RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

Check for updates

RESEARCH ARTICLE

Rewetting is not enough: *Sphagnum* transplants promote lowering of greenhouse-gas emissions in peatlands

Rima Bou Melhem[1,2], Line Jourdain[1], Sébastien Gogo[3], Fabien Leroy[4], Adrien Jacotot[5,6], Jean-Sébastien Moquet[4], Fatima Laggoun-Défarge[4], Christophe Guimbaud[1]

Abstract

Introduction: Degraded peatlands contribute up to 2 gigatons CO_2-equivalent annually (approximately 5% of anthropogenic greenhouse gas emissions). As restoration efforts increase, the effectiveness of combined hydrological and vegetation restoration strategies remains insufficiently understood.

Objectives: This study investigates the short-term impacts of rewetting, topsoil removal, and *Sphagnum* transplantation on carbon fluxes and greenhouse gas carbon balance in La Guette peatland in France, a disturbed temperate peatland invaded by *Molinia caerulea*.

Methods: Carbon dioxide and methane fluxes, vegetation, and environmental variables were monitored between 2014 and 2017 at La Guette peatland, across Control (unchanged), Bare (top-soil removed), and *Sphagnum* (top-soil removed + *Sphagnum* transplants) plots within rewetted and non-rewetted subsites. Empirical models for ecosystem respiration, gross primary production, and methane fluxes were used to estimate annual carbon budgets, considering only ecosystem–atmosphere exchanges (excluding the carbon physically lost through topsoil stripping).

Results: Rewetting elevated the water table by approximately 7 cm and slightly reduced carbon emissions (by approximately 124 gCO_2-eq m^{-2} yr^{-1}) when implemented alone. Control plots showed the highest emissions. Top-soil removal lowered emissions, and when coupled with *Sphagnum* reintroduction in rewetted areas, achieved the greatest greenhouse gas mitigation. Methane emissions increased post-rewetting, but this increase remained outweighed by reductions in carbon dioxide emissions. One *Sphagnum*-restored plot approached carbon neutrality within the third year.

Conclusions: Although restored plots remained net carbon sources, combined hydrological and vegetation interventions significantly limited carbon losses and CO_2-equivalent emissions compared to degraded conditions. Restoration thus prevents further carbon stock deterioration in disturbed peatlands while reducing climate impacts.

Implications for Practice: While most peatland restoration projects focus solely on rewetting, this approach can require extended periods before full ecosystem recovery. Combining with vegetation interventions can accelerate restoration and deliver greater greenhouse gas emission reductions. Rewetting raises the water table, limiting aerobic decomposition and CO_2 release, while vegetation restoration fosters conditions that support native peatland plant communities. This integrated approach not only speeds the return of ecosystem functions but also enhances biodiversity, strengthens climate change mitigation, and improves ecosystem resilience. Practitioners should explicitly consider carbon outcomes in restoration planning and prioritize integrated hydrological and vegetation interventions to maximize ecosystem recovery and services.

Key words: carbon sequestration, greenhouse gas emissions, hydrological restoration, peatland degradation, *Sphagnum* transplantation, topsoil removal

Author contributions: RBM, FL conducted the modeling, performed data analysis, and wrote the manuscript; LJ, SG, CG, J-SM supervised the study; SG, FL, AJ, CG collected the field data; SG, FL-D designed the experimental setup.

[1]Laboratoire de Physique et Chimie de l'Environnement et de l'Espace (LPC2E), UMR 7328, OSUC, Université d'Orléans/CNRS, Orléans, France
[2]Address correspondence to R. Bou Melhem, email boumelhem.rima@gmail.com
[3]Ecobio - Ecosystèmes, Biodiversité, Evolution, UMR 6553, Université de Rennes, CNRS, Rennes, France
[4]Institut des Sciences de la Terre d'Orléans (ISTO), UMR 7327, OSUC, Université d'Orléans, CNRS, BRGM, Orléans, France
[5]Chrono-Environnement, UMR 6249, Université Marie et Louis Pasteur, CNRS, Besançon, France
[6]SARL SEMBIOSE, Saint-Denis-de-Gastines, France

© 2025 The Author(s). Restoration Ecology *published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.*
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.70224
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70224/suppinfo

Introduction

Natural peatlands are waterlogged ecosystems with anoxic conditions that slow organic matter (OM) decomposition, thus allowing the gradual accumulation of partially decomposed plant material. These wet conditions also support key ecosystem services—water regulation and habitat provision—and make them among the most carbon-dense ecosystems (Temmink et al. 2022). Although covering only 3% of the Earth's terrestrial surface, they store approximately 30% of global soil carbon (C) (Leifeld & Menichetti 2018). Their role in C storage was formally recognized by the United Nations Framework Convention on Climate Change (UNFCCC) in 2012 (Wiegandt 2024). However, peatlands are highly vulnerable to anthropogenic factors. Currently, 12.1% of known peatlands are degraded (Bonn et al. 2016), with this proportion increasing by 0.1% annually—10 times faster than their natural expansion rate (Joosten & Clarke 2002).

Drainage through ditch building is a prerequisite for most anthropogenic disturbances, including land-use changes, road construction, and other practices. By increasing oxygen availability in peat, drainage enhances aerobic microbial activity, accelerating OM decomposition (Li et al. 2021), and potentially shifting peatlands from C sinks to sources (Ojanen et al. 2013; Mishra et al. 2021). Drainage can also induce vegetation shifts. In nutrient-poor, acidic peatlands such as bogs and poor fens, drying leads to the loss of *Sphagnum* mosses—the species responsible for key peatland functions, including long-term C accumulation, hydrological regulation, and nutrient retention (Minayeva et al. 2017). Meanwhile, the increasing dominance of shrubs and graminoids in drained peatlands is thought to enhance microbial activity and hence C mineralization and greenhouse gas (GHG) emissions (Antala et al. 2022). Drained peatlands contribute up to 2 Gt of carbon dioxide equivalents (CO_2-eq) globally each year—around 5% of total anthropogenic GHG emissions (Bonn et al. 2016) and could emit GHGs for centuries (Leifeld & Menichetti 2018). This consequence underscores the importance of implementing peatland restoration as a climate mitigation strategy (Wilson et al. 2015).

Peatland restoration activities depend on site conditions but aim to recover hydrological function and biodiversity (Bacon et al. 2017). Rewetting is a prerequisite to raising the water table (WT) in drained peatlands. By reducing oxygen diffusion into the soil, rewetting promotes an environment that slows the decomposition of OM and reduces carbon dioxide (CO_2) emissions (Couwenberg et al. 2011; Kim et al. 2012; Günther et al. 2020; Evans et al. 2021), although the efficiency of emission reduction may vary substantially between sites, depending on factors such as previous land use, rewetting strategy, and peatland type. Recent syntheses show that, after rewetting, CO_2 balances generally stabilize within about a decade, and although temporary methane peaks can occur, they are usually short-lived and decline as vegetation establishes and WT stabilizes (Balliston et al. 2024). Nevertheless, some long-rewetted sites remain net GHG sources, particularly where restoration focused on hydrology while vegetation recovery was left to spontaneous succession (Samaritani et al. 2011; Vanselow-Algan et al. 2015). Overall, rewetting is preferable to maintaining drained conditions because avoiding CO_2 emissions outweighs any methane (CH_4) increases (Günther et al. 2020). Thus, rewetting is necessary but often insufficient to re-establish a net C sink (Dinesen & Hahn 2019).

Reintroducing native peat-forming vegetation accelerates C sequestration in degraded peatlands (Waddington et al. 2010; Mazzola et al. 2022). When coupled with stable hydrological conditions, this approach further enhances the development of new C sinks (Wilson et al. 2012). Revegetation efforts are tailored to the specific type and condition of the site; for instance, temperate peatlands, commonly dominated by *Sphagnum* species before degradation, often require their reintroduction during restoration (Joosten 2021). The *Sphagnum* genus decomposes three times more slowly than most vascular plants (Graf & Rochefort 2009), shaping the surrounding environment to support peat formation (Bacon et al. 2017). Also, *Sphagnum* species possess greater water retention and higher recovery capacity after desiccation (Titus & Wagner 1983). Topsoil removal (TSR) removes the topsoil layer, eliminating the nutrient-rich and highly decomposed peat layer and the roots and seeds of undesirable plants (Joosten 2021), thus reducing nutrient availability and preventing strong GHG emissions (Harpenslager et al. 2015). Recent work demonstrates that even removing as little as 5 cm of topsoil can substantially reduce methane emissions (Quadra et al. 2023) and achieve comparable *Sphagnum* biomass to deeper removal treatments, with lower vascular plant dominance (Käärmelahti et al. 2024). When combined, rewetting, TSR, and *Sphagnum* reintroduction support effective recovery of peat-forming vegetation (Joosten 2021). Yet how disturbance, rewetting success, and measures such as TSR and *Sphagnum* transfer shape early post-restoration C balance remains unclear.

