Hydrological and temperature controls on CO_2 and CH_4 exchange between a mid-altitude mountain peatland and the atmosphere

Alexandre Lhosmot[1,2], Marc Steinmann[1], Adrien Jacotot[3,4], Philippe Binet[1], Robin Calisti[5], Edward A.D. Mitchell[5], Marie-Laure Toussaint[1], Anne Boetsch[1,6], Fatima Laggoun-Défarge[7], Guillaume Bertrand[1]

[1] Chrono-Environnement, Université Marie et Louis Pasteur, UMR6249, CNRS, France
[2] Département de géographie, Université de Montréal, Montréal, Canada
[3] SARL SEMBIOSE, Saint-Denis-de-Gastines, France
[4] Sol, Agro et hydrosystèmes, Spatialisation (SAS), UMR1069, INRAE, Institut Agro, Rennes, France
[5] Laboratoire de Biodiversité du Sol, Université de Neuchâtel, Neuchâtel, Switzerland
[6] OSU Theta, Besançon, France
[7] Institut Des Sciences de La Terre d'Orléans (ISTO), UMR7327, CNRS, Université d'Orléans, Orléans, France

SUMMARY

The aim of the present study is to understand the variability and the environmental factors controlling the fluxes of carbonaceous greenhouse gases (GHGs), methane (CH_4) and carbon dioxide (CO_2) between a temperate *Sphagnum*-dominated mid-altitude mountain peatland and the atmosphere. We conducted monthly measurements of GHG fluxes over 20 months using the chamber method. Specifically, we assessed the effects of (1) air temperature and (2) water level (WL) on GHG emissions. Open Top Chambers (OTC) were used to simulate a warming effect by passive heating of the air above the soil. To assess the effect of WL, we studied a hydrological gradient along a 35 m long transect from a near-surface "WET" area, through an "INTER" area with an intermediate WL, to a "DRY" area with a lower WL. The WET area featured a higher cover of *Sphagnum* species while the vegetation cover in the DRY area contained more vascular plants. Although all plots showed the same seasonality of GHG fluxes, considerable variability was observed among them. Raising the temperature using OTCs, which increased annual average air temperature by 0.2 °C to 0.6 °C, did not significantly affect CH_4 and CO_2 respiration (Reco) fluxes. In contrast, hydrological conditions played an important role in explaining flux variability. CH_4 fluxes were significantly higher in the WET and INTER areas (median [95 % CI] values: 17.5 [14.2, 29.0] and 20.0 [14.8, 30.4] nmol m^{-2} s^{-1}) compared to the DRY area (3.4 [1.9, 9.4] nmol m^{-2} s^{-1}) during all hydrological periods, i.e., humid spring, humid summer and dry summer. Reco did not vary significantly along the hydrological gradient overall, but the fluxes were lower in the WET area under humid spring (0.4 [0.3, 0.6] µmol m^{-2} s^{-1}) and summer (1.7 [1.25, 2.75] µmol m^{-2} s^{-1}) conditions compared to the DRY area (1.6 [1.3, 2.0] µmol m^{-2} s^{-1} in spring and 3.8 [2.7, 4.6] µmol m^{-2} s^{-1} in summer). Conversely, greater fluxes (by ~ 0.5 µmol m^{-2} s^{-1}) were observed in the WET area during summer drought. Given that Reco emissions are expected to be higher during droughts in the DRY area, we hypothesise a possible threshold effect, such as inhibition of phenoloxidase activity and/or other enzymatic activities, which would limit organic matter decomposition. Moreover, increasing WL in the WET and INTER areas led to a drastic drop in gross primary production (GPP) corresponding to *Sphagnum* immersion.

KEY WORDS: chambers, greenhouse gas, hydrology, Open Top Chamber, *Sphagnum*

INTRODUCTION

Greenhouse gas (GHG) exchanges between terrestrial surfaces and the atmosphere are spatially and temporally heterogeneous due to the large variability of ecosystems and human land uses (Luyssaert *et al.* 2012, Premke *et al*. 2016). Peatlands, which occupy only a small proportion (~3 %) of the global land area, constitute an outstanding carbon stock of about one-third of total soil organic matter (Yu *et al.* 2010, Xu *et al*. 2018, Nichols & Peteet 2019). As a result, GHG exchanges between peatlands and the atmosphere have played a significant role in climate regulation during the Holocene, through the sequestration of atmospheric CO_2 (Yu 2011, IPCC 2013). The current and future carbon exchanges between peatlands and the atmosphere are therefore crucial for evaluating their carbon sink or source strength (Humpenöder *et al.* 2020, Loisel *et al.* 2021, Tanneberger *et al.* 2021).

In peatlands, the two main GHGs (CO_2 and CH_4) are produced or consumed by biogeochemical processes which are directly and indirectly influenced by water level (WL) and soil temperature (Moore & Dalva 1993, Lafleur *et al.* 2005, Abdalla *et al.* 2016, Samson *et al.* 2018, Evans *et al.* 2021). These two factors play key roles in controlling the biotic participants (vegetation, microorganisms) involved in carbon dynamics and, as a result, have become a major focus for research (Andersen *et al.* 2013, Jassey *et al*. 2018, Antala *et al*. 2022). While anaerobic conditions enable peat accumulation and carbon storage by limiting the decomposition of organic matter, they also lead to production of CH_4, a powerful GHG with global warming potential 28 to 32 times that of CO_2 over a 100-year horizon (IPCC 2013, Etminan *et al.* 2016, Dean *et al*. 2018). In contrast, the respiration of aerobic microorganisms produces CO_2 and favours oxidation of CH_4 before it is released to the atmosphere (Moore & Dalva 1993, Lai 2009). Prolonged aerobic conditions caused by drainage lead to peat decomposition (i.e., peat mineralisation) and have several long-term effects on peat properties (reduced macro-porosity, elasticity and water storage capacity, increased compaction and consolidation, surface elevation loss, and overall homogenisation of soil properties and ecosystem functionality; Price *et al.* 2003, Gabriel *et al.* 2018, Gauthier *et al.* 2018, Howie & Hebda 2018, Liu *et al.* 2020). The recovery of peat properties to the pre-degradation state after rewetting is strongly influenced by the duration and intensity of prior drainage, which can lead to significant physical and chemical alterations of the peat. Severely disturbed and long-drained peatlands often exhibit increased bulk density, reduced porosity and decreased hydraulic conductivity, all of which impede rapid restoration. While rewetting can stabilise carbon losses and initiate recovery, natural conditions may take decades or longer to re-establish, depending on the severity of the degradation (Kreyling *et al*. 2021). Rewetting, which aims to slow down peat degradation and to restore the carbon sink function of peatlands, generally leads to a short-term (years to decades) increase in CH_4 production (Vanselow-Algan *et al.* 2015, Abdalla *et al*. 2016). However, the positive radiative effect of CH_4 emission over the short term is expected to be compensated by CO_2 sequestration over the long term (spanning several decades to centuries; Nugent *et al.* 2019, Günther *et al.* 2020, Humpenöder *et al*. 2020, Zak & McInnes 2022).

Climate change including an associated rise in air temperature has, together with anthropogenic disturbance (e.g., drainage for agriculture, forestry, and peat extraction), led to the desiccation of temperate and tropical peatlands. This, in turn, promotes CO_2 fluxes to the atmosphere and leads to contrasting and unclear effects on CH_4 emissions (Swindles *et al*. 2019, Loisel *et al.* 2021, Kang *et al.* 2022). In addition, increased temperature and lowered WL favour the colonisation of peatlands by vascular plants, resulting in positive feedback that further amplifies the decrease in WL and the increase of CO_2 emissions (Antala *et al.* 2022).

Moreover, the complex interactions between vegetation, microorganisms, peat properties, water chemistry and WL complicate the assessment of consequences for GHG exchange between peatlands and the atmosphere (Parish *et al*. 2008, Bragazza *et al.* 2013, Waddington *et al.* 2015, Arsenault *et al.* 2019, Antala *et al.* 2022). Therefore, these global changes lead to non-linear responses in the carbon cycles of peatlands, with threshold effects (Bragazza 2008, Page & Baird 2016, Jassey *et al.* 2018, Li *et al.* 2021b, Liu *et al.* 2022).

Peatlands are also highly diversified ecosystems and thus subject to small-scale variations in WL, vegetation, microtopography and hydrophysical peat properties (Joosten & Clarke 2002, Lindsay 2010, Juszczak *et al*. 2013, Arsenault *et al.* 2019, Ahmad *et al.* 2020a, Miaorun Wang *et al.* 2021, Briones *et al.* 2022, Couwenberg *et al.* 2022). For example, microtopography causes significant variability in water depth with respect to surface vegetation, which leads to diversified microhabitats (e.g., hummocks, lawns or hollows). Microtopography also influences organic matter recycling, leading to variations in peat growth rates and GHG emissions (Chaudhary *et al.* 2018, Ming Wang *et al.* 2021, Perryman *et al.* 2022).

Beyond the internal heterogeneity of an individual peatland, considerable differences exist in peatland types and locations depending on altitude, latitude or geological framework (Joosten 2016, Wheeler & Proctor 2000). All of these heterogeneities, operating across spatial and temporal scales, influence GHG exchange with the atmosphere and must therefore be quantified to better delineate the future of peatlands regarding their ecosystem services (Limpens *et al.* 2008). Within this general scheme, temperate peatlands located at the southern distribution limit of northern peatlands (Xu *et al.* 2018) may be regarded "as 'ecosystem sentinels' for climate change, acting as early warning indicators of climate–carbon feedbacks" (Briones *et al.* 2022). Indeed, they may experience temperature conditions that ecosystems farther north will not reach until later.

Temperature is a key driver for aerobic and anaerobic respiration, as well as for photosynthesis. Therefore, the increase of air temperature induced by climate change raises questions about the direct and indirect (e.g., vegetation, WL) effects of temperature on GHG exchange between peatlands and the atmosphere (Harenda *et al.* 2018, Bertrand *et al.* 2021, Li *et al.* 2021b, Antala *et al.* 2022). One approach to improving our ability to predict future fluxes is to install Open Top Chambers (OTC) which can locally induce passive warming of the air above ground (Arft *et al*. 1999, Li *et al.* 2021a). To our knowledge, few recent studies have investigated the effects of OTCs on GHG fluxes in temperate peatlands, and even fewer have been conducted in mid-altitude mountain settings (Johnson *et al.* 2013, Ward *et al.* 2013, Pearson *et al.* 2015, Lamentowicz *et al.* 2016, Oestmann *et al.* 2022, Salmon *et al.* 2022).

METHODS

Study site

The study site is located in the French Jura Mountains near the town of Frasne (840 m a.s.l., 46.826° N, 6.173° E; Figure 1A). The Frasne peatland is a large (> 300 ha) complex of different peatland types (e.g., fen, raised bog, wooded and transitional peatland). Its ecological value has been recognised by the RAMSAR convention (RAMSAR site), it is part of the European Natura 2000 network, and approximately 100 ha of the complex is also a regional nature reserve. The Forbonnet site is a transitional peatland within the complex that has been monitored since 2008. The site has belonged to the National Observatory of Peatlands (SNO Tourbières; Bertrand *et al.* 2021, Gogo *et al.* 2021) since 2012 and is integrated into the French Critical Zone research infrastructure (OZCAR; Gaillardet *et al.* 2018). The site also serves as an observatory for the Zone Atelier of Arc Jurassien, which is dedicated to studying the interplay between humans and nature (ZAAJ website). As a French priority research site, Forbonnet benefits from detailed spatio-temporal monitoring of meteorology and hydrology.

According to the Köppen-Geiger classification the climate of the site falls between classes Cfb and Dfb (Rubel *et al*. 2017), defining a temperate climate with contrasted seasons. Average annual air temperature is 7 °C and monthly averages range from 0 °C (December to February) to 15 °C in July and August. Annual precipitation ranges from 1293 to 2110 mm (average ± standard deviation = 1618 ± 258 mm) and is uniformly distributed throughout the year with a mean of 135 ± 25 mm month^{-1} (averages over the period 2009–2019; Toussaint *et al.* 2020a).

