Seasonal patterns of greenhouse gas emissions from a forest-to-bog restored site in northern Scotland: Influence of microtopography and vegetation on carbon dioxide and methane dynamics

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Abstract

Northern peatlands play an important role in the regulation of the atmospheric greenhouse gas (GHG) balance, functioning as a net carbon sink with low rates of organic decomposition. However, perturbations such as drainage increase peat oxidation, which may lead to enhanced gaseous release of carbon. For this reason, the number of restoration projects that aim to rewet blanket bogs has increased in the last few years, but there is still a lack of understanding of the impact of restoration on emissions of greenhouse gases, such as methane, particularly in sites restored from forestry. In this paper, we investigate the seasonal greenhouse gas dynamics in a forest-to-bog restoration site in Scotland. We analyse the effects of restoration on both carbon dioxide and methane fluxes, and investigate which site factors (microtopography, vegetation type, soil moisture and temperature) drive the processes of gaseous exchange between the bog surface and the atmosphere. Our results show that the original surface is near greenhouse gas equilibrium at $-0.28 \text{gCO}_2\text{eq m}^{-2}\text{day}^{-1}$ and that microtopographic features act as a net greenhouse gas sink (ridges $= -0.94 \text{gCO}_2\text{eq m}^{-2}\text{day}^{-1}$ and furrows $= -0.86 \text{gCO}_2\text{eq m}^{-2}\text{day}^{-1}$), whereas the bog pool is a net source of greenhouse gases ($0.98 \text{gCO}_2\text{eq m}^{-2}\text{day}^{-1}$). We found different vegetation species play a key role in greenhouse gas flux dynamics, especially in forestry-derived microtopographical features, and their presence and influence on greenhouse gas dynamics should be accounted for to provide a more comprehensive understanding of emissions associated with restoration management practices.

Highlights

- GHG (CO₂ and CH₄) dynamics in a boreal peatland restored from forestry are mainly affected by microtopography and vegetation.
1 | INTRODUCTION

Peat soils only cover 3% of the world land surface, but are a key component of the global carbon (C) cycle due to their high organic C content. Northern peatlands alone are estimated to hold about 500 Gt C, which corresponds to almost a third of the total soil C pool of the world (Scharlemann, Tanner, Hiederer, & Kapos, 2014). In Scotland, peatlands extend for over 1.8 Mha and hold around 1,620 ± 70 Mt C stock (assuming an average peat depth of 2 m; Chapman, Bell, Donnelly, & Lilly, 2009). The Flow Country and surrounding area hosts 0.4 Mha of blanket bogs (Lindsay et al., 1988), which are estimated to store up to 400 Mt C, with a C accumulation rate of around 16.3 g·m⁻²·year⁻¹ (Ratcliffe et al., 2018). In the current climate, C accumulation in the soil is possible because rates of decomposition tend to be low compared to photosynthetic inputs (Whiting & Chanton, 2001) as a result of factors such as low temperature, anoxic conditions, small microbial populations and recalcitrant plant litter. As a result, peatlands act as net sinks of C (Gorham, 1991).

Anthropogenic impacts on peatlands, however, have led to a degradation of these ecosystems, and in the UK more than 0.19 Mha of deep peats (peat layer >50 cm) have been drained since World War II for plantation forestry, predominantly Sitka spruce (Holden et al., 2007). Drainage is used to ensure aeration of the upper peat surface and allows tree root survival by lowering the water table relative to the ground surface. This has been achieved by deep cultivation to provide a raised root zone and aid drainage of the peat, with creation of the distinct microtopographic features: furrows, ridges and strips of residual original surface. Hambley et al. (2019) identified that peatland drainage enhances and extends aerobic soil environments, creating conditions for peat decomposition that lead to a loss of C (Silvola, Alm, Ahlholm, Nykanen, & Martikainen, 1996), turning the afforested peat soil from a net sink to a net source of greenhouse gases (GHGs). Ciais et al. (2014) stated that degraded peatlands are net CO₂ sources, globally emitting 270 Mt C·year⁻¹ (1 Gt·year⁻¹ carbon dioxide, CO₂) into the atmosphere.

Many blanket bogs are now subject to environmental protection legislation and the number of restoration projects has increased in recent years. In 2010, there were at least 50 bog restoration projects around the UK (Anderson, 2010). Since 2013, approximately 10,000 ha of peatlands have been restored (under the Peatland Action Initiative) through actions funded by the Scottish Government and coordinated by Scottish Natural Heritage (Scottish Environment Protection Agency, 2019). The Scottish Government has formerly issued a call for 50,000 ha of peatlands to be in good condition or under restoration management by 2020, extending the plan to 250,000 ha of restored peatland by 2030 (Scottish Environment Protection Agency, 2019).

In the Flow Country, almost 0.07 Mha of blanket bogs were planted with commercial conifers between 1970 and 1980. The Royal Society for the Protection of Birds (RSPB) started the first restoration work in the late 1990s, felling trees and putting them into the furrows, and later progressing to blocking drains and flipping stumps. Restoration practices aim to re-establish the original conditions that encourage peat accumulation and C storage (Kimmel & Mander, 2010; Vasander et al., 2003). Other studies (Wheeler & Shaw, 1995) underline the importance of restoring bogs to the development stage that immediately preceded the disturbance (in this case, afforestation). Bain, Hornsey, Bongiorno, and Jeffries (2012) suggested that peatland restoration could be one option for reducing GHG emissions to below Kyoto protocol targets, although the assessment of restored function and renewed storage is problematic.

Restoration practices have been shown to reduce net CO₂ losses to the atmosphere and to return the functioning of the bog to a “sink behaviour” (Komulainen, Tuittila, Vasander, & Laine, 1999; Tuittila, Komulainen, Vasander, & Laine, 1999). This can be achieved after 5–50 years, depending on the local site conditions and restoration practices adopted (Hambley et al., 2019; Nykanen, Alm, Lang, Silvola, & Martikainen, 1995; Ojanen, Mikkinkinen, Alm, & Penttilä, 2010; Samaritani et al., 2011; Strack & Zuback, 2013; Waddington &
However, restoration practices aim to raise the water table and consequently increase soil water saturation, creating anaerobic conditions that encourage methane (CH$_4$) emissions (Saarnio, Winiwarter, & Leitao, 2009). Peatland restoration indeed does not necessarily result in lower GHG emission rates (Campbell & Robson, 2019), especially at the beginning (Sirin & Laine, 2008). Rewetting of drained peatlands increases CH$_4$ emissions by an average of 46% during the first period after rewetting compared to the original prewetting emission (Abdalla et al., 2016), and sometimes this increase may offset the reduction in CO$_2$ losses (Thompson, 2008). Morison et al. (2012) suggested that restored peatlands from forestry might lead to an increase in CH$_4$ emissions, particularly over the short term, turning the bog into a net GHG source. This increase, however, may not be limited to a short period; indeed, Vanselow-Algan et al. (2015) reported increased emissions of CH$_4$ continuing for 30 years after rewetting.