In this context, we conducted a field experiment on a drained, temperate, nutrient-poor, acidic fen (poor fen) functioning as a C source (D'Angelo et al. 2021). The objective of the study was to investigate how rewetting, topsoil removal, and *Sphagnum* transplantation can impact the peatland's greenhouse gas carbon balance (GGCB). Three different vegetation treatments (unchanged vegetation, topsoil removed, topsoil removed combined with retransferred *Sphagnum* spp.) were implemented within a rewetted and a non-rewetted subsite of the peatland. The TSR treatment in our case was a prerequisite for any vegetation treatment because of the initial conditions of the ecosystem: heavily dominated by *Molina caerulea* (purple moor grass) in all sites. CO_2 and CH_4 fluxes were regularly measured for 4 years after restoration in the 24 plots spanning the rewetted and the non-rewetted subsites. Flux measurements were related to biotic and abiotic environmental factors using empirical ecological models to estimate the annual C budget of each treatment, as well as its GGCB in CO_2-eq. The aims of the study were to:

(1) Assess the impact of different treatments on vegetation and C flux dynamics within the first 4 years after restoration.
(2) Compare how implemented rewetting and vegetation treatment strategies differ in their potential to mitigate GHG emissions.

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Methods

Site Description

The study was conducted at La Guette peatland, an originally *Sphagnum*-dominated site in Neuvy-sur-Barangeon, Cher, France (47°19′44″N, 2°17′04″E). The site is best described as an acidic transitional poor fen primarily rain-fed but also influenced to some extent by groundwater/lateral inflow, with a pH of 4–5 and electrical conductivity <80 µS cm^{-1} (Binet et al. 2013; Devau et al. 2021). Over the 2014–2017 period, the mean annual air temperature (T_a) and mean annual precipitation were 10.8°C and approximately 745 mm yr^{-1}, respectively (4-year mean); for a detailed hydrological balance of La Guette peatland, see Binet et al. (2013). The site is part of the national peatland observation services (Service National d'Observation, SNO Tourbières) due to its ecological importance and its history of anthropogenic disturbances since the 1960s (SNO-Tourbières, 2017; Gogo et al. 2021). Disturbances include pine plantations along the edges, the building of a road across its southern part, accompanied by a drainage ditch installed in the 1970s for flood and fire control. These alterations caused prolonged droughts, lowered water levels, and invasion by vascular plants such as *Pinus sylvestris* (pine), *Betula* spp. (birch), and *Molinia caerulea* (Gogo et al. 2011), shifting the site from a C sink to a C source (approximately 220 gC m^{-2} yr^{-1} in 2013–2014; D'Angelo et al. 2021).

Experimental Design and Monitored Parameters

In February 2014, two restoration strategies were implemented (Fig. 1). A hydrological restoration in the downstream subwatershed was implemented to elevate the WT by constructing eight dams and extending the roadside ditch with sand-bentonite-filled trenches. Meanders were added to slow drainage (Laggoun-Défarge et al. 2016). A vegetation treatment was conducted at both rewetted and non-rewetted subsites. It included three types of plots: Control (unchanged vegetation), Bare (top 5 cm of peat removed, as this surface layer was expected to contain the majority of *Molinia* seeds, while minimizing disturbance to deeper peat), and *Sphagnum* (top 5 cm peat removed with *Sphagnum capitula*–mostly *Sphagnum palustre* and some *Sphagnum rubellum*–reintroduced at 0.5 kg m^{-2} as 3–5 cm green fragments evenly spread). The peat removed was used to fill drains in the nature reserve. Each plot measured 2 × 2 m (4 m^2), with four replicates per treatment, resulting in 24 experimental plots (Laggoun-Défarge et al. 2016). Between April 2014 and September 2017, vegetation, GHG fluxes, and environmental parameters were monitored. Manual measurements included T_a, atmospheric pressure (P), photosynthetically active radiation (PAR), chamber temperature (T_{ch}), and water table depth (WTD; referenced to the local ground surface of each plot or the top of the *Sphagnum capitulum* when present, with negative/positive values referring to WT below/above the reference surface). Measurements were conducted multiple times per year during the growing season and transitional months: six campaigns in each year between 2014 and 2016 and four in 2017. Automated sensors recorded WTD, relative humidity (RH), T_a, soil temperature (T_s), and soil permittivity at depths of 5, 10, 20, 30, and 40 cm, with one sensor per subsite for each variable, except T_s and soil permittivity, which were each measured with one sensor per treatment type per subsite. Automated WTD was also referenced to the local ground surface at the piezometer.

Measurements of GHG Fluxes

Fluxes were measured during 22 campaigns (2014–2017) using permanent PVC collars (30 cm diameter) installed in each plot.

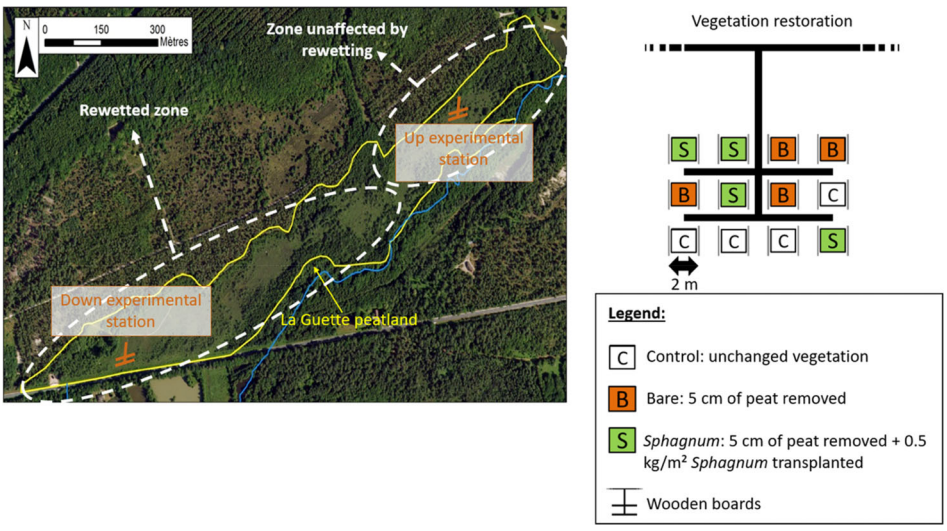


Figure 1. Map of La Guette peatland (Neuvy-sur-Barangeon, Cher, France) showing experimental stations located in the rewetted and non-rewetted zones. The vegetation restoration experiment consists of 24 plots across the two stations, each assigned to one of three treatments: Control (unchanged vegetation), Bare (5 cm of peat removed), and *Sphagnum* (5 cm of peat removed plus *Sphagnum* moss transplantation). Plot arrangement and access paths are shown in the schematic to the right.

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

CO_2 was measured twice daily using a GMP343 sensor (Vaisala, Finland) with a closed static chamber following the protocol by D'Angelo et al. (2016). Each session lasted 2–5 minutes, with a 5-second resolution. CH_4 was measured using a certified infrared spectrometer (Guimbaud et al. 2011) and a Los Gatos Research Ultra-Portable GHG Analyzer (CA, U.S.A.) with a dynamic closed chamber. CH_4 measurements lasted a mean of 5 minutes with 1-second resolution, ranging from a few minutes up to 20 minutes depending on the intensity of the CH_4 emission (Guimbaud et al. 2011). Fluxes (μmol m^{-2} s^{-1}) were calculated using:

$$F = \frac{dX}{dt} \times \frac{P}{R \times T} \times \frac{V}{S} \quad (1)$$

where:

- F is the net gas flux (μmol m^{-2} s^{-1}).
- $\frac{dX}{dt}$ is the concentration rate (μmol mol^{-1} s^{-1}).
- P is the atmospheric pressure (Pa).
- R is the gas constant (J mol^{-1} K^{-1}).
- T is the chamber temperature (K).
- V is the chamber volume (m^3).
- S is the chamber surface area (m^2).

Net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}) were measured under light and dark conditions, respectively, with darkness achieved by covering the chamber with an insulated, opaque bubble-wrap cover. Gross primary production (GPP) was estimated as:

$$GPP = NEE - R_{eco} \quad (2)$$

Estimation of Plant Species Abundance and Vegetation Index

Vegetation abundance was visually monitored based on the green photosynthetic parts of each species. Only the following species were observed in the plots: bryophytes (*Sphagnum* spp.), graminoids (*Molinia caerulea*, *Eleocharis multicaulis* [spike-sedge], *Eriophorum angustifolium* [common cottongrass]), and shrubs (*Erica tetralix* [cross-leaved heath], *Calluna vulgaris* [heather]). A vegetation index (VI), following D'Angelo et al. (2021), was calculated as:

$$VI = \frac{BS + HS + SS}{TC} \quad (3)$$

where:

- BS is the bryophyte cover (%).
- HS is the graminoid cover (%).
- SS is the shrub cover (%).
- TC is the total potential cover ($TC = n \times 100$, with n representing the number of vegetation strata recorded [$n = 3$] and 100 representing the maximum potential cover).

VI quantified the overall vegetation abundance, enabling its integration into C flux modeling.

C Flux Modeling

R_{eco} Flux. R_{eco} fluxes were modeled as a funciton of WTD, VI, and T_s (Bortoluzzi et al. 2006; Equation 4). To adapt the model to our experimental design, we introduced an additional parameter, b, to account for soil respiration in the absence of vegetation and when the WT is close to the surface, which was necessary for the Bare plots in the first year. Although both T_a and soil temperature at 5 cm depth (T_s) were initially tested as temperature drivers, only T_s was retained in the main analysis because it provided better model performance, as indicated by higher adjusted R^2 values (Table S6). The resulting model was as follows:

$$R_{eco} = \left[\left(a \times \frac{WTD}{WTD_{ref}} + b\right) + c \times VI\right] * \left(\frac{T_s - T_{min}}{T_{ref} - T_{min}}\right)^d \quad (4)$$

where:

- R_{eco} is expressed in μmol CO_2 m^{-2} s^{-1}.
- WTD is the water table depth measured by automatic piezometers (m).
- VI is the vegetation index.
- T_s is soil temperature at 5 cm (T_s at 5 cm was selected due to the best model fit and fewer missing values).
- a, b, c, and d are fitted coefficients.
- WTD_{ref} is the reference WTD, set to −0.365 m (lowest WTD observed during CO_2 measurements).
- T_{min} and T_{ref} are the minimum temperature at which positive respiration occurred ($T_{min} = -5°C$) and the reference temperature at which optimal respiration took place ($T_{ref} = 15°C$), as defined by Bortoluzzi et al. (2006) and used by Leroy et al. (2019) in modeling R_{eco} in mesocosm from La Guette.

