An incubation study of GHG flux responses to a changing water table linked to biochemical parameters across a peatland restoration chronosequence

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SUMMARY

Large areas of northern peatlands have been drained and afforested with conifers in the 20th century. This has led to changes in the hydrology of the peatlands, the quality and quantity of organic matter inputs and soil microbial communities, which are all likely to impact on greenhouse gas (GHG) fluxes. Considerable areas of these forest plantations are undergoing restoration, and our aim was to assess whether contrasting compositions of peat, in conjunction with hydrological changes in a controlled lab experiment, impact on GHG fluxes. We incubated vegetation free cores (at 8 °C) from a near-natural bog, restoration sites felled in 1998, 2006, 2012 and a current forest plantation at (a) low water tables, (b) high tables or (c) water tables that were changed from low to high. Results show that peat quality and nutrient availability in the pore water have been altered by the forest plantations, which resulted in dissimilar carbon dioxide (CO_2) fluxes between the sites under the same temperature and water table conditions. Higher CO_2 fluxes were found in the peat cores from the forest plantations than from sites that have undergone restoration and from the near-natural bog. However, there were few differences in methane (CH_4) fluxes from the different sites, indicating that on its own (i.e., in the absence of biotic interactions under field conditions) the effects of forestry on CH_4 flux are limited.

KEY WORDS: CO_2, CH_4, carbon, peat quality, pore water chemistry

INTRODUCTION

Drainage and afforestation of peatlands alters soil hydrology with further impacts on the chemical quality and quantity of organic matter inputs and soil microbial associations. Large areas of peatland in Scotland have undergone such changes in the 20th century (Andersen *et al.* 2010, Bellamy *et al.* 2012, Creevy *et al.* 2018). These new hydrological and biochemical conditions mean that the processes governing organic matter formation and greenhouse gas (GHG) exchange are likely to be impacted, since the quality of dead organic matter entering organic soils is an important factor in determining its rates of stabilisation and decomposability (Conant *et al.* 2011). De Deyn *et al.* (2008) have shown that in some environments, vegetation can be a good proxy for soil carbon (C) dynamics, because the quality of the litter is controlled by the vegetation. The deeper peat of bogs is highly recalcitrant (Bridgham *et al.* 1998) and it is likely that recent C inputs from plants drive carbon dioxide (CO_2) and methane (CH_4) fluxes (Joabsson & Christensen 2001, Ström *et al.* 2003, Chanton *et al.* 2008). Drainage of the soil in afforested peatlands also influences litter decay and soil organic matter (SOM) transformations (Wickland *et al.* 2010). From the 1990s onwards, increased awareness of the negative impacts of deep drainage and afforestation of peatlands, and a better understanding of the importance of peatlands for other ecosystem services, has led to a shift in land management in the UK (Anderson *et al.* 2016). Large areas of formerly afforested peatlands, approximately 10 % of peatlands in the UK (JNCC 2011), are already undergoing restoration, with over 2200 ha of forestry felled to date, with plans to restore more. However, little is known about the legacy of forested areas on the soil biochemical composition, or whether previous forest cover has had significant impacts on the quality of organic matter found within the peat body, and consequently on microbial decomposability and GHG production.

Soil carbon cycling in peatlands depends predominantly on the soil temperature, water table depth, plant community composition, chemical characteristics of the peat and the microbial activity in the peat (McGuire *et al.* 2002, Weltzin *et al.* 2003, Gunnarsson *et al.* 2004, Bragazza *et al.* 2013, Hodgkins *et al.* 2014). Previous studies on the effects of water table depth on CO_2 and CH_4 fluxes show

that, in general, raising the water table increases CH_4 fluxes and decreases CO_2 fluxes from the peat (Blodau *et al.* 2004, Dinsmore *et al.* 2008, Estop-Aragonés *et al.* 2016). However, no assessment of how the chemical legacy of tree litter in the peat soils after restoration may impact GHG fluxes has been carried out thus far.

The goal of this experiment is to understand how the composition of peat changes following forest removal and a rise in the water table, and to investigate how this may be linked to GHG fluxes. We hypothesise that: (1) sites with different time since restoration show differences in biochemical composition of soil organic matter (SOM), (2) the biochemical composition of SOM influenced by different legacies of forestry litter input leads to different GHG fluxes under identical hydrological and temperature conditions, and (3) the response in GHG flux to a short-term change in water table differs according to time since felling.

METHODS

Study site

The peat cores used in this study came from the Flow Country in the north of Scotland (58° 22' N, 3° 53' W), one of the largest areas of blanket peat bogs in Europe. The average annual precipitation between 1981–2010 was 970.5 mm with an average air temperature of 11.4°C, measured at the Kinbrace weather station approximately 20 km from our research sites (Location: 58° 13′ 58″ N, 3° 55′ 01″ W; Altitude: 103 m amsl; Met Office data). In the 1980s, large areas of the Flow Country were drained and planted with non-native trees (*Picea sitchensis* (Bong.) Carr.; *Pinus contorta var. latifolia* Engelm.). At the time of afforestation, the peat was double-ploughed creating a regular micro-topography with low lying furrows (approximately 1.5 m wide) flanked by high ridges (plough throws; c. 0.75 m wide) on either side. In between two plough throws, there is distance of approximately 0.5 m width of the original (unploughed) surface. The height from the bottom of the furrow to the top of the plough throw is about 0.5 m and from the original surface to the base of the plough throw is about 0.15–0.2 m. In general, conifer seedlings were planted on the plough throws because of the improved drainage compared to the original surface. All forest-to-bog sites used in this study still have this microtopography. According to the literature it is very likely that fertilisers (phosphate, potassium and nitrogen) were applied during planting and regularly afterwards until canopy closure (Taylor 1991).

Ongoing felling of trees and blocking of collector drains to restore the peatlands has resulted in a chronosequence of different restoration ages. For this study, we used soil cores from a number of sites that span the duration of the restoration process; cores from near-natural blanket bog sites that were never afforested or drained, forest plantation plots and restoration sites that include plots felled in 1998 (R98), 2006 (R06) and 2012 (R12) (Table 1).

Table 1. Site descriptions, with dominant species, ground cover and destination of trees after felling.

Site	Dominant species	Ground cover	Trees left in furrows?
Forest plantation plots	*Picea sitchensis*, *Pinus contorta* (both around 30 years old), sporadic patches of *Hypnum jutlandicum* and *Sphagnum* mosses.	No vascular understory, mainly needle litter	N/A
R12	Patches of *Polytrichum commune*, *Eriophorum* sp., *Calluna vulgaris* and, in some instances, *Sphagnum fallax* and *Sphagnum capillifolium* in furrows.	Mainly bare peat	Yes
R06	*Polytrichum commune*, *Eriophorum* sp., *Calluna vulgaris*. *Sphagnum fallax* and *Sphagnum capillifolium* in furrows.	Almost completely covered by vegetation	Yes
R98	*Deschampsia flexuosa*, *Eriophorum*, *Sphagnum* spp., *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*	Completely covered by vegetation	Yes
Bog plots	Dominated by *Sphagnum* spp. Also present: *Erica tetralix*, *Calluna vulgaris*, *Eriophorum vaginatum*, *Myrica gale*, *Pleurozia purpurea*.	Completely covered by vegetation	N/A

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Vegetation composition

Forest plots

The forest control plots (58° 22′ 22″ N, 3° 59′ 27″ W) contained a mixture of *P. sitchensis* and *P. contorta*, which were approximately 30 years old. Stand density was high (about 5000 trees per ha), with no vascular vegetation understory, but sporadic patches of moss, predominantly feather moss, e.g. *Hypnum jutlandicum*, *Hylocomium splendens* and in some instances, *Sphagnum fallax* and *S. capillifolium* in furrows. The average diameter at breast height (DBH) for the *P. sitchensis* trees was 13.3 cm (n = 22) and for *P. contorta* 17.9 cm (n = 33), with an average ratio per area of *P. sitchensis* / *P. contorta* of 0.6. Average canopy cover was 76.3 % (RSPB unpublished data, Smith *et al.* 2014, Smith & Hancock 2016).