There is little evidence on the effect of tree removal and peatland restoration on complete C and GHG balances for the UK (Morison et al., 2012). The few studies available are based on data collected from eddy covariance towers (Fowler, Hargreaves, Macdonald, & Gardiner, 1995; Hargreaves, Milne, & Cannell, 2003). These measurements work at the ecosystem scale and are not able to detect fluxes from local microtopographical features (microforms), so they tell us nothing about the impact of different microforms and vegetation on GHG dynamics. Furthermore, some of these studies only focus on CO$_2$ fluxes (Hambley et al., 2019). Forestry-derived microtopography is known to affect water table depth (WTD) and vegetation composition (Campbell & Robson, 2019; Hancock, Klein, Andersen, & Cowie, 2018) and, consequentially, GHG fluxes (Cresto-Aleina et al., 2015; Hermans, 2018). Drier microforms such as ridges, showing a lower WTD and moisture, tend to emit more CO$_2$ due to peat oxidation and host vegetation more adapted to dry conditions. Furrows, on the other hand, are characterized by higher WTD and moisture and are consequently regarded as CH$_4$ sources.

In the Flow Country, restoration practices that involve stump flipping and reshaping the microforms created during forestry operations (i.e., terraforming) aim to recreate a landscape similar to the original surface and pools, which were once the major components of the landscape. This management aims to favour the re-establishment of the original bog species, such as Sphagnum spp. and Eriophorum spp., and promote a return to “near natural” conditions and a net GHG sink (Hancock et al., 2018). However, there is still scant evidence regarding the actual benefits that the terraforming may bring and its impact on the GHG dynamics of the restored bog (Campbell & Robson, 2019; Hambley et al., 2019; Hermans et al., 2019).

In this study, we investigate the main drivers of the GHG (CO$_2$ and CH$_4$) dynamics of a restored site, focusing on different microforms (ridges, furrows, original surfaces and pools) and their associated vegetation. We considered the contribution of nitrous dioxide (N$_2$O) to the total GHG negligible based on recent evidence in the same study area (Hermans, 2018). In some cases, accounting only for environmental variables, such as soil moisture and temperature, is not enough to explain both CO$_2$ and CH$_4$ fluxes (Acosta et al., 2017). Many studies show that vascular plants with aerenchymatous tissues, such as Eriophorum spp. and Trichophorum spp., can play an important role in CH$_4$ transport at the soil–atmosphere interface (Bartlett, Crill, Sass, Harriss, & Di, 1992; Couwenberg, 2009; Davidson et al., 2016; Frenzel & Rudolph, 1998; Greenup, Bradford, McNamar, Ineson, & Lee, 2000; Joabsson, Christensen, & Wallen, 1999). Root and stem structures of these vascular plants may act as direct pathways through which CH$_4$ can diffuse and be emitted from the soil, bypassing the aerobic layers of the peat without oxidation. The contribution of vascular species to overall CH$_4$ emissions has been estimated to be 25–97% (Whalen, 2005). We might expect higher CH$_4$ fluxes from areas with a higher percentage of these “methane shunt” species (Davidson et al., 2016), suggesting that vegetation composition will play a decisive role in mediating microtopographical flux responses behind GHG dynamics. We describe the influence of microtopography and vascular plant assemblage on GHG fluxes and use this information to identify options for more effective peatland restoration management.

We hypothesize that CO$_2$ and CH$_4$ fluxes will be mostly driven by microtopography and plant species. We expect: (a) the original surface to have a GHG balance close to equilibrium; (b) ridges to be a drier and warmer microform, and so to provide a larger source of CO$_2$; (c) furrows and the pool to exhibit a waterlogged microform, so acting as sources of CH$_4$ due to their high moisture content and saturated condition; and (d) increased CH$_4$ emissions in the presence of vascular plants with aerenchymatous root tissue, such as Eriophorum spp. and Trichophorum spp.

We furthermore compare CO$_2$ and CH$_4$ fluxes for two periods in summer 2018 and summer 2019 (respectively, 3 and 15 months after restoration work) and try to assess whether time since restoration had any effect on GHG dynamics. We expect a rise in CH$_4$ and a reduction in CO$_2$ fluxes due to a possible increase of water and soil moisture levels at the site.
2 | MATERIALS AND METHODS

2.1 Study site

The project was undertaken in the RSPB Forsinard Flows National Nature Reserve. The reserve covers an area of 0.0215 Mha and ranges from 45 to 580 m above sea level (asl), with a predominance of deep blanket bog between 120 and 438 m asl. The climate is cool and wet, with average annual precipitation of 970 mm (between 1981 and 2010) and average daily maximum temperature of 11.4°C (Kinbrace weather station, 58°15’32”N, 3°56’26”W, 103 m asl, approximately 20 km from the study site). Measurements were carried out in the Lonielist field site (58°23’29”N, 3°45’59”W, Figure 1), at 180 m asl, with a slope of about 1–3° (original surface) and average peat depth of 2 m, maximum of 6 m. It is characterized by the presence of furrows (~0.3 m below the original peat surface) and ridges (0.15–0.25 m above the original peat surface), created by forestry ploughing in the 1980s.

The peat overturned during deep furrow ploughing formed ridges, sufficiently raised above the drained water table to enhance the establishment and survival of trees after planting. The original surface is the part of the land that was not directly affected by either ploughing or compaction (Figure 2), plus areas left uncultivated as firebreaks or “rides” during the forest cycle.

The site, planted in 1981 with sitka spruce (Picea sitchensis, (Bong). Carr.) and lodgepole pine (Pinus contorta, Douglas ex Loudon), went through its first restoration work in 2003/2004. This involved premature felling of the plantation and main collector drain blocking using peat and plastic dams. Trees were entirely left on site and placed into the furrows to further impede drainage (Hambley et al., 2019). The aim of the restoration was to encourage the re-occurrence of original peat-forming species, such as Sphagnum spp. and Eriophorum spp. (Hancock et al., 2018). A vegetation survey in May 2017 found sphagnum mosses (Sphagnum capillifolium and Sphagnum papillosum) and deer grass (Trichophorum cespitosum, L. Hartm.) dominating the original surfaces. On ridges, the most common species were haircap moss (Polytrichum commune Hedw), common cottongrass (Eriophorum angustifolium, Honck.) and ling heather (Calluna vulgaris (L.) Hull), whereas S. capillifolium, S. papillosum and P. commune typically dominated furrows.

These vegetation and microtopographic characteristics are not visible anymore for the greater part of the area due to subsequent restoration work from March 2018. This involved stump flipping and smoothing of the microtopographic features, practices that left the site compacted, flattened and covered with small pools (Figure 3). These pools may have been created after water filled former furrows or hollows where tree roots had been removed during stump flipping. The depth and size of these small pools were

FIGURE 1 Lonielist field site in Forsinard. The image was taken prior to restoration in March 2018. In this picture, microtopographic features are still visible, as the entire trees crushed into the furrows. The study transect is 40 m long (yellow dashed line). White dashed lines indicate the boardwalk. The picture is north orientated [Color figure can be viewed at wileyonlinelibrary.com]
difficult to detect, as they seemed to change dimensions many times during the study period (they seemed to be largely influenced by wetter and drier weather conditions). The measurement transect used in this study was not affected and all types of microforms were represented for the duration of the survey. However, assuming that terraforming will have had hydrological effects similar to those of plough furrow blocking, we think that the second part of the restoration work may have had an indirect (not quantified) effect on the site due to adjacency effects.

