

Greenhouse gas emissions from two rewetted peatlands previously managed for forestry

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SUMMARY

The aim of this study was to investigate the controls on carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) dynamics on a blanket bog (at Pollagoona) and a raised bog (at Scohaboy) in Ireland after felling of plantation forestry and rewetting, and to produce annual balances for each gas at both sites. Gas fluxes were measured during a twelve-month period using the chamber method. Microsite types reflecting the dominant plant species at the chamber plots were identified and classified as *Eriophorum-Sphagnum*, *Cladonia-Calluna* and *Molinia* at Pollagoona and *Eriophorum-Sphagnum*, *Cladonia*-mosses, *Eriophorum* and brash (logging residues) at Scohaboy. The relationships between gas fluxes and environmental variables were assessed, and regression models were used to estimate annual CO₂ and CH₄ gas balances for each microsite type. Annual estimates of N₂O exchange were calculated using seasonal means. Over the course of the study both sites acted as CO₂ and CH₄ sources. Although Pollagoona was an overall net source of CO₂-C (131.6 ± 298.3 g m⁻² yr⁻¹), one microsite type (*Cladonia-Calluna*) acted as a strong sink for CO₂-C (-142.8 g m⁻² yr⁻¹). *Molinia* microsites exhibited the highest CH₄-C emissions (2.53 ± 1.01 g m⁻² yr⁻¹). Nitrous oxide emissions at Pollagoona were calculated as 12 µg m⁻² yr⁻¹. Scohaboy acted as a large CO₂-C source (585.3 ± 241.5 g m⁻² yr⁻¹) (all microsite types) despite re-vegetation of non-brash plots, due to the availability of fresh organic matter across the site. Scohaboy was also a CH₄-C source, emitting 3.25 ± 0.58 g m⁻² yr⁻¹. Emissions of both CO₂-C (819.31 ± 57.7 g m⁻² yr⁻¹) and CH₄-C (4.76 ± 0.98 g m⁻² yr⁻¹) were highest from the brash plots. Annual N₂O-N emissions were small over the study period (72 µg m⁻² yr⁻¹). Our results indicate that, despite remedial work being conducted on both peatlands to raise the water table, the C sink function has not yet been restored at either site.

KEY WORDS: blanket bog, carbon dioxide, methane, nitrous oxide, raised bog, rewetting

INTRODUCTION

Although peatlands cover just 3 % of the world's land surface they store as much carbon (C) as all terrestrial biomass and double that of global forest biomass (Parish *et al.* 2008). Carbon stocks in peatlands are estimated to be approximately 600 Pg (Yu *et al.* 2011), the majority of which is found in the northern hemisphere (Strack 2008). Decomposition in peatlands is impeded by saturated anaerobic conditions caused by a high water table leading to accumulation of organic matter (Moore 1987, Renou-Wilson *et al.* 2011). The C cycle in peatlands involves carbon dioxide (CO₂) uptake by plants during photosynthesis, plant and soil respiration where CO₂ is released, and methane (CH₄) production and consumption. Besides gaseous losses to the atmosphere, C is also lost through waterborne fluxes in runoff from peatlands, in forms that include dissolved organic carbon (DOC), particulate organic

carbon (POC), and dissolved inorganic carbon (DIC), CO₂ and CH₄ (Evans *et al.* 2016). Surface waters from peatland catchments, supersaturated with CO₂ and CH₄, represent a significant pathway connecting the C store with the atmosphere (Dinsmore *et al.* 2009).

Peatlands provide many services such as supporting biodiversity (Bullock *et al.* 2012), maintaining water quality (NPWS 2013), a significant C sink (Joosten *et al.* 2016), a fuel source (Rydin & Jeglum 2006), providing land for agriculture (Joosten & Clarke 2002) and amenity (Moors for the Future Partnership 2012). In their undrained condition peatlands act as sinks of CO₂ (Laine *et al.* 2006, Aurela *et al.* 2009), sources of CH₄ (Hommeltenberg *et al.* 2014, Juszczak & Augustin 2013, Sundh *et al.* 1994) and low emitters of N₂O (Regina *et al.* 1996, Minkinen *et al.* 2002). Drainage precedes peatland utilisation for agriculture, forestry and fuel extraction. Lowering the water table alters microbial activity and nutrient conditions, increases

aeration of the surface peat thereby increasing decomposition and C loss, causes subsidence, and increases peat bulk density (Minkinen & Laine 1998, Laine *et al.* 2006, Laine *et al.* 2009). The falling water table also affects greenhouse gas (GHG) dynamics - CO₂ emissions increase, CH₄ emissions decrease and N₂O is produced (Martikainen *et al.* 1995, Silvola *et al.* 1996, Drewer *et al.* 2010, Turetsky *et al.* 2014).

Irish peatlands are estimated to cover between 1,205,235 and 1,657,500 ha (Xu *et al.* 2018, Eaton *et al.* 2008), of which approximately 322,000 ha is forested (NFI 2013) and 75 % is on blanket peatland (Black *et al.* 2008). Afforestation of peatlands is now limited, with the emphasis on reforestation or other management options. Since 2002, Coillte (the Irish state forestry company) has carried out rewetting works on approximately 1,967 ha of blanket bog (Delaney & Murphy 2012). Previous studies of C dynamics in forested peatlands in Ireland and Scotland have reported high respiration and low emissions of both CH₄ and N₂O (Yamulki *et al.* 2013, Jovani-Sancho *et al.* 2017).

Rewetting and restoration are seen as viable means of restoring the C sink function of peatlands (Höper *et al.* 2008). The primary aim of peatland restoration must be to reduce additional peat degradation (Schumann & Joosten 2008) and subsequently re-establish an ecosystem similar to the one that was degraded (Konvalinková & Prach 2014). In order to accomplish this, drainage ditches must be blocked to raise the water table (Quinty & Rochefort 2003). If the site is successfully rewetted, recolonisation by peatland species may occur, eventually leading to C accumulation (Komulainen *et al.* 1998, Waddington *et al.* 2010). Rewetting often leads to a decrease in both CO₂ and N₂O emissions and an increase in CH₄ emissions (Tuittila *et al.* 2000, Waddington & Price 2000, Regina & Myllys 2009, Beyer & Höper 2015); although these changes can take years to occur, with the result that sites may persist as C sources after rewetting (Petroni *et al.* 2003, Wilson *et al.* 2007b, Samartitani *et al.* 2011). The greenhouse (GHG) dynamics of peatlands are affected by a number of factors including time since rewetting, pH, nutrient status, peat type, vegetation cover and hydrology, which implies that rewetting requires a site-specific approach (Wilson *et al.* 2016a).

Although there is a growing literature on peatland restoration (e.g. Laine *et al.* 2007, Aurela *et al.* 2009, Laine *et al.* 2009, Urbanová *et al.* 2012, Renou-Wilson *et al.* 2016, Wilson *et al.* 2016a), few studies have investigated the changes that occur following rewetting of peatland forests (e.g. Komulainen *et al.* 1999, Haapalehto *et al.* 2011, Koskinen *et al.* 2016).

The objectives of this study are: (1) to identify the environmental variables controlling GHG fluxes at two felled and rewetted peatland forestry sites on (a) a blanket bog and (b) a raised bog in Ireland; (2) to estimate the annual GHG balances for a range of microsite types at both of these sites; and (3) to compare our findings with results from other rewetted peatland sites and suggest management options for increasing the C sink potential of the sites.

METHODS

Study sites

Pollagoona (53° 00' N, 8° 32' W) is a blanket bog in the Slieve Aughty Mountains, County Clare, Ireland, lying at an altitude of 156 m above sea level. The mean annual air temperature is 10 °C and mean annual rainfall 1435 mm (1984–2015 average at Gort Meteorological Station, 20 km from Pollagoona, from the Irish meteorological service Met Éireann). The site was formerly a treeless ombrotrophic blanket bog which, following drainage and ploughing, was afforested with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in the 1980s and felled in 2006. Following felling of the trees, the brash (logging residues) was windrowed (i.e. an excavator was used to collect harvest residues into long narrow piles) and drains were blocked. The peatland is dominated by *Molinia caerulea* while *Calluna vulgaris*, *Potentilla erecta* and *Eriophorum angustifolium* occur frequently (Figure 1). *Eriophorum vaginatum* was also present in small quantities.

Schoaboy (52° 59' N, 8° 02' W) is a raised bog located 4 km south-east of Borrisokane in County Tipperary, Ireland, and lies at an altitude of 78 m above sea level. The mean annual air temperature is 9.8 °C and the mean annual rainfall is 948.2 mm (1981–2010 average at the Met Éireann Gurteen Meteorological Station). The rewetted site covers 71.80 ha and was mainly planted with Sitka spruce in the 1980s. Prior to afforestation, the site was drained and ploughed. Felling was carried out on approximately 19 ha of the site in 2011, without removal of biomass (clear felling). Windrowing the trees limited the area of ground they covered to approximately 40 %, allowing maximum recovery of bog vegetation. In 2013, drains were blocked with plastic piling on both the clear-felled plantation and the remaining natural bog (John Connolly, Coillte, personal communication). Furrows and ridges are still evident on the rewetted bog, creating contrasting habitats for colonisation by plants (Figure 2). The furrows are permanently flooded while the ridges between furrows and drains are drier.



Figure 1. The Pollagoona site at different times during the two years of the study. Clockwise from top left: June 2014, October 2014, February 2015 and August 2015.

Vegetation

Following a survey in January 2014, eight permanent sample plots (P1–P8 at Pollagoona and S1–S8 at Scohaboy) were established on each site using stainless steel collars ($60 \times 60 \times 30$ cm). The vegetation at Pollagoona was dominated by *Molinia caerulea*, with mosses (both *Sphagnum* and non-*Sphagnum*) as the next dominant group of species (Table 1). The plots were located within the representative vegetation assemblages (microsite types): *Eriophorum-Sphagnum* ($n=1$), *Cladonia-Calluna* ($n=1$) and *Molinia* ($n=6$). Two of the *Molinia* plots (P4 and P8) were situated in a former lane of brash. At Scohaboy, plots were established in the following vegetation types: *Eriophorum-Sphagnum* ($n=2$), *Cladonia*-mosses ($n=2$), *Eriophorum* ($n=1$) and brash with no vegetation at the start of the survey ($n=3$).

A wooden boardwalk was built on each site to minimise compression of the peat surface and damage to vegetation. Green leaf area (*GAI*) ($\text{m}^2 \text{m}^{-2}$) was calculated in order to include the seasonal changes of vegetation in the CO_2 exchange models.

Within each collar, five sub-plots (8×8 cm) were established, one in each corner and one in the middle, to capture the vegetation range within the microsite type (see Figure A1 in the Appendix). At fortnightly intervals, the total numbers of leaves and stems of individual plant species within the sub-plots were counted and used to estimate the average numbers of leaves and stems of each species per m^2 . In order to avoid disturbance to the plants inside the sample plots, three individual plants of each species growing outside the sample plots were tagged and their leaves were measured. The tagged plants were similar in age and stature to those inside the sample plots. The length and width of each leaf was measured and these dimensions were used to estimate leaf area using species-specific formulae based on the geometric shape of the leaf (e.g. ellipse, circle, rectangle). The measurements were made on the same day as leaves were counted. For each sample plot, non-linear regression analysis was used to determine the seasonal development of a plot-specific *GAI*. For a detailed description of the method see Wilson *et al.* (2007a).



Figure 2. The Scohaboy site at different times during the two years of the study. Clockwise from top left: March 2014, August 2014, November 2015 and June 2015.

Table 1. Plant species recorded in the study plots, listed in descending order of dominance at the end of the study period. Key to species abbreviations: Calluna = *Calluna vulgaris*, Cam = *Campylopus* spp., Cladonia = *Cladonia portentosa*, Eri ang = *Eriophorum angustifolium*, Eri vag = *Eriophorum vaginatum*, Erica = *Erica tetralix*, Hypnum = *Hypnum jutlandicum*, Juncus = *Juncus effusus*, Molinia = *Molinia caerulea*, Polytrichum = *Polytrichum commune*, Potentilla = *Potentilla erecta*, Rac = *Racomitrium lanuginosum*, Rhy = *Rhytidiadelphus* spp., Sp cap = *Sphagnum capillifolium*, Sp pap = *Sphagnum papillosum*.

Pollagoona			Scohaboy			
<i>Eriophorum-Sphagnum</i> (P1)	<i>Cladonia-Calluna</i> (P5)	<i>Molinia</i> (P2, P3, P4, P6, P7, P8)	<i>Eriophorum-Sphagnum</i> (S1, S5)	<i>Cladonia-mosses</i> (S3, S6)	<i>Eriophorum</i> (S2)	brash (S4, S7, S8)
Eri vag Polytrichum Sp pap Molinia Eri ang	Molinia Sp cap Calluna Cladonia Eri vag Potentilla	Molinia Polytrichum Hypnum Sp cap Rhy Rac Sp pap Cam Juncus	Sp cap Sp pap Eri vag Erica	Cladonia Calluna Hypnum Erica Eri ang Sp pap Sp cap	Eri vag Hypnum Sp cap Calluna Cam	Hypnum Sp pap

Environmental variables

Water table depth (*WT*) was measured in perforated PVC pipes (dipwells; 90 cm long, 2 cm internal diameter) installed adjacent to each collar prior to the start of the study, using a Pocket Dipmeter Kill Mini (Hydrokit, Dorset, UK). A meteorological station (Watchdog 1400 Micro Station, Spectrum Technologies Inc., Illinois USA) was installed at each site to measure photosynthetic photon flux density (*PPFD*; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and soil temperature at depths of 5 and 10 cm, at ten-minute intervals beginning in March 2014 until September 2015.