Restoration plots

The plots felled in 2012 (R12) (58° 24′ 48″ N, 3° 44′ 36″W) had *Polytrichum commune, Eriophorum sp., Calluna vulgaris* and *S. fallax* and *S. capillifolium* in furrows, with some bare patches of peat. Trees here were felled and left in the furrows, as the extraction of stems was not economically viable. In the plots felled in 2006 (R06) (58° 23′ 36″ N 3° 47′ 25″ W), vegetation was also similar to the R12 plots; however, *Sphagnum spp.* were also present and the ground was completely covered with vegetation. Trees here were also left in the furrows after felling, but they were smaller than the trees in R12. The plots felled in 1998 (R98) (58° 24' 46" N, 3° 48' 06" W) were dominated by *E. vaginatum*, *Sphagnum* spp., *C. vulgaris*, *Erica cinerea* and *E. tetralix.* There was also re-growth of *P. sitchensis* at low densities throughout the site. During harvest, trees here had also been felled and left in the furrows, although these trees were smaller than the trees in R06.

All the restoration sites used in this study have undergone collector drain blocking either with peat or plastic dams. Furrows were not managed in any way and continued to provide some element of drainage, especially on more sloping ground.

Near-natural bog plots

The bog control plots (58° 22′ 55″ N, 3° 58′ 42″ W) were located in three different sites and were dominated by *Sphagnum* spp., *E. tetralix, C. vulgaris, E. vaginatum, E. angustifolium* and *Pleurozia purpurea.*

Soil sampling

A total of 150 soil cores of 10-cm depth and a diameter of 6.5 cm, were collected from the original surface of all plots in March 2015. Cores were taken by hammering 10-cm long PVC pipe sections into the peat and cutting underneath the core. Within each site, five sampling locations, spaced about 10 m apart, were chosen to capture spatial variations. At each location, three shallow (0–10 cm depth) and three deep cores (10–20 cm depth) were collected, which included where present, the moss and litter layer. Surface vegetation was removed during collection, and soils were kept in dark incubators (see below) to prevent re-growth of the vegetation. The sampling was carried out in that way to differentiate processes in the superficial and slightly deeper zones of these deep peat soils. Each within-site location acted as one experimental block, such that each of the three water table treatments (see below) was allocated to each of the three replicate 10-cm cores per depth. Cores were kept in the PVC pipe sections and sealed in plastic bags for transport to the laboratory, where the pipes with the cores were placed in plastic tubs (9.5 cm diameter and 11 cm tall). Distilled water was added to a set level (see below) and topped up twice per week during the experiment. Soils were maintained at 3 °C in incubators (MIR-153, Sanyo, Gunma, Japan) for 10 weeks, to allow for the moisture conditions in the samples to adjust. Then the temperature was increased to 8 °C, close to the seasonal average. CO_2 and CH_4 flux measurements started five days after the temperature adjustment.

Three water table treatments were set up, where shallow and deep cores from each sampled site/block had water tables adjusted to either a low level (8.5 cm below the surface), high water table (1 cm below the soil surface) or had water tables first set to the lower level for two weeks from the start of flux measurements, before the water tables were increased to the 'high' level.

Flux measurements

CO_2 and CH_4 fluxes were measured from all cores on four occasions between the beginning of June and mid-October 2015. Measurements were initiated by closing the containers with an airtight lid and monitoring the change in CO_2 and CH_4 concentrations by connecting the plastic tub to a fast GHG analyser (FGGA-24EP, Los Gatos, San Jose, California, USA). Concentrations were recorded continuously for 10 minutes under dark conditions. Air temperature and humidity were not monitored during enclosure.

Flux rates were calculated using the *HMR* package (Pedersen 2017) in RStudio (Version 1.0.136). Concentrations were regressed against time since container closure using either a linear or a non-linear function, whichever best fitted the data, in order to calculate the flux based on container volume

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and surface area (Pedersen 2010). Fluxes were expressed in units of mole CO_2 evolved per mass of C in soil cores (determined after the flux experiments had finished). Only fluxes based on regressions with a p-value < 0.1 were considered as robust estimates, and considered for further analysis. This led to a rejection of 2.4 % of CH_4 fluxes, whilst none of the CO_2 fluxes were rejected. To eliminate outliers, fluxes with more than three times the standard deviation of average fluxes per gas species were also eliminated, which led to 0.9 % rejection of CH_4 fluxes and 1 % for CO_2 fluxes.

A number of flux measurements showed a decrease in CO_2 concentration over the 10-minute period, and passed the data quality criteria (see above). As a net uptake of CO_2 in the absence of photosynthesis (under dark conditions) is not plausible, these apparent negative fluxes are considered artefacts associated with the measurement set-up, likely associated with a slight drift in the signal of the analyser. Measurements of empty containers confirmed that small apparent negative or positive fluxes could result for this set-up, but there was no reliable pattern that allowed a retrospective correction of these small effects. As the sequence by which flux measurements were carried out was strictly by experimental blocks, this artefact affected all treatments without bias. We acknowledge the possibility of some error on flux estimates but are confident that the relative flux magnitudes and hence impacts of site treatments and soil depths are robust.

Pore water chemistry

Pore water samples were taken with Rhizon MOM samplers (Rhizosphere Research Products B.V., Wageningen, the Netherlands) for the first and last sampling rounds. These samplers have a diameter of 2.5 mm and a mean pore size of 0.15 µm, and the porous area of the sampler is 10 cm long. The samplers were inserted vertically in the middle of the core immediately after flux measurements, and samples were obtained 24 hours after flux measurements by connecting to an evacuated glass vial (Exetainer, Labco Limited, Lampeter, UK). Approximately 10 ml of sample were collected each time, and were stored in a dark fridge at 3.5 °C before analysis.

For the three replicates per treatment, we determined nitrate, phosphate and sulphate concentrations in pore water samples using an ion chromatograph (DX-120, Dionex Corporation, Sunnyvale, USA), and dissolved organic carbon (DOC) concentrations were measured on a Total Organic Carbon analyser (TOC-V CSN, Shimadzu Corporation, Kyoto, Japan). Instrument downtime meant that most samples were analysed up to five months after collection. In order to quantify any changes in concentrations, one batch of 60 samples was analysed both after 2–4 weeks and after 5 months. For the determination of pH, 3 g of homogenised dried (at 80 °C for 72 hours) soil was suspended in 54 ml of distilled water (1:19 dilution) and measured with a FiveEasy pH meter (Mettler Toledo, Columbus, USA).

Fibre analysis

Fibre analyses were carried out at the University of Aberdeen in April 2016 on a sub-set of cores of which the pore water had also been analysed (n = 3 per site for each depth increment).

The shallow cores (0–10 cm) were divided into two smaller depth increments to improve the resolution of the superficial peat layers. The top layer (hereafter shallow top) is defined as organic matter consisting of litter and moss, and the lower layer (hereafter shallow bottom) defined as organic matter consisting of amorphous peat. Where no distinct layers were evident, the cores were halved. The dried samples (at 80 °C for 72 hours) were homogenised with a mortar and pestle, resulting in a grain size suitable for the mesh bags used in the fibre analysis. Roots were extracted from dried samples by picking them out by hand.

The fibre analysis followed the Carnegie protocol "Carbon extractions to determine hemicellulose, cellulose and lignin in leaf tissue" (Carnegie Institution for Science, Stanford, CA, USA) with a few alterations. As this protocol is designed for leaves, there was a risk of losing some peat material through the mesh of the sampling bags. To account for this, an additional step was added to the protocol, where bags were submerged in boiling de-ionised water and agitated five times (for two minutes each time). After this, the neutral detergent fibre (NDF) extraction step was carried out in which carbohydrates, lipids, pectin, starch, soluble proteins and non-protein nitrogen were extracted. Then the hemicellulose and membrane-bound proteins were extracted (the acid detergent fibre (ADF) step), the cellulose was extracted and the lignin and recalcitrant materials were left behind (the acid determined lignin (ADL) step), and finally the ashing step to determine the percentage of mineral soil. The other alteration to the Carnegie protocol was to rinse the samples in acetone after the NDF and ADF steps (Ankom technology NY, USA), as some of the NDF and ADF solution could stick to the fibres, which would be left in the sample when only rinsing with de-ionised water. The NDF and ADF steps were run in an Ankom 2000 fibre analyser (Ankom technology NY, USA).

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C:N ratio

The C and N content of the same cores that were used for fibre analysis were determined on a Flash Combustion Elemental analyser (CE Instruments (Carlo Erba) NA2500, Wigan, UK). Materials were dried at 105 °C overnight and ball milled prior to analysis.