Ecologically, the Forbonnet peatland is a *Sphagnum*-dominated zone, where species such as *Andromeda polifolia*, *Vaccinium oxycoccos*, *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Drosera* spp. and *Calluna vulgaris* are also observed. The peatland is surrounded by more mature and topographically higher peatlands covered with pine and spruce trees, that are progressively colonising the centre of the site. In addition, patches of *Phragmites* on the contours of the Forbonnet peatland indicate localised minerotrophic (i.e., nutrient-rich) conditions.

The Forbonnet peatland was equipped with an experimental research station in 2008 to study the effect of air temperature warming using OTC devices according to the ITEX protocol (Arft *et al.* 1999, Laggoun-Défarge *et al.* 2008). The chambers were installed along a hydrological gradient (Figures 1B–D) characterised by differences in WL (Toussaint *et al.* 2020b), microtopography and vegetation cover. The "WET" area is almost flat and homogeneous (lawn area) while the "DRY" area is characterised by more-pronounced microtopography with hummocks. The proportion of *Sphagnum* is significantly lower in the DRY than in the WET area, and reciprocally for vascular plants (Buttler *et al.* 2015). Along this hydrological gradient, which includes an intermediate location (referred to as INTER), measuring plots were distributed across the gradient with both "control" and "heated" OTC stations: DC (control) and DH (heated) in the DRY area, IC (control) and IH (heated) in the INTER area; and WC (control) and WH (heated) in the WET area.

Hydrometeorological monitoring

Air temperature was measured at each plot 10 cm above the soil surface using thermocouples (Mesurex, TT20100T). The research station is also equipped with a meteorological station recording air temperature and relative humidity (T, RH, HMP155A, Vaisala, Vantaa Finland), atmospheric pressure (278, SETRA, Boxborough MA, USA), Photosynthetic Photon Flux Density (PPFD, SKP215 Skye Ltd, Llandrindod Wells, UK), wind direction, and wind speed every 30 minutes (Windsonic Gill, Lymington, UK; see Gogo *et al.* (2021) for more details). Due to technical issues with the automatic raingauge during the study period, precipitation was measured monthly on site with a rain collector normalised for isotope characterisation (Palmex Rain Sampler 1C; see Lhosmot *et al.* 2022a). The WL was monitored every 30 minutes by two piezometers equipped with OTT Orpheus Mini pressure probes and installed in the WET and DRY areas along the research station boardwalk (± 0.1 %; Toussaint *et al.* 2020b).

GHG flux and auxiliary data measurements

Carbonaceous greenhouse gas (CO_2 and CH_4) fluxes between the peatland and the atmosphere were measured monthly from February 2020 to September 2021, using the non-steady state closed chamber method (Hutchinson & Livingston 1993). Fluxes were measured on six plots, constituting three pairs of control (C) and OTC (H) plots (Figure 1C). These three pairs were placed along the hydrological DRY-INTER-WET gradient (Figure 1C).

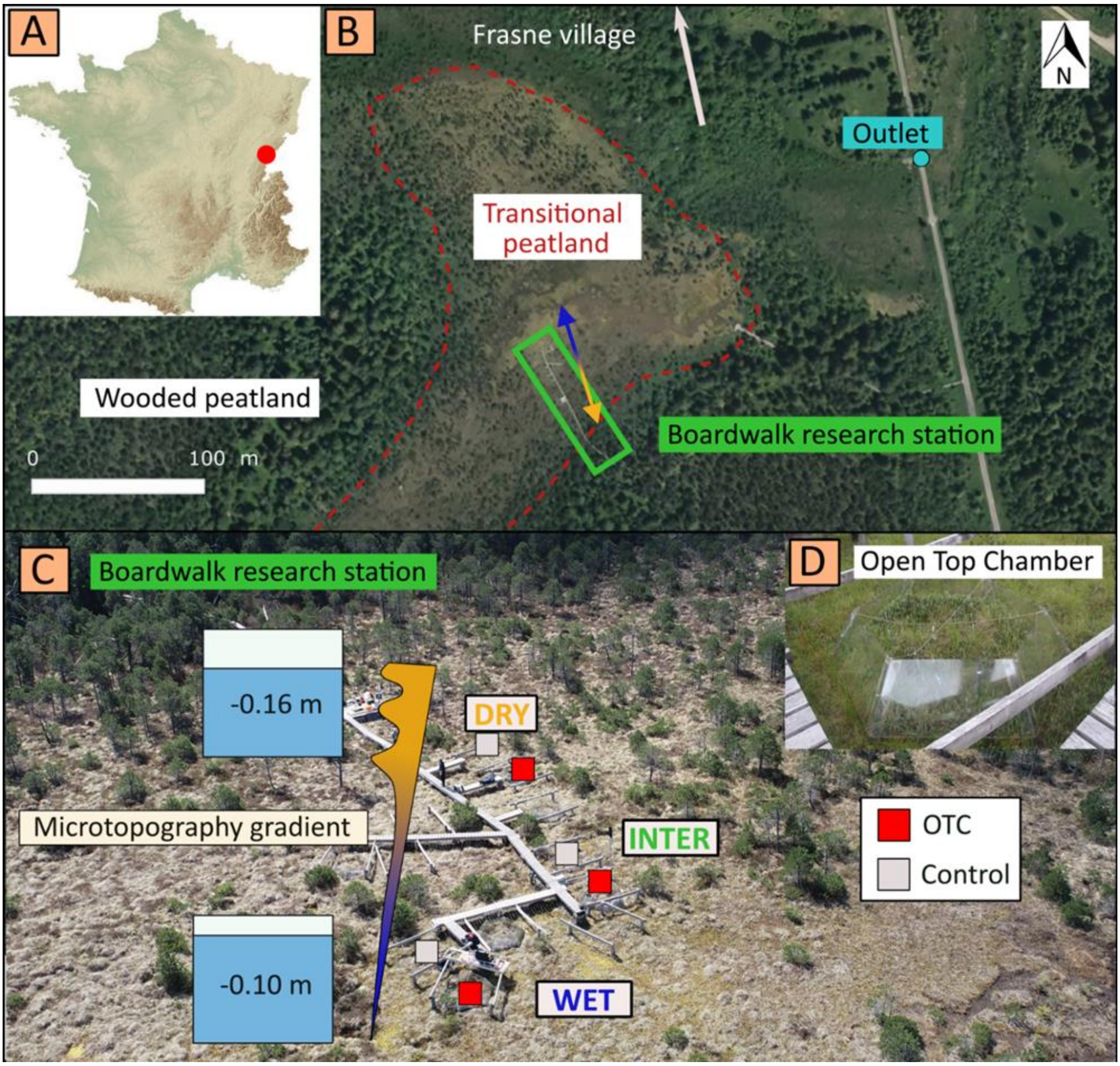

Figure 1. (A) Location of the Frasne peatland (CapCarto, 2016). (B) Location of the study plot and the boardwalk research station (IGN, 2018). (C) Location of the WET, INTER and DRY study areas (Open Lab Dream, UBFC, G. Bertrand, March 2021). The beige-blue graph next to the boardwalk is a simplified microtopographic cross-section along the WET-INTER-DRY transect. It symbolises the hummocks in the DRY area in beige and the transition towards the almost flat and wetter INTER and WET areas in blue. The median water level over the two study years (2020 and 2021) was -0.10 m and -0.16 m for the DRY and WET areas, respectively, based on 30 minute interval data. (D) Open Top Chamber.

To determine the GHG fluxes, we used a Los Gatos Research infrared laser spectrometer analyser (LGR "Greenhouse Gas Analyzer [CH4, CO2, H2O] Ultraportable," 2019), connected to a transparent plexiglass chamber (29 cm diameter and 51 cm height) in which GHG concentrations were measured for 2–4 minutes. To ensure proper homogenisation, the air inside the chamber was continuously mixed using an internal pump system. Since the chamber is translucent, the measurements represent the Net Ecosystem Exchange (NEE) of CO_2. To measure the ecosystem respiration (Reco), a second measurement was conducted using the same chamber, this time with an opaque cover. After the opaque cover was installed, measurements were considered following a stabilisation period of up to 20 seconds. The gross primary production (GPP) was then calculated as follows:

$$(\mathrm{NEE} = \mathrm{Reco} - \mathrm{GPP}) \qquad [1]$$

where Reco and GPP are expressed as absolute values. In this study, negative fluxes are defined as fluxes from the atmosphere to the soil, and reciprocally. Accordingly, a negative sign was assigned to GPP values. Methane measurements were similarly performed with and without the opaque cover, but no difference was observed. All flux measurements were conducted during daytime, typically between 10 a.m. and 6 p.m. Finally, the flux of GHG between the peatland and the atmosphere ($F_{CO2, CH4}$) was calculated using Equation 2 (Jacotot *et al.* 2019, Korkiakoski *et al.* 2019):

$$F_{(CO2,\ \mathrm{CH4})} = \frac{\frac{\frac{V}{S}\times dC}{dt}\times P}{R\times T} \qquad [2]$$

where $F_{(CO2, CH4)}$ is the flux (µmol m^{-2} s^{-1}) of CO_2 and CH_4 respectively, V the volume of the chamber (m^3), S the area of soil covered by the chamber (m^2), dC the difference of GHG concentration in the chamber between the start and the end of the measurement (ppm), dt the duration of the measurement (s), P the air pressure in the chamber (Pa), R the universal gas constant (8.314 J mol^{-1} K^{-1}), and T the air temperature inside the chamber (K).

During each measurement, both air temperature and pressure were measured in the chamber with a Hobo Tidbit V2 probe (accuracy ± 0.21 °C) and a Baro Diver (Van Essen instruments, accuracy ± 49 Pa), respectively. In addition, the Photosynthetic Photon Flux Density (PPFD) was recorded every 30 seconds in the chamber with a light meter (ULM-500, WALZ).

Evaluation of CO_2 ecosystem respiration (Reco) sensitivity to temperature: the apparent Q_{10}

The sensitivity of ecosystem respiration to temperature variation is critical in the context of global warming. This sensitivity can be quantified using the Q_{10} parameter (Davidson *et al.* 2006), which is a temperature coefficient based on the Arrhenius (1889) law that relates variations of chemical reaction rates to temperature changes. More precisely, k, the reaction rate (s^{-1}), is related to the temperature and the activation energy by the following equation (Arrhenius 1889):

$$k = Ae^{\frac{-E_a}{RT}} \qquad [3]$$

where A is the Arrhenius constant in s^{-1} with ln(A) representing the y-intercept of the Arrhenius plot (ln(k) = 1/T), E_a is the activation energy required to initiate a chemical reaction in J mol^{-1}, R is the universal gas constant in J mol^{-1} K^{-1} and T is the absolute temperature (K).

The change in GHG production rates as a function of temperature variation serves as an indicator of organic matter decomposition sensitivity to temperature (Curiel Yuste *et al.* 2004, Davidson *et al.* 2006). As our study is not directly based on GHG production rates, but on GHG fluxes at the peatland–atmosphere interface, the calculated E_a and Q_{10} values correspond to apparent values (referred to as E_a and Q_{10}; Davidson *et al.* 2006). Q_{10} is an index based on the difference in reaction rate triggered by a temperature change of 10 °C. It can therefore be expressed as follows:

$$Q_{10} = e^{\left(\frac{E_a}{R}\left(\frac{10}{T(T+10)}\right)\right)} \qquad [4]$$

E_a was calculated by the following equation after using the logarithm:

$$F_{GHG} = Ae^{\frac{-E_a}{RT}} \qquad [5]$$

The air temperature measured in each plot at 10 cm above the soil surface was used to calculate Q_{10}. We showed in a previous study that methanotrophy is an important process controlling methane fluxes in the Forbonnet peatland (Lhosmot *et al.* 2022b). Hence, measured CH_4 fluxes integrate both production and oxidation of CH_4. Consequently, apparent Q_{10} is not a direct indicator of the CH_4 production alone, and we did not use Q_{10} for CH_4.

Analysis of GHG fluxes

To assess the effect of warming on GHG emissions (Reco and CH_4), we considered measurement campaigns for which OTC and control plot data were available along with all hydrological conditions (WET, INTER and DRY). Given that passive warming does not appear to be a discriminating factor (see section "*Reco and CH_4 fluxes for OTC and control plots*"), we finally merged the OTC and control plot data and grouped them only by hydrological conditions. This allowed a larger dataset to be used to assess the influence of WL on Reco and CH_4 fluxes. Considering the occurrence of two contrasting hydrological conditions during the summers of 2020 and 2021 and the implementation of a high frequency GHG measurement campaign during the wet spring of 2021, we split the dataset into three seasonal conditions: (1) dry/drought summer (June–September 2020), (2) wet summer (June–September 2021), and wet spring (May 2021).