2.2 Measurement of gaseous emissions, species composition and environmental conditions

Measurements of net ecosystem exchange (NEE) of CO₂ only and CH₄ were taken every month between November 2017 and October 2018. A second group of measurements was carried out in summer 2019, throughout two campaigns for a period of 5 and 6 days in July and August, respectively. We decided to measure net ecosystem exchange because “NEE is a primary gauge of ecosystem C sink strength” (Kramer et al., 2002). We did not consider the use of dark chambers at this stage of the research, because we were not interested in partitioning ecosystem respiration (Reco).

At the same time, new vegetation analysis was carried out to monitor species changes in every collar. Auxiliary measurements of soil temperature and moisture were collected to identify key environmental drivers and how they interacted with the microtopography.

In May 2017, we installed 29 collars into the soil along a 40-m-long transect (Figure 1), capturing four different types of microforms (ridges, furrows, original surface and pool), and recorded vegetation classification (percentage cover of species per collar). The only pool in our study was located between the area that was excluded from forestry work (original surface) and the area with

**FIGURE 2** Double-mouldboard plough creates a furrow in the original bog surface (a) and pushes excavated peat into ridges. The ridges are raised above the drained water table, enhancing the survival and early growth chances of planted trees (b). Photo: Double-mouldboard ploughing. Schematic representations (a) and (b) based on work by Hambley (2016) [Color figure can be viewed at wileyonlinelibrary.com]

**FIGURE 3** Lonielist field site in April 2019, 1 year after terraforming practices. The site appeared flat (ridges and furrows not more visible) and covered with small pools [Color figure can be viewed at wileyonlinelibrary.com]
presence of furrows and ridges. We counted 11 collars on the original surface, nine on ridges, six on furrows and three on the pool. We positioned the collars as far as we could from the boardwalk, but close enough to allow us to place the chamber and take measurements (~50 cm). Pool measurements were initially taken using collars that were anchored to the underwater peat with the support of cane sticks. Because the cane sticks tended to sink into the peat when the chamber was placed on top (with the risk of damaging the gas analyser due to intake of water into the system), we then opted for a manual approach, where the person in charge of measurements held the chamber on water at a distance from the boardwalk. If any unusual flux was detected by the gas analyser (due to sudden movements during sampling) we repeated the measurement after some time to allow the pool environment to normalize. Collars were allocated to the vegetation type according to the most dominant species growing inside the collar. Vegetation surveys were conducted together with a member of the Forest Research Technical Support Unit. We initially gave a specific percentage (%) cover in relation to the area covered by each species inside the collar. The result was a total % coverage (sum of all species) that most of the time exceeded 100%. We then normalized the results, obtaining a normalized covered area for every species in the collar. For example, collar No 1 had 100% of the area covered by S. capillifolium (layer 1), with the presence of 5% of E. angustifolium (layer 2), for a total of 105%. Normalising the data, the % area covered by the species became 95% for Sphagnum and 5% for Eriophorum. We use the same approach to quantify the % cover in different microforms.

The collars were made from polyvinyl chloride, with a diameter of 20 cm, and inserted 5 cm into the soil with 3 cm left above ground. A wooden access boardwalk from the parking lot to the study site (around 350 m long and including also the length of the transect) was built prior to collar installation in order to minimize damage to the vegetation and soil during fieldwork. Greenhouse gas measurements were taken using a cylindrical transparent Plexiglas chamber (area = 0.03 m², total volume = 0.009 m³; University of York, York, UK), connected through Bev-a-line tubing (return connection) to an Ultra-Portable Greenhouse Gas analyser (UGGA, Los Gatos Inc., San Jose, CA, USA). A portable 12 V lead acid battery placed in a power case (ACC-DCCASE, Los Gatos Research, Inc.) powered the system. The chamber was placed on the collars for 3 min in order to reach a stable increase in CO₂ and CH₄ concentration within the chamber headspace. After every measurement, the chamber was removed to allow air to flow again and re-establish ambient gas concentration for approximately 2 min before being placed on the next collar. The flow rate of the UGGA ensured good air circulation inside the chamber and maintained stable headspace pressure. Before measurements, the chamber was left on the collar to allow pressure inside to stabilize over the course of 10 to 20 seconds. Data from the steady state phase were manually removed during the analysis from each collar.

Ancillary measurements of soil temperature at 2 cm (Ts2) and 10 cm (Ts10) below the soil surface and soil moisture (θ, ML3 Tetha probe, Delta-T Devices Ltd, Cambridge, UK) at 6 cm were collected outside each collar to minimize disturbance. Occasional gaps in soil temperature and moisture data due to faulty instruments were filled using measurements collected by eight probes permanently located along the transect (4107-Temperature Probe equipped with a Beta Therm 100K6A1IA Thermistor and 4 CS616 Water Content Reflectometer, Campbell Scientific, Inc., Logan, UT), connected to a CR1000 logger (Campbell Scientific, Inc., Logan, UT) with a recording interval of 30 min. The eight probes covered all the microforms except the pool.

Fluxes were calculated based on changes in CO₂ and CH₄ concentration in the chamber headspace over time, using the linear slope fitting technique:

\[ F = \frac{P \times V \times \Delta v}{R \times T \times t \times A} \]

where \( F \) is the CH₄ or CO₂ flux (µmol m⁻² s⁻¹), \( P \) is the atmospheric pressure (atm), \( \Delta v \) is the change in gas concentration in the chamber headspace over the closure time (µmol·mol⁻¹), \( V \) is the total volume of the chamber (m³), \( R \) is the gas constant (atm·K⁻¹·mol⁻¹), \( T \) is the temperature in the chamber (K), \( t \) the enclosure time (s) and \( A \) is the chamber area (m²). We report NEE, CH₄ and total GHG flux in g m⁻² day⁻¹ of CO₂ equivalents (CO₂ eq), calculated by estimating a global warming potential (GWP) for CH₄ of 28 CO₂ eq over 100 years with no feedbacks (Myhre et al., 2013). Photosynthetically active radiation (PAR) values were not considered. This information was not the focus of our hypothesis, being mainly centred in understanding the role of vegetation in CH₄ emission.

2.3 Statistical analysis

All the analysis was performed using R (Version 1.0.143 – © 2009–2016, RStudio, Inc.). Results are presented as means with standard error. We tested the significance of the differences in the CO₂ and CH₄ fluxes between different microforms and plant species by performing an
analysis of variance (ANOVA). Differences were considered significant at \( p < .05 \). Pearson correlation analysis was conducted to explore the relationships of CO\(_2\) and CH\(_4\) emissions with environmental variables, micro-forms and vegetation types. Based on normal statistical convention, we decided to consider a correlation to be strong if the correlation coefficient \( r \geq 0.5 \) and significant if \( p < .05 \).