GPP Flux. We modeled GPP as a rectangular hyperbolic function of PAR, incorporating the effects of T_a and vegetation (Kandel et al. 2013):

$$GPP = \frac{[(e \times VI + f) \times T_{scale}] \times PAR}{k + PAR} \quad (5)$$

where:

- GPP is expressed in μmol CO_2 m^{-2} s^{-1}.
- VI is the vegetation index.
- PAR is the photosynthetically active radiation (μmol photons m^{-2} s^{-1}).
- k is the half-saturation constant for light (μmol photon m^{-2} s^{-1}).
- e and f are fitted parameters.
- T_{scale} is the temperature sensitivity of photosynthesis.

T_{scale} was calculated as per Raich et al. (1991):

$$T_{scale} = \frac{(T_a - T_{min}) \times (T_a - T_{max})}{(T_a - T_{min}) \times (T_a - T_{max}) \times (T_a - T_{opt})^2} \quad (6)$$

where:

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

- T is air temperature (°C).
- T_{min}, T_{opt}, and T_{max} represent the minimum, optimum, and maximum air temperatures for photosynthesis and were set to 0, 20, and 40°C, respectively, as in (Mahadevan et al. 2008) and in Leroy et al. (2019) for La Guette peatland.

The term $[(e \times \mathrm{VI} + f) \times T_{scale}]$ represents maximum gross primary production (GPP_{max}), which can be estimated by modeling measured GPP fluxes under different radiation levels. However, as these measurements were lacking, we integrated it directly into the model and optimized its parameters (e, f, and k; Equation 5).

CH_4 Flux. The modeling of CH_4 flux was based on the framework proposed by Leroy et al. (2019), incorporating WTD, vegetation, and T_s as primary drivers of CH_4 emissions. The CH_4 flux model is expressed as follows:

$$\mathrm{CH_4} = \left[\left(g \times \frac{\mathrm{WTD}}{\mathrm{WTD_{ref}}} + h\right) + i \times VI\right] * \left(\frac{T_s - T_{min}}{T_{ref} - T_{min}}\right)^j \quad (7)$$

where:

- CH_4 is expressed in μmol CH_4 m^{-2} s^{-1}.
- WTD is the water table depth measured by automatic piezometers (m).
- T_s is the soil temperature at 5 cm (T_s at 5 cm was selected due to the best model fit and fewer missing values).
- WTD_{ref} is the reference WTD, set to −0.36 m (the lowest WTD observed during CH_4 measurements).
- T_{min} and T_{ref} are constants, same as defined in the R_{eco} model.
- g, h, and i are fitted coefficients specific to the methane flux model.

Calibration and Evaluation of Models

Fluxes were randomly divided into two datasets following Leroy et al. (2019). The first dataset comprised two-thirds of the fluxes for model calibration. The second dataset, consisting of the remaining one-third of the fluxes, was used for model evaluation. Models were established for each replicate of Control, Bare, and *Sphagnum* treatments at both rewetted and non-rewetted subsites. The optimization of the fitted parameters was achieved by minimizing the root mean square error (RMSE) between observed and modeled fluxes using the "Nelder–Mead" method from the optim() function in R (R Core Team 2016). Model performance was assessed by adjusted determination coefficient (R^2_{adj}) and p-values from the linear regression between measured and modeled fluxes. R^2_{adj} evaluates the proportion of variance in the data explained by the model while accounting for the model's complexity through the number of predictors. Meanwhile, the p-value addresses its statistical significance.

GGCB Estimation

The optimized parameters of R_{eco}, GPP, and CH_4 were integrated with hourly interpolated vegetation and environmental variables collected from the experimental stations between April 2014 and April 2017. This allowed the calculation of R_{eco} and GPP annual means and CH_4 budgets for each plot. The GGCB, representing the net rate of C release from GHG emissions in the ecosystem, was then calculated using a simplified approach adapted from Leroy et al. (2019):

$$\mathrm{GGCB} = \mathrm{GPP} + R_{eco} + F_{CH_4} \quad (8)$$

where all terms are expressed in gC m^{-2} yr^{-1}. GGCB >0 indicates net release to the atmosphere.

Additionally, GGCB was also expressed in gCO_2-eq. m^{-2} yr^{-1} as:

$$\mathrm{GGCB_{CO_2-eq}} = \left[(x+y) \times \frac{\mathrm{MW\ of\ CO_2}}{\mathrm{MW\ of\ C}}\right] + \left[z \times \frac{\mathrm{MW\ of\ CH_4}}{\mathrm{MW\ of\ C}} \times \mathrm{GWP_{100}}\right] \quad (9)$$

where:

- MW is the molecular weight in g mol^{-1}.
- x, y, and z represent the annual GPP, R_{eco}, and CH_4 means in gC m^{-2} yr^{-1}.
- GWP_{100} is the 100-year global warming potential of CH_4, equal to 27 (Forster et al. 2021).

Statistical Analysis of Datasets

To assess the effects of rewetting and vegetation on C fluxes and budgets, we performed a two-way analysis of variance (ANOVA) with the factors hydrology (rewetted/non-rewetted) and vegetation (Control, Bare, and *Sphagnum*). The model included their interaction (Hydrology × Vegetation). Dependent variables were CO_2 and CH_4 fluxes as well as GGCB. Normality of residuals was assessed using the Shapiro–Wilk test, and homogeneity of variance with Levene's test. Log transformation was applied if assumptions were violated ($p < 0.05$); however, it did not improve normality or homogeneity. Thus, in such cases, non-parametric aligned rank transform (ART) ANOVA was applied. Post-hoc comparisons employed either Tukey's honestly significant difference (HSD) or ART contrasts.

Results

Hydrological and Vegetation Conditions

From 2014 to 2017, the rewetted subsite exhibited a significantly shallower WT compared to the non-rewetted subsite (difference of 6.87 ± 0.08 cm, $p < 0.05$) and showed a less pronounced summer decline (Table S3; Fig. 2). Manual measurements confirmed that Bare and *Sphagnum* plots exhibited significantly shallower WTs than Control plots in the rewetted subsite ($p < 0.05$). In contrast, in the non-rewetted subsite, WT levels in Bare and *Sphagnum* plots matched those of Control plots after 2015.

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

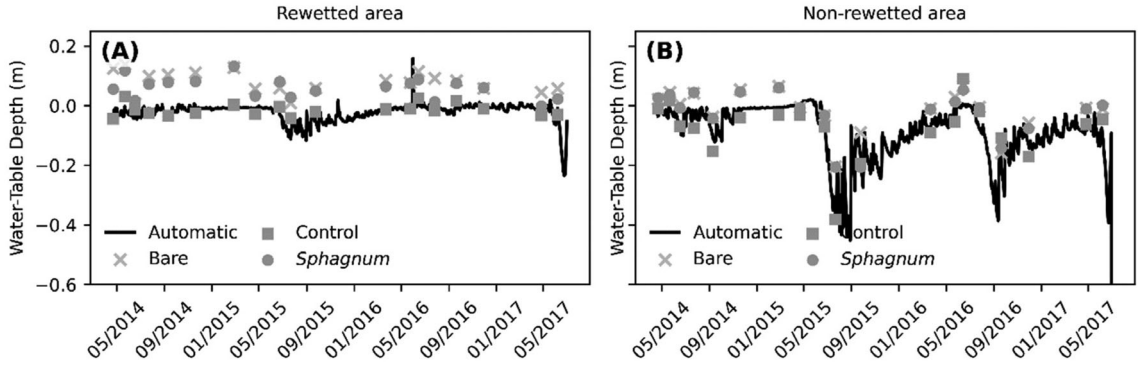


Figure 2. Water-table depth (m) from automatic measurements at the rewetted and non-rewetted areas (solid lines), and from manual measurements in Control, Bare, and *Sphagnum* plots (symbols) during 2014–2017.