PPFD, which strongly controls GPP (Haraguchi & Yamada 2011, Leroy *et al.* 2019), showed coherent seasonal variations but high within-day variation due to cloud cover and diurnal cycles (Figure 2). Consequently, rapid variations in both PPFD and T data limited the availability of simultaneous

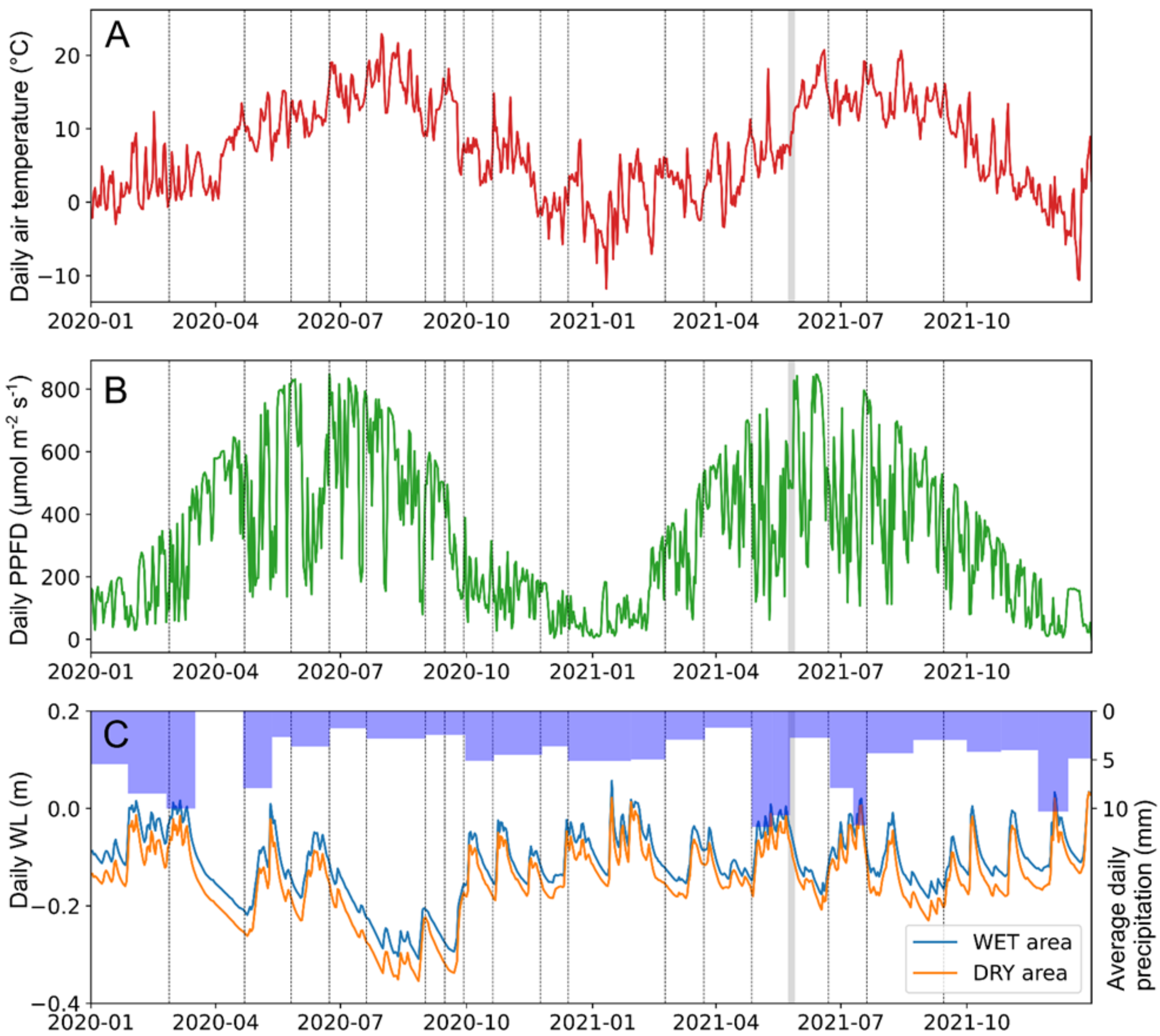

Figure 2. Daily means of hydro-meteorological data measured at the meteorological station. (A) Air Temperature. (B) Photosynthetic Photon Flux Density (PPFD, µmol m^{-2} s^{-1}). (C) Water Level (WL, m) at the WET and DRY areas (left y-axis) and average daily precipitation (mm, right y-axis). The black vertical dashed line indicates the days of chamber GHG flux measurements. The grey vertical band in May 2021 indicates an intensive campaign of chamber GHG flux measurements.

measurements across the plots, thereby restricting the analysis of the relationship between GPP, air temperature and WL. To address this, the dataset was divided into two groups (DRY and WET-INTER areas) and environmental conditions favourable for photosynthetic activity (air temperature above 10 °C and PPFD between 100 and 2000 µmol m^{-2} s^{-1}) were selected. This approach allowed us to identify a hydrological influence on GPP (see section "*GPP response to different hydrological conditions*").

Statistical comparison

Statistical tests were conducted to assess differences in data distribution across similar periods for WL (between WET and DRY areas), air temperature above the soil surface (between OTC and control plots), and GHG fluxes (between OTC and control plots, as well as across different hydrological conditions [WET, INTER, DRY]). Due to the lack of normality and/or homoscedasticity in the datasets and because measurements were paired, the Wilcoxon signed-rank test was employed.

RESULTS

Hydrometeorological conditions

The study period integrated two growing seasons (2020 and 2021, Figures 2A and 2B). The daily air temperatures in the peatland were highest in summer, reaching 23 °C in July 2020, and lowest in winter, reaching -11.9 °C in January 2021, with a mean of 7.2 °C for 2020–2021 (Figure 2A). The PPFD showed a seasonal pattern similar to that for temperature, with the highest mean daily (24 hours) values in summer (848 µmol m^{-2} s^{-1}) and values close to 0 in winter (Figure 2B). The cumulative rainfall in 2020 (from 28 Jan 2020 to 14 Dec 2020) and 2021 (from 29 Jan 2021 to 14 Dec 2021) was 1328 and 1618 mm, respectively. Reflecting precipitation, WL median in the WET area was significantly lower in 2020 (median [95 % CI]; -0.13 [-0.14, -0.11] m) compared to 2021 (-0.10 [-0.11, -0.10] m; p-value < 0.001; Figures 2C, 3A and 3B). The growing seasons (May to September) were particularly contrasting, with rainfall totalling 653 mm in 2020 and 1016 mm in 2021, resulting in a significant WL difference during this period (2020: -0.19 [-0.21, -0.17] m and 2021: -0.11 [-0.12, -0.09] m; p-value < 0.001; data from the WET area; Figure 2C). The cumulative potential evapotranspiration over May to September, calculated from daily air temperature using the formula of Oudin *et al.* (2005), was slightly higher in 2020 (472 mm) than in 2021 (449 mm). Furthermore, the WL distribution over the two years showed significantly lower values in the DRY (-0.16 [-0.17, -0.15] m) compared to the WET area (-0.10 [-0.11, -0.10] m; p-value < 0.001; Figures 3A and 3B).

The effect of OTC on air T was evaluated across the different plots for 2020–2021 (Table S1 in the supplementary material). For all areas (DRY, INTER, WET), mean annual air T was 0.2 to 0.6 °C higher in OTC plots compared to their corresponding control plots. This temperature difference increased with PPFD (p-value < 0.001; Table S1, Figures 4A and 4B). For PPFD values above 1000 µmol m^{-2} s^{-1}, OTCs increased air T from 0.6 to 1.5 °C. The temperature difference reached 1.7 to 2.0 °C for PPFD above 2000 µmol m^{-2} s^{-1} (Table S1). In contrast, for PPFD below 1 µmol m^{-2} s^{-1} the temperature difference dropped to 0.2 to 0.5 °C (Figure 4A).

GHG fluxes

Seasonal variations of Reco, NEE, GPP and CH_4 fluxes

Raw flux data with associated environmental variables are available in the supplementary material (Table S2). While all fluxes were close to zero in winter, Reco reached 5.9 µmol m^{-2} s^{-1} on 23 Jun 2020, and 5.1 µmol m^{-2} s^{-1} on 14 Sep 2021. GPP reached

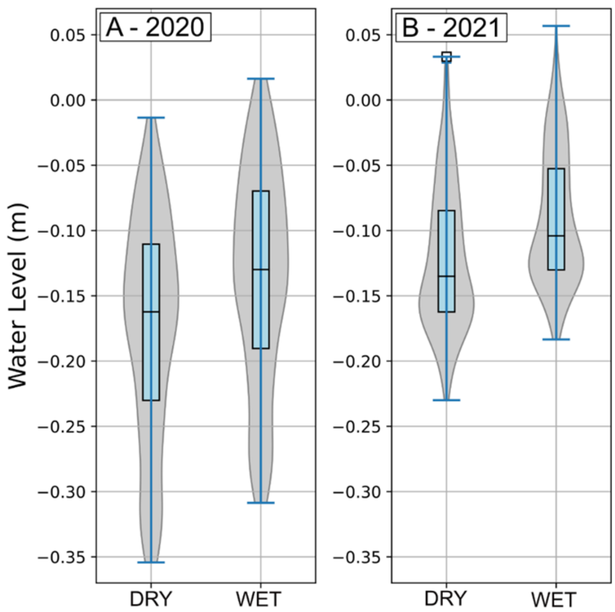

Figure 3. Violin plot showing the distribution of water level (WL) measurements for DRY and WET areas in 2020 (A) and 2021 (B), based on data for 30-minute intervals. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR.

-9.6 and -8.9 μmol m^{-2} s^{-1} on 20 July in 2020 and 2021, respectively. NEE ranged from 3.4 to -6.1 μmol m^{-2} s^{-1}. Over the two years, the highest NEE values were recorded on 20 Jul 2020 (-4.6 μmol m^{-2} s^{-1}) and 20 Jul 2021 (-6.1 μmol m^{-2} s^{-1}). Finally, CH_4 fluxes were mostly between 0 and 100 nmol m^{-2} s^{-1}, reaching 187 and 344 nmol m^{-2} s^{-1} on 20 Jul 2020 and 14 Sep 2021, respectively. Flux variability between plots was close to zero in winter and fluxes increased in summer, reaching maxima of 4.6, 5.8, 8.1 μmol m^{-2} s^{-1} and 326 nmol m^{-2} s^{-1} for NEE, Reco, GPP and CH_4, respectively (Figures 5A, 5B, 5C, 5D). The general trend indicates that the contrast between plots increases with increasing fluxes.

Reco and CH_4 fluxes for OTC and control plots

The statistical comparison showed no significant differences in Reco and CH_4 fluxes between the OTC and control plots along the hydrological gradient (Figures 6A and 6B; p-value > 0.05; Wilcoxon signed-rank test).

Reco and CH_4 fluxes along the hydrological gradient

Figures 7A and 7B show a statistical comparison of the Reco and CH_4 fluxes along the WET-INTER-DRY hydrological gradient, including OTC and control plots (Wilcoxon signed-rank test). For this comparison, only datasets from field campaigns where fluxes were available for all six plots were used.