Statistical analysis

All statistical analysis was carried out in RStudio (RStudio Team 2016). Statistically significant differences and correlations were determined using p-values, where the p-value is used to weigh the strength of the evidence against the null hypothesis (no difference/correlation). P-values less than, or equal to, 0.05, indicate that the null hypothesis should be rejected in favour of the alternative ('working') hypothesis. P-values between 0.05 and 0.1 suggest marginal significance and are interpreted as such throughout. P-values greater than 0.1 are too large to reject the null hypothesis. Fluxes were analysed using linear mixed effect models for each core depth, using the *nlme* package (Pinheiro *et al.* 2017). Both CO_2 and CH_4 fluxes were square root transformed to meet normality requirements. Model selection was based on the information theory (Burnham & Anderson 2002); first the most complex model was built, which included *site*, *water table* and *time since start of experiment* as fixed effects, with an interaction between them and *incubator* and *plot within site* as a random effect. All possible combinations of this model were identified using the 'dredge' function in the *MuMIn* package (Barton 2017). Goodness of model fit was assessed with the small-sample size corrected Akaike's information criterion (AICc), which is calculated using the number of parameters and either the maximum likelihood estimate for the model or the residual sum of squares. "Likelihood" here is a measure of the extent to which a sample provides support for particular values of a parameter in a parametric model. AICc values of different models can be compared and the model with the lowest AICc is selected as the 'best approximating model' (Burnham & Anderson 2002).

Peat quality data was analysed using linear models, with *site* and *core depth* as fixed effects and an interaction between them. The pore water chemicals were also analysed with linear models, where the most complex model used *site*, *core depth*, *water table* and *time since start of experiment* as fixed effects with interactions between them. Then 'dredge' was used again to find the 'best approximating model'. Linear models per core depth were used to find parameters that could predict CO_2 and CH_4 fluxes, with peat properties and *site* as fixed effects.

Principle components analysis (PCA) was performed on the peat properties, using the 'rda' function in the *Vegan* package (Oksanen *et al.* 2017). The variables chloride, nitrate, soluble cell component and lignin and recalcitrant materials were log transformed to meet normality requirements. Post hoc testing against *site* was applied using the 'adonis' function.

RESULTS

CO_2 fluxes

Overall, CO_2 fluxes (expressed throughout as CO_2-C) from peat cores averaged 35.52 (±2.53) nmol g^{-1} h^{-1}, showing consistent temporal patterns between sites and the significant influences of water table treatments (see below). Mean fluxes over all sites and water table treatment from the shallow peat cores (57.43 ±4.42 nmol g^{-1} h^{-1}) were significantly greater than from the deeper depth (10.89 ±3.29 nmol g^{-1} h^{-1}, $p<0.001$). The fluxes were therefore analysed for site and water table treatment effects per core depth.

Shallow soil cores

The low water table treatment resulted in significantly higher CO_2 flux rates (93.15 ±7.95 nmol g^{-1} h^{-1}) than the high (37.69 ±5.51 nmol g^{-1} h^{-1}) or changed (24.18 ±5.79 nmol g^{-1} h^{-1}) water level treatments ($p<0.001$) (Figure 1). However, there was no significant difference between the latter two water level treatments ($p=0.64$). A slight trend of decreasing CO_2 fluxes across all sites over the time of the incubation was statistically significant ($p<0.001$) and this was strongest in the cores where the water level was raised (Figure 1).

Regardless of water table treatment, the forest plantation showed the highest CO_2 flux rates (97.96 ±13.80 nmol g^{-1} h^{-1}), significantly higher than those from the restored sites R12 (44.07 ±8.26 nmol g^{-1} h^{-1}, $p<0.001$) and R06 (37.78 ±6.27 nmol g^{-1} h^{-1}, $p<0.001$), from the bog cores (41.07 ±7.24 nmol g^{-1} h^{-1}, $p<0.001$) and were marginally significantly higher than from R98 (67.29 ±10.28 nmol g^{-1} h^{-1}, $p=0.09$). Fluxes from the cores from R98 were marginally higher than from the R06 cores ($p=0.08$), with no further significant differences between sites ($p>0.2$; Figure 2).

Deep soil cores

The CO_2 flux rates measured from the deep cores showed less differentiation between sites than that observed for the shallow peat cores. Fluxes were generally lower compared to shallow peat cores, irrespective of water table, with several sites showing average flux rates not significantly different from

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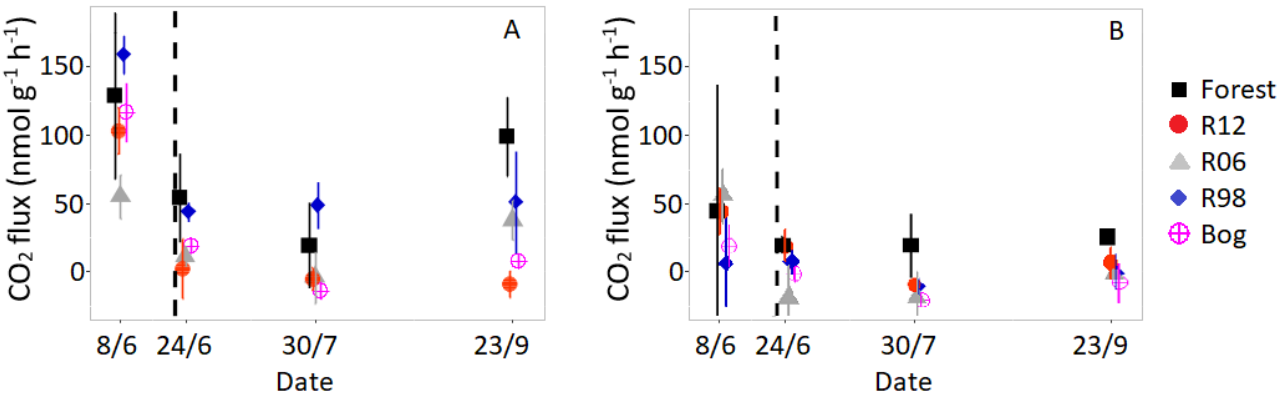

Figure 1. Carbon dioxide (CO_2) fluxes for changed water table levels, per core depth over time (n=5). Error bars are standard error. Dotted vertical line is timing of water table change (from low to high). A) Shallow cores, B) Deep cores.

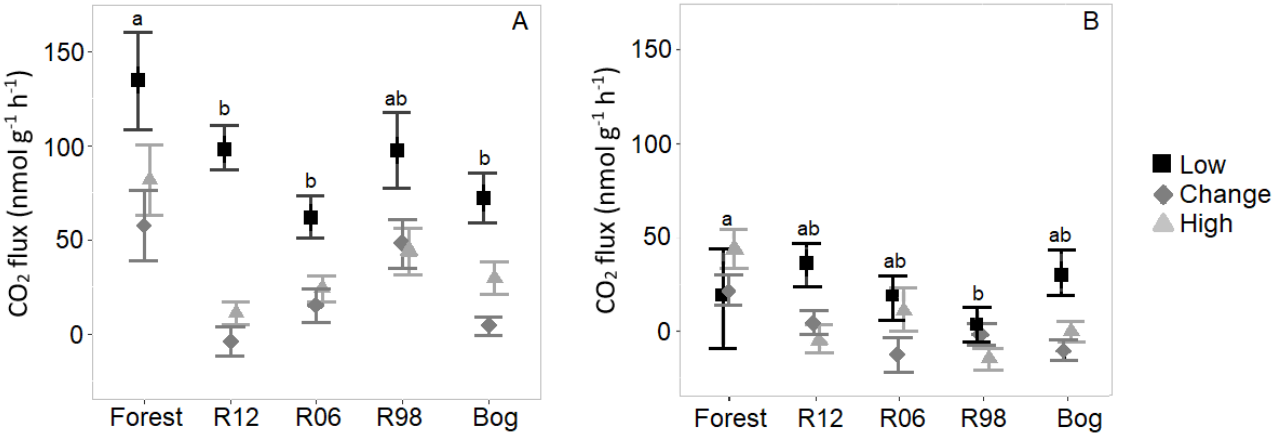

Figure 2. Carbon dioxide (CO_2) fluxes per core depth, points are averages over all measurement rounds (n=5). Error bars are standard errors. A) Shallow cores, B) Deep cores.

zero. Across all water table treatments and core depths, the forest plantation cores had the highest fluxes (26.77 ±11.40 nmol g^{-1} h^{-1}), and the lowest rates were found for cores from R98 (Figure 1). The mean flux difference between these two sites was significant ($p<0.02$), with no further significant differences between any of the other sites ($p>0.2$; Figure 2). Across all sites, water table treatments did not produce a significant effect on CO_2 fluxes in the deep cores ($p>0.2$). A trend of decreasing fluxes over time was significant ($p=0.001$) with no detectable interaction between time and water table treatments (Figure 1).