3 | RESULTS

3.1 | November 2017 to October 2018

3.1.1 | Environmental variables

Soil temperature at 2 and 10 cm was statistically different between microforms (\( p < .05 \)) and in different seasons (\( p < .001 \)) (Figure 4). During summer, we saw an increase in soil temperature for all microforms. Ridges showed the warmest average value (21.6 ± 0.5°C), followed by furrows (19.9 ± 0.2°C) and original surfaces (17.0 ± 0.8°C). July was the hottest month of the year, with the temperature reaching 26.1 and 24.8°C for the original surface and ridges, respectively. Soil moisture was statistically different in different seasons (\( p < .01 \)) and microforms (\( p < .05 \)). Forestry-derived microforms (ridges and furrows) seemed to be more affected by drier conditions in summer (Figure 5), especially furrows, which showed the lowest moisture value by far (0.25 ± 0.03 m\(^3\).m\(^{-3}\)). Original surfaces maintained instead a stable moisture content throughout the year (moisture average of 0.42 ± 0.02 m\(^3\).m\(^{-3}\)). Ridges were confirmed to be the driest microform, with an annual average moisture content of 0.38 ± 0.02 m\(^3\).m\(^{-3}\), whereas furrows were the wettest (0.46 ± 0.02 m\(^3\).m\(^{-3}\)). No correlations were found between either NEE or CH\(_4\) fluxes and the environmental variables, except for a significant weak negative correlation (\( R = -0.18 \) and \( p < .05 \)) between NEE and soil moisture (Figure 6).

3.1.2 | Net ecosystem exchange and methane fluxes in different microforms

Our results showed significant differences between NEE values in different microforms (\( p < .001 \)) and different seasons (\( p < .001 \); Figure 7). The pool was found to be a source of both gases, whereas all the other land types acted as a sink of CO\(_2\), with higher NEE (in absolute value) for furrows and ridges (Table 1). Over the whole study period, the original surface acted as a weaker CO\(_2\)
sink than forestry-derived microforms in all periods of the year except for summer. In autumn, we observed the highest NEE values for all microforms except for the pool. An especially strong C sink was observed in the ridges, with mean NEE = −2.20 ± 0.30 gCO₂eq m⁻²·day⁻¹. The pool continued to act as a source of CO₂ throughout the measurement period (0.80 ± 0.20 gCO₂eq m⁻²·day⁻¹). All microforms, except the pool, acted as sinks of CO₂ in every season. During summer, ridges showed the lowest values of NEE, especially in June when the lowest soil moisture value of the year was observed (0.22 ± 0.03 m³·m⁻³).

Significant differences in CH₄ fluxes were also found in different microforms (p < .001) and different seasons (p < .001). The original surface was observed to be the strongest CH₄ source (0.42 ± 0.03 gCO₂eq m⁻²·day⁻¹), with the maximum CH₄ emissions occurring in autumn from the original surface (0.48 ± 0.05 gCO₂eq m⁻²·day⁻¹), followed by furrows (0.24 ± 0.06 gCO₂eq m⁻²·day⁻¹), ridges (0.16 ± 0.03 gCO₂eq m⁻²·day⁻¹) and

**FIGURE 5** Soil moisture in different seasons per each microform (2017–2018)

**FIGURE 6** Correlations for (a) NEE and (b) CH₄ fluxes with soil temperature at 10-cm (Ts10) and 2-cm (Ts2) depth and soil moisture (θ) in the period 2017–2018. F is the flux expressed in gCO₂eq m⁻²·day⁻¹. Soil moisture is expressed in m³ m⁻³ and θ is expressed in °C [Color figure can be viewed at wileyonlinelibrary.com]
the pool (0.14 ± 0.04 gCO₂eq m⁻² day⁻¹). The pool and ridges showed the smallest CH₄ fluxes in winter, with mean fluxes of 0.08 ± 0.01 gCO₂eq m⁻² day⁻¹ and 0.14 ± 0.04 gCO₂eq m⁻² day⁻¹, respectively. Even if the pool contributed less to CH₄ emissions in the overall studied period, in summer we measured a peak CH₄ flux of 0.77 ± 0.03 gCO₂eq m⁻² day⁻¹, which was the highest among all microforms. Overall, measurements grouped by microform across the assessment period showed that ridges and furrows acted as net GHG sinks, the original surface was found to be close to equilibrium and the pool was the only GHG source (Table 1).

### 3.1.3 Net ecosystem exchange and methane fluxes in different vegetation types

Based on plant species abundance (percentage cover) per collar, we identified five key species to classify and summarize fluxes. These were *C. vulgaris*, *E. angustifolium*, *P. commune*, *Sphagnum* spp. (*S. capillifolium* and *S. papillosum*) and *T. cespitosum*. We therefore assessed the species abundance per each microform (Table 2). Our results showed significant differences in NEE among the different vegetation types.
(i.e., different dominant species) \( p < .001 \) and different seasons \( p < .001 \). Interdependence between vegetation types and microforms was inevitable, and it clearly reflected the habitat preference of the species. The highest NEE values measured were in vegetation dominated by *Eriophorum* \(-1.30 \pm 0.30 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), followed by *Polytrichum* \(-1.20 \pm 0.20 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), *Calluna* \(-0.80 \pm 0.20 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), *Trichophorum* \(-0.70 \pm 0.30 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), and *Sphagnum* spp \(-0.60 \pm 0.10 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\). All species showed uptake of CO2 in different seasons, except for *Trichophorum*, where we detected small CO2 losses during spring \(0.06 \pm 0.03 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) and winter \(0.10 \pm 0.10 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) (Figure 8). Autumn was the season where we measured the highest NEE during the year, with a mean value across all vegetation types of \(-1.60 \pm 0.95 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), with *Eriophorum* showing the highest values for CO2 uptake among all species \((-2.70 \pm 0.50 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\)\). Spring, by contrast, displayed the lowest NEE values \(-0.50 \pm 0.50 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\).

We found significant differences in CH4 fluxes among vegetation types \( p < .001 \) and seasons \( p < .001 \). Data for *Trichophorum* showed the highest CH4 fluxes compared to other species, with a mean CH4 emission of \(0.69 \pm 0.06 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) averaged across the studied period (Figure 8). Collars with *Sphagnum* \(0.39 \pm 0.03 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) had similar fluxes to *Eriophorum* \(0.35 \pm 0.03 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\), whereas *Polytrichum* and *Calluna* were the smallest CH4 sources (respectively, \(0.09 \pm 0.02 \text{ and } 0.18 \pm 0.03 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\)). Our data showed peak emissions of CH4 in spring \(0.79 \pm 0.08 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) and summer \(0.79 \pm 0.17 \text{ gCO}_2\text{eq m}^{-2}\text{day}^{-1}\) for *Trichophorum*, whereas in winter (collars were covered in snow due to snowfalls occurring between December 2017 and February 2018) (Table 3) the CH4 emitted was the smallest of the study period for all the species investigated. The total GHG balance of all vegetation

### Table 2

Percentage relative abundance of key species identified during the 2017 vegetation survey on different microforms

| Microform          | Original | Furrow | Ridge |
|--------------------|----------|--------|-------|
| *Calluna*          | 3.8      | 8.3    | 8.8   |
| *Deshampsia*       | 0        | 0      | 0     |
| *Polytrichum*      | 0        | 29.3   | 59.8  |
| *Trichophorum*     | 18.9     | 0      | 1     |
| *Eriophorum* spp   | 5        | 2.5    | 14.2  |
| *Sphagnum* spp     | 64.5     | 36.1   | 1.5   |
| Others             | 7.8      | 23.8   | 14.7  |

### Figure 8

Net ecosystem exchange (NEE) and CH4 averages (bars) with standard errors for the different dominant plant species per each season expressed in gCO2eq m\(^{-2}\) day\(^{-1}\) (2017–2018)
types was negative (GHG sink), except for *Trichophorum*-dominated collars, which showed a GHG balance equal to zero (equilibrium) (Table 4).