CO₂ flux measurements

Carbon dioxide flux measurements were conducted at intervals of two weeks from August 2014 until September 2015, making up to three measurements per collar per day between sunrise and late afternoon. To carry out the measurements, a transparent polycarbonate chamber (60 × 60 × 30 cm) was placed on top of the collar. A water filled channel at the top of the collar created an airtight seal. A small vent in the chamber (to ensure pressure equilibrium) was closed after the chamber was placed on the collar. The chamber was fitted with a battery-operated fan to mix the air within the chamber headspace and a quantum sensor to measure *PPFD* (PAR sensor, PP Systems, UK) inside the chamber. Air temperatures inside the chamber were also measured (Ted Pella Inc., 28163 Traceable Total-Range Thermometer, USA.). The chamber was connected to a cooling system that maintained the internal temperature within 1 °C of the ambient temperature. Carbon dioxide fluxes were measured using a portable infrared gas analyser (EGM- 4, PP Systems, UK). During gas flux measurements, soil temperatures at 5 and 10 cm ($T_{5\text{cm}}$, $T_{10\text{cm}}$) depths were measured with a temperature probe (Jenway 220, Jenway, USA.).

In order to measure instantaneous *NEE*, CO₂ concentration was measured at 15 s intervals over a period of 60–180 s under stable ambient illumination. The chamber was vented for a short time following the initial measurement of CO₂ at each collar. To better establish a relationship between *PPFD* and photosynthesis, artificial shades were sometimes used to obtain fluxes under a greater range of *PPFD*. Following measurements in daylight, the same procedure was followed to determine total ecosystem respiration (R_{eco}) but with the chamber covered with an opaque material. Carbon dioxide flux rates ($\text{mg m}^{-2} \text{h}^{-1}$) were calculated from the linear change in CO₂ concentration in the chamber headspace over time, chamber volume, collar area and air temperature. A flux was accepted if the coefficient of determination (r^2) was at least 0.90. A positive flux indicated a net loss of CO₂ from the peatland and a

negative value indicated a net uptake. Gross photosynthesis (P_G) was estimated as the sum of *NEE* and R_{ECO} (Alm *et al.* 2007).

CH₄ and N₂O flux measurements

Methane sampling was conducted at fortnightly to monthly intervals from March 2014 to July 2015. Fluxes were measured using a 60 × 60 × 30 cm opaque polycarbonate chamber which was placed on the collar. The water filled channel at the top of the collar created an airtight seal during sampling. Each chamber had a vent to ensure pressure equilibrium, which was closed after the chamber had been placed on the collar. The chamber was fitted with a fan that circulated air inside the chamber. Four gas samples were taken at five-minute intervals in summer months and at ten-minute intervals in winter months when flux rates are low due to colder conditions and low plant cover. Gas samples were taken in 50 ml plastic syringes fitted with stopcocks and transferred to pre-evacuated glass vials (Extrainer®, Labco Ltd., UK) for transport to the laboratory.

Samples were analysed for CH₄ and N₂O at Justus Liebig University, Giessen, Germany within two months of collection using a gas chromatograph (Bruker Greenhouse Gas Analyser 450-GC) fitted with a flame ionisation detector (FID) and an Electron Capture Detector (ECD). The temperature of both detectors was 300 °C and the oven temperature was 70 °C. Nitrogen was used as the carrier gas (22 ml min⁻¹). The CH₄ (1.02, 1.81, 5.02, 20.9 and 100.1 ppm) and N₂O (0.248, 0.321, 2.01, 15.1 and 100.1 ppm) standards were supplied by Deuste Steininger GmbH. Gas concentrations were calculated using Galaxie software (Varian Inc. 2006).

Fluxes ($\text{mg m}^{-2} \text{h}^{-1}$) were calculated from the linear change in gas concentration as a function of time, chamber volume, collar area and air temperature. A flux was accepted if the coefficient of determination (r^2) was at least 0.90. Positive values indicated losses of CH₄ and N₂O to the atmosphere, and negative flux values indicated CH₄ and N₂O uptake. When analysing CH₄ data, in cases where there was evidence for ebullition or sampling error during the measurement period the measurement was discarded. It is possible that ebullition was caused by the sampling method itself. Therefore, a maximum of one discarded sample per plot was permitted. If vial leakage was evident the sample was also discarded. From a total of 1,024 samples, 97 % of CH₄ samples were deemed acceptable. From the same number, 30 % of N₂O samples were discarded.

Modelling of GHG fluxes

The CO₂ components, R_{eco} and P_G , were modelled separately for each microsite type using nonlinear

regression. In instances where vegetation characteristics and controlling variables were similar, plots were grouped. For Pollagoona, the first group consists of sample plot P1 containing *Sphagnum* spp. and *Eriophorum* spp.; the second group is P5 which, although *Molinia* was present, was the only plot to contain *Calluna vulgaris* and *Cladonia portentosa* and demonstrated a different relationship with the recorded variables than the remaining plots; and the third group is made up of the remaining collars P2, P3, P4, P6, P7 and P8. *Molinia caerulea* was dominant in these collars with moss species occurring in the undergrowth (Table 1). The Scohaboy plots were divided on the basis of their dominant vegetation into groups labelled *Eriophorum-Sphagnum* (n=2), *Cladonia*-mosses (n=2), *Eriophorum* (n=1) and brash (n=3).

The Levenberg-Marquardt multiple non-linear regression technique was used to estimate parameters (SPSS Version 22 for Windows statistical package, SPSS, Inc., Chicago, USA).

Modelling of gross photosynthesis (P_G)

Soil temperature at 5 cm, GAI and $PPFD$ were used as explanatory variables for the P_G models (Equations 1–4 below). GAI was used in the CO_2 flux models to account for the relationship between plant growth and CO_2 flux. The Michaelis-Menten relationship was used to relate $PPFD$ to P_G , describing the dependence of P_G on light [1]. GAI was added to the model as either a linear [2] or an exponential [3] term. Temperature was added to the model as a linear [1 and 2] or Gaussian [3] term. Models were adapted from Wilson *et al.* (2015) [1 and 2] and Laine *et al.* (2009) [3]. Only variables that increased the explanatory power of the model were included. Water table improved the Scohaboy model and was added as a Gaussian term [4]. Model acceptance was based on the following criteria: (a) statistically significant model parameters ($p < 0.05$); (b) highest possible coefficient of determination; (c) lowest possible parameter error; and (d) normality of residuals and residuals scattered around zero.

$$P_G = P_{\max} \left(\frac{PPFD}{PPFD + k_{PPFD}} \right) * T_{5cm} \quad [1]$$

$$P_G = P_{\max} \left(\frac{PPFD}{PPFD + k_{PPFD}} \right) * T_{5cm} * GAI \quad [2]$$

$$P_G = P_{\max} \left(\frac{PPFD}{PPFD + k_{PPFD}} \right) * EXP \left[-0.5 \left(\frac{T_{5cm} - T_{opt}}{T_{tol}} \right)^2 \right] * [1 - EXP(-E * GAI)] \quad [3]$$

$$P_G = P_{\max} \left(\frac{PPFD}{PPFD + k_{PPFD}} \right) * (EXP(-0.5 \left(\frac{WT - WT_{opt}}{WT_{tol}} \right)^2)) \quad [4]$$

where P_G is gross photosynthetic CO_2 flux ($mg\ m^{-2}\ hr^{-1}$), P_{\max} is maximum photosynthesis, $PPFD$ is photosynthetic photon flux density, k_{PPFD} is the value at which P_G reaches half its maximum, T_{5cm} (K) is soil temperature at 5 cm depth, GAI is green area index, T_{opt} is the temperature optimum, T_{tol} is the temperature tolerance for photosynthesis and E is a fitted model parameter. The P_G model parameters are given in Table A1 (Appendix).

Modelling of total soil respiration (R_{eco})

To model soil respiration (Equations 5–8), R_{eco} was linked to soil temperature at 5 cm depth, expressed in Kelvin (K), using the exponential relationship described by Lloyd & Taylor (1994). GAI did not improve the models on either site and was not included. The addition of WT did not improve the performance of the models for the *Eriophorum-Sphagnum* or *Calluna-Cladonia* plots so it was excluded [5]. The *Molinia caerulea* communities displayed a quadratic relationship with WT [6]. At Scohaboy, WT displayed a linear relationship with R_{eco} in some plots, improving the explaining power of the model [8].

$$R_{eco} = [A * EXP[B \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0} \right)]] \quad [5]$$

$$R_{eco} = [A * EXP[B \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0} \right)]] + (WT * C)^2 \quad [6]$$

$$R_{eco} = [A + (B * WT) * EXP[C \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0} \right)]] \quad [7]$$

$$R_{eco} = [A * EXP[C \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0} \right)]] + (B * WT) \quad [8]$$

where R_{eco} is the CO_2 flux due to ecosystem respiration ($mg\ m^{-2}\ hr^{-1}$) and A , B , C are fitted model parameters. Air temperatures (T) are in Kelvin. The temperature minimum at which respiration reaches zero is denoted by T_0 and was set at 227.13 K; T_{ref} was set at 283.15. The R_{eco} model parameters for each sample plot are given in Table A2.

The annual balance of fluxes was calculated using the models created in conjunction with the recorded environmental data for the period 01 Mar 2014 to 28 Feb 2015. Due to sampling errors, annual CH_4 fluxes displayed for Scohaboy are for the year 01 May 2014 to 30 Apr 2015. Daily WT was interpolated from sample day measurements.

Annual CH_4 and N_2O fluxes

No relationships between any of the measured variables and either CH_4 or N_2O fluxes were established at either site. Therefore, annual CH_4 balances were estimated by linear interpolation

between sampling days for each collar and summed to calculate the annual flux. Due to the high number of discarded values for N₂O, interpolation was deemed inadequate and N₂O emissions were estimated using seasonal means. The growing season mean was calculated using data collected from mid-April to mid-October and the winter mean from the remainder of the measurements.

Statistical and uncertainty analysis

Statistical uncertainties associated with the models used for annual P_G and R_{eco} reconstruction were estimated using the standard error of estimation E_r, where the standard error of the model is determined as a percentage of the mean of the fluxes then related to the annual balance (e.g. Renou-Wilson *et al.* 2016). The formula used was:

$$E_r = \sqrt{\frac{\sum_{i=1}^n (F_{obs} - F_{mod})^2}{(n-1)*n}} \quad [9]$$

where E_r is the standard error of the model, F_{obs} is the sampled flux, F_{mod} is the modelled flux and n is the total number of flux measurements. This estimate of error denotes the collective effect of random errors due to statistical uncertainties of the measurements and the scatter of the model results. As net ecosystem exchange was not directly modelled, error in the annual NEE estimate was determined following the law of error of propagation, as the square root of the sum of the squared standard errors of P_G and R_{eco}.

The significance threshold used in this study was p ≤ 0.05. A one-way ANOVA test confirmed a significant difference between sample plot means.

RESULTS

Environmental variables

During the study year March 2014 to February 2015, the annual rainfall of 1411 mm in Pollagoona was similar to the 30-year average of 1435 mm (Figure 3a). Precipitation in Scohaboy for the same period was 912.5 mm, 4 % less than the long-term average of 948.2 mm (Figure 3c). The rainfall recorded during the November–February period was higher than for the summer months. Mean air temperature (Athenry Meteorological Station near Pollagoona) was 9.9 °C for the same period, with the maximum air temperature (26.6 °C) being recorded in July 2014 and the minimum (-5.4 °C) in February 2015 (Figure 3b). Mean air temperature at Gurteen Meteorological Station, near Scohaboy, was 9.9 °C for the study year. Soil temperatures reached their maximum values in July 2014 and their minimum values during January and February 2015 (Figure 3d).

Annual mean WT was -13.4 cm (standard deviation 9.1) at Pollagoona and -6.9 cm (standard deviation 7.5) at Scohaboy. The water table in all sample plots fell during the summer months, below -30 cm in two plots at Pollagoona (Figure 4a). The largest fall in any of the plots was observed in P7 (a *Molinia caerulea* dominated plot) in October 2014, where WT reached -56 cm. The deepest mean annual WT (-25.4 cm) was observed in P7, while the shallowest (-6.6 cm) was observed in P3 (also a *Molinia caerulea* dominated plot). The deepest mean WT (-18.9 cm) for a microsite type was observed in *Cladonia-Calluna* microsites. At Scohaboy, despite a drop during the summer months, WT remained above -30 cm throughout the study period (Figure 4b). Both the lowest and the highest mean annual WT during 2014 and 2015 were observed in the brash plots.