CH_4 fluxes

Overall, CH_4 fluxes (expressed throughout as CH_4-C) from the peat cores averaged 1.49 (± 5.84) pmol g^{-1} h^{-1}, and there was no consistent pattern between sites and water table treatments. Across all sites and water tables, mean fluxes from the shallow peat cores (14.96 ±10.90 pmol g^{-1} h^{-1}) were significantly higher than from the deep cores (-15.75 ±7.84 pmol g^{-1} h^{-1}, $p<0.001$). There were no significant differences in CH_4 fluxes between sites ($p>0.7$), water table treatments ($p>0.2$) or time since the start of the experiment ($p=0.3$) across all shallow peat cores (Figure 3 and Figure 4). A similar result was found for deep peat cores; no significant differences were observed between sites ($p>0.1$), water table treatments ($p>0.3$) or time since the start of the experiment ($p=0.3$; Figure 3, Figure 4).

Pore water chemistry

The five months of storage of the water samples did not have a significant effect on the concentrations of DOC ($p=0.9$), nitrate ($p=0.3$), sulphate ($p=0.7$) or phosphate ($p=0.5$).

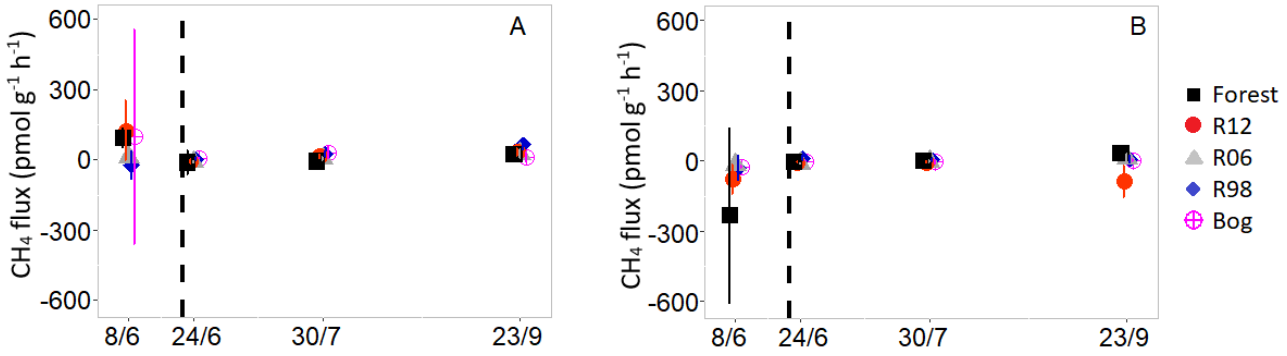

Figure 3. Methane (CH_4) fluxes for the changed water level over the running time of the experiment (n=5). Error bars are standard errors. Dotted vertical line is timing of water table change (from low to high). A) Shallow cores, B) Deep cores.

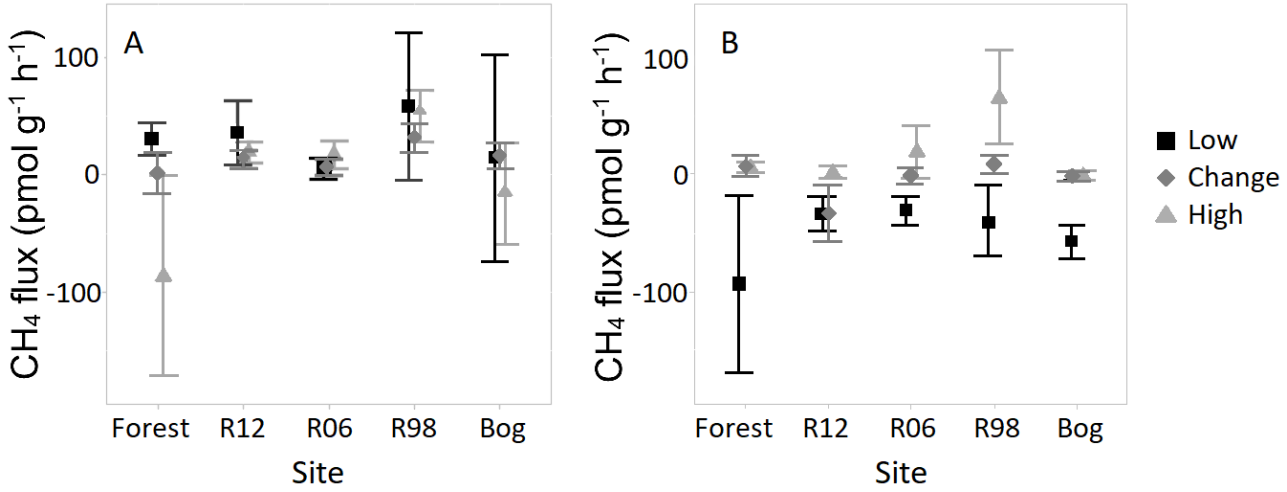

Figure 4. Methane (CH_4) fluxes from the different core depths, points are averages over all measurement rounds (n=5). Error bars are standard errors. A) Shallow cores, B) Deep cores.

DOC

The DOC levels in the pore water of the peat cores ranged from 0 to 253.2 mg L^{-1}. There was no difference between sites in DOC levels in the pore water ($p>0.1$; Table 2). Depth had a significant impact on the DOC concentrations in the pore water ($p=0.003$), with higher concentrations in the shallow cores (83.0 ±4.9 mg L^{-1}mg L^{-1}) compared to the deep cores (67.4 ±3.9 mg L^{-1}).

Nitrate

Nitrate concentrations in the pore water were very low in most cores, except in cores R98 and R06, and ranged from 0 to 40.3 mg L^{-1}. There were some significant differences between the sites; nitrate concentrations in the pore water of the forest planation (0.3 ±0.08 mg L^{-1}) cores were lower than in the pore water of the R98 cores (2.7 ±0.03, $p=0.01$). The concentrations in the pore waters of the R12 (0.2 ±0.06 mg L^{-1}) and bog (0.2 ±0.03) cores were significantly lower than from the R06 (3.2 ±1.1, $p=0.02$ and 0.004 respectively) and R98 cores ($p=0.002$ and <0.001 respectively; Table 2). Across all sites, the deep cores had significantly lower concentrations than the shallow cores (0.4 ±0.08 mg L^{-1} and 2.0 ±0.7 mg L^{-1}, respectively; $p < 0.01$).

Sulphate

The concentrations of sulphate across all samples ranged from 0 to 24.1 mg L^{-1}. Across all core depths and water table treatments, the forest plantation (2.1 ±0.4 mg L^{-1}) cores had significantly lower concentrations of sulphate than R06 (4.3 ±0.7, $p=0.02$) and R98 (4.1 ±0.8, $p=0.003$), with no further differences between sites (Table 2). The shallow cores (1.8 ±0.3 mg L^{-1}) had significantly less sulphate in the pore water than the deep cores (4.2 ±0.5, $p<0.001$).

Table 2. Pore water chemical composition (mg L^{-1} per site) at restored sites R12 (felled in 2012), R06 (felled in 2006) and R98 (felled in 1998), at both core depths (S=Shallow and D=Deep). Standard error in brackets.