**TABLE 3** Monthly total precipitation (mm) and relative average air temperature (T, °C) during winter 2017–2018 (Lonielist EC tower, Coyle et al., personal communication)

|          | Total precipitation | Air T average |
|----------|--------------------|--------------|
| Dec 2017 | 74                 | 2.62         |
| Jan 2018 | 68                 | 0.99         |
| Feb 2018 | 39                 | 0.71         |

**TABLE 4** Plant species average contribution of CH₄ and NEE over the assessment period (2017–2018) and standard error of the mean (±SE) and overall net GHG balance

|                | CH₄          | NEE         | GHG balance |
|----------------|-------------|-------------|-------------|
|                | Mean        | SE          | Mean        | SE          | Mean        | SE          |
| *Sphagnum*     | 0.39        | 0.03        | −0.60       | 0.10        | −0.21       | 0.13        |
| *Calluna*      | 0.18        | 0.03        | −0.80       | 0.20        | −0.62       | 0.23        |
| *Eriophorum*   | 0.35        | 0.03        | −1.30       | 0.30        | −0.95       | 0.33        |
| *Trichophorum* | 0.69        | 0.06        | −0.70       | 0.30        | 0.01        | 0.36        |
| *Polytrichum*  | 0.09        | 0.02        | −1.20       | 0.20        | −1.11       | 0.22        |

*Note:* NEE, CH₄ and GHG are expressed as CO₂eq in g m⁻² day⁻¹. GHG, greenhouse gas; NEE, net ecosystem exchange.

**3.2 | Comparison of summers 2018 and 2019 (3 and 15 months after restoration)**

**3.2.1 | Environmental variables**

Environmental variables collected during summer 2019 were wetter and colder compared to those collected in summer 2018 (Figures 9 and 10). Overall in the summer 2019 period, soil temperatures on ridges were the lowest (14.6 ± 0.1°C), followed by the pool (14.7 ± 0.5°C), original surfaces (14.9 ± 0.1°C) and furrows (15.1 ± 0.1°C). In July, the soil temperature reached the maximum for all microforms.
(Table 5) but remained lower than in summer 2018. Data from the Scottish Environment Protection Agency (SEPA, 2019) relative to Forsinain weather station (58°24′48″N; 3°51′48″W, ~10 km west from Lonielist) reported higher monthly rainfalls in summer 2019 in comparison to 2018 (Figure 11) and this could have influenced the soil moisture values of our transect (wetter in 2019 compared to 2018). In 2019, original surfaces were the wettest microforms on a summer average (0.95 ± 0.00 m³·m⁻³), followed by ridges (0.93 ± 0.01 m³·m⁻³) and furrows (0.88 ± 0.01 m³·m⁻³) and with specific monthly averages reported in Table 6. The only significant correlation observed was a weak positive one between NEE and Ts2 (r = 0.25, p < .001).

### 3.2.2 Changes in vegetation after restoration

The vegetation survey conducted in summer 2019 revealed that almost all the collars in our study site went through changes in their vegetation composition (Figure 12). The cover of *Sphagnum* spp increased in all collars, with important increments on ridges (+196%), which had very...
little Sphagnum in 2017. *Calluna vulgaris* decreased in all the three microforms, with the biggest losses from ridges and furrows, and so did *Trichophorum*, on the original surface and ridges. *Polytrichum* decreased by 4 and 12% on furrows and ridges, respectively, and was confirmed to be a species only present in forestry-derived microforms. *Eriophorum* increased greatly on furrows but declined on ridges. The vegetation survey after restoration showed the appearance of a new species, commonly found in restored sites, *Deshampsia flexuosa*. On ridges and furrows, its cover reached almost 20 and 10%, respectively.

In general, we observed an increase in *Sphagnum* spp in all microforms and a decrease in other vegetation types, such as *Calluna*, which tends to increase on drier surfaces, and *Polytrichum*, which often grows on bared peat, such as forestry-derived microforms.

### 3.2.3 Greenhouse gas dynamics in different summers

In summer 2019, NEE and CH₄ fluxes were significantly different among some of the microforms and vegetation species. The NEE sink increased significantly for original surfaces, ridges and furrows, whereas the pool was confirmed again to be the only CO₂ emitter of the system, with its fluxes not significantly different from those in summer 2018 (Figure 13). Forestry-derived microforms had the highest NEE, with furrows absorbing the most CO₂. Methane emissions in summer 2019 were significantly different from those in summer 2018 only for original surfaces and the pool, whereas they did not differ much for forestry-derived microforms. The pool was the only microform that showed decreased values from the ones reported in 2018 (Table 7). Methane emissions doubled or almost doubled for all microforms between 2018 and 2019, except for the pool, which, on the contrary, showed very low values in 2019 compared to the previous summer. However, only original surfaces and the pool were significantly different from 2018.

In 2019, the overall balance of GHG emissions gave a stronger sink for ridges and furrows (followed similarly by original surfaces), whereas the pool acted again as a net source.

#### TABLE 6 Soil moisture (m³ m⁻³) in the summer months of 2018 and 2019 and relative percentage increases

| June       |          |          |          |          |          |          |          |          |          |          |          |          |          |          |          |          |          |          |
|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
|            | 2018a    | 2019b    | +%       | 2018a    | 2019a    | +%       | 2018b    | 2019b    | 2019a    | +%       |
| Original surface | 0.54 0.04 | 0.90 – 66 | Mean SE | 0.26 0.03 | 0.85 0.02 | 228 26 | 0.79 – 1.00 | 0.01 21 |
| Ridge      | 0.34 0.05 | 0.87 – 158 | Mean SE | 0.22 0.03 | 0.80 0.02 | 260    | 0.80 – 0.97 | 0.01 21 |
| Furrow     | 0.24 0.03 | 0.91 – 282 | Mean SE | 0.26 0.03 | 0.85 0.03 | 223    | 0.83 – 0.88 | 0.01  6 |

aData collected using the portable ML3 Theta probe.