Vegetation dynamics

Moss cover varied along the WT gradient at Pollagoona. Plots with WT > -20 cm tended to contain more *Sphagnum* species such as *Sphagnum capillifolium* and *Sphagnum papillosum* as well as non-*Sphagnum* mosses, e.g. *Campylopus* spp., *Polytrichum commune* and *Hypnum jutlandicum*, than plots where the water table was below this level for much of the growing season. A strong seasonal dynamic in GAI was evident in all sample plots throughout the study. Plant growth increased during spring and early summer due to rising soil temperatures and increased PPF_D values. GAI peaked at midsummer before decreasing through the autumn due to *Molinia caerulea* senescence. Throughout the winter months, GAI remained above zero, signifying the presence of evergreen species (Table 2) in addition to *Molinia caerulea* in all sample plots. The highest variation in GAI occurred in plots with high *Molinia caerulea* density and least change in GAI was observed in the *Eriophorum-Sphagnum* plot.

This study took place soon after rewetting of Scohaboy, which caused a clear change in the vegetation. *Eriophorum vaginatum* was spreading rapidly, as were *Sphagnum* spp., particularly in the wetter old plough furrows. Despite this, vegetation remained patchy, reflecting the early successional stage of the site. The sample plots in furrows (S1, S2 and S5) were the wettest and by the end of the study were covered by a dense carpet of *Sphagnum capillifolium* and *Sphagnum papillosum*, along with *Eriophorum vaginatum*. *Erica tetralix* also grew in the wetter areas of these ‘furrow plots’. *Calluna vulgaris* and *Cladonia* spp. growing in plots situated along the tree lines on the old plough ridges, (S3, S6) reflect drier conditions. Sample plots situated in the brash line (S4, S7 and S8) provided conditions quite

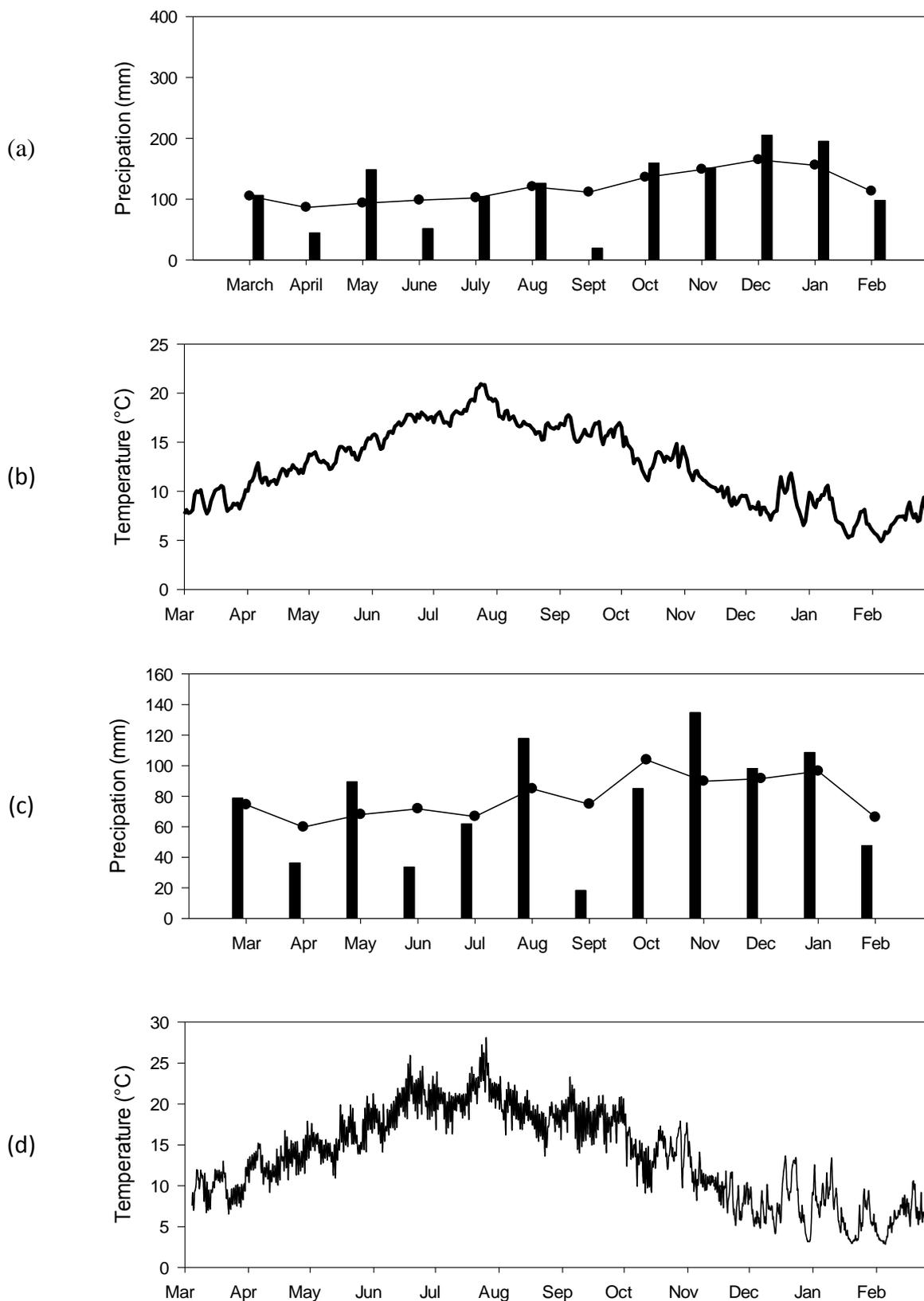


Figure 3. Rainfall and soil temperature data for Pollagoona, County Clare and Scohaboy Bog, County Tipperary, during the study period March 2014 to February 2015: (a) monthly rainfall (mm) (Met Eireann, Gort rainfall Station); (b) soil temperature (°C) at 5 cm depth at Pollagoona; (c) monthly rainfall (mm) (Met Eireann, Gurteen Station); (d) soil temperature (°C) at 5 cm depth at Scohaboy. The filled circles and lines indicate 30-year averages (1981–2010, www.met.ie).

unlike those in the other sample plots. Here, little or no vegetation was present at the start of the study, but over time *Sphagnum papillosum* and *Hypnum jutlandicum* started to colonise the plots.

Model performance

The strength of the relationship between CO₂ fluxes and the environmental variables differed between vegetation communities at both sites (Tables A1 and A2; see Appendix). At Pollagoona, *PPFD* alone accounted for 25 % of the variability amongst the *Molinia caerulea* dominated plots for P_G. The addition of soil temperature and *GAI* increased the explanatory power of the model to 68 %. Plots P1 and P5 behaved differently from *Molinia* plots. *PPFD* accounted for 42–55 % of the variation, while adding soil temperature at 5 cm to the model improved P1 to 79 % and further incorporation of *GAI* raised the explaining power of the model for P5 to 84 %.

At the *Eriophorum-Sphagnum* and *Cladonia-Calluna* sample plots, soil temperature at 5 cm was the sole explanatory variable in the R_{eco} models [5] and explained 63–74 % of the flux variability. The addition of *WT* improved the explanatory power of

the model for the *Molinia caerulea* plots from 54 % to 63 %. Both models tended to overestimate low and underestimate high fluxes.

PPFD explained 45–53 % of the variability in P_G across all vegetation communities at Scohaboy. The addition of *WT* [4] increased the explanatory power of the model to 77 % (S1 and S5), 64 % (S3 and S6) and 68 % (S2). No significant relationship between *GAI* and CO₂ flux was observed, so *GAI* was not included. At S2, soil temperature at 5 cm was the sole explaining variable in the R_{eco} models [5] and explained 61 % of the flux variability. The addition of *WT* to the model [7] increased the variability explained to 45 % (S1 and S5) and 45 % (brash collars). *WT* was the controlling variable in the *Cladonia*-mosses sample plots [8] and the addition of soil temperature at 5 cm improved the explanatory power of the model, explaining 77 % of the variability.

Annual GHG balance

All study plots across both study sites, apart from the *Cladonia-Calluna* plot at Pollagoona, were net sources of CO₂ during the study period. Strong

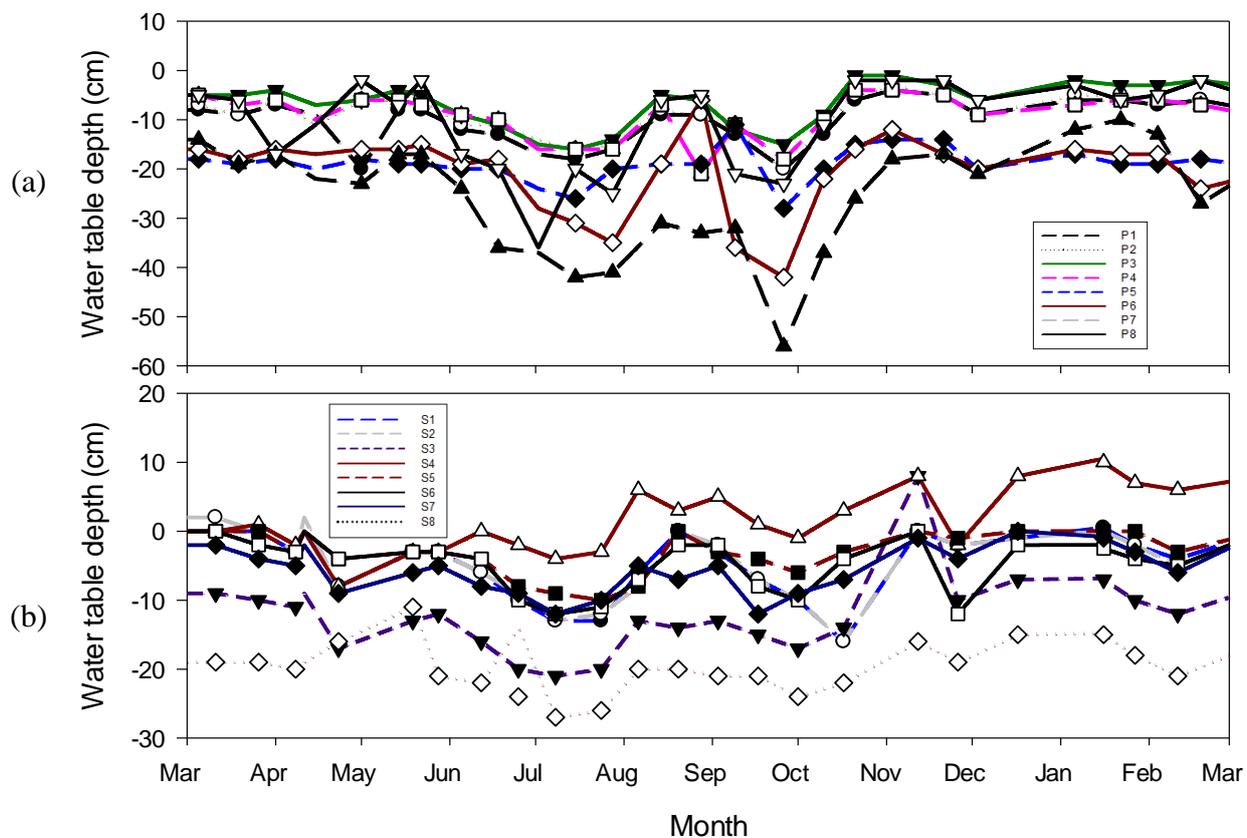


Figure 4. Interpolated water table depths (cm) in all study plots at (a) Pollagoona and (b) Scohaboy from March 2014 to February 2015. Markers show observations while lines show interpolated values.

seasonal variation was seen in modelled P_G , R_{eco} and NEE (Figures 5 and 6). Highest fluxes were observed in all plots in the summer season (May to August) while the lowest modelled fluxes occurred in the winter season (November to February).

At Pollagoona, NEE generally followed the *WT* gradient. The annual CO_2 -C balance was highest in the plots where *WT* dropped below -20 cm during the summer months of June to August, namely P7 (243.2 g m^{-2}) and P6 (313.4 g m^{-2}). Although *WT* values below -10 cm were recorded for P5, it acted as a CO_2 -C sink over the course of this study (-142.8 g m^{-2}), suggesting that other factors control its CO_2 emissions. Both the *Eriophorum-Sphagnum* and *Molinia caerulea* dominated communities acted as small C sinks during the summer months. Gross photosynthesis remained above zero during daylight hours throughout the study, including winter. The annual CO_2 balance varied between microsites (Table 2). The *Eriophorum-Sphagnum* plot was the

largest annual CO_2 -C source at 184.8 g m^{-2} while the *Cladonia-Calluna* plot was a sink of -142.84 g m^{-2} in the year studied. The average CO_2 -C balance across all study plots for the year March 2014 to February 2015 was estimated as 131.6 ± 298.3 g m^{-2} yr^{-1} .