Chemical	Forest		R12		R06		R98		Bog	
	S	D	S	D	S	D	S	D	S	D
DOC	74.0 (14.6)	87.0 (9.9)	108.6 (8.4)	66.5 (7.4)	82.6 (6.3)	59.4 (6.9)	76.8 (14.2)	53.2 (6.6)	68.3 (7.7)	71.4 (10.3)
Nitrate	0.3 (0.1)	0.4 (0.1)	0.4 (0.1)	0.2 (0.04)	4.1 (2.4)	0.8 (0.3)	5.2 (2.5)	0.7 (0.2)	0.2 (0.05)	0.1 (0.03)
Sulphate	1.1 (0.3)	2.6 (0.7)	1.2 (0.3)	4.01 (1.08)	1.8 (0.5)	4.8 (1.05)	3.9 (1.2)	4.4 (1.2)	0.8 (0.2)	5.2 (1.2)
Phosphate	3.8 (1.9)	0.3 (0.3)	8.4 (1.5)	1.2 (0.4)	10.4 (2.8)	0.9 (0.4)	1.4 (1.2)	0.09 (0.04)	0.09 (0.05)	0.3 (0.3)

Phosphate

Phosphate concentrations in the pore water ranged from 0 to 45.8 mg L^{-1}. There was hardly any phosphate in the pore water of most of the cores, except in the shallow cores from R06, R12 and the shallow core of the forest plantations. Concentrations in the pore water from the forest plantations (2.8 ±1.2 mg L^{-1}) was significantly higher than the R98 (0.7 ±0.5 mg L^{-1}, p=0.005) and the bog cores (1.2 ±1.1 mg L^{-1}, p<0.001) and significantly lower than the cores from R12 (4.8 ±0.9 mg L^{-1}, p=0.003) and R06 (5.8 ±1.6 mg L^{-1}, p=0.003). The phosphate concentrations in the R06 and R12 cores were significantly higher than the R98 (p<0.001) and bog cores (p<0.001; Table 2). Across all sites, phosphate concentrations in the pore water of the deep cores (0.6 ±0.1 mg L^{-1}) were significantly lower compared to the shallow cores (4.9 ±0.9 mg L^{-1}, p<0.001).

Peat quality

Soluble components

The soluble components of peat biomass include carbohydrates, lipids, pectin, starch, soluble proteins and non-protein nitrogen. In general, the percentage of soluble cell components increased towards the deeper layers and there was a gradient from the forest plantation cores towards the bog cores across the age of restoration sites (Figure 5). The forest plantation cores (18.2 ±1.3 %) had a significantly lower percentage of soluble cell components than the R06 (23.0 ±1.3 %, p=0.01), R98 (25.2 ±1.5 %, p<0.001) and bog cores (22.3 ±1.0 %, p=0.05), whilst R12 had a significantly lower percentage than R98 (p=0.004). Across all sites, the deep cores (24.4 ±0.9 %) contained more soluble cell components than the upper (19.0 ±1.0 %, p<0.001) and lower parts of the shallow cores (21.8 ±1.1 %, p=0.05). The difference in soluble cell components between the lower and upper parts of the shallow cores was statistically significant (p=0.03; Figure 5A).

Hemicellulose

The hemicellulose contents increased from the forest plantation cores towards the bog cores, and from the shallow to the deep cores (Figure 5). Forest plantation (14.7 ±1.8 %), R12 (13.4 ±1.5 %) and R06 (14.9 ±1.5 %) cores had significantly less hemicellulose than the R98 (20.3 ±1.5 %, p=0.03, p=0.007 and p=0.05 respectively) and bog cores (21.8 ±1.0 %, p=0.005, p<0.001and p=0.006 respectively). The shallow top cores (15.2 ±1.2 %) had significantly less hemicellulose than the deep cores (18.9 ±1.0%, p=0.03). When comparing sites by depth of the cores, there were a number of significant differences; the forest shallow bottom cores (10.0 ±1.5 %) had significantly less hemicellulose than the R98 (23.7 ±2.2 %, p=0.01) and the bog shallow bottom cores (24.5 ±1.6 %, p=0.006), and the R12 shallow bottom cores (12.7 ±1.5 %) had significantly less hemicellulose than the bog shallow bottom cores (p=0.05; Figure 5).

Cellulose

There was a higher percentage of cellulose in the shallow top (22.8 ±0.5%) and shallow bottom (20.5 ±0.8 %) layers compared to the deep layers (18.7 ±0.8 % p<0.001and p=0.02 respectively) across all sites (Figure 5). The bog cores (23.9 ±0.9 %) had significantly higher percentages of cellulose than the restored sites (18.6-20.7 %; p<0.05), but were not significantly higher than the forest cores (Figure 5).

Lignin and recalcitrant materials

The percentages of lignin and recalcitrant material levels showed an apparent decrease from the forest

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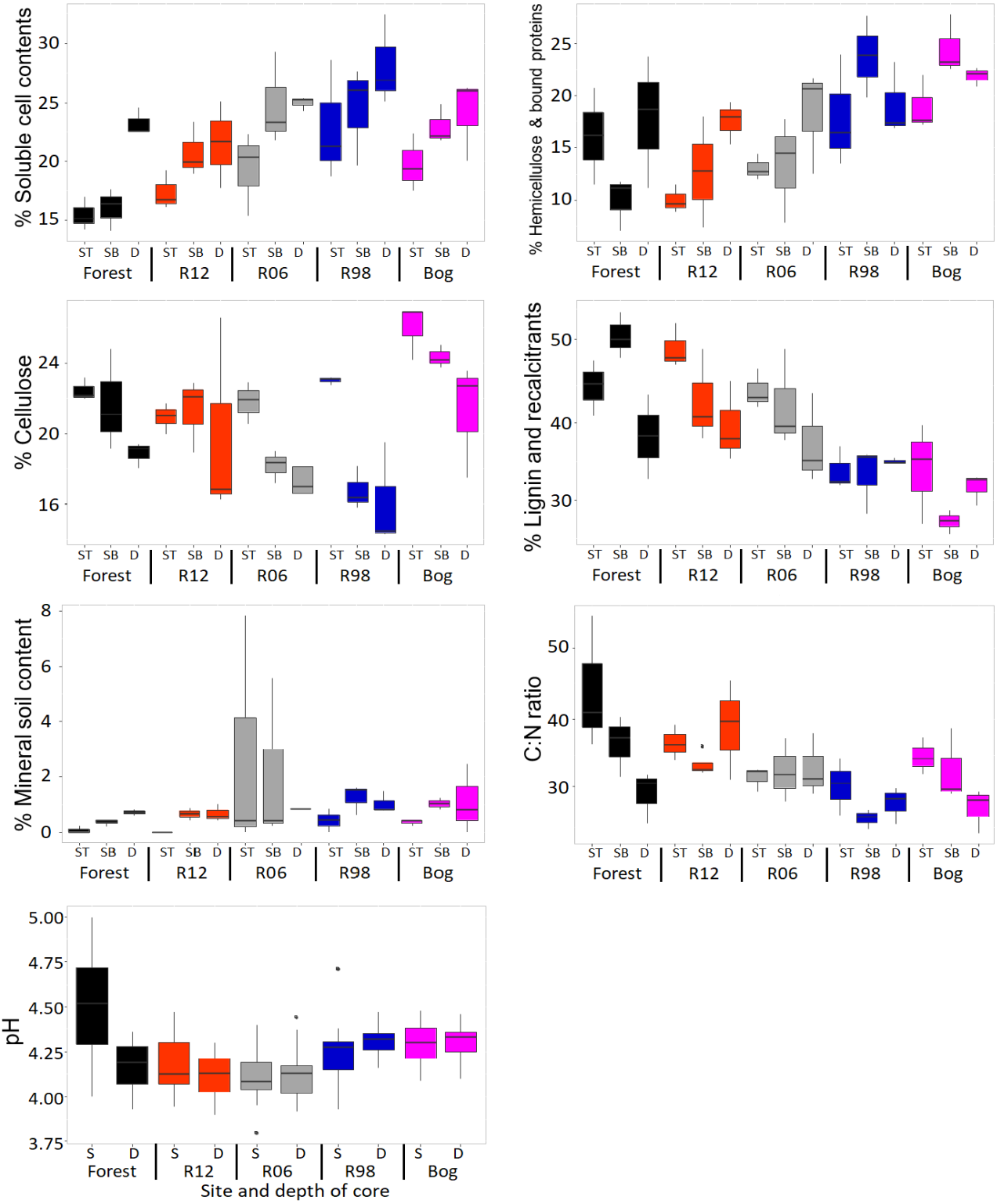

Figure 5. Peat quality per site divided by core depth; Deep (D), and shallow cores separated into top (ST) and bottom (SB) sections. Hinges correspond to the first and third quartiles and whiskers to 1.5 * inter-quartile range. See text for statistical indicators. With A) Percentage soluble components, B) Percentage hemicellulose, C) Percentage cellulose, D) Percentage lignin and recalcitrant materials, E) Percentage mineral soil, F) C:N ratio of the soil and G) soil pH.

plantation towards the bog cores (Figure 5) and from the shallow to the deeper layers in the restored sites, with significantly higher levels in the forest plantation (44.9 ±2.2 %), R12 (44.2 ±2.1 %) and R06 cores (41.3 ±1.8 %) compared to the R98 (34.1 ±0.9 %, $p \leq 0.01$) and bog cores (31.0 ±1.5 %, $p < 0.001$). The deep cores (36.4 ±1.2 %) had significantly lower levels of lignin and recalcitrant material than the shallow top cores (41.4 ±1.9 %, p=0.01), whilst the shallow bottom cores (39.5 ±2.5 %) were not significantly different from either the deep or the shallow top cores ($p \geq 0.2$).