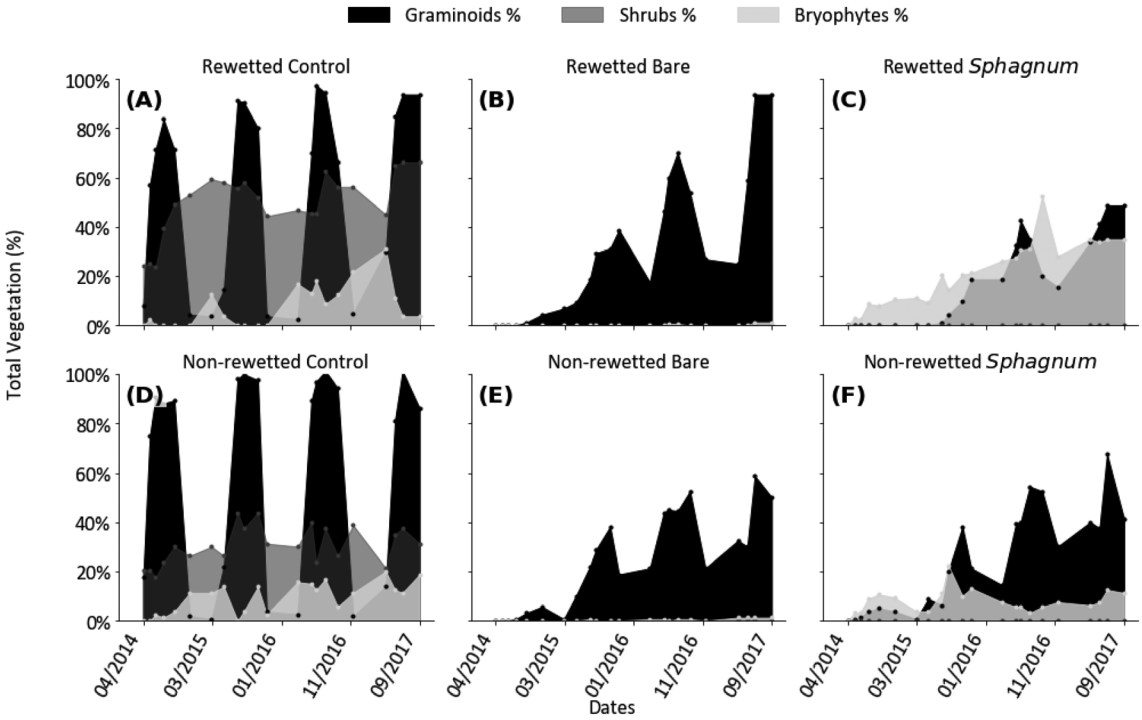


Figure 3. Vegetation cover by plant functional groups—graminoids (black), shrubs (dark gray), and bryophytes (light gray, all *Sphagnum* spp.)—in six plot types at La Guette peatland from January 2015 to July 2017. Panels show: (A) rewetted Control, (B) rewetted Bare, (C) rewetted *Sphagnum*, (D) non-rewetted Control, (E) non-rewetted Bare, and (F) non-rewetted *Sphagnum*. Filled areas depict percentage cover for each stratum (non-stacked, starting from zero), and point markers indicate vegetation measurement dates.

Graminoids and shrubs dominated Control plots throughout the study period (Fig. 3A & 3D), *Molinia caerulea* during growing seasons, and *Erica tetralix* all year (Fig. S1). In 2014, Bare plots had minimal vegetation (approximately 5%), but by 2015, their cover increased to approximately 40%, thus transitioning to sedge dominance (Fig. 3B & 3E), primarily *Eleocharis multicaulis* in the rewetted subsite and *Eriophorum angustifolium* in the non-rewetted subsite (Fig. S2). Bryophytes in rewetted *Sphagnum* plots, consisting solely of *Sphagnum* spp., increased steadily, reaching 35% by year four. In contrast, non-rewetted *Sphagnum* plots exhibited more variability and lower bryophyte cover (approximately 10% by year four, $p < 0.05$). Since 2015, graminoids (mainly *E. angustifolium*) also expanded in both *Sphagnum* plots, increasing from approximately 5–10% in year one, reaching approximately 40–50% by the end of the experiment (Fig. S2).

GHG Flux Measurements

Seasonal variations were observed in all GHG fluxes, with peak GPP, R_{eco}, and CH_4 activity during growing seasons (Figure S3). NEE fluxes followed a similar pattern, with net CO_2 uptake

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Adjusted R^2 values of calibration (Cal) and evaluation (Eval) of net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), gross primary production (GPP), and methane (CH_4) models across different vegetation plots (Control, Bare, and *Sphagnum*) of rewetted and non-rewetted subsites. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; and +$p > 0.05$).

	R_{eco}		*GPP*		CH_4	
Plots	*Cal*	*Eval*	*Cal*	*Eval*	*Cal*	*Eval*
Rewetted Control	0.75***	0.51***	0.76***	0.47***	0.80***	0.58***
Rewetted Bare	0.89***	0.54***	0.80***	0.72***	0.57***	0.29***
Rewetted *Sphagnum*	0.64***	0.49***	0.56***	0.65***	0.48***	0.16*
Non-rewetted Control	0.84***	0.57***	0.69***	0.45***	0.38***	0.81***
Non-rewetted Bare	0.92***	0.49***	0.71***	0.81***	0.50***	0.59***
Non-rewetted *Sphagnum*	0.79***	0.41***	0.67***	0.58***	0.66***	0.15*

in summer and reduced or positive fluxes in winter. In both rewetted and non-rewetted subsites, Bare and *Sphagnum* plots exhibited significantly lower GPP (absolute value) and R_{eco} than Control plots ($p < 0.05$; Table S1), although GPP increased after 2015 due to graminoid expansion. CH_4 fluxes were significantly higher in Bare and *Sphagnum* plots compared to Control plots ($p < 0.05$), especially in the rewetted subsite. CH_4 fluxes exhibited a generally decreasing trend over time, more pronounced in Bare and *Sphagnum* plots (initial fluxes > 0.2 μmol m^{-2} s^{-1}).

Calibration and Evaluation of Models

Calibration of the R_{eco} model showed good agreement between observed and modeled fluxes (R^2_{adj}: 0.64–0.92). The evaluation of this model showed a reduction in R^2_{adj} (Table 1), likely due to the smaller validation dataset (approximately 35% of the total data), which may have limited the model's ability to capture variance. The calibration of the GPP model showed good performance with R^2_{adj} values ranging from 0.56 to 0.80 across plots (Table 1). The evaluation performance of the GPP model experienced variations among plots. However, all plots still obtained a significant *p*-value ($p < 0.05$), confirming the overall reliability of the model as a tool for estimating GPP fluxes. The CH_4 model calibration exhibited lower agreement than R_{eco} and GPP models, with R^2_{adj} values ranging from 0.38 to 0.81 (Table 1). Evaluation performance varied (Table 1) with most plots maintaining acceptable R^2_{adj} values and significant *p*-values ($p < 0.05$). However, the CH_4 model yielded low prediction abilities for *Sphagnum* plots with $R^2_{adj} < 0.2$, though remaining statistically significant ($p < 0.05$).

Gap-Filled Fluxes and GGCB Budget

R_{eco} and GPP annual means exhibited consistent trends at both rewetted and non-rewetted subsites (Fig. 4A & 4B and Table S2, S4), with Bare and *Sphagnum* plots presenting lower R_{eco} and less negative GPP than Control plots ($p < 0.05$). Bare plots were statistically similar to each other and to *Sphagnum* plots ($p > 0.05$). Control plots were also statistically similar to each other ($p > 0.05$), albeit rewetted Control plots showed slightly lower R_{eco} and less negative GPP than those of the non-rewetted subsite. Only rewetted *Sphagnum* plots had significantly lower R_{eco} than non-rewetted ones ($p < 0.05$). CH_4 budgets were higher in Bare and *Sphagnum* plots than in Control plots ($p < 0.05$; Fig. 4C and Table S5). In the non-rewetted subsite, *Sphagnum* plots had the highest emissions, differing from Bare plots ($p < 0.05$), whereas in the rewetted subsite, differences were not significant.

The GGCB was analyzed across hydrology status (rewetted, non-rewetted), vegetation (Control, Bare, *Sphagnum*), and plots (Table 2). Both rewetted and non-rewetted plots acted as net C sources without significant differences, although the rewetted plots displayed slightly lower emissions than the non-rewetted plots ($p > 0.05$; Table 2). Bare and *Sphagnum* plots had significantly lower C emissions than Control plots ($p < 0.05$), without significant differences between them ($p > 0.05$; Table 2). However, Bare plots exhibited slightly higher GGCB values than *Sphagnum* plots. All plots acted as net C sources (Table 2; Fig. 4D) with the non-rewetted Control plot exhibiting the highest emissions and the rewetted *Sphagnum* plot exhibiting the lowest ($p < 0.05$). Furthermore, one rewetted *Sphagnum* replicate showed a near-neutral GGCB by year four.

The statistical analysis of GGCB in gCO_2-eq m^{-2} yr^{-1} across hydrology and vegetation factors gave the same result as previously presented for GGCB in gC m^{-2} yr^{-1} (Table 2). At the plot level, non-rewetted Controls recorded the highest CO_2-eq losses, while rewetted *Sphagnum* plots exhibited the lowest ($p < 0.05$), in agreement with previous results for GGCB in expessed in gC. But the remaining plots—Bare plots of both subsites and non-rewetted *Sphagnum* plots—displayed intermediate values and did not differ from either the Control plots, the rewetted *Sphagnum* plots, or between them ($p > 0.05$; Table 2).