During the same period, the mean annual CO_2 -C release in the Scohaboy study plots was much greater, estimated at 585.3 ± 241.52 g m^{-2} yr^{-1} (Table 2) but varied spatially across the site. In the brash plots, NEE followed the *WT* gradient, with the highest rates of CO_2 -C loss at Plots S7 (761.3 g m^{-2}) and S8 (1136.8 g m^{-2}) which both recorded the lowest water tables. Despite high annual mean *WT* (-5, -5, 2 and -3 cm, respectively), CO_2 -C emissions at S1 (785.9 g m^{-2}), S2 (382.3 g m^{-2}), S4 (559.8 g m^{-2}) and S5 (668.3 g m^{-2}) were high; while the lowest annual CO_2 -C emissions occurred at S3 (25.1 g m^{-2}), which was the driest plot (mean annual *WT* -12cm).

High levels of variance in CH_4 emissions were evident both temporally within and spatially between

Table 2. Summary of annual sums and averages of greenhouse gases from the Pollagoona sample plots of (a) *Eriophorum-Sphagnum*, (b) *Cladonia-Calluna* and (c) *Molinia*; and from the Scohaboy sample plots of (d) *Eriophorum-Sphagnum*, (e) *Cladonia*-mosses, (f) *Eriophorum* and (g) brash. Standard errors of estimates for fluxes calculated from more than one sample plot are shown in brackets. Positive values indicate a loss of C from the site and negative values indicate an uptake of C by the site. T_{5cm} = soil temperature ($^{\circ}C$) at 5 cm depth, *WT* = water table depth in cm. Standard deviation is not shown for T_{5cm} which was recorded continuously at site rather than at plot level.

	T_{5cm} ($^{\circ}C$)	<i>WT</i> (cm)	P_G as CO_2 -C (g m^{-2} yr^{-1})	R_{eco} as CO_2 -C (g m^{-2} yr^{-1})	NEE as CO_2 -C (g m^{-2} yr^{-1})	CH_4 -C (g m^{-2} yr^{-1})	N_2O -N (μg m^{-2} yr^{-1})
Pollagoona							
(a) <i>Eriophorum-Sphagnum</i>	12.6	-10.2	-1089.8 (68.1)	1274.7 (47.1)	184.8 (82.8)	1.99	56.29
(b) <i>Cladonia-Calluna</i>	12.6	-18.9	-1179.8 (86.3)	1037.0 (30.1)	-142.8 (91.4)	0.54	-107.86
(c) <i>Molinia</i>	12.6	-13.4	-954.4 (204.7)	1122.9 (103.8)	168.4 (229.5)	2.53 (1.01)	29.08 (0.06)
Site value			-999.5 (267.8)	1131.1 (131.4)	131.6 (298.3)	2.94 (1.03)	-12.00 (79.82)
Scohaboy							
(d) <i>Eriophorum-Sphagnum</i>	13.5	-3.8	-1159.6 (179.9)	1886.7 (240.4)	727.1 (300.3)	2.30 (0.03)	34.90 (25.10)
(e) <i>Eriophorum</i>	13.5	-4.6	-1138.4 (167.6)	1520.7 (77.6)	382.3 (184.7)	2.25	43.60
(f) <i>Cladonia</i> -mosses	13.5	-4.6	-634.1 (92.6)	828.1 (31.5)	194.1 (97.9)	2.40 (1.00)	180.60 (26.00)
(g) brash	13.5	-7.5	0	819.3 (57.7)	819.3 (57.7)	4.80 (1.00)	29.80 (37.80)
Site value			-590.7 (153.0)	1176.0 (186.9)	585.3 (241.5)	3.25 (0.58)	72.00 (36.25)

the sample plots at Pollagoona (Figure 7a). A significant but weak relationship was found between the measured CH₄ emissions and soil temperature ($r^2 = 0.20$, $p < 0.05$), while no correlation was found between CH₄ fluxes and either *WT* or *GAI*. All plots were CH₄ sources for the study period, with interpolated annual CH₄-C emissions ranging from 0.081 g m⁻² yr⁻¹ (P7) to 8.24 g m⁻² yr⁻¹ (P4). An annual CH₄-C release of 2.94 ± 1.03 g m⁻² yr⁻¹ was calculated for Pollagoona by interpolation of measured emissions (Table 2).

The annual CH₄-C release was higher for Scohaboy (3.25 ± 0.58 g m⁻² yr⁻¹) (Table 2). As with Pollagoona, high temporal and spatial variability in

fluxes was evident between the sample plots. All plots were CH₄-C sources for the study period, with mean annual emissions ranging from 1.4 g m⁻² yr⁻¹ (S6) to 8.5 g m⁻² yr⁻¹ (S7).

Pollagoona was estimated to be a net N₂O-N sink of -12 μg m⁻² year⁻¹ (Table 2) and Scohaboy a net source of 72 μg m⁻² yr⁻¹. Considerable variation was seen between sample plots. At Pollagoona, the *Cladonia-Calluna* plot acted as a N₂O sink for the duration of the study while the remaining microsite types were N₂O sources throughout the same period. At Scohaboy, the *Cladonia*-mosses plots were the largest N₂O sources and the brash plots were the smallest.

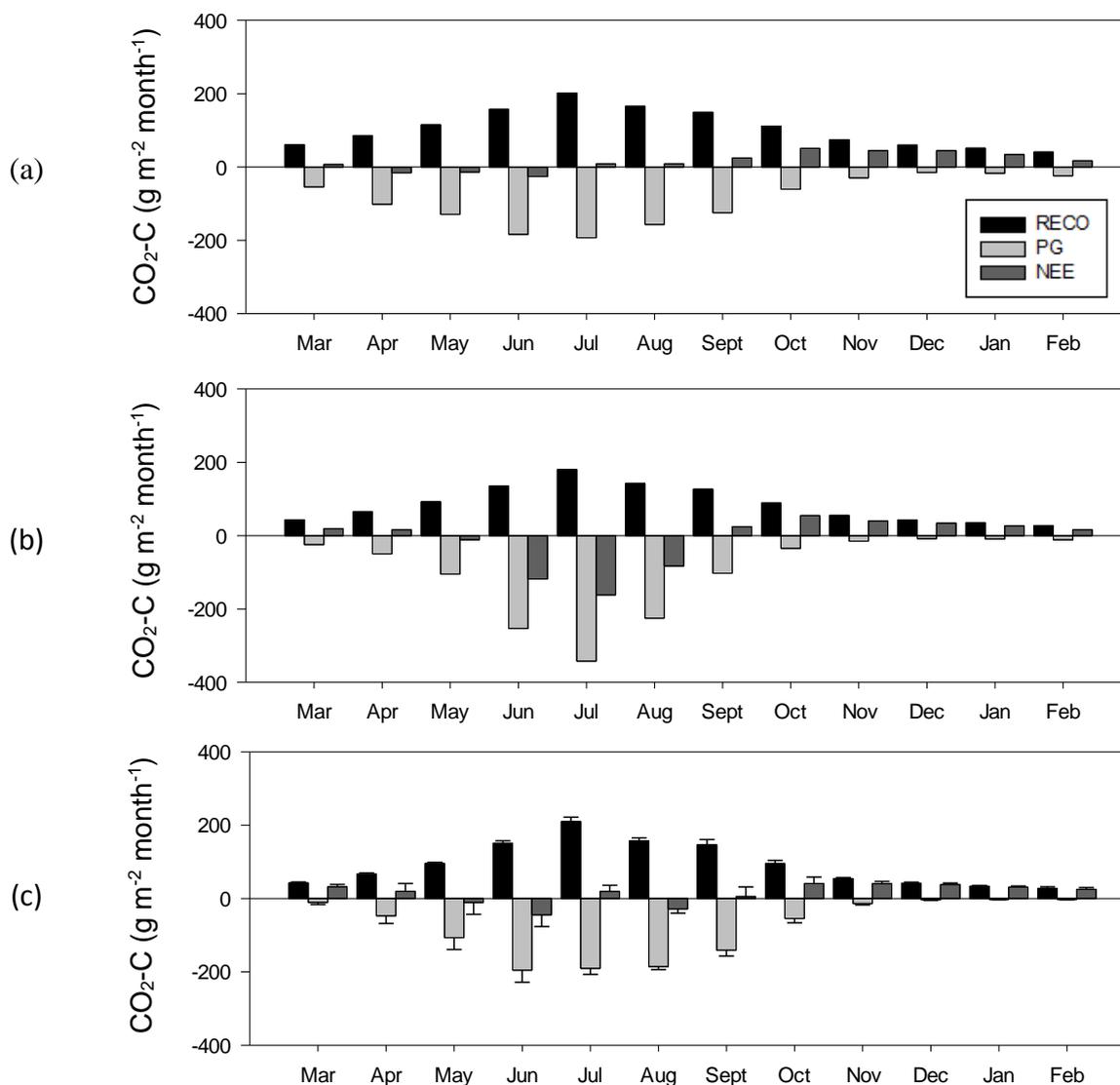


Figure 5. Average monthly modelled gross photosynthesis (P_G), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE) as CO₂-C (g m⁻² month⁻²) for (a) *Eriophorum-Sphagnum* (b) *Cladonia-Calluna*, and (c) *Molinia caerulea* sample plots at Pollagoona from March 2014 until February 2015. Positive values indicate losses of CO₂ to the atmosphere while negative values indicate CO₂ uptake by the peatland. Error bars indicate standard errors for microsite types represented by more than one sampling plot.

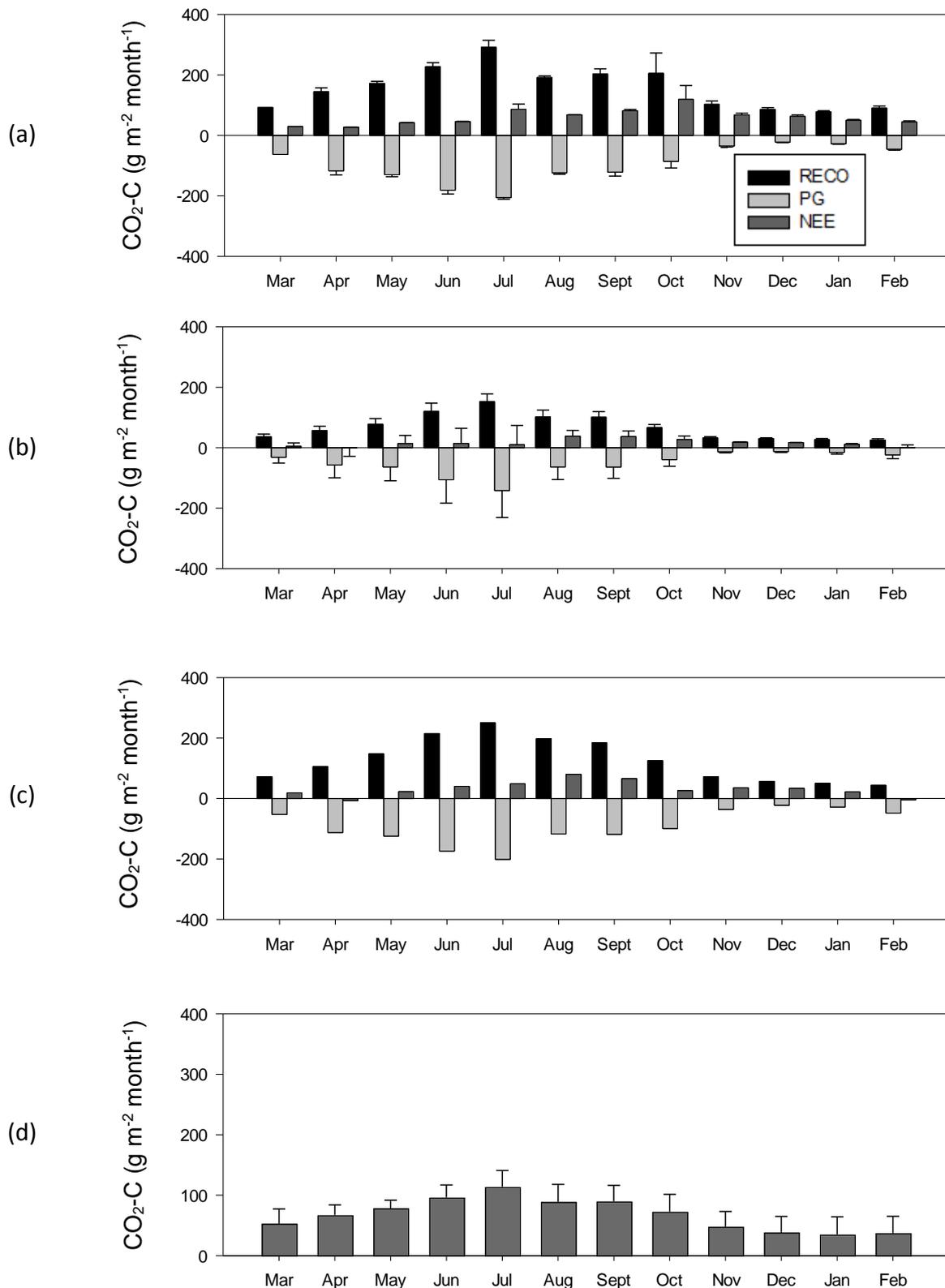


Figure 6. Average monthly modelled gross photosynthesis (P_G), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE) as CO_2-C ($g\ m^{-2}\ month^{-1}$) for (a) *Eriophorum-Sphagnum*, (b) *Cladonia*-mosses, (c) *Eriophorum* and (d) brush sample plots at Scohaboy from March 2014 to February 2015. Positive values indicate losses of CO_2 to the atmosphere while negative values indicate CO_2 uptake by the peatland. Note the different scales on the y axes. Error bars indicate standard errors for microsite types represented by more than one sampling plot.