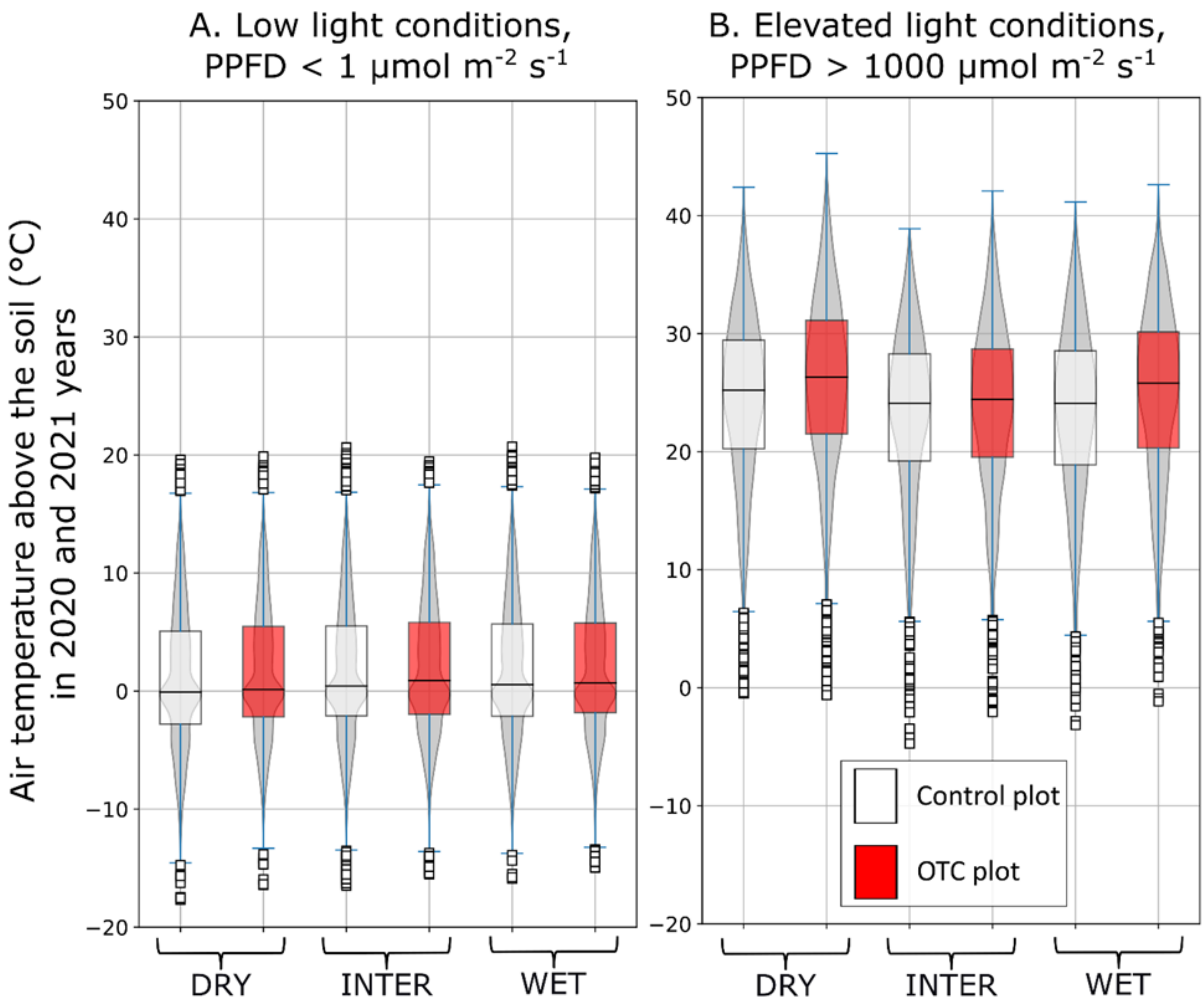

Figure 4. Violin plot showing air temperature (T, °C) distribution for the six plots over the 2020–2021 period. The measurements were taken every 30 minutes at 10 cm above the soil surface. Subplots show (A) low light conditions (PPFD < 1 μmol m^{-2} s^{-1}) and (B) elevated light conditions (PPFD > 1000 μmol m^{-2} s^{-1}), respectively. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR.

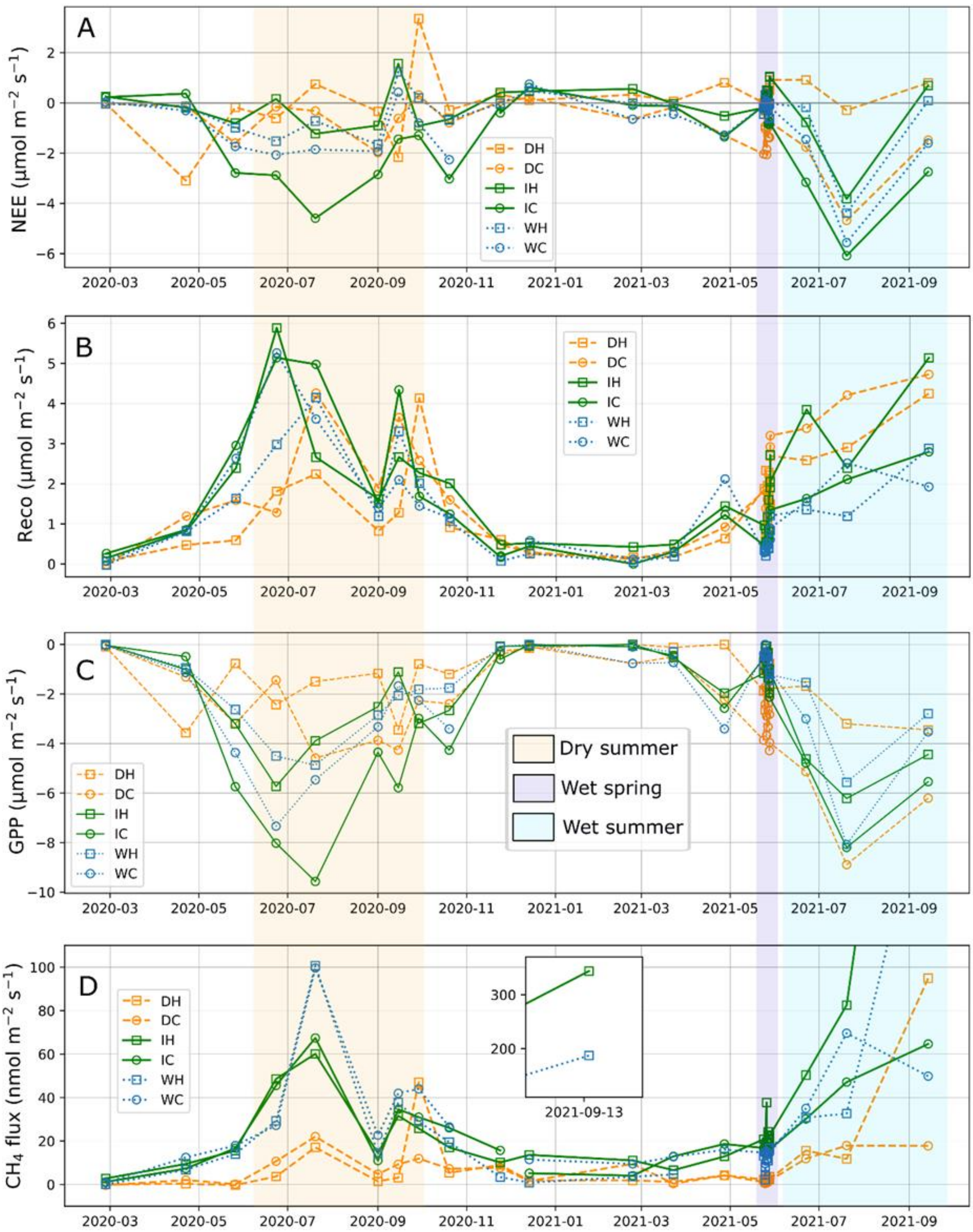

Figure 5. GHG fluxes of the individual plots. DC: control plot in the DRY area; DH: OTC plot in the DRY area; IC: control plot in the INTER area; IH: OTC plot in the INTER area; WC: control plot in the WET area; and WH: OTC plot in the WET area.

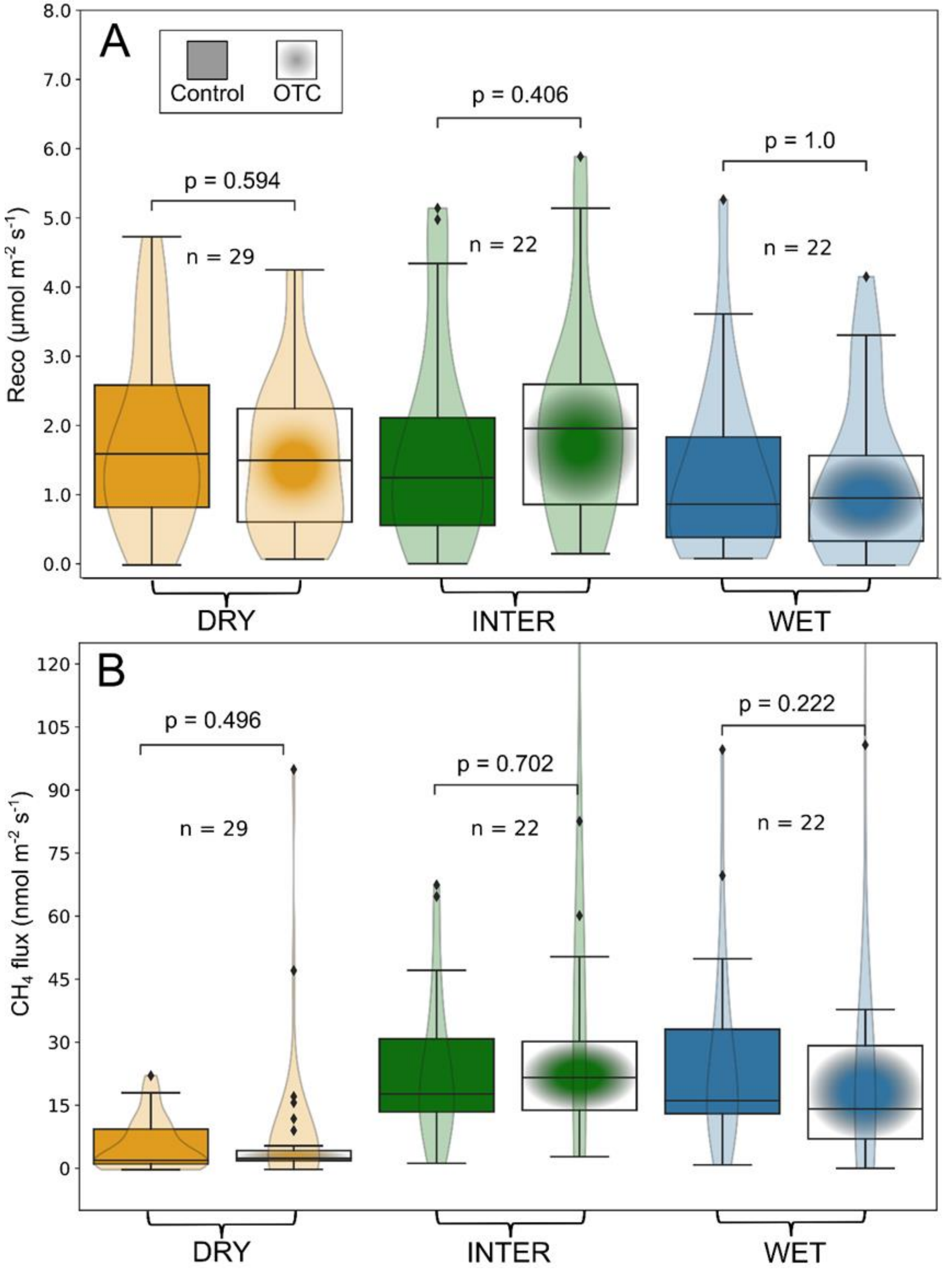

Figure 6. Violin plot showing Reco (A) and CH_4 flux (B) distribution for each study plot. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR. The statistical comparison (p-value) between control and OTC plots was realised using the Wilcoxon signed-rank test. The y-axis of subplot B has been shortened to improve readability and to prevent the display of two extreme values (for IH, CH_4 flux = 344 nmol m^{-2} s^{-1}; and for WH, CH_4 flux = 187 nmol m^{-2} s^{-1}).