Discussion

Restoring Vegetation Requires More than Successful Rewetting

Our experiment showed that an approximately 7 cm rise in WT occurred in the rewetted subsite, consistently detected by both automatic (7.6 cm) and manual (7.2 cm) measurements. This confirms the effectiveness of the implemented strategy in reducing water loss and aligns with the findings of Laggoun-Défarge et al. (2016). However, rewetting alone did not significantly

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

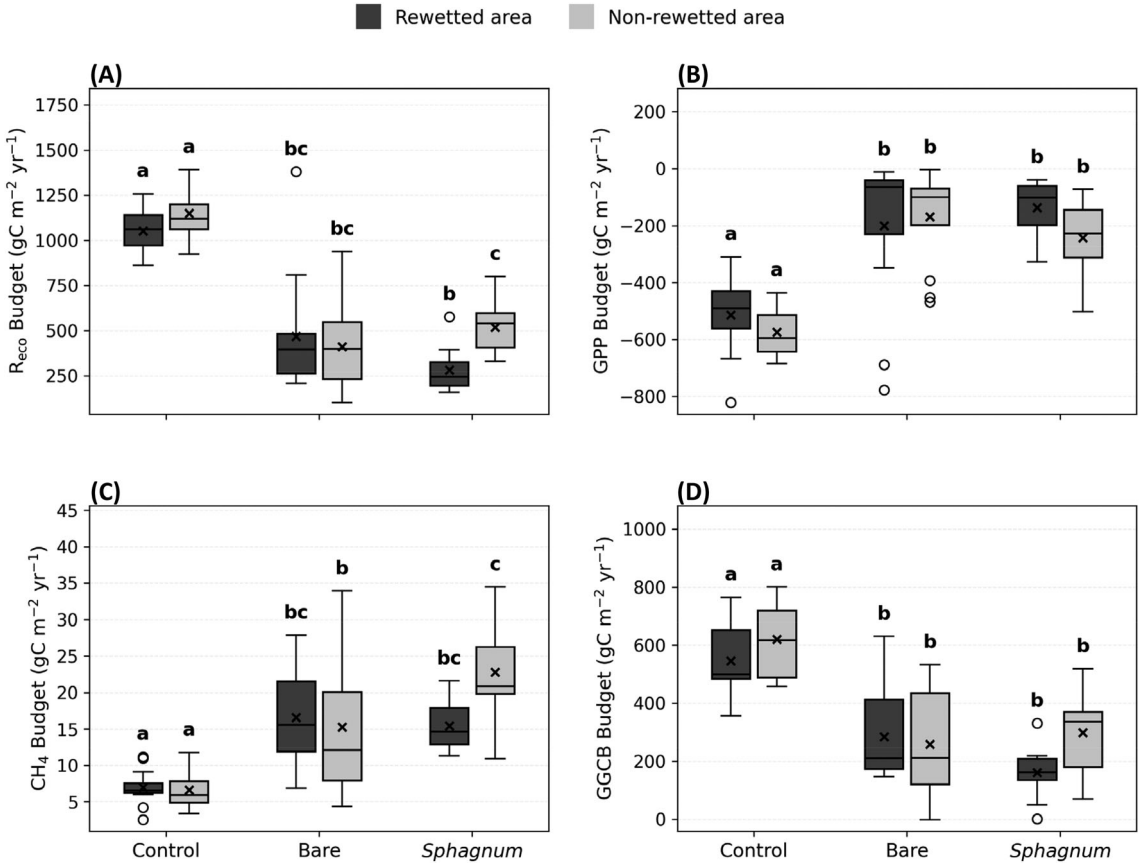


Figure 4. Annual budgets (gC m^{-2} yr^{-1}) of (A) ecosystem respiration, (B) gross primary production (GPP), (C) methane (CH_4), and (D) greenhouse gas carbon balance for Control, Bare, and *Sphagnum* plots in rewetted (dark gray) and non-rewetted (light gray) areas. Boxes show interquartile ranges, horizontal lines the medians, and crosses the means. Statistically different groups ($p < 0.05$) are indicated by different letters; groups sharing the same letter do not differ significantly.

Table 2. Summary of annual mean ± SE of greenhouse gas carbon budget (GGCB) in gC m^{-2} yr^{-1} and in gCO_2-eq m^{-2} yr^{-1} comparing rewetted and non-rewetted subsites, comparing Control, Bare, and *Sphagnum* treatments, and comparing all plots. Different letters indicate statistically significant differences between groups ($p < 0.05$).

		gC m^{-2} yr^{-1}	*gCO_2-eq m^{-2} yr^{-1}*
Hydrology	Rewetted	330 ± 34^{a}	1,632 ± 115^{a}
	Non-rewetted	380 ± 34^{a}	1874 ± 115^{a}
Vegetation	Control	564 ± 24^{a}	2,287 ± 90^{a}
	Bare	272 ± 34^{b}	1,512 ± 148^{b}
	Sphagnum	230 ± 27^{b}	1,461 ± 119^{b}
Hydrology × Vegetation	Rewetted Control	545 ± 35^{b}	2,225 ± 131^{a}
	Rewetted Bare	285 ± 45^{a}	1,580 ± 206^{ab}
	Rewetted *Sphagnum*	161 ± 24^{a}	1,090 ± 93^{b}
	Non-rewetted Control	583 ± 33^{b}	2,349 ± 126^{a}
	Non-rewetted Bare	259 ± 52^{a}	1,443 ± 219^{ab}
	Non-rewetted *Sphagnum*	298 ± 39^{a}	1,831 ± 159^{a}

change vegetation in Control plots, where *Molinia caerulea* and *Erica tetralix* dominated 4 years post-restoration, with limited *Sphagnum* establishment. This aligns with broader European restoration assessments showing that rewetting alone often fails to promote the return of native species, particularly *Sphagnum* (Andersen et al. 2017; Kreyling et al. 2021).

In our study, sedges such as *Eleocharis multicaulis* and *Eriophorum angustifolium* colonized Bare plots by year two and peaked by year four, especially at the rewetted subsite. This agrees with reports of sedges, particularly *Eriophorum* spp., acting as early colonizers of rewetted peat (Lavoie et al. 2005a; Kozlov et al. 2016). Sedges can promote *Sphagnum*

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

establishment by dampening temperature and evaporative stress (Pouliot et al. 2011; Keightley et al. 2023) and producing little litter (Guêné-Nanchen et al. 2017). However, at La Guette, this potential function did not lead to *Sphagnum* recovery within the four years after TSR in Bare plots, as bryophyte cover remained approximately 1%. The *Eleocharis/Eriophorum* dominance likely reflects acidic, nutrient-poor fen conditions where sedges are competitive in early successional stages (González et al. 2013). In contrast, *Molinia caerulea*, a colonizing species shown to contribute to the C source function at La Guette peatland (D'Angelo et al. 2021), did not recolonize Bare plots, likely due to competitive exclusion in low-nutrient, water-saturated conditions created by TSR and its removal from the seed bank.

TSR followed by *Sphagnum* transplantation allowed the increase of *Sphagnum* spp. cover up to approximately 35% within four years in the rewetted plots, demonstrating the effectiveness of moss transplantation under suitable hydrological conditions (Rochefort et al. 2003; Pouliot et al. 2011). In contrast, *Sphagnum* establishment was more variable in the non-rewetted plots, likely due to WT fluctuations exposing transplants to drying, which limited their survival and expansion (Robroek et al. 2009). This highlights the critical role of stable, water-saturated conditions in promoting bryophyte succession (Lavoie et al. 2005b). Notably, our study represents one of the most southerly successful *Sphagnum* transplantations reported, suggesting that relatively high mean annual air temperatures do not hinder successful re-establishment when hydrological conditions are adequate. Overall, the absence of *Molinia caerulea,* together with the emergence of sedges and *Sphagnum* in TSR plots, suggests an ecosystem reset toward vegetation communities typical of functional peatlands. However, long-term monitoring is required to fully assess the impact of restoration measures on vegetation dynamics.

Rewetting Alone Does Not Reduce C Emissions

Non-rewetted Control plots functioned as net C sources, consistent with D'Angelo et al. (2021), who reported similar results for La Guette peatland in 2013 and 2014 before the restoration. However, their reported Net Ecosystem Carbon Balance (NECB, GGCB + dissolved organic carbon [DOC]) was lower, averaging 220 ± 33 gC m^{-2} yr^{-1}, with DOC accounting for approximately 3–12% of the total C losses. To explore this difference, we compared R_{eco}, GPP, and CH_4 data from non-rewetted Control plots with their results. The higher C emissions in our study (583 ± 33 gC m^{-2} yr^{-1}) were driven by a smaller GPP uptake (574 ± 24 gC m^{-2} yr^{-1} in absolute terms) compared to the stronger uptake reported by D'Angelo et al. (2021) (>1,000 gC m^{-2} yr^{-1}). R_{eco} and CH_4 did not differ widely between studies, while DOC—which was not included in our budget—could not account for the observed differences. These GPP differences likely reflect variations in vegetation composition or differences in GPP modeling approaches and data fitting.

Rewetted Control plots also functioned as net C sources, suggesting that hydrological restoration alone was insufficient to reinstate peatland C sink functionality. This observation aligns with the findings from Huth et al. (2022) and Balode et al. (2024), who highlight that rewetting alone may not restore full C sink functioning primarily in temperate and boreal zones where long-term drainage alters the peat's physical properties. Furthermore, although rewetted Control plots exhibited lower GGCB than non-rewetted Control plots, this decrease was not significant ($p > 0.05$). In our study, the WTD difference between rewetted and non-rewetted Control plots was around +6.45 cm, and the GGCB difference was +1.24 tCO_2-eq ha^{-1} yr^{-1}, that is, 2 tCO_2-eq ha^{-1} yr^{-1} for a 10 cm rise. These values broadly agree with published ΔWTD–ΔCO_2-eq relationships based on a large dataset covering near-neutral to managed peatlands, which estimate that each 10 cm rise in WT can lower the GGCB by at least approximately 3 tCO_2 ha^{-1} yr^{-1} (e.g., Evans et al. 2021). Taken together, these results suggest that the non-significant GGCB difference observed between rewetted and non-rewetted Control plots (i.e., the effect of rewetting alone) is likely due to the relatively small difference in WTD.