aData derived from CR1000 logger.
4 | DISCUSSION

4.1 | Effect of microtopography and vegetation on net ecosystem exchange

As expected, furrows were found to be the wettest microform, excluding the pool. They absorbed more CO₂ than all the other land classes, with sink strength peaking in spring and autumn. In summer though, we observed a decrease in their sink strength. Because we found a weak negative correlation between NEE and soil moisture, it is possible that soil moisture in furrows (as well as in other microforms) affected the peat decomposition rate. In summer, low moisture levels may have increased peat oxidation and relative CO₂ emissions, whereas in autumn higher moisture levels may have slowed down peat decomposition, reducing CO₂ release from the soil. Furthermore, in accordance with Acosta et al. (2017), we
believe that vegetation composition played a key role in these GHG dynamics. Dominant plant species in furrows were *Sphagnum* spp. and *Polytrichum*. *Polytrichum* showed higher NEE values, especially in autumn, suggesting that higher absorption of CO₂ in furrows may have occurred due to its possible efficient photosynthetic activity for that period (Sveinbjörnsson & Oechel, 1981). *Polytrichum* photosynthetic activity, though, may be inhibited by low water content (and equally by high temperature), resulting in lower NEE, as reported by Callaghan, Collins, and Callaghan (1978). Indeed, summer trends of NEE based on the dominant vegetation type showed that *Polytrichum* emitted more CO₂ in summer than in other seasons. In periods of water stress, *Polytrichum* is able to fold its leaves against the stem, thus reducing water loss, but, at the same time, this inhibits photosynthesis (Groeneveld & Rochefort, 2002). During summer then, *Polytrichum* may have suffered from drier soil, especially in June, which had the lowest soil moisture values of the studied period. It is also possible that warmer and drier conditions may have desiccated its leaves, reducing the plant photosynthetic rate (Penny & Bayfield, 1982).

A similar pattern is reported for ridges, which showed a peak in CO₂ uptake in autumn, whereas in summer NEE values were very close to zero. The species composition may explain the observed behaviour. Ridges were indeed mostly covered with *Polytrichum* (60%), with occasional *Calluna* and *Eriophorum*. NEE from ridges may have been affected by *Polytrichum* in the same way as in the furrows. The intensity of the fluxes may be different though (more severe from ridges), because of higher abundance of *Polytrichum* on ridges and almost total lack (1.5%) of sphagnum, which is known to have the ability to minimize evaporative water loss and retain water to differing degrees dependent on species (Robroek, Limpens, Breeuwer, & Schouten, 2007).

On the original surface, *Sphagnum* was the species most commonly found and it tended to create a bedding layer for different plants. In every collar on original surfaces, a layer of *Sphagnum* nurtured *Trichophorum*, followed by small amounts of *Eriophorum* and *Calluna*. Seasonal trends in NEE on the original surface were correlated with those of *Trichophorum*. Both showed stronger sinks in autumn and summer, whereas in winter and spring there were losses of CO₂ from collars with *Trichophorum*. Uptake of CO₂ in summer may be associated with a possible intense photosynthetic activity by *Trichophorum*. Korrensalo et al. (2017) assessed that *Trichophorum*, with only 1% of areal cover, made up 12% of the seasonal vascular net photosynthesis at their boreal peatland study site.

The pool showed positive NEE values throughout the studied period, acting as a net source of CO₂. This is in line with studies conducted on ombrotrophic bogs with sparse pools in Canada (McEnroe, Roulet, Moore, & Garneau, 2009; Pelletier, Strachan, Garneau, & Roulet, 2014; Pelletier, Strachan, Roulet, & Garneau, 2015). These studies underlined how CO₂ would originate predominantly from the degradation of peat sediments in the pools and how deeper pools tend to emit less CO₂. Where the pools are small and shallow (<45 cm deep, roughly the dimension of the pool in our study), these sediments tend to degrade faster and more consistently, due to warmer water and less humified and recalcitrant peat at the pool bottom. In spring, we observed the highest CO₂ emissions, probably due to thawing. In winter, a thin layer of ice covered the pool, which may have prevented gases from escaping to the atmosphere (McEnroe et al., 2009). Once the layer melted, the CO₂ might have been released. This pattern can be seen in winter, too. During winter, even if the pool was covered by a thin layer of ice, we were still able to detect CO₂ fluxes. We think that although the thin ice sheet was preventing the gases from escaping to the atmosphere, during field measurements the layer may have been broken, releasing the CO₂ underneath.

### 4.2 Effect of microtopography and vegetation on methane emissions

Methane emissions were significantly different for different microtopographic levels, echoing the finding of Creevy, Payne, Andersen, and Rowson (2019), who assessed the C budgets from a forest-to-bog restoration site between England and Wales.

According to our hypothesis, we expected higher CH₄ emissions from the pool and furrows, but we found the original surface made the largest contribution to CH₄ emissions. Couwenberg (2009) reported CH₄ emissions to be dependent on the balance between CH₄ production, CH₄ consumption and CH₄ transport. Methane production is correlated with labile substrate availability and decreases when labile substrates are depleted (Davidson et al., 2016). In summer, we measured the greatest CH₄ fluxes in all the microforms. Because a large supply of available labile C substrate can cause a substantial amount of CH₄ to be emitted (Charman, 2002; Clymo, Pearce, & Conrad, 1995), it is possible that during spring new labile C was produced and, in summer, part of this was released largely through diffusion, ebullition or plant transport. Diffusion is usually smaller than the other two transport types (Lai, 2009), and our experiment design did not consider the deployment of specific equipment.
(i.e., bubble traps) able to detect ebullition episodes. In view of this, and because we found no correlation between environmental variables and CH₄ fluxes, we believe that the presence of wetland vascular plants played a key role in the CH₄ dynamics, especially on the original surface. Schimel (1995) stated that measurement of total CH₄ production per se is not a good predictor of CH₄ emissions, and he considered plants’ composition and their ability to transport CH₄ to be essential for a complete understanding of CH₄ dynamics. Greenup et al. (2000) and Joabsson et al. (1999) identified that photosynthetic activity of vascular plants can have an impact on the rate of methanogenesis. They found that E. vaginatum, for example, could increase C supply to methanogens and therefore create the conditions for CH₄ production. When this is associated with the presence of aerenchymous species, which can mediate CH₄ transport, the result is higher CH₄ emission rates (Schütz, Seiler, & Conrad, 1990). In fact, a considerable amount of the CH₄ emitted from peatlands flows through vascular plants (Schimel, 1995; Thomas, Benstead, Davies, & Lloyd, 1996) by molecular diffusion (Sirin & Laine, 2008), bypassing the attacks of methanotrophs.

We have observed similar patterns during summer for Trichophorum, which showed the highest NEE values. Moreover, emissions from Trichophorum confirmed our hypothesis, with higher CH₄ emissions during the study compared to other species. This result is in line with other studies focused on the importance of the investigated wetland vascular species in predicting CH₄ emissions from peatlands and wetlands (Bohdalkova, Čufík, Kuběna, & Bůzek, 2012; Couwenberg, 2009; Creevy et al., 2019; Davidson et al., 2016; Greenup et al., 2000; Joabsson et al., 1999). Polytrichum, in contrast, exhibited lower CH₄ emissions throughout all seasons. Because Polytrichum was more abundant in furrows and ridges, matched by an absence of Trichophorum, it is possible that CH₄ emissions were lower due to smaller vegetation-mediated transport effects. No comparative evidence was available in the literature and thus, further study is required as Polytrichum may be a key species for CH₄ emissions for restored peatlands.