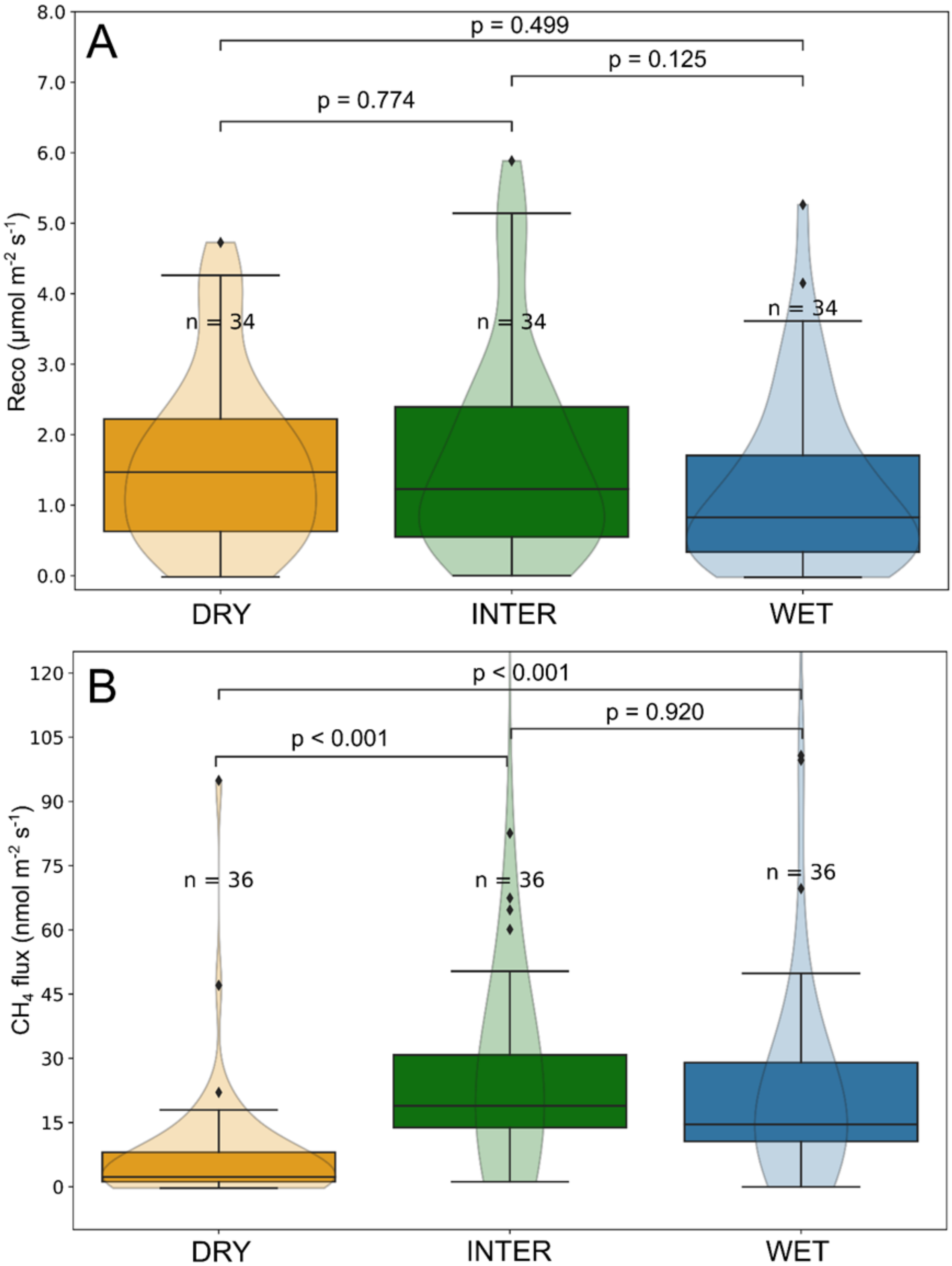

Figure 7. Violin plot showing Reco (A) and CH_4 flux (B) distribution for each hydrological condition (DRY, INTER and WET areas) including OTC and control plots. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR. The statistical comparison (p-value) between plots of different hydrological condition was realised using the Wilcoxon signed-rank test. The y-axis of subplot B has been shortened to improve readability and to prevent the display of two extreme values (for IH, CH_4 flux = 344 nmol m^{-2} s^{-1}; and for WH, CH_4 flux = 187 nmol m^{-2} s^{-1}).

For Reco, the median flux for the DRY (median [95 % CI]; 1.7 [0.9, 2.3] µmol m^{-2} s^{-1}) and INTER (1.7 [1.0, 2.4] µmol m^{-2} s^{-1}) plots was slightly higher than for the WET area (1.2 [0.8, 1.7] µmol m^{-2} s^{-1}; Figure 7A). Regarding specific hydrological conditions (i.e., dry/drought summer [Jun–Sep 2020], wet summer [Jun–Sep 2021] and wet spring [May 2021]), the WET–DRY gradient was consistent with the gradient observed for the entire dataset in 2021 (with wet summer and wet spring conditions). For the wet summer and wet spring periods of 2021, Reco was substantially lower for the WET (1.7 [1.25, 2.75] µmol m^{-2} s^{-1} and 0.4 [0.3, 0.6] µmol m^{-2} s^{-1}) than for the DRY area (3.8 [2.7, 4.6] µmol m^{-2} s^{-1} and 1.6 [1.3, 2.0] µmol m^{-2} s^{-1}, respectively). However, during the dry summer of 2020, Reco for the DRY area (2.0 [1.3, 3.8] µmol m^{-2} s^{-1}) was slightly lower than for the INTER and WET areas (2.7 [1.7, 5.0] and 2.5 [1.4, 3.8] µmol m^{-2} s^{-1}, respectively). In addition, Reco for the DRY area was lower in the dry (2.0 [1.3, 3.8] µmol m^{-2} s^{-1}) than in the wet summer (3.8 [2.7, 4.6] µmol m^{-2} s^{-1}), while average WL was -0.27 [-0.29, -0.25] m for the dry and -0.15 [-0.17, -0.15] m for the wet summer (June–September, DRY area, Figure 2C).

The mean CH_4 fluxes calculated from all measurements were significantly higher (p-value < 0.001) for the WET and INTER areas (17.5 [14.2, 29.0] and 20.0 [14.8, 30.4] nmol m^{-2} s^{-1}) compared to the DRY area (3.4 [1.9, 9.4] nmol m^{-2} s^{-1}, Figure 7B). In contrast, the mean CH_4 fluxes for INTER and WET areas were not significantly different (p-value = 0.92, Figure 7B). This spatial pattern was also observed at the seasonal scale.

GPP response to different hydrological conditions

In the WET-INTER areas, GPP showed a slight negative correlation with WL, with a distinct break observed at a WL of approximately -8 cm. For WL values below -8 cm GPP exhibited strong variability, ranging from 0 to -10 µmol m^{-2} s^{-1}. In contrast, for shallow WL values above -8 cm, GPP converged towards a narrow range between -2 and 0 µmol m^{-2} s^{-1} (Figure 8A). No similar trend was observed for the DRY area, where GPP did not display a clear relationship with WL (Figure 8B).

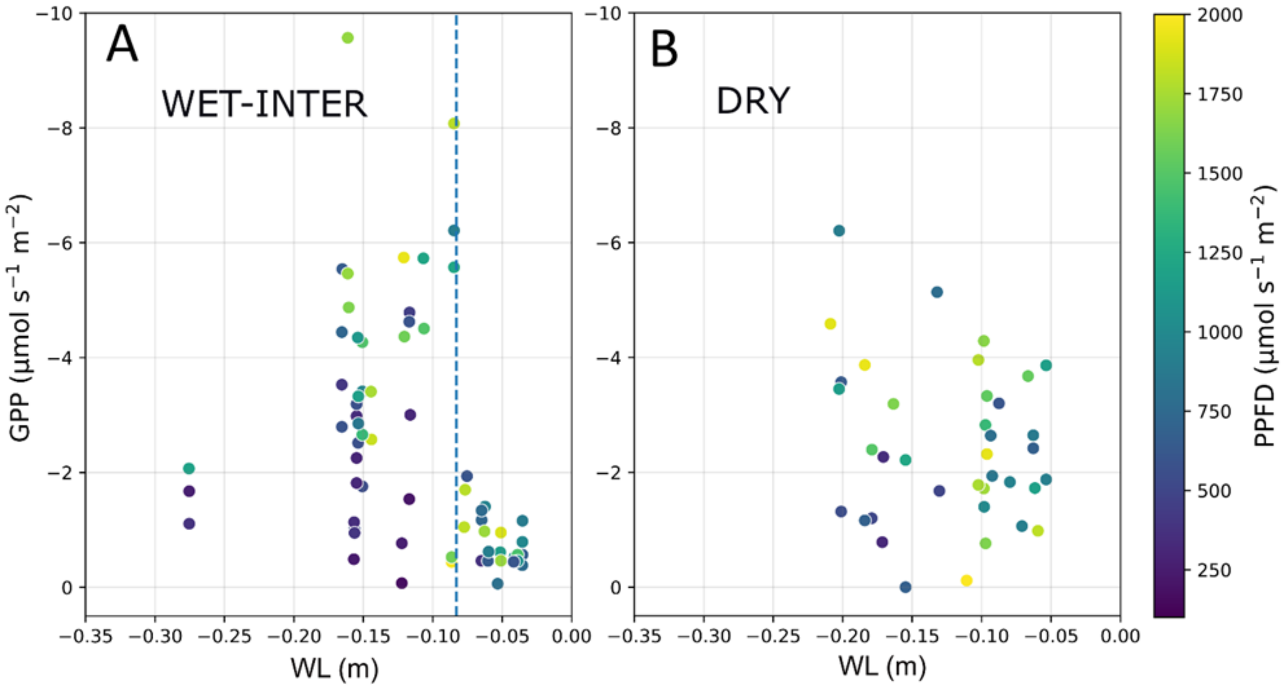

Figure 8. Correlation plot between GPP (µmol m^{-2} s^{-1}) and WL (m) (A) in the WET and INTER areas and (B) in the DRY area. Flux data are shown only for air temperatures above 10 °C and PPFD values between 100 and 2000 µmol m^{-2} s^{-1}. The blue dashed line in subplot A represents the WL threshold of -0.08 m discussed in the text. The colours of the plot symbols reflect the PPFD conditions when fluxes were measured, specified by the gradient bar to the right.

Apparent temperature sensitivity of ecosystem respiration

We sorted the GHG fluxes by plot using all available data and then calculated the apparent Q_{10} and the apparent E_a for Reco (Table 1). E_a ranged from 48 to 88.6 KJ mol^{-1} (average of 65 KJ mol^{-1}). It was slightly lower in the DRY area (~ 48 KJ mol^{-1}) compared to the INTER and WET areas (60.3 to 88.6 KJ mol^{-1}). No discernible difference was observed between OTC and control plots. Consequently, the Q_{10} (0–10 °C) was around 2.1 in the DRY area and achieved higher values of 2.6–4 in the INTER and WET areas (Table 1).

DISCUSSION

Northern peatlands have captured significant amounts (545–1055 Gt) of carbon from the atmosphere over the past millennia (Gorham 1991, Nichols & Peteet 2019). However, both climate and land use changes currently affect the complex functioning of these ecosystems, which in turn influences the rate of carbon exchange with the atmosphere (Loisel *et al.* 2021). Understanding the processes involved in the control of these exchanges remains a major challenge, particularly for modelling fluxes at continental scale and for their integration into global climate models (Frolking *et al.* 2009). In the present study, the flux ranges observed at Forbonnet are comparable to those measured in other temperate peatlands. For instance, Reco ranges from 0 to 5.9 µmol m^{-2} s^{-1}, which is within the range reported by Samson *et al.* (2018) for northern Poland (0 to 4.9 µmol m^{-2} s^{-1}) and by Lafleur *et al.* (2005) for southern Canada (< 1 to 4.5 µmol m^{-2} s^{-1}). However, the values are lower than those observed by Juszczak *et al.* (2013) in western Poland (up to 15 µmol m^{-2} s^{-1}). Regarding GPP, the fluxes remained below -10 µmol m^{-2} s^{-1} in our study, which is consistent with results from other *Sphagnum*-dominated temperate peatlands (Johnson *et al.* 2013, Leroy *et al.* 2019), although higher values have also been documented (e.g., up to 20 µmol m^{-2} s^{-1}; Ueyama *et al.* 2020). Similarly, our CH_4 fluxes, predominantly ranging from 0 to 100 nmol m^{-2} s^{-1}, agree with other studies conducted in temperate peatlands (Leroy *et al.* 2019, Ueyama *et al.* 2020).