Regarding CH_4 emissions, rewetting is expected to promote higher CH_4 release, as elevated WTs favor anaerobic methanogenesis—an effect confirmed by several review studies, such as Zhong et al. (2020), Balode et al. (2024), and Darusman et al. (2023). In contrast to these studies, our findings showed statistically similar CH_4 budgets across rewetted and non-rewetted Control plots. However, CH_4 raw flux measurements were slightly higher at the rewetted subsite, indicating possible model bias, which we note as a limitation.

Topsoil Removal Affects CO_2 and CH_4 Emissions Differently

Our findings demonstrated that TSR, with and without *Sphagnum* transplantation, effectively reduced net CO_2 emissions compared to Control plots across rewetted and non-rewetted subsites. Although R_{eco} and GPP (absolute values) decreased in Bare and *Sphagnum* plots compared to Control plots, the greater reduction in R_{eco} led to net CO_2 reduction. This may be attributed to increased net primary productivity (NPP) following the removal of established root systems. In addition, it may be due to reduced heterotrophic respiration resulting from the removal of the nutrient-rich topsoil layer, as well as from the TSR plot surface being brought closer to the WT compared to the Control plots. TSR enhanced CH_4 emissions, particularly in the first year, with fluxes nearly doubling Control fluxes—likely due to ebullition events observed during early measurements. In non-rewetted Bare plots, CH_4 returned to Control levels; however, in rewetted Bare plots, emissions remained higher through the last year. The increase in CH_4 emissions in TSR plots is likely due to the removal of the approximately upper 5 cm of oxic peat layer, together with the TSR-induced rise in WT, both of which reduce methanotrophic activity. Rapid sedge regrowth at La Guette may also have increased labile C inputs and plant-mediated gas transport. This aligns with Putkinen et al. (2018), who argued that vegetation recovery and its associated microbial communities can enhance CH_4 after rewetting.

Our results in terms of CO_2 reduction are in agreement with several studies (e.g., Huth et al. 2022; Quadra et al. 2023) that reported that removing the upper 5–15 cm of peat can effectively eliminate the nutrient-rich, oxidized topsoil layer that sustains high microbial activity and mineralization rates. In terms of CH_4 emissions, our

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

results contrast with other studies that found strong CH_4 emission reduction after TSR (by 25–60 cm), such as in Huth et al. (2022) and Zak et al. (2018), and even with shallower TSR (5 cm), such as in Quadra et al. (2023). The differences reflect baseline substrate differences: their reductions followed the removal of agricultural, nutrient-rich topsoil with abundant methanogenic substrate. More importantly, they reflect the different experimental setups used in the other studies where TSR plots and Control plots had the same WT, allowing the investigation of the sole effect of TSR. Here, TSR removed the upper oxidized peat and raised the surface closer to the WT, which reduced methanotrophic activity. Furthermore, the layer removed was shallow; thus, it likely did not impair methanogenic activity taking place deeper in the peat.

Sphagnum Transplantation Lowers C Loss Despite Elevated CH_4

Combining TSR with *Sphagnum* transplantation further reduced CO_2 emissions, especially in the rewetted subsite, compared to TSR alone, likely due to the reestablishment of *Sphagnum*, the key peat-forming species. *Sphagnum* is known for its slow decomposition rates, microbial inhibition, nutrient depletion, and acidification, factors that slow C loss (Putkinen et al. 2018). Our observations coincided with previous studies that emphasize the climate benefits of coupling TSR with *Sphagnum* establishment rather than using TSR alone (e.g., Huth et al. 2022).

TSR with *Sphagnum* transplantation leads to the same level of CH_4 emissions as TSR alone in the rewetted area in our study. This is inconsistent with studies indicating that *Sphagnum* mosses support methane oxidation via symbiosis with methanotrophic bacteria (Basiliko et al. 2004; Raghoebarsing et al. 2005; Kip et al. 2010). However, *Sphagnum* cover establishment remained limited (approximately 10% in the non-rewetted subsite and approximately 35% in the rewetted subsite), while *Eriophorum* expanded to approximately 40% after four years. The aerenchyma of *Eriophorum* likely enhanced CH_4 transport, overwhelming the limited oxidation from sparse *Sphagnum*. In contrast, Huth et al. (2022) reported rapid and dense *Sphagnum* establishment when restoring a nutrient-rich, agriculturally drained raised bog. They applied shredded *Sphagnum* fragments at 1–5 cm thickness, then covered with straw to protect from desiccation, which yielded a full *Sphagnum* cover within a year and supported a substantial CH_4 decrease. In our study, low *Sphagnum* cover—likely constrained by nutrient loss from TSR (Käärmelahti et al. 2024)—together with *Eriophorum* dominance helps explain the sustained CH_4 emissions. Furthermore, previous studies suggest that effective long-term *Sphagnum*-driven C sequestration requires 50–70% cover (Rochefort et al. 2003; Caporn et al. 2017), a threshold unmet here. Despite elevated methane emissions, one rewetted *Sphagnum* replicate approached C neutrality by the end of the monitoring period, with net C loss around 0 gC m^{-2} yr^{-1}.

Reducing CO_2 Emissions Offsets Increasing CH_4 Emissions

While some studies suggest that GHG balances in rewetted peatlands can remain CH_4-dominated for long periods (e.g., Vanselow-Algan et al. 2015), our results showed reduced net CO_2-eq emissions despite increased CH_4, consistent with meta-analyses indicating that raising the WT generally reduces climate warming (Couwenberg et al. 2011; Günther et al. 2020; Evans et al. 2021). Notably, *Sphagnum* plots, despite the highest CH_4 fluxes, recorded the lowest overall CO_2-eq emissions, highlighting the dominant role of CO_2 uptake in shaping the net GHG balance. This supports findings from several studies (e.g., Frolking et al. 2006; Günther et al. 2020; Mander et al. 2024), demonstrating that CH_4 emissions do not undermine the climate change mitigation potential oreducing f CO_2 emissions in rewetted peatlands.

Restoring Peatlands: A Slow Road Back to C Sink Function

Despite implementing hydrological and vegetation restoration strategies, the C sink function at La Guette peatland was not fully restored within four years. Faster recovery has been observed under favorable conditions: for instance, Wilson et al. (2022) and Huth et al. (2022) reported near-immediate return to a net sink where rewetting was successful and *Sphagnum* rapidly re-established. In contrast, Nugent et al. (2018) observed recovery within 14 years, and Beyer and Höper (2015) estimated up to 30 years under less intensive measures. These differences indicate that recovery trajectories are system-dependent and shaped by site-specific factors such as disturbance history, hydrological conditions, and the effectiveness of peat-forming vegetation reestablishment. Understanding these dependencies is critical for management: to secure lasting climate benefits, restoration efforts should therefore combine hydrological and vegetation measures with long-term assessments of C emissions from removed soil and potential impacts on biodiversity components, such as insects and soil fauna.

Acknowledgments

We gratefully acknowledge financial support from the European Regional Development Fund through Interreg North-West Europe—Care-Peat: Restoring the carbon storage capacity of peatlands; the Fonds européen de développement régional (FEDER)—Europe—Région Centre, Conseil Général du Cher-18, CARBIODIV: Restauration hydrologique de la tourbière de la Guette en Sologne: effets sur le stockage du carbone et la biodiversité (grant 2012-00073566); the ANR Investissements d'Avenir Program, LabEx VOLTAIRE (grant ANR-10-LABX-100-01). This work has received support under the JUNON Program, with the financial support of the Région Centre-Val de Loire (France) (grant 2022-00121803).

LITERATURE CITED

Andersen R, Farrell C, Graf M, Muller F, Calvar E, Frankard P, Caporn S, Anderson P (2017) An overview of the progress and challenges of peatland restoration in Western Europe. Restoration Ecology 25:271–282. https://doi.org/10.1111/rec.12415

Antala M, Juszczak R, van der Tol C, Rastogi A (2022) Impact of climate change-induced alterations in peatland vegetation phenology and composition on

15261100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

carbon balance. Science of the Total Environment 827:154294. https://doi.org/10.1016/j.scitotenv.2022.154294

Bacon KL, Baird AJ, Blundell A, Bourgault MA, Chapman PJ, Dargie G, et al. (2017) Questioning ten common assumptions about peatlands. Mires and Peat 19:12. https://doi.org/10.19189/MaP.2016.OMB.253

Balliston N, Artz R, Couwenberg J, Gauthier L, Huth V, Jurasinski G, et al. (2024) Peatland restoration, rewetting, and greenhouse gas balances. Pages 308–358. In: Strack M (ed) Peatlands and climate change. 2nd edition. International Peatland Society, Jyväskylä, Finland

Balode L, Bumbiere K, Sosars V, Valters K, Blumberga D (2024) Pros and cons of strategies to reduce greenhouse gas emissions from peatlands: review of possibilities. Applied Sciences 14:2260. https://doi.org/10.3390/app14062260

Basiliko N, Knowles R, Moore TR (2004) Roles of moss species and habitat in methane consumption potential in a northern peatland. Wetlands 24:178–185. https://doi.org/10.1672/0277-5212(2004)024[0178:ROMSAH]2.0.CO;2