When comparing sites by depth of the cores, the shallow top core R12 (49.8 ±1.7 %) had significantly higher levels of lignin and recalcitrant materials than the R98 (33.9 ±1.6 %, p=0.007) and bog cores (34.0 ±3.8 %, p=0.007). The shallow bottom cores R12 (43.0 ±3.5 %), R06 (42.4 ±3.7 %) and the forest plantation cores (51.5 ±1.7 %) had significantly higher levels than the bog cores (27.3 ±0.9 %, p=0.008, p=0.01 and $p < 0.001$ respectively), and the forest plantation cores had significant higher levels than the R98 cores (33.3 ±2.5 %, p=0.001; Figure 5).

Mineral soil

There was very little mineral soil material in any of the peat cores (range 0 to 7.8 %) with no significant differences between sites or soil core depth (Figure 5).

C:N ratio of the soil

The C:N ratio ranged from 24.2:1 to 54.4:1, with an apparent downward trend from the forest plantation cores to the bog cores. The R98 cores (28.4 ±1.0) had significantly lower C:N ratios than the forest plantation (36.8:1 ±2.7, p=0.002) and R12 cores (36.2:1 ±1.3, p=0.003), but no other significant differences between sites were detected. Across all sites, the deep cores (31.6:1 ±1.5) had a significantly lower C:N ratio than the shallow top cores (35.7:1 ±1.6, p=0.03). The shallow bottom cores exhibited intermediate mean C:N ratios (32.6:1 ±1.1), which did not differ significantly from the other core depths (Figure 5).

Soil pH

The soil pH measured in all cores ranged from 3.8 to 5 (Figure 5). Across all depths, the pH of the bog (4.3 ±0.02) and forest (4.3 ±0.05) soil were significantly higher than the soil in sites R06 (4.1 ±0.02, $p < 0.001$ and $p < 0.001$ respectively) and R12 (4.2 ±0.03, p=0.02 and p=0.01 respectively). The pH of the soil in site R98 (4.3 ±0.02) was significantly higher than the pH in R06 (p=0.04). The deep cores had a marginally lower pH than the shallow cores (4.2 ±0.02 and 4.3 ±0.03 respectively, p=0.04). The interaction between site and depth of the cores led to significant differences between sites for the shallow cores, but not for the deep cores; the pH of the forest shallow cores was significantly higher than the pH in the bog shallow (p=0.01), R06 shallow ($p < 0.001$), R12 shallow ($p < 0.001$) and R98 shallow ($p < 0.001$). The only significant difference within a site was in the forest plantation where the shallow cores had significantly higher pH values than the deep cores ($p < 0.001$) (Figure 5).

Effects of pore water chemistry and peat quality on fluxes

CO_2 fluxes

In the shallow cores, CO_2 flux showed negative correlations with DOC ($p < 0.01$) and phosphate (p=0.01) concentrations in the pore water, and a positive correlation with soil pH ($p < 0.01$; Table 3). There was an indication that CO_2 flux decreased with increasing percentage of mineral soil (p=0.06). None of the other chemical variables had a significant influence on the CO_2 fluxes from the shallow cores ($p > 0.1$; Table 3). CO_2 fluxes measured from the deep cores did not follow similar trends to those seen in the shallow cores. There were no significant

Table 3. Correlations of carbon dioxide (CO_2) fluxes with biochemical parameters across the shallow cores from all sites. Values in bold indicate a significant correlation with CO_2 flux.

Variable	Pearson correlation coefficient	p-value
DOC	**-0.39**	**<0.01**
Nitrate	-0.039	0.7
Sulphate	0.12	0.2
Phosphate	**-0.26**	**0.01**
Soluble components	-0.086	0.5
Hemicellulose	-0.076	0.6
Cellulose	-0.20	0.1
Lignin and recalcitrant material	0.14	0.28
Mineral soil	**-0.24**	**0.06**
C:N	-0.096	0.5
Soil pH	**0.28**	**<0.01**

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correlations between CO_2 flux and biochemical properties of the peat or pore water (Table 4).

CH_4 fluxes

In the shallow cores, CH_4 fluxes increased with increasing percentages of soluble cell components ($p<0.01$) and appeared to decrease with increasing soil pH ($p=0.06$). The other biochemical properties of the peat or pore water did not have a significant effect on CH_4 fluxes in the shallow cores ($p>0.2$; Table 5). In the deep cores, there were no significant correlations between CH_4 fluxes and the biochemical properties of the peat or pore water ($p>0.2$; Table 6).

Principle component analysis

The principle component analysis (PCA) indicated some consistent patterns, which separated the soil quality components according to sites. For the shallow cores, there was a continuous transition from forest to bog sites via restoration sites of increasing age influenced by PC1 and PC2 (Figure 6). This consistent trend disappeared in the deep cores (Figure 6). The trend observed in the PCA of the shallow cores was significant ($p<0.001$); the sites did differ in overall peat quality and pore water chemicals between sites, in contrast to the deep cores ($p=0.27$).

Table 4. Correlations of carbon dioxide (CO_2) fluxes with biochemical parameters across the deep cores from all sites.

Variable	**Pearson correlation coefficient**	**p-value**
DOC	0.008	0.9
Nitrate	-0.06	0.6
Sulphate	0.13	0.2
Phosphate	-0.028	0.8
Soluble components	-0.12	0.4
Hemicellulose	0.12	0.4
Cellulose	-0.045	0.7
Lignin and recalcitrant material	0.0063	1.0
Mineral soil	0.22	0.1
C:N	-0.0015	0.9
Soil pH	-0.028	0.6

Table 5. Correlations of methane (CH_4) fluxes with biochemical parameters across the shallow cores from all sites. Values in bold indicate a significant or marginally significant correlation with CH_4 flux.

Variable	**Pearson correlation coefficient**	**p-value**
DOC	-0.054	0.6
Nitrate	0.0038	1.0
Sulphate	0.0027	1.0
Phosphate	-0.044	0.7
Soluble components	**0.34**	**<0.01**
Hemicellulose	-0.062	0.6
Cellulose	-0.18	0.2
Lignin and recalcitrant material	-0.065	0.6
Mineral soil	-0.026	0.9
C:N	-0.15	0.3
Soil pH	**-0.11**	**0.06**

Table 6. Correlations of methane (CH_4) fluxes with biochemical parameters across the deep cores from all sites.