However, the data reported in the present study indicate that both Reco and CH_4 fluxes exhibit large variability over a distance of only 35 m (Figure 5). Identification of the drivers behind this variability represents a substantial challenge for our comprehension of GHG emissions from peatlands. The aim of the following sections is, therefore, to examine CO_2 respiration and CH_4 fluxes with respect to the two primary forcing parameters, which are air temperature and hydrological conditions.

Passive warming does not directly affect GHG emissions

The comparison of Reco and CH_4 fluxes between the OTC and control plots across the different hydrological conditions (DRY, INTER and WET) did not show significant differences (Figure 6). This outcome differs from the findings of Oestmann *et al.* (2022) and Samson *et al.* (2018), who both observed increased GHG emissions in OTC plots on temperate peatland, although the patterns were complex. Oestmann *et al.* (2022) observed increased GHG emissions, dominated by CH_4 fluxes, in OTCs on a near-natural bog in north-western Germany. Samson *et al.* (2018) observed higher Reco in OTC plots under WET and DRY conditions (due to water level manipulation) in a poor fen in northern Poland. Over the course of a two-year experiment, these authors

Table 1. Apparent E_a and Q_{10} of the Reco fluxes for the different plots.

Hydrological gradient	Temperature control	Plot	E_a (KJ mol^{-1})	Q_{10} (0–10 °C)	Q_{10} (10–20 °C)
DRY	Control	DC	48.0	2.1	2.0
	OTC	DH	48.3	2.1	2.0
INTER	Control	IC	88.6	4.0	3.6
	OTC	IH	60.3	2.6	2.4
WET	Control	WC	66.1	2.8	2.6
	OTC	WH	79.1	3.4	3.1

measured the highest Reco in plots under both DRY and OTC conditions, demonstrating that the combined effect of drying and warming is stronger than either factor alone. However, in a cold-temperate peatland in the northern USA, no contrasts in Reco and CH_4 fluxes were observed between OTC and control plots (Johnson *et al.* 2013). Similarly, Pearson *et al.* (2015) found no significant differences in Reco and CH_4 fluxes between OTC and control plots across three boreal peatlands in Finland, under a variety of hydrological conditions (pristine, short-term and long-term drainage).

The non-uniform response of GHG fluxes to OTC treatment might be explained by several factors. First, the OTC effect on soil temperature is not homogeneous. Johnson *et al.* (2013) found no difference in the seasonal average peat temperature between OTC and control plots. Regarding daily patterns, they observed that the difference in peat temperature at 5 cm depth was highly variable, depending on radiation and wind conditions. We observed that OTC increased air temperature above the soil most noticeably under high PPFD conditions (Table S1) but, using the OTC and control plots of the Forbonnet station, Delarue *et al.* (2011) found no significant temperature differences in peat below 7 cm depth. In contrast to an expected increase of soil temperature (on average 0.3 to 0.5 °C) in OTC plots, as observed by Oestmann *et al.* (2022), some studies have even showed that the surface peat temperature in OTC plots is lower due to enhanced latent heat energy loss (Dabros *et al.* 2010, Górecki *et al.* 2021). As the temperature of the peat surface is a key driver for CH_4 and Reco fluxes (Ueyama *et al.* 2020, Li *et al.* 2021b), the non-significant or possible cooling effect of OTC on peat temperature could partially explain the absence of coherent trends.

Also working at Forbonnet, Binet *et al.* (2017) showed that the OTC effect changed the fungal root symbiosis and enzyme activities of *A. polifolia* that are involved in carbon cycling and the associated Reco, albeit to varying degrees depending on the hydrological gradient. Hence, the temporal variability of sunlight and wind (Figure 2B), as well as the complexity of the OTC effect on peat temperature and microbial activity, could explain the lack of observable OTC effects on Reco and CH_4 fluxes. Given the superposition of various and complex factors controlling carbon fluxes in peatlands, the OTC effect might be overridden by other drivers. In our study the variability amongst plots of vegetation, microbial communities and peat properties introduces potential for a significant OTC effect on GHG fluxes to be obscured owing to the small number of plots, consistently with observations elsewhere (Juszczak *et al.* 2013, Ward *et al.* 2013). For instance, Ward *et al.* (2013) observed that CH_4 emissions were more strongly controlled by vegetation composition than by warming in a temperate blanket bog in northern England.

Hydrological contrasts affect GHG emissions depending on the season

CO_2 ecosystem respiration (Reco)

The higher Reco measured in the DRY area aligns with expectations. The drier conditions, coupled with a higher proportion of vascular plants and their associated litter, favour aerobic decomposition of organic matter, thereby increasing Reco (Limpens *et al.* 2008, Leroy *et al.* 2017, Li *et al.* 2021b). The evaluation of the apparent sensitivity of Reco (Q_{10}, E_a) to temperature variations highlighted consistent differences between the WET-INTER (Q_{10} between 2.6 and 4) and DRY areas (Q_{10} = 2.1; Table 1). The difference in Q_{10} values is even more significant than the absolute value of Q_{10} itself. The temperature range over which Q_{10} is calculated (i.e., Q_{10} for temperature variation between 0 and 10 °C) and the specific temperature utilised (i.e., air or different soil depths) can change the absolute value of Q_{10} (Samson *et al.* 2018, Helbig *et al.* 2019). The variability of Q_{10} observed at Forbonnet may reflect variations between the WET-INTER and DRY areas in terms of the lability of organic matter, which is a determining factor triggering CO_2 production from organic carbon decomposition (Conant *et al.* 2008). This hypothesis is consistent with observations from Leroy *et al.* (2017), who conducted a mesocosm experiment with peat cores from a temperate peatland. These authors observed higher sensitivity of Reco to temperature in plots dominated by *Sphagnum* (Q_{10} = 3.75, E_a = 92.2 KJ mol^{-1}) compared to plots with vascular plants (*Molinia*, Q_{10} = 2.58, E_a = 65.7 KJ mol^{-1}) that were suspected to release exudates of labile organic compounds. Consistent with our findings, Samson *et al.* (2018), found higher Q_{10} for wetter (from 2.9 to 6.1) than for drier areas (2 to 4) in a temperate peatland. However, this is the opposite of what is generally observed in peatlands, i.e., an increase in Q_{10} under drier conditions (Liu *et al.* 2024). This contrast suggests that, in the studies of Samson *et al.* (2018) and ourselves, higher temperatures were generally associated with lower water level and thus drier conditions. According to Samson *et al.* (2018), the higher Q_{10} in the wettest area indicated “a high reactivity of respiration rate when the organic matter got exposed to aerobic conditions”.

Interestingly, the higher Reco observed in the DRY area did not persist during the dry summer period of 2020. Although the difference was not significant, it may indicate a threshold at which Reco slows down. While it is commonly accepted that Reco increases with WL drawdown, the underlying processes are complex and non-linear. For instance, Jassey *et al.* (2018) showed, in a peatland in northern Poland, that the increase in Reco only became significant at WL below -25 cm. In contrast, Liu *et al.* (2022) found in a mountainous peatland in China that Reco increased with WL drawdown until a value of -30 cm was reached, beyond which the flux no longer changed with WL depth. Other studies concluded that the heterotrophic respiration of microorganisms and the related activity of phenol-oxidase enzymes may be drastically reduced during intense droughts (Criquet *et al.* 2000, Kang *et al.* 2022). This mechanism may explain why Reco was lower in the DRY area during 2020, when WL dropped below -30 cm (Figure 2C).

CH_4 fluxes

Higher CH_4 fluxes for the WET and INTER areas strongly suggest a hydrological control over these fluxes. The reduced thickness of the aerobic peat layer due to the near-surface WL in these environments might limit oxidation and simultaneously favour CH_4 production by the thicker anaerobic compartment. Consistently, a positive relationship between CH_4 emissions and WL has been observed in numerous studies (Moore & Knowles 1989, Turetsky *et al.* 2014, Abdalla *et al*. 2016). In addition, our results align with those of Johnson *et al.* (2013), who observed lower CH_4 emissions in the driest hydrological environment (hummocks) of a cold-temperate peatland.

The hydrological WET-INTER-DRY gradient promoted non-gradual significant differences in CH_4 fluxes. Indeed, there was a marked change at the DRY-INTER transition, suggesting rapid lateral shifts in the biogeochemical behaviour of the peatland at the metre scale. Additional factors beyond WL may have contributed to this rapid spatial change of CH_4 fluxes. One of these could be the WL-controlled spatial variation of vegetation between the DRY and WET-INTER areas. This botanical contrast, characterised by denser vascular plant coverage in the DRY area, could have led to changes in plant litter and microbial communities, both of which play key roles in organic matter recycling (Trinder *et al.* 2008, Jassey *et al.* 2011a,b, Andersen *et al.* 2013). For instance, Strakova *et al.* (2011) showed that vegetation type and its associated litter influence microbial activity more strongly than decreasing WL. While the flat terrain in our experimental transect suggested gradual WL changes, it is likely that the pronounced microtopography in the DRY area accentuated the WL difference compared to the INTER and WET areas.

Effect of water level on GPP

While the variability of GPP reflected the seasonality of PPFD intensity and of plant phenological stages (Figures 2A and 2B), our data also show faster fluctuations superimposed on this seasonality (Figure 5C). The seasonal dynamics of plant phenology and differences in vegetation cover between plots, as well as hydrological and passive warming effects, provide a potential explanation of this short-term and inter-plot variability in GPP (Tuittila *et al.* 2004, Korrensalo *et al.* 2017, Walker *et al.* 2017, Järveoja *et al.* 2018, Peichl *et al*. 2018). GPP responds rapidly to changes in PPFD (e.g., diurnal cycle, fluctuations in cloud cover; Chojnicki *et al.* 2010) because the photosynthetic rate increases with PPFD until it reaches a saturation point which depends on plant species (Haraguchi & Yamada 2011, Leroy *et al.* 2019). In our experiment, the variability of PPFD complicated the analysis of the forcing factors influencing GPP, which is an essential component of the net ecosystem carbon balance (Chapin *et al*. 2006). A more extensive dataset, including many GPP values across a wide range of PPFD fluxes under different conditions and seasons (e.g., by using different light filters on the chambers) would be necessary to disentangle the forcing effects on GPP. Nevertheless, our results show a clear influence of hydrological conditions on GPP (Figures 8A and 8B). The abrupt drop in GPP in the WET and INTER areas at WL above -8 cm could be attributed to the immersion of *Sphagnum* mosses, which significantly limited GPP due to the lower diffusion of CO_2 in water compared to air (Williams & Flanagan 1996). Field observations indicated that *Sphagnum* mosses in the WET and INTER areas are indeed partially immersed when WL exceeded -8 cm. This result aligns with Tuittila *et al.* (2004), who observed the photosynthetic response of *Sphagnum* in a restored peatland. They reported a unimodal response curve with a WL optimum of -12 cm and a significant decrease below -22 cm and above 1 cm.

These findings support the observation that GPP decreases significantly in peatlands in response to extreme hydrological conditions (Ratcliffe *et al.* 2019). While low WL can also inhibit photosynthetic activity, this was not observed in our study (Williams & Flanagan 1996). Ahmad *et al.* (2020b), however, provided evidence that rewetting improves the hydrological buffering capacity, reducing the water level fluctuations in response to precipitation events. In pristine and restored peatlands, an upper elastic peat layer is often present, albeit not always and with spatial variability (Morris *et al.* 2011, Baird *et al.* 2016). This layer enables a hydrological self-regulating mechanism known as “bog breathing”, which stabilises WL relative to vegetation (Howie & Hebda 2018, Morton & Heinemeyer 2019). However, in northern temperate latitudes, climate change exacerbates hydrological extremes such as droughts and heavy precipitation events. This intensification may increase WL variability, pushing extremes beyond the buffering capacity of bog breathing (Spinoni *et al.* 2018, Bertrand *et al*. 2021). These contrasting forces on WL variability raise significant uncertainties regarding the future of GPP values in peatlands.