Methane emissions from the pool confirmed our hypothesis that it was an emitter of CH₄. However, the amount of CH₄ emitted from the pool is smaller than that from other microforms. This may be related to lower availability of fresh C substrates in pools, which may slow down CH₄ production and thus efflux (McEnroe et al., 2009; Miller, Ghiorse, & Yavitt, 1999). However, in summer we observed a spike in CH₄, the highest among microforms and seasons. This peak is not related to any ebullition episodes, because the only CH₄ peak value measured in July was considered to be an outlier and removed from the analysis. Peacock, Evans, Fenner, and Freeman (2013) reported that pool depth was correlated with CH₄ emissions. They measured CH₄ fluxes from 60 bog pools created following ditch blocking on a blanket bog in north Wales and found that shallower pools emitted more methane. According to their study, shallow pools can favour invasion of Eriophorum, creating an ideal environment for methanogenesis, and they can also make for a shorter distance for methane diffusion through water (so that it has no time to oxidize before being emitted to the atmosphere). Indeed, during summer the pool was considerably shallower compared to other seasons and this may have influenced the amount of methane emitted by shortening the travel time to the atmosphere. In normal conditions, the level of the pool was deep enough to allow a net separation between the pool and the original surface (where the Eriophorum was vegetating close to the pool). Hence, when taking measurements from the boardwalk, the chamber was free from any traces of vegetation. In the dry summer of 2018, the level of the pool diminished, to an extent that the boardwalk was further from the water and parts of the vegetation (Eriophorum) may have been included in the chamber without being noticed and possibly contributed to CH₄ emission by transport.

Ultimately, we observed that all microforms showed appreciable winter CH₄ emission. This may be related to snow cover. Sirin and Laine (2008) suggested that a substantial amount of CH₄ (and also CO₂) could be released through the snow pack via diffusion during winter. This release can be significant and account for 5–33% of the annual total (Alm, Saarnio, Nykänen, Silvola, & Martikainen, 1999).

4.3 Annual GHG balance (November 2017 to October 2018)

The total GHG balance of the Forsinard site transect showed a negative flux of $-1.10 \pm 0.40$ gCO₂ eq m⁻²·day⁻¹, meaning the whole system was acting as a “GHG sink”. Contrary to our hypothesis, furrows and ridges contributed most to total GHG uptake, acting as efficient and strong sinks. We may assume this is primarily due to the extensive presence of P. commune, a species that can have a high rate of photosynthesis (high CO₂ uptake), combined with the absence of roots and vascular tissues (reduced CH₄ emissions). Original surfaces were weaker GHG sinks, confirming our hypothesis regarding original surfaces in a condition of GHG equilibrium. This microform, however, showed the highest total CH₄ rates, possibly due to the effect of Trichophorum. The pool confirmed our hypothesis that it is a GHG source, but, contrary to our expectations, the pool was not a hotspot for methane, because it mainly emitted CO₂.
4.4 | GHG balance 3 and 15 months after restoration (comparison between summer 2018 and summer 2019)

NEE and CH4 fluxes in 2019 were found to be significantly different from those in 2018, although only for some microforms. Carbon dioxide fluxes decreased (higher NEE), whereas CH4 emissions almost doubled for every microform, except for the pool. The observed GHG dynamics might be due to the adjacency effect of nearby restoration work at the site, differences in weather conditions between 2018 and 2019, long-term changes in vegetation or some combination of these.

4.4.1 | Restoration work at the site (adjacency effect)

Recent restoration work might have resulted in wetter and, in some periods (e.g., August 2019), even waterlogged conditions in our study area. Anoxic soil conditions can inhibit CO2 release, but can also favour CH4 production and subsequent emissions. In a study conducted on a blanket bog restored from forestry in northern Scotland, Anderson and Peace (2017) showed how restoration practices such as damming ditches and furrows could significantly raise the water table and promote development of aquatic microhabitats. Terraforming of the forestry-derived microforms by filling the furrows with trees left on site and compacting the peat may have reduced water runoff, favouring the occurrence of standing water and small pools, especially in the areas previously occupied by furrows. Even though our transect has not undergone terraforming, there is the possibility that the water content and hydrology could have been affected by terraforming in the surrounding area (simulating the effect of plough furrow blocking), causing the observed increase in soil moisture. Data from R. Artz et al. (unpublished data), relative to WTD in the area surrounding our transect (data from 4 replicate water table - conductivity, Odyssey, NZ - loggers), show indeed higher water tables for summer 2019 in comparison to summer 2018 (Figure 14). However, there is still little evidence on the effects of this type of restoration work on nearby areas (Hambley et al., 2019; Hermans et al., 2019).

4.4.2 | Differences in weather conditions

According to the Met Office (2019), summer 2019 was “unusually wet and ranked as the 7th wettest overall in the UK in a series dating back to 1910”. Scotland was very wet overall, recording its second wettest summer (only surpassed by summer 1985), with the heaviest rainfall in August. By contrast, the summer of 2018 has been described as the warmest since 2006 and driest since 2003, particularly during June and July (Met Office, 2019). SEPA (2019) reported total rainfall values of 393 mm in relation to summer 2019 and 138 mm during 2018 (Figure 11). At our site in 2019, the soil was 60–280% wetter than in 2018, suggesting that weather conditions may have had an impact on the hydrological state of the site in 2019, as reported also in Figure 14. Sirin and Laine (2008) reported that the annual GHG flux rate from peatlands could change between years with different weather conditions and this change could be very large, varying from absorption to high emission rates. Moreover, Bubier, Moore, Savage, and Crill (2005) found that CH4 emissions from a boreal wetland complex in Canada increased 60% between a dry and a wet summer 2 years apart, and Laine et al. (2019) underline how a high soil moisture and colder temperatures may limit CO2 emissions, due to inhibition of peat oxidation, reflecting the observed weak correlation between NEE and soil temperature at 2 cm in this study.

4.4.3 | Long-term changes in vegetation

Vegetation is another aspect that needs to be examined. From May 2017 to September 2019 vegetation cover inside the collars has gone through changes. These changes, however, may or may not have been triggered by the recent restoration works. It is possible that the system was already evolving into a new succession in response to the first restoration practices in 2003, which only involved felling to waste and ditch damming.
net emitter of CO2, and in summer 2019 net CO2 emissions were close to zero and this to a reduced methanogenesis due to lower sediment temperatures. A study by McEnroe et al. (2009) confirmed this pattern, reporting that CH4 fluxes from pools of 0.3-m depth were up to five times smaller than fluxes from pools of 0.7-m depth. Moreover, Bastviken, Cole, Pace, and Van de Bogert (2008) suggested that a decrease in CH4 fluxes can be linked to an increase of CO2 emissions. Methane, indeed, might get oxidized while travelling up the water column from the bottom of the pool to the atmosphere. The deeper the pool, the further the distance to travel and the more CH4 can be oxidized into CO2 (depending on the oxygen concentration profile of the pool). In relation to this, we indeed observed an increase in CO2 fluxes from the studied pool in summer 2019 and this might be related to an increase in its water level. NEE values from original surfaces, furrows and ridges decreased hugely. Although we found a weak positive and significant correlation between NEE and soil temperature at 2 cm, we believe (according to Ward et al., 2013) that the effect on NEE depended mostly on vegetation composition and possibly on the wetter conditions of the soil. Higher water contents, for example, may have inhibited CO2 loss from both peat and CH4 oxidation. Vegetation may have been crucial too; in forestry-derived microforms we measured the highest NEE values of the transect. This may be linked to the presence of *Polytrichum*, absent on original surfaces, which is known to function optimally in environments that tend not to be too dry (Groeneveld et al., 2007). The dry summer of 2018 might have limited the growth of this species and inhibited its photosynthesis (Callaghan et al., 1978). The increase in *Eriophorum* spp observed especially on furrows and original surfaces can also result in increased NEE due to the high total chlorophyll content of its leaves, which may enhance photosynthetic activity (Defoliart, Griffith, Chapin III, & Jonasson, 1988; Konings, Boyd, & Andersen, 2019).