Beyer C, Höper H (2015) Greenhouse gas exchange of rewetted bog peat extraction sites and a *sphagnum* cultivation site in northwest Germany. Biogeosciences 12:2101–2117. https://doi.org/10.5194/bg-12-2101-2015

Binet S, Gogo S, Laggoun-Défarge F (2013) A water-table dependent reservoir model to investigate the effect of drought and vascular plant invasion on peatland hydrology. Journal of Hydrology 499:132–139. https://doi.org/10.1016/j.jhydrol.2013.06.035

Bonn A, Allott T, Evans M, Joosten H, Stoneman R (2016) Peatland restoration and ecosystem services: an introduction. Pages 1–16. 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. https://doi.org/10.1017/CBO9781139177788.002

Bortoluzzi E, Epron D, Siegenthaler A, Gilbert D, Buttler A (2006) Carbon balance of a European mountain bog at contrasting stages of regeneration. New Phytologist 172:708–718. https://doi.org/10.1111/j.1469-8137.2006.01859.x

Caporn SJM, Rosenburgh AE, Keightley AT, Hinde SL, Riggs JL, Buckler M, Wright NA (2017) *Sphagnum* restoration on degraded blanket and raised bogs in the UK using micropropagated source material: a review of progress. Mires and Peat 20:1–17. https://doi.org/10.19189/map.2017.omb.306

Couwenberg J, Thiele A, Tanneberger F, Augustin J, Bärisch S, Dubovik D, et al. (2011) Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674:67–89. https://doi.org/10.1007/s10750-011-0729-x

D'Angelo B, Gogo S, Laggoun-Défarge F, Le Moing F, Jégou F, Guimbaud C (2016) Soil temperature synchronisation improves representation of diel variability of ecosystem respiration in *Sphagnum* peatlands. Agricultural and Forest Meteorology 223:95–102. https://doi.org/10.1016/j.agrformet.2016.03.021

D'Angelo B, Leroy F, Guimbaud C, Jacotot A, Zocatelli R, Gogo S, Laggoun-Défarge F (2021) Carbon balance and spatial variability of CO_2 and CH_4 fluxes in a sphagnum-dominated peatland in a temperate climate. Wetlands 41:5. https://doi.org/10.1007/s13157-021-01411-y

Darusman T, Murdiyarso D, Impron, Anas I (2023) Effect of rewetting degraded peatlands on carbon fluxes: a meta-analysis. Mitigation and Adaptation Strategies for Global Change 28:1–20. https://doi.org/10.1007/s11027-023-10046-9

Devau N, Gogo S, Andre L (2021) Development, calibration and validation of a numerical model for C-fluxes. BRGM report BRGM/RP-71118-FR. CarePeat Interreg NWE Project, Orléans, France. https://vb.nweurope.eu/media/15967/dt132_report_development_calibration_validation.pdf (accessed 25 Aug 2025)

Dinesen L, Hahn P (2019) STRP22 Doc.7.2: Draft Ramsar technical report on peatland restoration and rewetting methodologies in northern bogs. Ramsar Convention Secretariat, Gland, Switzerland. https://www.ramsar.org/document/strp22-doc72-draft-technical-report-peatland-restoration-and-rewetting-methodologies (accessed 25 Aug 2025)

Evans CD, Peacock M, Baird AJ, Artz RRE, Burden A, Callaghan N, et al. (2021) Overriding water table control on managed peatland greenhouse gas emissions. Nature 593:548–552. https://doi.org/10.1038/s41586-021-03523-1

Forster P, Storelvmo T, Armour KC, Collins W, Dufresne J-L, Frame D, et al. (2021) The Earth's energy budget, climate feedbacks, and climate sensitivity. Pages 923–1054. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds) Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York

Frolking S, Roulet N, Fuglestvedt J (2006) How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. Journal of Geophysical Research: Biogeosciences 111 (G1). https://doi.org/10.1029/2005jg000091

Gogo S, Laggoun-Défarge F, Delarue F, Lottier N (2011) Invasion of a *Sphagnum*-peatland by *Betula* spp and *Molinia caerulea* impacts organic matter biochemistry. Implications for carbon and nutrient cycling. Biogeochemistry 106:53–69. https://doi.org/10.1007/s10533-010-9433-6

Gogo S, Paroissien JB, Laggoun-Défarge F, Antoine JM, Bernard-Jannin L, Bertrand G, et al. (2021) The information system of the French Peatland Observation Service: Service National d'Observation Tourbières—a valuable tool to assess the impact of global changes on the hydrology and biogeochemistry of temperate peatlands through long term monitoring. Hydrological Processes 35:146–1475. https://doi.org/10.1002/hyp.14244

González E, Rochefort L, Boudreau S, Hugron S, Poulin M (2013) Can indicator species predict restoration outcomes early in the monitoring process? A case study with peatlands. Ecological Indicators 32:232–238. https://doi.org/10.1016/j.ecolind.2013.03.019

Graf M, Rochefort L (2009) Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. Ecoscience 16:158–166. https://doi.org/10.2980/16-2-3128

Guêné-Nanchen M, Pouliot R, Hugron S, Rochefort L (2017) Effect of repeated mowing to reduce graminoid plant cover on the moss carpet at a *Sphagnum* farm in North America. Mires and Peat 20:1–12. https://doi.org/10.19189/MaP.2016.OMB.250

Guimbaud C, Catoire V, Gogo S, Robert C, Chartier M, Laggoun-Défarge F, et al. (2011) A portable infrared laser spectrometer for flux measurements of trace gases at the geosphere-atmosphere interface. Measurement Science and Technology 22:075601. https://doi.org/10.1088/0957-0233/22/7/075601

Günther A, Barthelmes A, Huth V, Joosten H, Jurasinski G, Koebsch F, Couwenberg J (2020) Prompt rewetting of drained peatlands reduces climate warming despite methane emissions. Nature Communications 11:1644. https://doi.org/10.1038/s41467-020-15499-z

Harpenslager SF, Van Den Elzen E, Kox MAR, Smolders AJP (2015) Rewetting former agricultural peatlands : topsoil removal as a prerequisite to avoid strong nutrient and greenhouse gas emissions. Ecological Engineering 84:159–168. https://doi.org/10.1016/j.ecoleng.2015.08.002

Huth V, Günther A, Bartel A, Gutekunst C, Heinze S, Hofer B, et al. (2022) The climate benefits of topsoil removal and *Sphagnum* introduction in raised bog restoration. Restoration Ecology 30:e13490. https://doi.org/10.1111/rec.13490

Joosten H (2021) Global guidelines for peatland rewetting and restoration. Ramsar Technical Report No. 11. Secretariat of the Convention on Wetlands, Gland, Switzerland

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

Käärmelahti SA, Fritz C, Quadra GR, Gardoki ME, Gaudig G, Krebs M, Temmink RJM (2024) Topsoil removal for *sphagnum* establishment on rewetted agricultural bogs. Biogeochemistry 167:479–496. https://doi.org/10.1007/s10533-023-01096-x

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Kandel TP, Elsgaard L, Lærke PE (2013) Measurement and modelling of CO_2 flux from a drained fen peatland cultivated with reed canary grass and spring barley. GCB Bioenergy 5:548–561. https://doi.org/10.1111/gcbb.12020

Keightley AT, Field CD, Rowson JG, Wright NA, Caporn SJM (2023) Engineering restoration and gaseous carbon uptake on a degraded bog: the role of *Eriophorum angustifolium* and micropropagated *Sphagnum*. Mires and Peat 29:23. https://doi.org/10.19189/MaP.2023.OMB.Sc.2108595

Kim D-G, Vargas R, Bond-Lamberty B, Turetsky MR (2012) Effects of soil rewetting and thawing on soil gas fluxes: A review of current literature and suggestions for future research. Biogeosciences 9:2459–2483. https://doi.org/10.5194/bg-9-2459-2012

Kip N, Van Winden JF, Pan Y, Bodrossy L, Reichart GJ, Smolders AJP, Jetten MSM, Damsté JSS, Op Den Camp HJM (2010) Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. Nature Geoscience 3:617–621. https://doi.org/10.1038/ngeo939

Kozlov SA, Lundin L, Avetov NA (2016) Revegetation dynamics after 15 years of rewetting in two extracted peatlands in Sweden. Mires and Peat 18:1–17

Kreyling J, Tanneberger F, Jansen F, van der Linden S, Aggenbach C, Blüml V, et al. (2021) Rewetting does not return drained fen peatlands to their old selves. Nature Communications 12. https://doi.org/10.1038/s41467-021-25619-y

Laggoun-Défarge F, Gogo S, Bernard-Jannin L, Guimbaud C, Zocatelli R, Rousseau J, Binet S, D'angelo B, Leroy F, Jozja N (2016) Does hydrological restoration affect greenhouse gases emission and plant dynamics in *Sphagnum* peatlands? Mires and Peat 18:1–12

Lavoie C, Marcoux K, Saint-Louis A, Price JS (2005a) The dynamics of a cottongrass (*Eriophorum vaginatum* L.) cover expansion in a vacuum-mined peatland, Southern Québec, Canada. Wetlands 25:64–75. https://doi.org/10.1672/0277-5212(2005)025[0064:TDOACE]2.0.CO;2

Lavoie C, Saint-Louis A, Lachance D (2005b) Vegetation dynamics on an abandoned vacuum-mined peatland: 5 years of monitoring. Wetlands Ecology and Management 13:621–633. https://doi.org/10.1007/s11273-005-0126-1