Concluding perspectives

This study investigated the spatio-temporal variability of GHG emissions in the peatland of Forbonnet at Frasne, a long-term observatory of a mid-altitude mountain peatland. This site allows the study of GHG fluxes and associated hydrometeorological and ecological conditions at various timescales. Our study documents the added value of such an observatory, especially when combined with additional point measurements to highlight the spatial variability of GHG fluxes. Our analysis of monthly chamber flux data over 20 months revealed several key findings: (1) the Open Top Chamber (OTC), which warms the air above the soil surface, had no measurable effect on CO_2 and CH_4 fluxes. Instead, we found (2) that CO_2 and CH_4 fluxes evolved along a 35 m transect with a natural hydrological gradient from WET area with a near-surface water level to DRY area with a lower water level. However, replicating this kind of study with a larger number of plots and at higher temporal resolution, especially during periods with strongly contrasting air and soil temperatures between OTC and control plots, could potentially clarify the effects of OTC on GHG fluxes.

Our results confirm the well-established hydric control on CO_2 and CH_4 emissions (Reco and CH_4 fluxes). However, we found that this control is non-linear, raising questions about the future effects of climate change. Projections predict increasingly extreme weather conditions for the study area, with wetter and warmer winters on the one hand and drier and hotter summers on the other (Bertrand *et al*. 2021), which will have implications for GHG emissions from peatlands. However, in the driest area during summer drought conditions, our data did not confirm the expected higher CO_2 ecosystem respiration. We attribute this observation to a threshold effect during droughts that limits the aerobic decomposition of organic matter.

The contrasting responses of Reco to hydrological conditions highlight the complexity of mechanisms and feedback loops involved in organic matter recycling under aerobic conditions and the associated CO_2 emissions (Gilbert *et al.* 1998, Andersen *et al*. 2013, Binet *et al.* 2017, Jassey *et al*. 2018). As a result, a more comprehensive dataset is needed to further explore the above mechanisms, especially during droughts combined (or not) with heatwaves, which are becoming more frequent and more severe in temperate latitudes (Samaniego *et al.* 2018, Spinoni *et al.* 2018, IPCC 2022). The non-linear response of Reco to WL variations raises questions about its effect on NEE, provided that GPP is also limited under more extreme conditions (Tuittila *et al.* 2004).

CH_4 emissions from peatlands are known to increase with wetter conditions, a behaviour observed in the present study at the scale of a few metres. Nonetheless, the non-progressive transition between low- and high-emission areas suggests that WL is not the sole controlling factor. Other factors such as peat materials and/or microbial communities (methanogens and methanotrophs) may also play a role in modulating CH_4 emissions. Studies including the characterisation of both microbial communities and GHG exchanges with the atmosphere should aid in improving our understanding of the processes that govern these fluxes.

ACKNOWLEDGEMENTS

The authors warmly thank the managers of the Regional Natural Reserve of Frasne-Bouverans for allowing access to the site. This study is part of the CRITICAL PEAT project funded by the region of Bourgogne Franche-Comté (Accueil de Nouvelle Equipe de Recherche Agreement n2019-Y09069), the French National Network of Peatland Observatories "SNO Tourbières" (https://www.sno-tourbieres.cnrs.fr/) and the French Network of Critical Zone Observatories "OZCAR" (https://wwwozcar-ri.org/fr/ozcar-observatoires-de-la-zone-critique-applicationse t-recherche/). The SNO Tourbières observing system was created thanks to incentive funding from the French Ministry of Research, which allowed existing local observatories to be merged into a national observatory network. The continuity of field monitoring was made possible by continuous CNRS-INSU funding since 2008. A. Lhosmot benefited from a Ph.D. fellowship from the French Ministry of Research. The authors thank the two anonymous reviewers for their pertinent comments, which helped to substantially improve the manuscript.

AUTHOR CONTRIBUTIONS

AL wrote the original draft. AL, GB, AJ and PB participated in conception of the study, designed the methodology and analysed the data. AL, GB, PB, MLT, RC and AB participated to the GHG field measurements. MLT acquired soil-meteorological data. Supervision and funding management of the study: GB. All authors contributed to writing, and approved the definitive version of the manuscript.

DATA AVAILABILITY

Chamber GHG fluxes measured in this study are available in supplementary data files. Meteorological and water level data are available on the Zenodo repository https://zenodo.org/record/3763342 and https://zenodo.org/record/3763766. Complementary data on the Forbonnet hydrology and eddy covariance measurements are available at https://onlinelibrary.wiley.com/doi/10.1002/eco.2315, https://onlinelibrary.wiley.com/doi/10.1002/hyp.14781 and https://link.springer.com/10.1007/s10021-022-00809-x.

REFERENCES

Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, Ü., Smith, P. (2016) Emissions of methane from northern peatlands: a review of management impacts and implications for future management options. *Ecology and Evolution*, 6, 7080–7102. https://doi.org/10.1002/ece3.2469

Ahmad, S., Liu, H., Beyer, F., Kløve, B., Lennartz, B. (2020a) Spatial heterogeneity of soil properties in relation to microtopography in a non-tidal rewetted coastal mire. *Mires and Peat*, 26, 04. https://doi.org/10.19189/MaP.2019.GDC.StA.1779

Ahmad, S., Liu, H., Günther, A., Couwenberg, J., Lennartz, B. (2020b) Long-term rewetting of degraded peatlands restores hydrological buffer function. *Science of The Total Environment*, 749, 141571. https://doi.org/10.1016/j.scitotenv.2020.141571

Andersen, R., Chapman, S.J., Artz, R.R.E. (2013) Microbial communities in natural and disturbed peatlands: A review. *Soil Biology and Biochemistry*, 57, 979–994. https://doi.org/10.1016/j.soilbio.2012.10.003

Antala, M., Juszczak, R., van der Tol, C., Rastogi, A. (2022) Impact of climate change-induced alterations in peatland vegetation phenology and composition on carbon balance. *Science of The Total Environment*, 827, 154294. https://doi.org/10.1016/j.scitotenv.2022.154294

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M. and 25 others (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69, 491. https://doi.org/10.2307/2657227

Arrhenius, S. (1889) Uber die Reaktions-geschwindigkeit bei der Inversion von Rohrzucker durch Sauren (On the reaction rate during the inversion of cane sugar by acids). *Zeitschrift für Physikalische Chemie*, 4, 226–248. https://doi.org/10.1515/zpch-1889-0416

Arsenault, J., Talbot, J., Moore, T.R., Beauvais, M.-P., Franssen, J., Roulet, N.T. (2019) The spatial heterogeneity of vegetation, hydrology and water chemistry in a peatland with open-water pools. *Ecosystems*, 22, 1352–1367. https://doi.org/10.1007/s10021-019-00342-4

Baird, A.J., Milner, A.M., Blundell, A., Swindles, G.T., Morris, P.J. (2016) Microform-scale variations in peatland permeability and their ecohydrological implications. *Journal of Ecology*, 104, 531–544. https://doi.org/10.1111/1365-2745.12530

Bertrand, G., Poncets, A., Pohl, B., Lhosmot, A., Steinmann, M., Johannet, A., Pinel, S., Caldirak, H., Artigue, G., Binet, P., Bertrand, C., Collin, L., Magnon, G., Gilbert, D., Laggoun-Deffarge, F., Toussaint, M.-L. (2021) Statistical hydrology for evaluating peatland water table sensitivity to simple environmental variables and climate changes application to the mid-latitude/altitude Frasne peatland (Jura Mountains, France). *Science of The Total Environment*, 754, 141931. https://doi.org/10.1016/j.scitotenv.2020.141931

Binet, P., Rouifed, S., Jassey, V.E.J., Toussaint, M.-L., Chiapusio, G. (2017) Experimental climate warming alters the relationship between fungal root symbiosis and *Sphagnum* litter phenolics in two peatland microhabitats. *Soil Biology and Biochemistry*, 105, 153–161. https://doi.org/10.1016/j.soilbio.2016.11.020

Bragazza, L. (2008) A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. *Global Change Biology*, 14, 2688–2695. https://doi.org/10.1111/j.1365-2486.2008.01699.x

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D. (2013) Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, 3, 273–277. https://doi.org/10.1038/nclimate1781

Briones, M.J.I., Juan-Ovejero, R., McNamara, N.P., Ostle, N.J. (2022) Microbial “hotspots” of organic matter decomposition in temperate peatlands are driven by local spatial heterogeneity in abiotic conditions and not by vegetation structure. *Soil Biology and Biochemistry*, 165, 108501. https://doi.org/10.1016/j.soilbio.2021.108501

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., Bragazza, L. (2015) Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science*, 26, 964–974. https://doi.org/10.1111/jvs.12296

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B. and 25 others (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9, 1041–1050. https://doi.org/10.1007/s10021-005-0105-7

Chaudhary, N., Miller, P.A., Smith, B. (2018) Biotic and abiotic drivers of peatland growth and microtopography: a model demonstration. *Ecosystems*, 21, 1196–1214. https://doi.org/10.1007/s10021-017-0213-1

Chojnicki, B.H., Michalak, M., Acosta, M., Juszczak, R., Augustin, J., Drösler, M., Olejnik, J. (2010) Measurements of carbon dioxide fluxes by chamber method at the Rzecin wetland ecosystem, Poland. *Polish Journal of Environmental Studies*, 19, 283–291.

Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., Six, J., Steinweg, J.M. (2008) Sensitivity of organic matter decomposition to warming varies with its quality. *Global Change Biology*, 14, 868–877. https://doi.org/10.1111/j.1365-2486.2008.01541.x

Couwenberg, J., Baumann, M., Lamkowski, P., Joosten, H. (2022) From genes to landscapes: Pattern formation and self-regulation in raised bogs with an example from Tierra del Fuego. *Ecosphere*, 13(4), e4031. https://doi.org/10.1002/ecs2.4031

Criquet, S., Farnet, A.M., Tagger, S., Petit, J.L. (2000) Annual variations of phenoloxidase activities in an evergreen oak litter: influence of certain biotic and abiotic factors. *Soil Biology and Biochemistry*, 32, 1505–1513. https://doi.org/10.1016/S0038-0717(00)00027-4

Curiel Yuste, J., Janssens, I.A., Carrara, A., Ceulemans, R. (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, 10, 161–169. https://doi.org/10.1111/j.1529-8817.2003.00727.x

Dabros, A., Fyles, J.W., Strachan, I.B. (2010) Effects of open-top chambers on physical properties of air and soil at post-disturbance sites in northwestern Quebec. *Plant and Soil*, 333, 203–218. https://doi.org/10.1007/s11104-010-0336-z

Davidson, E.A., Janssens, I.A., Luo, Y. (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. *Global Change Biology*, 12, 154–164. https://doi.org/10.1111/j.1365-2486.2005.01065.x

Dean, J.F., Middelburg, J.J., Röckmann, T., Aerts, R., Blauw, L.G., Egger, M., Jetten, M.S.M., De Jong, A.E.E., Meisel, O.H., Rasigraf, O., Slomp, C.P., In'T Zandt, M.H., Dolman, A.J. (2018) Methane feedbacks to the global climate system in a warmer world. *Reviews of Geophysics*, 56, 207–250. https://doi.org/10.1002/2017RG000559

Delarue, F., Laggoun-Défarge, F., Buttler, A., Gogo, S., Jassey, V.E.J., Disnar, J.-R. (2011) Effects of short-term ecosystem experimental warming on water-extractable organic matter in an ombrotrophic *Sphagnum* peatland (Le Forbonnet, France). *Organic Geochemistry*, 42, 1016–1024. https://doi.org/10.1016/j.orggeochem.2011.07.005

Etminan, M., Myhre, G., Highwood, E.J., Shine, K.P. (2016) Radiative forcing of carbon dioxide, methane, and nitrous oxide: A significant revision of the methane radiative forcing. *Geophysical Research Letters*, 43, 12,614–12,623. https://doi.org/10.1002/2016GL071930

Evans, C.D., Peacock, M., Baird, A.J., Artz, R.R.E. and 27 others (2021) Overriding water table control on managed peatland greenhouse gas emissions. *Nature*, 593, 548–552. https://doi.org/10.1038/s41586-021-03523-1

Frolking, S., Roulet, N., Lawrence, D. (2009) Issues related to incorporating northern peatlands into global climate models. In: Baird, A.J., Belyea, L.R., Comas, X., Reeve, A.S., Slater, L.D. (eds.) *Carbon Cycling in Northern Peatlands*, Geophysical Monograph 184, American Geophysical Union, Washington DC, 19–35. https://doi.org/10.1029/2008GM000809