### 4.4.4 Combined factors

The overall increase in CH4 emissions from original surfaces, furrows and ridges, might be explained by the concomitant effects of the generally wetter condition of the site (which might have promoted methanogenesis) and the expansion of vascular species such as *Eriophorum* spp (+30% on the original surface). Methane emissions from the pool were close to zero and this can be related to small amounts of fresh substrate available for methane production (e.g., dead plants; Miller et al., 1999). The pool continued to be the only net emitter of CO2, and in summer 2019 net CO2 emissions were marginally higher than in 2018, whereas methane emissions seemed to decrease significantly. Pelletier, Moore, Roulet, Garneau, and Beaulieu-Audy (2007) found that CH4 emission decreased with increasing pool depth at two sites and they attributed this to a reduced methanogenesis due to lower sediment temperatures. A study by McEnroe et al. (2009) confirmed this pattern, reporting that CH4 fluxes from pools of 0.7-m depth were up to five times smaller than fluxes from pools of 0.3-m depth. Moreover, Bastviken, Cole, Pace, and Van de Bogert (2008) suggested that a decrease in CH4 fluxes can be linked to an increase of CO2 emissions. Methane, indeed, might get oxidized while travelling up the water column from the bottom of the pool to the atmosphere. The deeper the pool, the further the distance to travel and the more CH4 can be oxidized into CO2 (depending on the oxygen concentration profile of the pool). In relation to this, we indeed observed an increase in CO2 fluxes from the studied pool in summer 2019 and this might be related to an increase in its water level. NEE values from original surfaces, furrows and ridges decreased hugely. Although we found a weak positive and significant correlation between NEE and soil temperature at 2 cm, we believe (according to Ward et al., 2013) that the effect on NEE depended mostly on vegetation composition and possibly on the wetter conditions of the soil. Higher water contents, for example, may have inhibited CO2 loss from both peat and CH4 oxidation. Vegetation may have been crucial too; in forestry-derived microforms we measured the highest NEE values of the transect. This may be linked to the presence of *Polytrichum*, absent on original surfaces, which is known to function optimally in environments that tend not to be too dry (Groeneveld et al., 2007). The dry summer of 2018 might have limited the growth of this species and inhibited its photosynthesis (Callaghan et al., 1978). The increase in *Eriophorum* spp observed especially on furrows and original surfaces can also result in increased NEE due to the high total chlorophyll content of its leaves, which may enhance photosynthetic activity (Defoliart, Griffith, Chapin III, & Jonasson, 1988; Konings, Boyd, & Andersen, 2019).

### 4.4.5 Implications for restoration strategy

Our findings regarding forestry-derived microforms acting as GHG sinks, cast a different light on the understanding of peatland restoration strategies. The final stage of forest-to-bog restoration currently ongoing in Forsinard, which aims to bring the bog to a “pristine” or natural condition, is carried out by obliterating furrows and ridges and creating flattened areas (original surfaces) that are at first mostly devoid of vegetation and interspersed with small pools. Based on our results, this restoration technique may have a negative impact on GHG...
emissions, at least in the short term. One of the main reasons for the increase of GHG emissions may be the temporary obliteration of bog vegetation (less CO₂ absorbed by photosynthesis) and in particular of *P. commune*, exclusively present on ridges and furrows. This species not only showed higher GHG absorption compared with other vegetation types, but it can also encourage the regrowth of original bog species, such as *Sphagnum*. Also known as a “nurse plant”, *Polytrichum* assists the growth of *Sphagnum*, offering shelter, providing a relatively moist atmosphere and creating a favourable microclimate by reducing temperature fluctuations (Groeneveld et al., 2007; Groeneveld & Rochefort, 2002). Another source of GHGs derived from terraforming is related to the creation of small and shallow pools, which we found to be the only net GHG source among other microforms. Peacock et al. (2013) suggested that to ensure the best restoration is achieved in terms of GHG balance, pools should be deeper than 0.5 m. Based on our results, together with studies by Anderson and Peace (2017) and Hancock et al. (2018), we suggest, as an alternative to terraforming, the application of plough furrow blocking in addition to ditch blocking to restore the former habitat and carbon sink function of the blanket bog. Contrary to terraforming, plough furrow blocking can lead to the creation of deep pools in the space occupied by furrows and thus facilitate the rise of the water table, avoiding creation of bare peat areas and disturbance of vegetation, which might contribute to further GHG emissions.

5 CONCLUSIONS

There are few studies on bog restoration, particularly from forestry. In contrast to our hypotheses, we found that the two microforms derived from forestry (ridges and furrows) both acted as significant sinks of GHGs, far exceeding the flux of the original surface. The pool was confirmed to be a source of GHGs. Although both soil moisture and soil temperature were significantly different between microforms and seasons, we found either not significant or significant weak correlations between fluxes and these key “driving” environmental variables (cf. Joabsson et al., 1999). Plant species on the other hand, played a central role in both CO₂ and CH₄ emissions. Different microforms hosted distinct species, each with specific characteristics. *Polytrichum*, mostly found on forestry-derived microforms, may be the primary driver for the ridges and furrows becoming GHG sinks, mostly due to its small CH₄ emissions. This pioneer species can also encourage the regrowth of *Sphagnum*, an original bog species supposed to reduce GHG emissions (Albrecht & Glatzel, 2012; Beyer & Höper, 2015), which represents the goal of restoration practices in the study area (Hancock et al., 2018). Vascular plants were mainly responsible for CH₄ emissions in different seasons and microforms, whereas other vegetation types contributed to lower emission rates. Methane transport mediated by *Trichophorum* was the primary cause of the CH₄ emissions from the original surface. Therefore, it is important to know whether these species are present and how they may affect the GHG dynamics, especially in peatland management (Greenup et al., 2000). We also believe that a future quantification of the extent of pools is crucial for a complete and scaled-up overview of the total GHG balance of the studied area, given that this was the only microform acting as a net source of GHG. These investigations suggest that terraforming of previously afforested peat (and creation of more original surface and shallow pools and obliteration of the existing vegetation) may have negative impacts by increasing GHG emissions, at least in the short term, because forestry-derived microforms can host important species and microhabitats able to reduce GHG emissions. Peacock et al. (2013) reached a similar conclusion, asserting that restoration techniques should aim to minimize the extent of areas of bare peat between pools. We therefore suggest plough furrow blocking as an alternative restoration practice.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORSHIP

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DATA SHARING AND DATA ACCESSIBILITY REQUEST

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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