Variable	**Pearson Correlation coefficient**	**p-value**
DOC	0.14	0.2
Nitrate	0.093	0.4
Sulphate	-0.13	0.2
Phosphate	0.015	0.9
Soluble components	-0.14	0.3
Hemicellulose	-0.048	0.7
Cellulose	-0.031	0.8
Lignin and recalcitrant material	0.15	0.3
Mineral soil	-0.086	0.6
C:N	0.17	0.2
Soil pH	0.015	0.9

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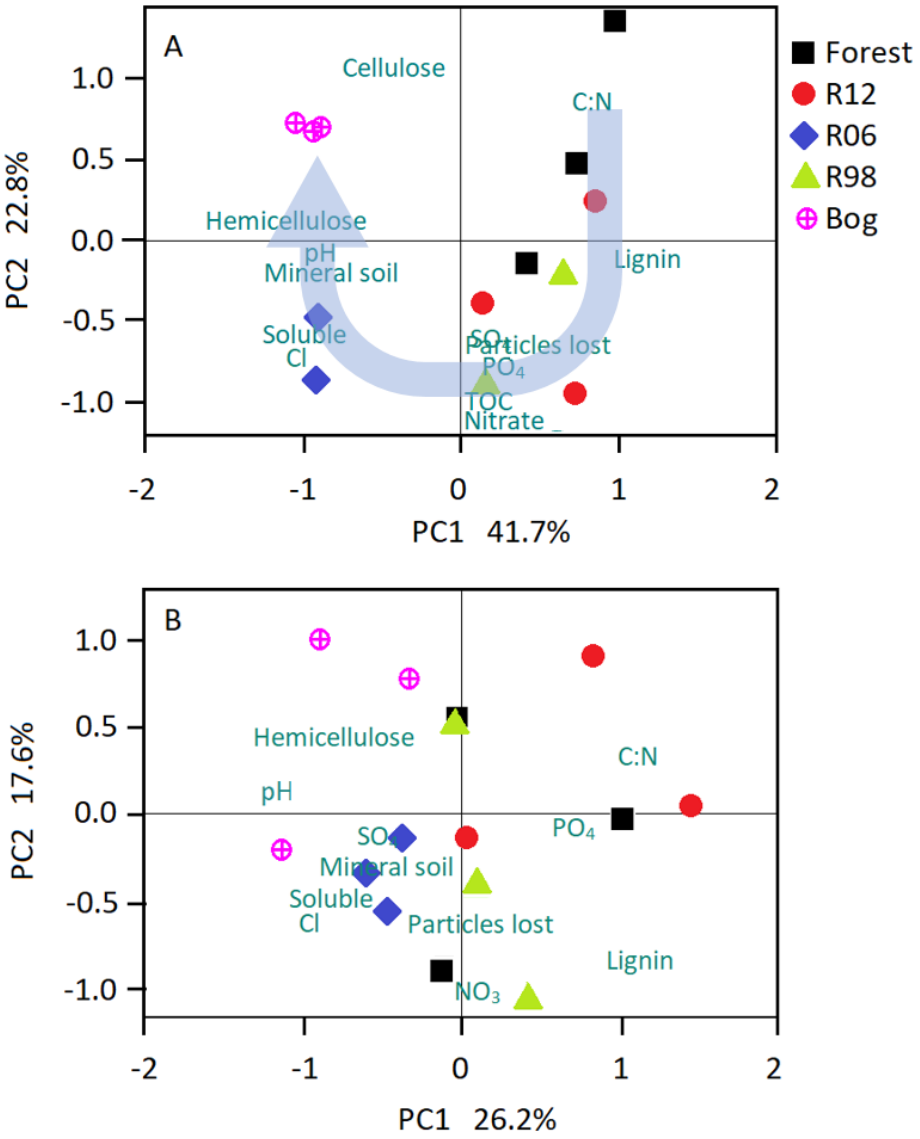

Figure 6. Principle component analysis for (A) shallow cores and (B) deep cores. The blue arrow shows an apparent trend of site clusters according to peat properties from forested sites to intact bogs, with restored sites of increasing age forming intermediate clusters.

DISCUSSION

The findings of this study indicate that under identical temperature and water table levels, there are significant differences in CO_2 and CH_4 fluxes from peat along a restoration chronosequence. CO_2 production in peat cores retrieved from forest plots was higher than that measured on cores from sites that have undergone restoration and where no forest had been planted. In contrast, CH_4 production did not show a direct influence of peat quality in the shallow depths, but some trends were evident in the deeper layers. This indicates an important impact of forest plantations on the biochemical peat constituents, and consequently the potential to produce GHG.

Role of pore water chemistry and peat quality in regulating CO_2 and CH_4 fluxes

Pore water chemistry

We did not find any statistical differences in DOC levels between sites. The DOC concentrations (low water table 60.6 ±3.2 mg L^{-1}, changed water table 113.5 ±9.1 mg L^{-1} and high water table 89.9 ±5.4 mg L^{-1}) are similar to the field pore and surface DOC concentrations found by Gaffney (2016) in the same sites, indicating that the mechanisms in the incubated peat are not too disturbed. However, our concentrations are higher than found by Dinsmore *et al.* (2008) in a grass-dominated, lowland ombrotrophic peatland with low intensity sheep grazing in Scotland (43 ±2.1 mg L^{-1}). Our results fall

within the same range as found by Clark *et al.* (2012) who carried out controlled drought simulation experiments on cores from UK peatlands. Nitrate concentration in the pore water of our cores are higher than found by Dinsmore *et al.* (2008) of 0.03 ±0.01 mg L^{-1} and by Proctor (2006) 0.017 ±0.012 mg L^{-1} in a blanket bog in England. The high levels in the oldest two restored sites, R06 and R98 (2.7 ±0.03 and 3.2 ±1.1 respectively), could be explained by the likelihood that these sites had been fertilised before planting, and that the trees where left in furrows after felling. Thus, higher levels of nitrate in the pore water of these sites could be due to the breakdown of tree biomass. Hancock *et al.* (2018) also found higher nitrogen levels in the vegetation of the R98 site than would be expected in bogs. The most recently harvested site (R12) also had decomposing tree material in the furrows, but had lower levels of nitrate in the pore water samples. The reasons for this pattern could relate to the lower rates of nitrification at these "younger" restoration sites, since the C:N ratio was higher in R12 than in R98, which could be linked to less N mineralisation and could result in lower nitrification rates (Booth *et al.* 2005). Another possible explanation could be that lower levels of fertilisation were applied prior to planting. In forest sites where continuous needle input and higher microbial activity (as indicated by the CO_2 flux results) likely transform organic nitrogen into mineral forms (including nitrate in the oxygenated layers), lower levels may result from higher nitrate uptake by roots.

Mean sulphate levels (3.30 ±0.16 mg L^{-1}) are similar to those found by Proctor (2006) in a blanket bog in England (4.71 ±1.17 mg L^{-1}). They show significant differences between sites, with forest plantation cores having significantly lower concentrations of sulphate than in R06 and R98, and the shallow cores have significantly less sulphate in the pore water than the deep cores. In general, sulphate is a good indicator of oxidation, since under aerobic conditions sulphur is oxidised to sulphate (Toivonen *et al.* 2013). However, sulphate reduction is faster in the periodically aerobic layers of the peat (Clymo 1965), which could possibly explain the low concentrations in the forest plantation cores, owing to the lower water table in forestry plots. Phosphate concentrations are highest in cores from recently felled sites (R06, R12) and forest plantations. This is expected, since these sites have most likely received phosphorus as a fertiliser when they were planted. Rodgers *et al.* (2010) found significant phosphorus enrichment in soils of forested peatlands that remained elevated for at least four years after the harvest of former forestry plots on blanket peat, especially where harvest residue (brash mats) covered the soil. Pore water phosphate concentrations in soils from the oldest restoration site (R98) are similar to those of unforested bog samples, which both fall within the range of phosphate concentrations found in pore water of peatland mesocosms by White *et al.* (2008). Kaila *et al.* (2016) measured soluble reactive phosphorus (SRP) in the pore water of peat columns from two nutrient-poor peatland forest sites in south-central Finland and from one nutrient-poor peatland forest site in the west of Ireland after rewetting in the laboratory. They found that concentrations ranged from an average of 0.31 to 15.5 mg L^{-1} SRP and the Irish peat column only ranged from 0.31 to about 6 mg L^{-1} SRP, our converted measurements in the forest plantation peat cores of 0.9 ±0.4 mg L^{-1} SRP are within this range, but at the lower end.

Peat quality

As hypothesised, the forest plantations have altered the quality of the peat. We found trends of increasing percentages of components with high decomposition potential, such as soluble cell components and hemicellulose (Berg & McClaugherty 2008), and a decreasing trend in compounds associated with slow turnover rates, such as lignin and recalcitrant material levels from the forest plantation towards the bog cores.