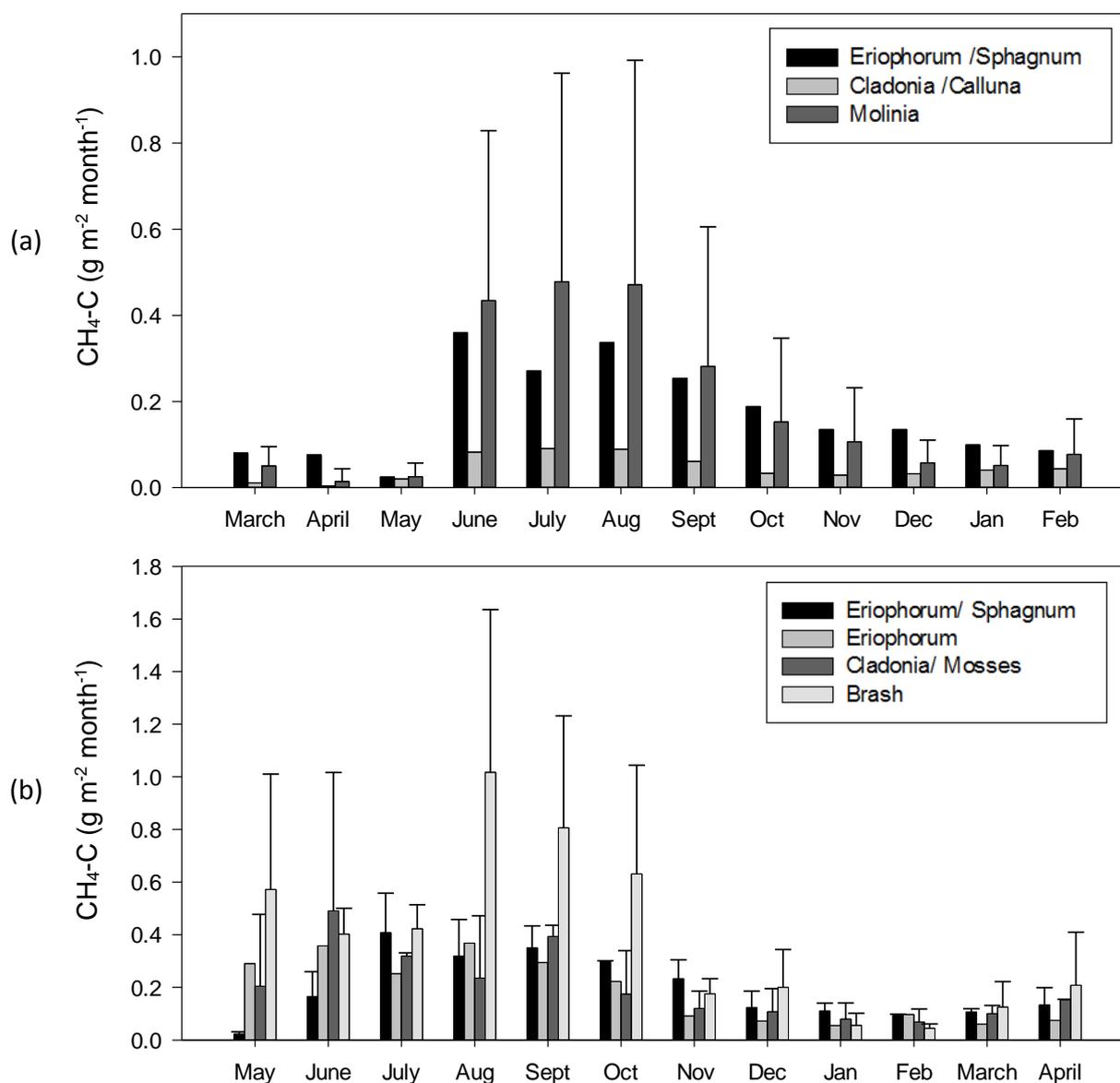


Figure 7. Interpolated monthly means of CH₄-C (g m⁻² month⁻¹) within the studied vegetation communities at (a) Pollagoona and (b) Scohaboy. Error bars represent standard deviation on the interpolated means. Positive values indicate losses of CH₄ to the atmosphere.

DISCUSSION

Similar dominant controls on GHG fluxes existed between the two study sites, despite their differing peat types. Pollagoona (blanket bog) was an annual source of CO₂-C (131.60 ± 298.3 g m⁻² yr⁻¹), a small annual source of CH₄-C (2.94 ± 1.03 g m⁻² yr⁻¹) and an annual sink of N₂O-N (-12 µg m⁻² year⁻¹) eight years after rewetting. Scohaboy (raised bog) was a large source of CO₂-C (585.3 ± 241.52 g m⁻² yr⁻¹) and a small source of both CH₄-C (3.25 ± 0.058 g m⁻² yr⁻¹) and N₂O-N (72 µg m⁻² year⁻¹) to the atmosphere during the study year.

Carbon dioxide

A significant relationship between soil temperature, *WT* and *R_{eco}* was determined (Table A2). The strong temperature dependence of *R_{eco}* has been described in many studies (Silvola *et al.* 1996, Bubier *et al.* 1998, Lafleur *et al.* 2005). High temperatures stimulate microbial activity which thereby emits a greater mass of CO₂ (e.g. Frolking & Crill 1994, Silvola *et al.* 1996). The chemical structure of substrates and the nutrients available also affect the heterotrophic respiration response to temperature (Updegraff *et al.* 2001, Blodau *et al.* 2004). In this study, near-surface temperatures displayed a closer relationship with *R_{eco}*

than deeper soil temperatures, as also described by Lafleur *et al.* (2005) and Minkinen *et al.* (2007). Soil temperatures recorded throughout this study were higher than in other studies on temperate peatlands (e.g. Laine *et al.* 2007, Wilson *et al.* 2016b) and remained high throughout the winter period, thereby maintaining high R_{eco} fluxes year-round. Thus, the mild winters in the temperate climate support peat decomposition (Höper *et al.* 2008). A weaker relationship was identified between R_{eco} and *WT* at Pollagoona, perhaps due to the deep water table in many plots over the course of the study year (*WT* values ranged from -2 to -56 cm). Water table regulation of peat respiration is a contentious issue and some studies have questioned or rejected its validity (e.g. Lafleur *et al.* 2005, Dimitrov *et al.* 2010). Soil respiration has been reported to cease increasing in response to *WT* falling below -30 cm (Silvola *et al.* 1996, Chimner & Cooper 2003) or -61 cm (Mäkiranta *et al.* 2009). Carbon dioxide fluxes were high in sample plots in the plough furrows at Scohaboy (*Eriophorum-Sphagnum* and *Eriophorum*) despite *WT* being no lower than -15 cm. Similarly, Saiz *et al.* (2006) found that higher soil respiration rates were found in the furrows of a forest stand on mineral soil, attributable to a thicker layer of organic matter gathering in the furrows than on the ridges or flat areas. The raised water table on Scohaboy could be expected to reduce peat decomposition while fine roots and the easily decomposable humus organic matter layer decompose creating an additional release of CO_2 during the initial phase of restoration, expected to last for 2–10 years (Höper *et al.* 2008). In addition to elevated soil temperatures, the brash (a source of highly decomposable fresh organic matter), remaining on both sites most likely contributed to the high R_{eco} rates observed (Mäkiranta *et al.* 2012). Recently, Jylhä *et al.* (2017) demonstrated that significant CO_2 emissions originate from stockpiled woodchips; 10.8 kg CO_2 for whole-tree and 9.3 kg CO_2 for stem wood per solid cubic metre of chips. Decomposing trees that remain in brash lines on both sites, coupled with the ‘priming effect’ i.e. the increased decomposition of peat beneath the brash due to the introduction of fresh organic material (Fontaine *et al.* 2004, Fontaine *et al.* 2007), could be elevating CO_2 losses from the sites particularly on Scohaboy, where the annual average $\text{CO}_2\text{-C}$ flux in the brash plots was almost double (819.9 g m^{-2}) that of the plots without brash (444.9 g m^{-2}).

Methane

Despite the absence of significant relationships between CH_4 fluxes and the variables measured, *WT* and temperature appeared to influence emissions.

Emissions at Pollagoona followed the *WT* gradient and seasonal trends in soil temperature, as in other studies (Beetz *et al.* 2013, Renou-Wilson *et al.* 2014, Renou-Wilson *et al.* 2016). At Scohaboy, brash collars had the greatest $\text{CH}_4\text{-C}$ fluxes of all four microsite types at 4.8 ± 1.0 g m^{-2} yr^{-1} . Similarly, Mäkiranta *et al.* (2012) found that brash plots emitted more CH_4 than control plots. Low emissions of CH_4 in this study are likely indicative of low quantities of methanogenic bacteria following drainage and subsequent rewetting (Juottonen *et al.* 2012); however, emissions would be expected to increase as time since rewetting progresses (Waddington & Day 2007), particularly if high *WT* is maintained and the peatland is recolonised by typical peatland plant communities. Annual $\text{CH}_4\text{-C}$ emissions estimated in this study are lower than those reported by Koskinen *et al.* (2016) from rewetted spruce swamps in Finland, while emissions from Pollagoona fall within the range (0.082–2.96 g m^{-2} yr^{-1}) estimated from the work of Juottonen *et al.* (2012) on rewetted forests in Finland.

Nitrous oxide

There is a high level of uncertainty associated with the N_2O values reported here and those published in previous studies due to huge spatial and temporal variation and the use of manual chambers which may fail to capture the variability associated with N_2O (Lai 2009, Hensen *et al.* 2013, Juszczak & Augustin 2013).

The influence of vegetation

Vegetation is significant in terms of both C sequestration and release on peatland sites. Pollagoona was fully vegetated eight years after rewetting, primarily by *Molinia caerulea*, with *Polytrichum commune* as the dominant moss species and *Hypnum cupressiforme* and *Sphagnum capillifolium* present in smaller quantities, indicating that the fluctuating water table and dry conditions of the site were preventing the return of *Sphagnum* as the dominant species. *Molinia caerulea* is well adapted to growth in nutrient-poor conditions and is known to be a successful and vigorous competitor on drained peatlands (Taylor *et al.* 2001). Its dominance here is indicative of less-than-optimum *WT* (Gatis *et al.* 2015). While Pollagoona displays a species assemblage typical of natural mountain blanket bogs, site conditions prior to rewetting have strongly influenced the recovery of micro-habitat heterogeneity, which is completely absent from this site. This together with the prolific *Molinia caerulea* limited species diversity on this site and the establishment of other peat forming species (Hákjová *et al.* 2009).

Vegetation change was observed at Scohaboy throughout the study period as *Eriophorum vaginatum* increased in both canopy size and spatial extent. The occurrence of *Sphagnum* also increased in the sample plots over the study period and attained cover >50 % in some plots which is a promising indicator. The plant species composition of a peatland can greatly influence CH₄ dynamics (Robroek *et al.* 2015). At this study site, the greatest CH₄ losses occurred in the *Cladonia*-mosses microsites. Aerenchymous plant species have been associated with higher CH₄ emissions by a large body of research (e.g. Marinier *et al.* 2004, Leppälä *et al.* 2011, Green & Baird 2012). A smaller number of authors have connected reduced CH₄ emissions from microsites containing aerenchymous species with an increase in oxygenation of the rhizosphere (Mitsch *et al.* 2009, Dinsmore *et al.* 2009). *Sphagnum* species have also been established as supporting methanotrophic bacteria (e.g. Raghoebarsing *et al.* 2005, Larmola *et al.* 2009) and emitting lower volumes of CH₄ (Parmentier *et al.* 2011). Large fluxes in late summer may be attributed to rising water table (Figure 5b) combined with high soil temperatures (Figure 4d) and may also be related to the addition of decaying plant material to the peatland due to the onset of senescence (Tuittila *et al.* 2000).