Leifeld J, Menichetti L (2018) The underappreciated potential of peatlands in global climate change mitigation strategies. Nature Communications 9:1071. https://doi.org/10.1038/s41467-018-03406-6

Leroy F, Gogo S, Guimbaud C, Bernard-Jannin L, Yin X, Belot G, Shuguang W, Laggoun-Défarge F (2019) CO_2 and CH_4 budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*. Biogeosciences 16:4085–4095. https://doi.org/10.5194/bg-16-4085-2019

Li Q, Gogo S, Leroy F, Guimbaud C, Laggoun-Défarge F (2021) Response of peatland CO_2 and CH_4 fluxes to experimental warming and the carbon balance. Frontiers in Earth Science 9:678906. https://doi.org/10.3389/feart.2021.631368

Mahadevan P, Wofsy SC, Matross DM, Xiao X, Dunn AL, Lin JC, Gerbig C, Munger JW, Chow VY, Gottlieb EW (2008) A satellite-based biosphere parameterization for net ecosystem CO_2 exchange: vegetation photosynthesis and respiration model (VPRM). Global Biogeochemical Cycles 22:GB2005. https://doi.org/10.1029/2006GB002735

Mander Ü, Espenberg M, Melling L, Kull A (2024) Peatland restoration pathways to mitigate greenhouse gas emissions and retain peat carbon. Biogeochemistry 167:523–543. https://doi.org/10.1007/s10533-023-01103-1

Mazzola V, Perks MP, Smith J, Yeluripati J, Xenakis G (2022) Assessing soil carbon dioxide and methane fluxes from a Scots pine raised bog-edge-woodland. Journal of Environmental Management 302:114061. https://doi.org/10.1016/j.jenvman.2021.114061

Minayeva TY, Bragg OM, Sirin AA (2017) Towards ecosystem-based restoration of peatland biodiversity. Mires and Peat 19:1–36. https://doi.org/10.19189/MaP.2013.OMB.150

Mishra S, Page SE, Cobb AR, Lee JSH, Jovani-Sancho AJ, Sjögersten S, Jaya A, Aswandi, Wardle DA (2021) Degradation of Southeast Asian tropical peatlands and integrated strategies for their better management and restoration. Journal of Applied Ecology 58:1370–1387. https://doi.org/10.1111/1365-2664.13905

Nugent KA, Strachan IB, Strack M, Roulet NT, Rochefort L (2018) Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. Global Change Biology 24:5751–5768. https://doi.org/10.1111/gcb.14449

Ojanen P, Minkkinen K, Penttilä T (2013) The current greenhouse gas impact of forestry-drained boreal peatlands. Forest Ecology and Management 289:201–208. https://doi.org/10.1016/j.foreco.2012.10.008

Pouliot R, Rochefort L, Karofeld E (2011) Initiation of microtopography in revegetated cutover peatlands. Applied Vegetation Science 14:158–171. https://doi.org/10.1111/j.1654-109X.2010.01118.x

Putkinen A, Tuittila ES, Siljanen HMP, Bodrossy L, Fritze H (2018) Recovery of methane turnover and the associated microbial communities in restored cutover peatlands is strongly linked with increasing *Sphagnum* abundance. Soil Biology and Biochemistry 116:110–119. https://doi.org/10.1016/j.soilbio.2017.10.005

Quadra GR, Boonman CCF, Vroom RJE, Temmink RJM, Smolders AJP, Geurts JJM, Aben RCH, Weideveld STJ, Fritz C (2023) Removing 10 cm of degraded peat mitigates unwanted effects of peatland rewetting: a mesocosm study. Biogeochemistry 163:65–84. https://doi.org/10.1007/s10533-022-01007-6

Raghoebarsing AA, Smolders AJP, Schmid MC, Rijpstra WIC, Wolters-Arts M, Derksen J, et al. (2005) Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436:1153–1156. https://doi.org/10.1038/nature03802

Raich JW, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Iii BM, Vörösmarty aC J, Rastetter EB (1991) Potential net primary productivity in South America application of a global model. Ecological Applications 1:399–429. https://doi.org/10.2307/1941899

Robroek BJM, van Ruijven J, Schouten MGC, Breeuwer A, Crushell PH, Berendse F, Limpens J (2009) *Sphagnum* re-introduction in degraded peatlands: the effects of aggregation, species identity and water table. Basic and Applied Ecology 10:697–706. https://doi.org/10.1016/j.baae.2009.04.005

Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. Wetlands Ecology and Management 11:3–20. https://doi.org/10.1023/A:1022011027946

R Core Team (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Samaritani E, Siegenthaler A, Yli-Petäys M, Buttler A, Christin P, Mitchell EAD (2011) Seasonal net ecosystem carbon exchange of a regenerating cutaway bog: How long does it take to restore the C-sequestration function? Restoration Ecology 19:480–489. https://doi.org/10.1111/j.1526-100x.2010.00662.x

SNO-Tourbières (2017) La Site de La Guette. https://www.sno-tourbieres.cnrs.fr/site-de-la-guette/ accessed 20 May 2025

Temmink RJM, Lamers LPM, Angelini C, Bouma TJ, Fritz C, van de Koppel J, et al. (2022) Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. Science 376:eabn1479. https://doi.org/10.1126/science.abn1479

Titus JE, Wagner DJ (1983) Contrasting water relations of photosynthesis for two *sphagnum* mosses. Ecology 64:1109–1115. https://doi.org/10.2307/1937821

Vanselow-Algan M, Schmidt SR, Greven M, Fiencke C, Kutzbach L, Pfeiffer EM (2015) High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. Biogeosciences 12:4361–4371. https://doi.org/10.5194/bg-12-4361-2015

Waddington JM, Strack M, Greenwood MJ (2010) Toward restoring the net carbon sink function of degraded peatlands: short-term response in CO_2 exchange to ecosystem-scale restoration. Journal of Geophysical Research: Biogeosciences 115: G01008. https://doi.org/10.1029/2009JG001090

Wiegandt K (ed) (2024) Pages 276. 3 Degrees more: the impending hot season and how nature can help us prevent it. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-031-58144-1

Wilson D, Dixon SD, Artz RRE, Smith TEL, Evans CD, Owen HJF, Archer E, Renou-Wilson F (2015) Derivation of greenhouse gas emission factors for peatlands managed for extraction in the Republic of Ireland and the

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

United Kingdom. Biogeosciences 12:5291–5308. https://doi.org/10.5194/bg-12-5291-2015

Wilson D, Mackin F, Tuovinen JP, Moser G, Farrell C, Renou-Wilson F (2022) Carbon and climate implications of rewetting a raised bog in Ireland. Global Change Biology 28:6349–6365. https://doi.org/10.1111/gcb.16359

Wilson D, Renou-Wilson F, Farrell C, Bullock C, Mueller C (2012) Carbon restore—the potential of restored Irish peatlands for carbon uptake and storage. CCRP Report No. 15. Environmental Protection Agency, Johnstown Castle, Wexford, Ireland. https://www.epa.ie/publications/research/climate-change/Carbon-Restore-The-potential-of-restored-Irish-peatlands-for-carbon-uptake-and-storage.php (accessed 20 May 2025)

Zak D, Goldhammer T, Cabezas A, Gelbrecht J, Gurke R, Wagner C, Reuter H, Augustin J, Klimkowska A, McInnes R (2018) Top soil removal reduces water pollution from phosphorus and dissolved organic matter and lowers methane emissions from rewetted peatlands. Journal of Applied Ecology 55:311–320. https://doi.org/10.1111/1365-2664.12931

Zhong Y, Jiang M, Middleton BA (2020) Effects of water level alteration on carbon cycling in peatlands. Ecosystem Health and Sustainability 6:1806113. https://doi.org/10.1080/20964129.2020.1806113

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Annual percentage covers of the different shrub species: *Calluna vulgaris* and *Erica tetralix*.
Figure S2. Temporal dynamics of different Graminoid species: *Eriophorum angustifolium*, *Molinia caerulea*, *Eleocharis multicaulis*, and *Rhynchospora alba*.
Figure S3. Seasonal dynamics of net ecosystem exchange (NEE) flux.
Table S1. Summary of mean ± SE fluxes in μmol m^{-2} s^{-1} of NEE, R_{eco}, GPP, and CH_4 in Control, Bare, and *Sphagnum* plots at rewetted and non-rewetted subsites (2014–2017).
Table S2. Summary of annual means ± SD fluxes in gC m^{-2} yr^{-1} of GPP in Control, Bare, and *Sphagnum* plots at rewetted and non-rewetted subsites.
Table S3. Summary of annual mean ± SE of WTD in cm in rewetted and non-rewetted subsites and in different plots.
Table S4. Summary of annual means ± SE fluxes in gC m^{-2} yr^{-1} of R_{eco} in Control, Bare, and *Sphagnum* plots at rewetted and non-rewetted subsites.
Table S5. Summary of annual means ± SE fluxes in gC m^{-2} yr^{-1} of methane in Control, Bare, and *Sphagnum* plots at rewetted and non-rewetted subsites.
Table S6. Adjusted R^2 values for calibration (Cal) and evaluation (Eval) data of ecosystem respiration (R_{eco}).

Coordinating Editor: Csaba Tölgyesi

Received: 15 June, 2025; First decision: 14 August, 2025; Revised: 24 September, 2025; Accepted: 24 September, 2025

1526100x, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/rec.70224 by Cochrane France, Wiley Online Library on [31/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License