The shallow cores have less soluble cell components and hemicellulose than the deep cores and they have more cellulose, lignin and recalcitrant material, and a higher C:N ratio than the deep cores. This is partly in contrast with what we expected, since according to Clymo (1984) more recalcitrant material is accumulated during peat formation, since the easily decomposable organic matter is lost in the process. This would mean that the deeper layers of peat should have more recalcitrant materials than the more superficial layers. However, the higher levels of recalcitrant material near the soil surface of forest plantation and younger restoration sites could be an indication of advanced peat decomposition (Klavins *et al.* 2008, Leifeld *et al.* 2012, Wüst-Galley *et al.* 2016), possibly due to the breakdown of previously anoxic organic matter that became oxic due to drainage and enhanced microbial activity due to fertilisation (Fenner & Freeman 2011).However, lower C:N ratios would then be expected in the top soil layers, since peat mineralisation appears to increase the relative nitrogen content of the soil (Malmer & Holm 1984, Kuhry & Vitt 1996, Krüger *et al.* 2015).We found higher C:N ratios in the top layers than in the deeper layers. Our results are similar to those of Bader *et al.* (2018) who argued that

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the higher levels of lignin and recalcitrant materials in the top layers of the forest soils is due the higher abundance of lignin rich (wood derived) plant residues and not due to advanced peat decomposition.

CO_2 flux explained by biochemical parameters

DOC, phosphate and soil pH emerged as generic predictors of CO_2 flux in the shallow cores across sites, and the mineral soil percentage also seems to correlate with CO_2 flux, but this was only marginally significant. However, as levels of DOC are not significantly different between sites, these cannot explain the observed differences in CO_2 fluxes. The negative correlation between phosphate concentration and CO_2 flux in the shallow cores is in contrast with what was expected, as the higher availability of a macronutrient such as phosphorus could plausibly lead to higher microbial activity and hence higher decomposition (Amador & Jones 1993). Conversely, it is possible that under certain conditions, demand for phosphate is reduced, which then results in an accumulation of phosphate. This has been shown in several studies for accumulation of a similar chemical compound; acetate (Shannon & White 1996, Avery *et al.* 1999, Hoehler *et al.* 1999, Duddleston *et al.* 2002). Soil pH was positively correlated with CO_2 flux. Moreover, pH is known to affect soil microbial communities in wetlands (Hartman *et al.* 2008), which in their turn affect the CO_2 flux. For soils with a pH between 4 and 7, pH is also a good proxy for nutrient availability (Härdtle *et al.* 2004); a higher nutrient availability is likely to lead to higher CO_2 fluxes (e.g. Shaver *et al.* 1998).

In the shallow cores, CO_2 flux from forest plantation cores was significantly higher than those from restored sites R12, R06 and from the bog cores. This could partly be explained by the biochemical results: Phosphate concentrations in the pore water of the forest plantations are lower than in the pore water of R12 and R06, but higher than the pore water of the bog cores. The soil pH in the forest plantation cores is significantly higher than in the R12, R06 and bog cores, correlating directly with CO_2 flux differences between these sites. However, there were also significant differences in the levels of phosphate and pH between other sites, which did not lead to a significant difference in CO_2 flux. For deep cores, there were no significant correlations between CO_2 flux and any of the chemical variables measured.

Overall, the results show that there are some biochemical constituents of peat (and of soil solution in peat) that emerge as good correlators for peat decomposability (measured as CO_2 flux). However, there is no clear-cut pattern by which peat decomposition can be explained by one or only a few parameters alone. We hypothesise that this is due to the different management of the forest plantations, e.g. variable amounts of fertiliser, and the dissimilar ages of the trees when felled, resulting in much smaller trees in the older restoration sites than in the younger ones and resulting in different ground vegetation at the time of felling. This will have resulted in different microbial communities, which are now re-adjusting after felling. Creevy *et al.* (2018) have shown a difference in the communities of the dominant microbial consumers, testate amoebae, between the forest plantations and the near-natural bogs in the Flow Country. They have also shown that the microbial communities in the R98 site are more similar to the forest plantations than the near-natural bog, so even though we see the peat quality recovering with restoration age, the microbial communities seem to recover more slowly. This could explain why it is so difficult to find good biochemical predictors for our sites. Two recent studies on SOM parameters and decomposition rates in peatlands also could not find strong relationships between CO_2 flux and chemicals (Bader *et al.* 2018, Säurich *et al.* 2017). Bader *et al.* (2018) focused on SOC content, soil pH and C:N ratios and Säurich *et al.* (2017) also focused on total nitrogen content, calcium carbonate content, bulk density, texture, oxalate extractable iron oxide content, calcium acetate lactate, extractable phosphorus content, $\delta^{13}C$ and $\delta^{15}N$.

CH_4 flux explained by biochemical parameters

In shallow cores, CH_4 fluxes increase with increasing percentages of soluble cell components and there seems to be a decrease in CH_4 flux with an increase in soil pH, although this correlation was only marginally significant. This pattern is largely based on within-site variability of soluble cell components, as there are no significant differences in CH_4 fluxes between sites. In contrast to shallow cores, we found no significant correlations between CH_4 fluxes and the biochemical parameters measured. CH_4 fluxes from the deep cores of the forest plantation were higher than from the R06 cores, but there are no significant differences in the levels of the biochemical predictors, so these cannot explain the differences in CH_4 flux between these two sites. In contrast to our results, White *et al.* (2008) found a negative relationship with pore water phosphate and ammonium (not measured here) in their bog mesocosms. Further, they report a positive relationship between DOC, nitrate and sulphate and CH_4 flux, but this correlation was only significant when they considered both the bog and fen mesocosms together and in their fen mesocosms

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separately, but not in their bog mesocosms They explained these inconsistencies by the fact that the concentrations of many of the pore water parameters are very low in the bog and, therefore, have a low predictive power. This is likely the case in our peat cores as well, and could explain the lack of significant correlations found here.

Role of water table

The water table treatment had, as expected, a significant effect on the CO_2 flux from shallow cores; fluxes from cores with a low water table were higher than those from cores with a high water table. However, in the deep cores there was no significant effect of water table treatment. This could be because the C in these deeper layers has become highly recalcitrant, due to the drainage of the sites, which has led to long-term aeration in the field (Laiho 2006). Other studies have also shown higher CO_2 fluxes from cores with lower water table than from cores with high water table, but these studies did not look at different core depths (e.g. Moore & Roulet 1993, Blodau *et al.* 2004, Dinsmore *et al.* 2008, Estop-Aragonés *et al.* 2016). The contrasting flux response to water table depth (and hence aeration of pore spaces in peat) indicate some fundamental differences in peat from the superficial or deeper soil layers. At our sites where the trees had been present over preceding years (or in the case of the forestry sites where they are still present), bulk density has been affected by layers of needle litter on the surface. This lower bulk density in superficial peat depths is likely to allow a much stronger aeration effect from lowered water tables compared to higher peat bulk density at greater depth, so that the oxygenation of peat pores in response to a lower water table may have a much smaller effect here.

There were no significant differences in CH_4 flux across both core depths between any of the water table treatments. This is in contrast with what was expected and with the literature where studies have found higher CH_4 fluxes in high water table treatments than in low water table treatments (Moore & Dalva 1993, Aerts & Ludwig 1997, MacDonald & Fowler 1998, Dinsmore *et al.* 2008) and where a change in water table from low to high has led to a pulse of CH_4 flux (Dinsmore *et al.* 2008). It is possible that a short-term flush of CH_4 was missed in our study (1-2 days after water table change), but overall, the lack of CH_4 flux response is surprising. The average water table depth in the field for the forest plantations is -40 cm and -10 cm in the bog (data not shown), which means that the low water table of -9 cm in the incubation study is only a moderate manipulation. Similarly, White *et al.* (2008) did not find a significant effect of water table treatment in their bog mesocosms, but they did find a significant effect in their fen mesocosms, indicating an interaction between peat composition and water table depth.

In this study, we show that forest plantations have altered the quality of the peat and nutrient availability in the pore water. Different CO_2 fluxes between sites under the same temperature and water table indicate that the chemical and physical legacies of the forest plantations shape the biogeochemical processes in peatlands. We have found some generic predictors for CO_2 and CH_4 fluxes, but it was difficult to interpret consistent changes in peat composition and water table depth in light of CO_2 and CH_4 flux responses. It appears that site-specific conditions, possibly linked to detailed management during periods of forestry, or linked to the method of forest removal seem to override global controls, which makes prediction of the data challenging. For CH_4 flux in particular, only very few differences between sites have emerged, with only two of the restoration sites displaying significant differences, which indicates that on its own (and in absence of biotic interactions under field conditions), the effects of forestry on CH_4 flux are limited.

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