Peatland vegetation also plays a crucial role in CH₄ emissions (Ström *et al.* 2003, Henneberg *et al.* 2015, Henneberger *et al.* 2015) by influencing the processes in CH₄ cycling (Joabsson *et al.* 1999). Some authors have suggested vegetation as a dominant control on CO₂ sequestration in the early stages of rewetting as the vegetation species that colonise the site and the amount of vegetation cover that a site displays can determine whether it is a sink or a source (Samaritani *et al.* 2011, Urbanová *et al.* 2012). At Pollagoona, R_{eco} was lowest and P_G highest in the *Cladonia-Calluna* plot, resulting in a small CO₂-C sink (-142.84 g m⁻² yr⁻¹). *Eriophorum vaginatum* is influential in CO₂ sequestration as it has a high rate of P_G throughout the growing season and high respiration rates (Tuittila *et al.* 1999, Marinier *et al.* 2004). *Eriophorum vaginatum* cover on Pollagoona is low and so the influence of other factors such as soil temperature and WT may negate any of its potential effects on CO₂ sequestration. However, work by Urbanová *et al.* (2012) also found *Molinia caerulea* to be a C sink and noted that photosynthesis levels dropped during senescence with large amounts of CO₂ released, which in our study caused the *Molinia caerulea* plots to be C sources. Methane flux has been found to be greater when graminoid species are present while the presence of mosses may reduce CH₄ emissions (Strack *et al.* 2017), as demonstrated by the larger

CH₄ emissions estimated from *Molinia* and *Eriophorum-Sphagnum* plots. Decaying vegetation and root exudates also increase substrate availability for heterotrophic microorganisms and eventually for methanogens (King & Reeburgh 2002, Saarnio *et al.* 2004). *Molinia caerulea* has been linked to low emission rates in some instances (Bhullar *et al.* 2014), and high rates in others (Vanselow-Algan *et al.* 2015). It has been suggested that *Molinia caerulea* contributes to CH₄ emissions by producing large amounts of litter, which is more easily decomposed than other plant species found on site (Berendse 1998, Vanselow-Algan *et al.* 2015), thereby contributing to the higher CH₄ fluxes seen in *Molinia caerulea* plots. Species specific differences in NEE and CH₄ emissions have been observed for the common peatland sedges *Carex*, *Eriophorum* and *Juncus*, and explained by variations in root exudation arrangement and radial oxygen loss (Ding *et al.* 2005, Ström *et al.* 2005, Koelbener *et al.* 2009). Mosses are likely to influence methanotrophic activity and lead to CH₄ oxidation (Liebner *et al.* 2011, Franchini *et al.* 2015), causing lower CH₄ losses. Our observation in this study that *Molinia caerulea* at Pollagoona emitted the highest levels of CH₄ during warmer periods is similar to the findings of Ward *et al.* (2013).

Effects of management

Rewetting is a long-term approach to the re-establishment of the C sink function of a peatland (Wilson *et al.* 2016a). It requires both the restoration of high WT and revegetation (Drösler *et al.* 2008). Despite implementation of rewetting management practices, the necessary hydrological conditions have not yet been restored at Pollagoona, as indicated by low WT throughout the study year and the dominance of *Molinia caerulea*, which grows freely on drier parts of blanket bog (Taylor *et al.* 2001). Despite a favourable (for rewetting) annual mean WT in the study plots (i.e. -13.4 cm), great variability was evident between plots and throughout the year. Evidence from the vegetation present suggests that a stable high water table has not been re-established, preventing the return of the C sink function as the water table is not high enough to reduce peat respiration. Published C balances from similar sites in Ireland or Britain are not available. However, comparing soil respiration values for Pollagoona (1131.1 ± 131.4) and Scohaboy (1176 ± 186.9) with the results of previous studies shows similarities. For Sitka spruce and lodgepole pine (*Pinus contorta*) plantations established on blanket peat, Jovani-Sancho *et al.* (2017) estimated annual soil respiration (as CO₂-C) at 1040 g m⁻² yr⁻¹ and 703 g m⁻² yr⁻¹, respectively. Other Irish authors have estimated

annual CO₂-C emissions by soil respiration in afforested peatland at 100–260 g m² yr⁻¹ (Byrne & Farrell 2005), while Yamulki *et al.* (2013) report a value of 450 g m² yr⁻¹ for total respiration of a lodgepole pine stand on a raised bog in central Scotland. However, despite modelled respiration being high, annual CO₂ emissions at Pollagoona are much lower than those from clear-felled peatland forests in Finland (e.g. Mäkiranta *et al.* 2007, Minkkinen *et al.* 2007) and the IPCC CO₂-C emission factor for temperate peatland forests (2600 kg ha⁻¹ yr⁻¹; Drösler *et al.* 2014), and N₂O emissions at this site are negligible. While CH₄ emissions remain lower than in other rewetting projects (e.g. Marinier *et al.* 2004, Juottonen *et al.* 2012, Wilson *et al.* 2016b), work by Green & Baird (2017) suggests that annual CH₄ balances estimated through linear interpolation are likely to be much lower than those estimated using empirical models. The effects of day-to-day variation in conditions are more evident in flux data for CH₄ than for the other gases and may not be represented accurately by interpolation. However, CH₄ emissions may increase if the water table is raised. On the other hand, CO₂ losses from Scohaboy are comparable to or greater than those from other clear-felled peatland sites (Mäkiranta *et al.* 2007, Minkkinen *et al.* 2007) and even peatland forests (Silvola *et al.* 1996), despite the apparent reinstatement of suitable hydrological conditions within the study area.

Implications

The C sink function of the rewetted peatland forests studied here was not successfully re-established, at least in the short term. Previous studies have demonstrated little consistency in the GHG dynamics of rewetted peatlands and results have proved to be unpredictable and highly site specific. A rapid return of the C sink function has been reported in some studies (Urbanová *et al.* 2012, Wilson *et al.* 2016b), while in others high CO₂ emissions have persisted for years after rewetting (Wilson *et al.* 2007b, Samartitani *et al.* 2011). In future forest rewetting projects, it is recommended that all clear-felled trees, including branches and timber of no commercial value, be removed and perhaps used for energy purposes (e.g. in co-firing boilers) in order to reduce the volume of fresh organic material on the site and thereby limit CO₂ emissions from brash decomposition, the priming effect and possibly the introduction of non-peatland species. Maintaining a stable high water table on the study sites will increase the likelihood of returning the C sink function of the peatland. Although drain blocking was not investigated in this study, the water table data for both sites indicate that more effective blocking of

drainage is required to encourage a stable and high water table, and thereby create optimum conditions for colonisation by peat forming vegetation. The results of research on drain-blocking methods for blanket bog in the UK (e.g. Armstrong *et al.* 2009) could be utilised to improve the effectiveness of rewetting in these ecosystems, for example by blocking with peat turves installed every 10 m on gentle slopes and every 5 m on steep slopes or in large drains. Alternatively, the drainage ditches could be completely filled if enough peat is available. More recently, techniques to address the drainage effects of peat cracks developed under forestry have been trialled with very promising results (Anderson 2017). Changes in the topography and hydrology of the peatland following drainage will also affect the success of rewetting. Therefore, sites should be assessed carefully before commencing tree felling and rewetting. In particular, careful attention to the hydrology of the site is needed in order to determine how altered it is following drainage and whether it will be possible to re-establish and maintain a high, stable water table. Holden *et al.* (2011) highlighted that rewetting peatlands may fail to re-establish natural water table dynamics even many years after rewetting. In situations where remedial works will not establish high WT and the rewetted peatland will remain a source of C, it is possible that the most favourable site carbon balance may in fact be achieved by leaving the trees growing on the peatland.

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REFERENCES

- Alm, J., Shurpali, N.J., Tuittila, E.-S., Laurila, T., Maljanen, M., Saarnio, S. & Minkkinen, K. (2007) Methods for determining emission factors for the use of peat and peatlands—flux measurements and modelling. *Boreal Environment Research*, 12, 85–100.
- Anderson, A.R. (2017) *Research Rewetting Trials*. Forest Research, Roslin, Midlothian, UK (website).

- Online at: <https://www.forestry.gov.uk/fr/bee-hajcevp>, accessed 10 Dec 2018.
- Armstrong, A., Holden, J., Kaya, P., Foulger, M., Gledhill, S., McDonald, A.T. & Walker, A.M., (2009) Drain-blocking techniques on blanket peat: A framework for best practice. *Journal of Environmental Management*, 90, 3512–3519.
- Aurela, M., Lohila, A., Tuovinen, J.P. & Laurila, T. (2009) Carbon dioxide exchange on a northern boreal fen. *Boreal Environmental Research*, 14(4), 699–710.
- Beetz, S., Liebersbach, H., Glatzel, S., Jurasinski, G., Buczko, U. & Höper, H. (2013) Effects of land use intensity on the full greenhouse gas balance in an Atlantic peat bog. *Biogeosciences*, 10, 1067–1082.
- Berendse, F. (1998) Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. *Biogeochemistry*, 42, 73–88.
- Beyer, C. & Höper, H. (2015) Greenhouse gas emissions from rewetted bog peat extraction sites and a *Sphagnum* cultivation site in Northwest Germany. *Biogeosciences*, 12, 2101–2117.
- Bhullar, G.S., Edwards, P.J. & Venterink, H.O. (2014) Influence of different plant species on methane emissions from soil in a restored Swiss wetland. *PLoS ONE*, 9(2), e89588.
- Black, K., O'Brien, P., Redmond, J., Barrett, F. & Twomey, M. (2008) The extent of recent peatland afforestation in Ireland. *Irish Forestry*, 65(1–2), 71–81.
- Blodau, C., Basiliko, N. & Moore, T.R. (2004) Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*, 67(3), 331–351.
- Bubier, J.L., Crill, P.M., Moore, T.R., Savage, K. & Varner, R.K. (1998) Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex. *Global Biogeochemical Cycles*, 12(4), 703–714.
- Bullock, C.H., Collier, M.J. & Convery, F. (2012) Peatlands, their economic value and priorities for their future management – The example of Ireland. *Land Use Policy*, 29(4), 921–928.
- Byrne, K.A. & Farrell, E.P. (2005) The effect of afforestation on soil carbon dioxide emissions in blanket peatland in Ireland. *Forestry*, 78, 217–227.
- Chimner, R.A. & Cooper, D.J. (2003) Influence of water table levels on CO₂ emissions in a Colorado subalpine fen: an in situ microcosm study. *Soil Biology and Biochemistry*, 35(3), 345–351.
- Delaney, M. & Murphy, P. (2012) Coillte and the EU LIFE Programme: 10 years of restoration works on afforested peatlands in Ireland. Extended Abstract No. 296, *Proceedings of the 14th International Peat Congress*, International Peat Society, Stockholm, 5 pp.
- Ding, W., Cai, Z. & Tsuruta, H. (2005) Plant species effects on methane emissions from freshwater marshes. *Atmospheric Environment*, 39(18), 3199–3207.
- Dimitrov, D.D., Grant, R.F., Lafleur, P.M. & Humphreys, E.R. (2010) Modeling the effects of hydrology on ecosystem respiration at Mer Bleue bog. *Journal of Geophysical Research*, 115, G40403, doi.org/10.1029/2010JG001312.
- Dinsmore, K.J., Skiba, U.M., Billett, M.F., Rees, R.M. & Drewer, J. (2009) Spatial and temporal variability in CH₄ and N₂O fluxes from a Scottish ombrotrophic peatland: implications for modelling and up-scaling. *Soil Biology and Biochemistry*, 41(6), 1315–1323.
- Drewer, J., Lohila, A., Aurela, M., Laurila, T., Minkinen, K., Penttilä, T., Dinsmore, K.J., McKenzie, R.M., Helfter, C., Flechard, C., Sutton, M.A. & Skiba, U.M. (2010) Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in Scotland and a minerotrophic sedge fen in Finland. *European Journal of Soil Science*, 61(5), 640–650.
- Drösler, M., Freibauer, A., Christensen, T.R. & Friborg, T. (2008) Observations and status of peatland greenhouse gas emissions in Europe. In Dolman, A.J., Valentini, R. & Freibauer, A. (eds.) *Observing the Continental Scale Greenhouse Gas Balance*, Springer, New York, 243–261.
- Drösler, M., Verchot, L.V., Freibauer, A., Pan, G., Evans, C.D., Bourbonniere, R.A., Alm, J.P., Page, S., Agus, F., Hergoualc'h, K., Couwenberg, J., Jauhiainen, J., Sabiham, S. & Wang, C. (2014) Chapter 2: Drained inland organic soils. In: Hiraiishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. & Troxler, T.G. (eds.) *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands*, IPCC, Switzerland.
- Eaton, J.M., McGoff, N.M., Byrne, K.A., Leahy, P. & Kiely, G. (2008) Land cover change and soil organic carbon stocks in the Republic of Ireland 1851–2000. *Climatic Change*, 91(3–4), 317–334.
- Evans, C.D., Renou-Wilson, F. & Strack, M. (2016) The role of waterborne carbon in the greenhouse gas balance of drained and re-wetted peatlands. *Aquatic Sciences*, 78(3), 575–590.
- Fontaine, S., Bardoux, G., Abbadie, L. & Mariotti, A. (2004) Carbon input to soil may decrease soil carbon content. *Ecology Letters*, 7(4), 314–320.
- Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B. & Rumpel, C. (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 450(7167), 277–280.
- Franchini, A.G., Henneberger, R., Aeppli, M. &

- Zeyer, J. (2015) Methane dynamics in an alpine fen: a field-based study on methanogenic and methanotrophic microbial communities. *FEMS Microbiology Ecology*, 91(3), fiu032. doi: 10.1093/femsec/fiu032.
- Frolking, S. & Crill, P. (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: Measurement and modelling. *Global Biogeochemical Cycles*, 8(4), 385–397.
- Gatis, N., Luscombe, D.J., Grand-Clement, E., Hartley, I.P., Anderson, K., Smith, D. & Brazier, R.E. (2015) The effect of drainage ditches on vegetation diversity and CO₂ fluxes in a *Molinia caerulea*-dominated peatland. *Ecohydrology*, 9(3), 407–420.
- Green, S.M. & Baird, A.J. (2012) A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane—including that due to episodic ebullition—from peatlands. *Plant and Soil*, 351(1), 207–218.
- Green, S.M. & Baird, A.J. (2017) Using ‘snapshot’ measurements of CH₄ fluxes from an ombrotrophic peatland to estimate annual budgets: interpolation *versus* modelling. *Mires and Peat*, 19(09), 1–9.
- Haapalehto, T.O., Vasander, H., Jauhiainen, S., Tahvanainen, T. & Kotiaho, J.S. (2011) The effects of peatland restoration on water-table depth, elemental concentrations, and vegetation: 10 years of changes. *Restoration Ecology*, 19(5), 587–598.
- Hájková, P., Hájek, M. & Kintrová, K. (2009) How can we effectively restore species richness and natural composition of a *Molinia* invaded fen? *Journal of Applied Ecology*, 46(2), 417–425.
- Henneberg, A., Elsgaard, L., Sorrell, B.K., Brix, H. & Petersen, S.O. (2015) Does *Juncus effusus* enhance methane emissions from grazed pastures on peat? *Biogeosciences*, 12(19), 5667–5676.
- Henneberger, R., Cheema, S., Franchini, A.G., Zumsteg, A. & Zeyer, J. (2015) Methane and carbon dioxide fluxes from a European alpine fen over the snow-free period. *Wetlands*, 35(6), 1149–1163.
- Hensen, A., Skiba, U. & Famulari, D. (2013) Low cost and state of the art methods to measure nitrous oxide emissions. *Environment Research Letters*, 8, 025022.
- Holden, J., Wallage, Z.E., Lane, S.N. & McDonald, A.T. (2011) Water table dynamics in undisturbed, drained and restored blanket peat. *Journal of Hydrology*, 402(1–2), 103–114.
- Hommeltenberg, J., Mauder, M., Drösler, M., Heidebach, K., Werle, P. & Schmid, H.P. (2014) Ecosystem scale methane fluxes in a natural temperate bog-pine forest in southern Germany. *Agricultural and Forest Meteorology*, 198–199, 273–284.
- Höper, H., Augustin, J., Cagampan, J.P., Drösler, M., Lundin, L., Moors, E., Vasander, H., Waddington, J.M. & Wilson, D. (2008) Restoration of peatlands and greenhouse gas balances. In: Strack, M. (ed.) *Peatlands and Climate Change*, International Peat Society, Jyväskylä, 182–210.
- Joabsson, A., Christensen, T.R. & Wallén, B. (1999) Vascular plant controls on methane emissions from northern peat forming wetlands. *Trends in Ecology and Evolution*, 14(10), 385–388.
- Joosten, H. & Clarke, D. (2002) *Wise Use of Mires and Peatlands - Background and Principles Including a Framework for Decision-making*. International Mire Conservation Group and International Peat Society, Saarijärvi, Finland, 304 pp.
- Joosten, H., Sirin, A., Couwenberg, J., Laine, J. & Smith, P. (2016). The role of peatlands in climate regulation. In: Bonn, A., Allott, T., Evans, M., Joosten, H. & Stoneman, R. (eds.) *Peatland Restoration and Ecosystem Services: Science, Policy and Practice*. Cambridge University Press, Cambridge, 66–79.
- Jovani-Sancho, A.J., Cummins, T. & Byrne, K.A. (2017) Collar insertion depth effects on soil respiration in afforested peatlands, *Biology and Fertility of Soils*, 53(6), 677–689.
- Juottonen, H., Hynninen, A., Nieminen, M., Tuomivirta, T.T., Tuittila, E.-S., Nousiainen, H., Kell, D.K., Yrjälä, K., Tervahauta, A. & Fritze, H. (2012) Methane-cycling microbial communities and methane emission in natural and restored peatlands. *Applied and Environmental Microbiology*, 78(17), 6386–6389.
- Juszczak, R. & Augustin, J. (2013) Exchange of the greenhouse gases methane and nitrous oxide between the atmosphere and a temperate peatland in Central Europe. *Wetlands*, 33(5), 895–907.
- Jylhä, P., Hytönen, J. & Alm, J. (2017) CO₂ release and dry matter loss of Scots pine forest chips stockpiled from late summer to winter. *Biomass and Bioenergy*, 104, 36–44.
- King, J.Y. & Reeburgh, W.S. (2002) A pulse-labeling experiment to determine the contribution of recent plant photosynthates to net methane emission in arctic wet sedge tundra. *Soil Biology and Biochemistry*, 34(2), 173–180.
- Koelbener, A., Ström, L., Edwards, P.J. & Olde Venterink, H. (2009) Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. *Plant and Soil*, 326(1), 147–158.
- Komulainen, V.M., Nykänen, H., Martikainen, P.J. & Laine, J. (1998) Short term effect of restoration on

- vegetation change and methane emissions from peatlands drained for forestry in southern Finland. *Canadian Journal of Forest Research*, 28, 402–411.
- Komulainen, V.M., Tuittila, E.S., Vasander, H. & Laine, J. (1999) Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO₂ balance. *Journal of Applied Ecology*, 36(5), 634–648.
- Konvalinková, P. & Prach, K. (2014) Environmental factors determining spontaneous recovery of industrially mined peat bogs: A multi-site analysis. *Ecological Engineering*, 69, 38–45.
- Koskinen, M., Maanaviija, L., Nieminen, M., Minkkinen, K. & Tuittila, E. (2016) High methane emissions from restored Norway spruce swamps in southern Finland over one growing season. *Mires and Peat* 17(02), 1–13.
- Lafleur, P., Moore, T., Roulet, N. & Frohling, S. (2005) Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8(6), 619–629.
- Lai, D.Y.F. (2009) Methane dynamics in northern peatlands: a review. *Pedosphere* 19(4), 409–421.
- Laine, J., Laiho, R., Minkkinen, K. & Vasander, H. (2006) Forestry and boreal peatlands. In: Wieder, R.K. & Vitt, D.H. (eds.) *Boreal Peatland Ecosystems*, Springer, Berlin Heidelberg, 331–357.
- Laine, A., Byrne, K., Kiely, G. & Tuittila, E.-S. (2007) Patterns in vegetation and CO₂ dynamics along a water level gradient in a lowland blanket bog. *Ecosystems*, 10(6), 890–905.
- Laine, A., Riutta, T., Juutinen, S., Väiliranta, M. & Tuittila, E.-S. (2009) Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. *Ecological Modelling*, 220(20), 2646–2655.
- Larmola, T., Tuittila, E.-S., Tiirola, M., Nykänen, H., Martikainen, P.J., Yrjälä, K., Tuomivirta, T. & Fritze, H. (2009) The role of *Sphagnum* mosses in the methane cycling of a boreal mire. *Ecology*, 91(8), 2356–2365.
- Leppälä, M., Oksanen, J. & Tuittila, E.-S. (2011) Methane flux dynamics during mire succession. *Oecologia*, 165(2), 489–499.
- Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E.-M. & Knoblauch, C. (2011) Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. *Journal of Ecology*, 99(4), 914–922.
- Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology*, 8(3), 315–323.
- Mäkiranta P., Hytönen, J., Aro, L., Maljanen, M., Pihlatie, M., Potila, H., Shurpali, N.J., Laine, J., Lohila, A., Martikainen, P.J. & Minkkinen, K. (2007) Soil greenhouse gas emissions from afforested organic soil croplands and cutaway peatlands. *Boreal Environmental Research*, 12(2), 159–175.
- Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J. & Minkkinen, K. (2009) Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. *Soil Biology and Biochemistry*, 41(4), 695–703.
- Mäkiranta, P., Laiho, R., Penttilä, T. & Minkkinen, K. (2012) The impact of logging residue on soil GHG fluxes in a drained peatland forest. *Soil Biology and Biochemistry*, 48, 1–9.
- Marinier, M., Glatzel, S. & Moore, T.R. (2004) The role of cotton-grass (*Eriophorum vaginatum*) in the exchange of CO₂ and CH₄ at two restored peatlands, eastern Canada. *Ecoscience*, 11(2), 141–149.
- Martikainen, P.J., Nykänen, H., Alm, J. & Silvola, J. (1995) Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophic. *Plant and Soil*, 168(1), 571–577.
- Minkkinen, K. & Laine, J. (1998) Effect of forest drainage on the peat bulk density of pine mires in Finland. *Canadian Journal of Forest Research*, 28(2), 178–186.
- Minkkinen, K., Korhonen, R., Savolainen, I. & Laine, J. (2002) Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. *Global Change Biology*, 8, 785–799.
- Minkkinen, K., Laine, J., Shurpali, N.J., Mäkiranta, P., Alm, J. & Penttilä, T. (2007) Heterotrophic soil respiration in forestry drained peatlands. *Boreal Environment Research*, 12, 115–126.
- Mitsch, W.J., Gooselink, J.G., Anderson, C.J. & Zhang, L. (eds.) (2009) *Wetland Ecosystems*. John Wiley & Sons Inc., Hoboken NJ, 256 pp.
- Moore, P.D. (1987) Ecological and hydrological aspects of peat formation. *Geological Society, London, Special Publications*, 32(1), 7–15.
- Moors for the Future Partnership (2012) *Science: Ecosystem services*. Moors for the Future Partnership, Edale, UK (website). Online at: <http://www.moorsforthefuture.org.uk/ecosystem-services>, accessed 18 Nov 2015.
- NFI (2013) *The Second National Forest Inventory - Republic of Ireland - Main Findings*. Forest Service, Department of Agriculture, Food and the Marine, Johnstown Castle Estate, Ireland, 60 pp.
- NPWS (2013) *National Peatlands Strategy Draft for Consultation*. National Parks & Wildlife Service (NPWS), Department of Culture, Heritage and the

- Gaeltacht, Dublin, Ireland. Online at: <https://www.npws.ie/sites/default/files/general/Final%20National%20Peatlands%20Strategy.pdf> services, accessed 21 Feb 2017.
- Parish, F., Sirin, A., Charman, D., Joosten, H., Minaeva, T. & Silviu, M. (eds.) (2008) *Assessment on Peatlands, Biodiversity and Climate Change: Main Report*. Global Environment Centre, Kuala Lumpur and Wetlands International, Wageningen, 179 pp.
- Parmentier, F.J.W., van Huissteden, J., Kip, N., Op den Camp, H.J.M., Jetten, M.S.M., Maximov, T.C. & Dolman, A.J. (2011) The role of endophytic methane-oxidizing bacteria in submerged *Sphagnum* in determining methane emissions of Northeastern Siberian tundra. *Biogeosciences*, 8(5), 1267–1278.
- Petrone, R.M., Waddington, J.M. & Price, J.S. (2003) Ecosystem-scale flux of CO₂ from a restored vacuum harvested peatland. *Wetlands Ecology and Management*, 11(6), 419–432.
- Quinty, F. & Rochefort, L. (2003) *Peatland Restoration Guide*. Canadian Sphagnum Peat Moss Association and New Brunswick Department of Natural Resources and Energy, Québec, Canada, 106 pp.
- Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijpstra, W.I.C., Wolters-Arts, M., Derksen, J., Jetten, M.S.M., Schouten, S., Sinninghe Damste, J.S., Lamers, L.P.M., Roelofs, J.G.M., Op den Camp, H.J.M. & Strous, M. (2005) Methanotrophic symbionts provide carbon for photosynthesis in peat bogs, *Nature*, 436(7054), 1153–1156.
- Regina, K. & Myllys, M. (2009) Mitigation of greenhouse gas fluxes from cultivated organic soils by raising water table. *IOP Conference Series: Earth and Environmental Science*, 6(24), 242034.
- Regina, K., Nykänen, H., Silvola, J. & Martikainen, P.J. (1996) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. *Biogeochemistry*, 35, 401–418.
- Renou-Wilson, F., Bolger, T., Bullock, C., Convery, F., Curry, J., Ward, S., Wilson, D. & Müller, C. (2011) *BOGLAND: Sustainable Management of Peatlands in Ireland*. STRIVE Report Series No. 75, Environmental Protection Agency, Johnstown Castle, County Wexford, Ireland, 158 pp.
- Renou-Wilson, F., Barry, C., Müller, C. & Wilson, D. (2014) The impacts of drainage, nutrient status and management practice on the full carbon balance of grasslands on organic soils in a maritime temperate zone. *Biogeosciences*, 11(16), 4361–4379.
- Renou-Wilson, F., Müller, C., Moser, G. & Wilson, D. (2016) To graze or not to graze? Four years greenhouse gas balances and vegetation composition from a drained and a rewetted organic soil under grassland. *Agriculture, Ecosystems & Environment*, 222, 156–170.
- Robroek, B.J., Jassey, V.E., Kox, M.A., Berendsen, R.L., Mills, R.T., Cécillon, L., Puissant, J., Meima-Franke, M., Bakker, P.A. & Bodelier, P.L. (2015) Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. *Journal of Ecology*, 103(4), 925–934.
- Rydin, H. & Jeglum, J.K. (2006) *The Biology of Peatlands*. Oxford University Press, Oxford, UK, 381 pp.
- Saarnio, S., Wittenmayer, L. & Merbach, W. (2004) Rhizospheric exudation of *Eriophorum vaginatum* L.—potential link to methanogenesis. *Plant and Soil*, 267(1–2), 343–355.
- Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V. & Farrell, E.P. (2006) Seasonal and spatial variability of soil respiration in four Sitka spruce stands. *Plant and Soil*, 287(1–2), 161–176.
- Samaritani, E., Siegenthaler, A., Yli-Petäys, M., Buttler, A., Christin, P.-A. & Mitchell, E.A.D. (2011) Seasonal net ecosystem carbon exchange of a regenerating cutaway bog: How long does it take to restore the C-sequestration function? *Restoration Ecology*, 19(4), 480–489.
- Schumann, M. & Joosten, H. (2008) *Global Peatland Restoration Manual*. Institute of Botany and Landscape Ecology, Greifswald University, Germany, 68 pp.
- Silvola, J., Alm, J., Ahlholm, U., Nykanen, H. & Martikainen, P.J. (1996) CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *Journal of Ecology*, 84(2), 219–228.
- Strack, M. (2008) Executive summary for policymakers “peatlands in global change”. In: Strack, M. (ed.) *Peatlands and Climate Change*, International Peat Society, Jyväskylä, 9–12.
- Strack, M., Mwakanyamale, K., Hassanpour Fard, G., Bird, M., Bérubé, V. & Rochefort, L. (2017) Effect of plant functional type on methane dynamics in a restored minerotrophic peatland. *Plant and Soil*, 410(1), 231–246.
- Ström, L., Ekberg, A., Mastepanov, M. & Røjle Christensen, T. (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Global Change Biology*, 9(8), 1185–1192.
- Ström, L., Mastepanov, M. & Christensen, T.R. (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from

- wetlands. *Biogeochemistry*, 75(1), 65–82.
- Sundh, I., Nilsson, M., Granberg, G. & Svensson, B. (1994) Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microbial Ecology*, 27, 253–265.
- Taylor, K., Rowland, A. & Jones, H. (2001) *Molinia caerulea* (L.) Moench. *Journal of Ecology*, 89(1), 126–144.
- Tuittila, E.-V., Komulainen, V.-M., Vasander, H. & Laine, J. (1999) Restored cut-away peatland as a sink for atmospheric CO₂. *Oecologia*, 120, 563–574.
- Tuittila E.S., Komulainen, V.M., Vasander, H., Nykänen, H., Martikainen, P.J. & Laine, J. (2000) Methane dynamics of a restored cut-away peatland. *Global Change Biology*, 6(5), 569–581.
- Turetsky, M., Kotowska, A., Bubier, J., Dise, N., Crill, P., Hornibrook, E.R.C., Minkinen, K., Moore, T.R., Myers-Smith, I., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N., Tuittila, E.S., Waddington, M.J., White, J., Wickland, K. & Wilking, M. (2014) A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Global Change Biology*, 20(7), 2183–2197.
- Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P. & Harth, C. (2001) Response of CO₂ and CH₄ emissions from peatlands to warming and water table manipulation. *Ecological Applications*, 11(2), 311–326.
- Urbanová, Z., Píček, T., Hájek, T., Buřková, I. & Tuittila, E.S. (2012) Vegetation and carbon gas dynamics under a changed hydrological regime in central European peatlands. *Plant Ecology and Diversity*, 5(1), 89–103.
- Vanselow-Algan, M., Schmidt, S.R., Greven, M., Fiencke, C., Kutzbach, L. & Pfeiffer, E.M. (2015) High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. *Biogeosciences*, 12(14), 4361–4371.
- Waddington, J.M. & Day, S.M. (2007) Methane emissions from a peatland following restoration. *Journal of Geophysical Research*, 112(G3), G03018, doi: 10.1029/2007JG000400.
- Waddington, J.M. & Price, J.S. (2000) Effect of peatland drainage, harvesting and restoration on atmospheric water and carbon exchange. *Physical Geography*, 21(5), 433–451.
- Waddington, J.M., Strack, M. & Greenwood, M.J. (2010) Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO₂ exchange to ecosystem-scale restoration. *Journal of Geophysical Research*, 115(G1), doi.org/10.1029/2009JG001090.
- Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A. & Bardgett, R.D. (2013) Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, 16(10), 1285–1293.
- Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K., Farrell, E.P. & Tuittila, E.S. (2007a) A high resolution green area index for modelling the seasonal dynamics of CO₂ exchange in peatland vascular plant communities. *Plant Ecology*, 190, 37–51.
- Wilson, D., Tuittila, E.S., Alm, J., Laine, J., Farrell, E.P. & Byrne, K.A. (2007b) Carbon dioxide dynamics of a restored maritime peatland. *Ecoscience*, 14(1), 71–80.
- Wilson, D., Dixon, S.D., Artz, R.R.E., Smith, T.E.L., Evans, C.D., Owen, H.J.F., Archer, E. & Renou-Wilson, F. (2015) Derivation of greenhouse gas emission factors for peatlands managed for extraction in the Republic of Ireland and the United Kingdom. *Biogeosciences*, 12(18), 5291–5308.
- Wilson, D., Blain, D., Couwenberg, J., Evans, C., Murdiyarso, D., Page, S., Renou-Wilson, F., Rieley, J., Sirin, A. & Strack, M. (2016a) Greenhouse gas emission factors associated with rewetting of organic soils. *Mires and Peat*, 17(04), 1–28.
- Wilson, D., Farrell, C.A., Fallon, D., Moser, G., Müller, C. & Renou-Wilson, F. (2016b) Multi-year greenhouse gas balances at a rewetted temperate peatland. *Global Change Biology*, 22(12), 4080–4095.
- Xu, J., Morris, P.J., Liu, J. & Holden, J. (2018) PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena*, 160, 134–140.
- Yamulki, S., Anderson, R., Peace, A. & Morison, J.I.L. (2013) Soil CO₂, CH₄ and N₂O fluxes from an afforested lowland raised peatbog in Scotland: implications for drainage and restoration. *Biogeosciences*, 10, 1051–1065.
- Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P. & Charman, D.J. (2011) Peatlands and their role in the global carbon cycle. *Eos, Transactions, American Geophysical Union*, 92(12), 97–98.

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Appendix

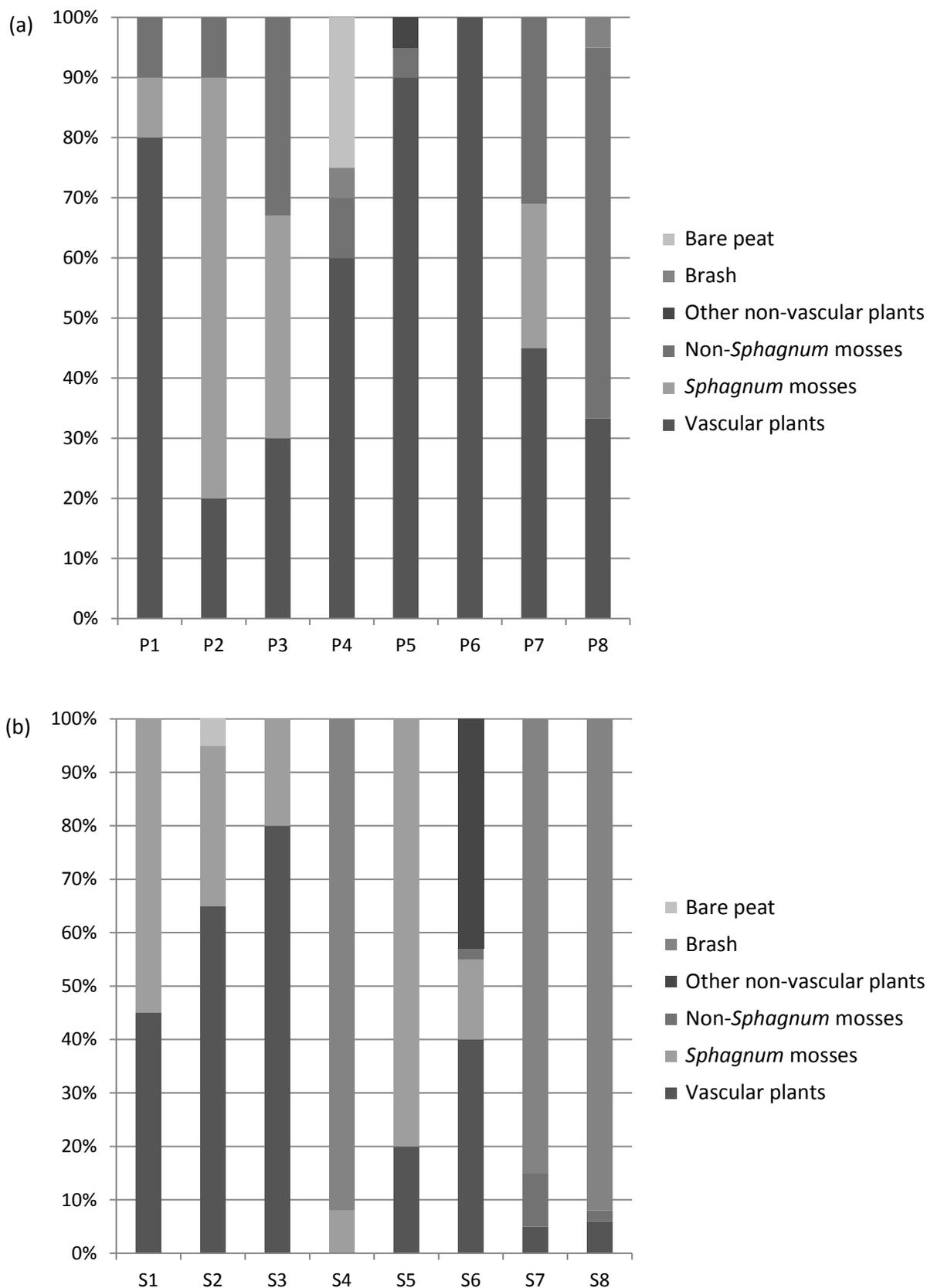


Figure A1. Percentage of each of six cover types on Plots 1–8 at (a) Pollagoona and (b) Scohaboy.

Table A1. Estimated factor values and goodness of fit (r^2) for P_G at Pollagoona and Scohaboy. The number of the equation used (see page 6) is given for each microsite type. Model errors for each term are shown in brackets.

	<i>Pollagoona</i>			<i>Scohaboy</i>		
	<i>Eriophorum-Sphagnum</i>	<i>Cladonia-Calluna</i>	<i>Molinia</i>	<i>Eriophorum-Sphagnum</i>	<i>Cladonia-mosses</i>	<i>Eriophorum</i>
P_{max}	247.92 (54.11)	133.72 (15.58)	3513.37 (312.85)	3274.46 (436.37)	3082.72 (694.90)	1563.49 (142.83)
k_{PPFD}	1026.72 (379.15)	388.99 (125.10)	422.04 (82.76)	466.92 (128.93)	432.78 (216.41)	194.92 (65.13)
T_{opt}			290.34 (0.38)			
T_{tol}			3.95 (0.45)			
WT_{opt}				-12.10 (1.68)	-13.59 (2.39)	-16.11 (1.03)
WT_{tol}				9.68 (1.58)	10.76 (2.84)	9.34 (1.35)
E			2.00 (0.39)			
R^2	0.785	0.839	0.678	0.77	0.68	0.64
Eq.	1	2	3	4	4	4

Table A2. Estimated parameter values and goodness of fit (r^2) for R_{eco} at Pollagoona and Scohaboy. The number of the equation used (see page 6) is given for each microsite type. Model errors for each parameter are shown in brackets.

	<i>Pollagoona</i>			<i>Scohaboy</i>			
	<i>Eriophorum-Sphagnum</i>	<i>Cladonia-Calluna</i>	<i>Molinia</i>	<i>Eriophorum-Sphagnum</i>	<i>Cladonia-mosses</i>	<i>Eriophorum</i>	<i>brash</i>
A	344.83 (48.11)	251.61 (36.04)	234.71 (21.91)	460.19 (86.77)	150.92 (21.04)	367.67 (58.47)	183.4 (39.64)
B	441.22 (80.51)	524.73 (75.80)	587.95 (46.61)	-52.75 (13.67)	-6.98 (2.09)	401.60 (75.15)	-11.55 (2.30)
C			-0.32 (0.07)	212.72 (99.99)	354.26 (54.53)		271.41 (109.06)
R^2	0.628	0.739	0.626	0.449	0.77	0.61	0.45
Eq	5	5	6	8	7	5	8