Gabriel, M., Toader, C., Faul, F., Roßkopf, N., Grundling, P., van Huyssteen, C., Grundling, A.T., Zeitz, J. (2018) Physical and hydrological properties of peat as proxies for degradation of South African peatlands: Implications for conservation and restoration. *Mires and Peat*, 21, 23. https://doi.org/10.19189/MaP.2018.OMB.336

Gaillardet, J., Braud, I., Hankard, F., Anquetin, S. and 145 others (2018) OZCAR: The French network of Critical Zone Observatories. *Vadose Zone Journal*, 17(1), 1–24. https://doi.org/10.2136/vzj2018.04.0067

Gauthier, T.-L.J., McCarter, C.P.R., Price, J.S. (2018) The effect of compression on *Sphagnum* hydrophysical properties: Implications for increasing hydrological connectivity in restored cutover peatlands. *Ecohydrology*, 11, e2020. https://doi.org/10.1002/eco.2020

Gilbert, D., Amblard, C., Bourdier, G., Francez, A.-J. (1998) The microbial loop at the surface of a peatland: structure, function, and impact of nutrient Input. *Microbial Ecology*, 35, 83–93. https://doi.org/10.1007/s002489900062

Gogo, S., Paroissien, J., Laggoun-Défarge, F., Antoine, J. and 32 others (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(6), e14244. https://doi.org/10.1002/hyp.14244

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łuców, D., Kayzer, D., Juszczak, R. (2021) Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate *Sphagnum*-peatland. *Science of The Total Environment*, 771, 145452. https://doi.org/10.1016/j.scitotenv.2021.145452

Gorham, E. (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1, 182–195. https://doi.org/10.2307/1941811

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

Haraguchi, A., Yamada, N. (2011) Temperature dependency of photosynthesis of *Sphagnum* spp. distributed in the warm-temperate and the cool-temperate mires of Japan. *American Journal of Plant Sciences*, 02, 716–725. https://doi.org/10.4236/ajps.2011.25086

Harenda, K.M., Lamentowicz, M., Samson, M., Chojnicki, B.H. (2018) The role of peatlands and their carbon storage function in the context of climate change. In: Zielinski, T., Sagan, I., Surosz, W. (eds.) *Interdisciplinary Approaches for Sustainable Development Goals*, Springer International Publishing, Cham, 169–187. https://doi.org/10.1007/978-3-319-71788-3_12

Helbig, M., Humphreys, E.R., Todd, A. (2019) Contrasting temperature sensitivity of CO_2 exchange in peatlands of the Hudson Bay lowlands, Canada. *Journal of Geophysical Research: Biogeosciences*, 124, 2126–2143. https://doi.org/10.1029/2019JG005090

Howie, S.A., Hebda, R.J. (2018) Bog surface oscillation (mire breathing): A useful measure in raised bog restoration. *Hydrological Processes*, 32, 1518–1530. https://doi.org/10.1002/hyp.11622

Humpenöder, F., Karstens, K., Lotze-Campen, H., Leifeld, J., Menichetti, L., Barthelmes, A., Popp, A. (2020) Peatland protection and restoration are key for climate change mitigation. *Environmental Research Letters*, 15, 104093. https://doi.org/10.1088/1748-9326/abae2a

Hutchinson, G.L., Livingston, G.P. (1993) Use of chamber systems to measure trace gas fluxes. In: Harper, L.A., Mosier, A.R., Duxbury, J.M., Rolston, D.E. (eds.) *Agricultural Ecosystem Effects on Trace Gases and Global Climate Change*, American Society of Agronomy, Crop Science Society of America and Soil Science Society of America, Madison WI, USA, 63–78. https://doi.org/10.2134/asaspecpub55.c4

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (eds.)], Cambridge University Press, Cambridge UK and New York NY, USA, 1535 pp.

IPCC (2022) *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (eds.)], Cambridge University Press, Cambridge UK and New York NY, USA, 3056 pp., https://doi.org/10.1017/9781009325844

Jacotot, A., Marchand, C., Allenbach, M. (2019) Biofilm and temperature controls on greenhouse gas (CO_2 and CH_4) emissions from a *Rhizophora* mangrove soil (New Caledonia). *Science of The Total Environment*, 650, 1019–1028. https://doi.org/10.1016/j.scitotenv.2018.09.093

Järveoja, J., Nilsson, M.B., Gažovič, M., Crill, P.M., Peichl, M. (2018) Partitioning of the net CO_2 exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland. *Global Change Biology*, 24, 3436–3451. https://doi.org/10.1111/gcb.14292

Jassey, V.E.J., Chiapusio, G., Gilbert, D., Buttler, A., Toussaint, M.-L., Binet, P. (2011a) Experimental climate effect on seasonal variability of polyphenol/phenoloxidase interplay along a narrow fen–bog ecological gradient in *Sphagnum fallax*. *Global Change Biology*, 17, 2945–2957. https://doi.org/10.1111/j.1365-2486.2011.02437.x

Jassey, V.E.J., Chiapusio, G., Mitchell, E.A.D., Binet, P., Toussaint, M.-L., Gilbert, D. (2011b) Fine-scale horizontal and vertical micro-distribution patterns of testate amoebae along a narrow fen/bog gradient. *Microbial Ecology*, 61, 374–385. https://doi.org/10.1007/s00248-010-9756-9

Jassey, V.E.J., Reczuga, M.K., Zielińska, M., Słowińska, S., Robroek, B.J.M., Mariotte, P., Seppey, C.V.W., Lara, E., Barabach, J., Słowiński, M., Bragazza, L., Chojnicki, B.H., Lamentowicz, M., Mitchell, E.A.D., Buttler, A. (2018) Tipping point in plant–fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. *Global Change Biology*, 24, 972–986. https://doi.org/10.1111/gcb.13928

Johnson, C.P., Pypker, T.G., Hribljan, J.A., Chimner, R.A. (2013) Open top chambers and infrared lamps: a comparison of heating efficacy and CO_2/CH_4 dynamics in a northern Michigan peatland. *Ecosystems*, 16, 736–748. https://doi.org/10.1007/s10021-013-9646-3

Joosten, H. (2016) Peatlands across the globe. In: Bonn, A., Allott, T., Evans, M., Joosten, H., Stoneman, R. (eds.) *Peatland Restoration and Ecosystem Services*, Cambridge University Press, Cambridge UK, 19–43. https://doi.org/10.1017/CBO9781139177788.003

Joosten, H., Clarke, D. (2002) *Wise Use of Mires and Peatlands - Background and Principles including a Framework for Decision-Making*. International Mire Conservation Group and International Peat Society, Saarijärvi, Finland, 304 pp.

Juszczak, R., Humphreys, E., Acosta, M., Michalak-Galczewska, M., Kayzer, D., Olejnik, J. (2013) Ecosystem respiration in a heterogeneous temperate peatland and its sensitivity to peat temperature and water table depth. *Plant and Soil*, 366, 505–520. https://doi.org/10.1007/s11104-012-1441-y

Kang, E., Li, Y., Zhang, X., Yan, Z., Zhang, W., Zhang, K., Yan, L., Wu, H., Li, M., Niu, Y., Yang, A., Wang, J., Kang, X. (2022) Extreme drought decreases soil heterotrophic respiration but not methane flux by modifying the abundance of soil microbial functional groups in alpine peatland. *CATENA*, 212, 106043. https://doi.org/10.1016/j.catena.2022.106043

Korkiakoski, M., Tuovinen, J.-P., Penttilä, T., Sarkkola, S., Ojanen, P., Minkkinen, K., Rainne, J., Laurila, T., Lohila, A. (2019) Greenhouse gas and energy fluxes in a boreal peatland forest after clear-cutting. *Biogeosciences*, 16, 3703–3723. https://doi.org/10.5194/bg-16-3703-2019

Korrensalo, A., Alekseychik, P., Hájek, T., Rinne, J., Vesala, T., Mehtätalo, L., Mammarella, I., Tuittila, E.-S. (2017) Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. *Biogeosciences*, 14, 257–269. https://doi.org/10.5194/bg-14-257-2017

Kreyling, J., Tanneberger, F., Jansen, F., Van Der Linden, S. and 36 others (2021) Rewetting does not return drained fen peatlands to their old selves. *Nature Communications*, 12, 5693. https://doi.org/10.1038/s41467-021-25619-y

Lafleur, P.M., Moore, T.R., Roulet, N.T., Frolking, S. (2005) Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8, 619–629. https://doi.org/10.1007/s10021-003-0131-2

Laggoun-Défarge, F., Gilbert, D., Buttler, A., Epron, D., Francez, A.-J., Grasset, L., Guimbaud, C., Mitchell, E., Roy, J.-C. (2008) Effects of experimental warming on Carbon sink function of a temperate pristine mire: The project PEATWARM. In: Farrell, C., Feehan, J. (eds.) *After Wise Use - The Future of Peatlands*, Proceedings of the 13th International Peat Congress, International Peat Society, Jyväskylä, 599–602.

Lai, D.Y.F. (2009) Methane dynamics in northern peatlands: a review. *Pedosphere*, 19, 409–421.

Lamentowicz, M., Słowińska, S., Słowiński, M. (2016) Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of *Sphagnum* peatlands to drought, fire and warming. *Mires and Peat*, 18, 20. https://doi.org/10.19189/MaP.2016.OMB.244

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., Laggoun-Défarge, F. (2017) Vegetation composition controls temperature sensitivity of CO2 and CH4 emissions and DOC concentration in peatlands. *Soil Biology and Biochemistry*, 107, 164–167. https://doi.org/10.1016/j.soilbio.2017.01.005

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

Lhosmot, A., Bouchez, J., Steinmann, M., Lavastre, V., Bichet, V., Loup, C., Stefani, V., Boetsch, A., Chevet, J., Toussaint, M.-L., Gaillardet, J., Bertrand, G. (2022a) The origin and transfer of water and solutes in peatlands: a multi tracer assessment in the carbonated Jura Mountains. *Hydrological Processes*, 36, e14781. https://doi.org/10.1002/hyp.14781

Lhosmot, A., Jacotot, A., Steinmann, M., Binet, P., Toussaint, M.-L., Gogo, S., Gilbert, D., Coffinet, S., Laggoun-Deffarge, F., Bertrand, G. (2022b) Biotic and abiotic control over diurnal CH_4 fluxes in a temperate transitional poor fen ecosystem. *Ecosystems*, 26, 951–968. https://doi.org/10.1007/s10021-022-00809-x

Li, Q., Gogo, S., Leroy, F., Guimbaud, C., Laggoun-Défarge, F. (2021a) Response of peatland CO_2 and CH_4 fluxes to experimental warming and the carbon balance. *Frontiers in Earth Science*, 9, 631368. https://doi.org/10.3389/feart.2021.631368

Li, Q., Leroy, F., Zocatelli, R., Gogo, S., Jacotot, A., Guimbaud, C., Laggoun-Défarge, F. (2021b) Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change. *Soil Biology and Biochemistry*, 153, 108077. https://doi.org/10.1016/j.soilbio.2020.108077

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G. (2008) Peatlands and the carbon cycle: from local processes to global implications - a synthesis. *Biogeosciences*, 5, 1475–1491.

Lindsay, R. (2010) *Peatbogs and Carbon: a Critical Synthesis to Inform Policy Development in Oceanic Peat Bog Conservation and Restoration in the Context of Climate Change*. Environmental Research Group, University of East London, 315 pp.

Liu, H., Price, J., Rezanezhad, F., Lennartz, B. (2020) Centennial-scale shifts in hydrophysical properties of peat induced by drainage. *Water Resources Research*, 56, e2020WR027538. https://doi.org/10.1029/2020WR027538

Liu, H., Gu, Y., Ge, J., Yu, Z., Xu, X., Zhang, Z., Cheng, S., Xie, S. (2022) The response of the Dajiuhu Peatland ecosystem to hydrological variations: Implications for carbon sequestration and peatlands conservation. *Journal of Hydrology*, 612, 128307. https://doi.org/10.1016/j.jhydrol.2022.128307

Liu, H., Rezanezhad, F., Zhao, Y., He, H., Van Cappellen, P., Lennartz, B. (2024) The apparent temperature sensitivity (Q10) of peat soil respiration: A synthesis study. *Geoderma*, 443, 116844. https://doi.org/10.1016/j.geoderma.2024.116844

Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G. and 66 others (2021) Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, 11, 70–77. https://doi.org/10.1038/s41558-020-00944-0

Luyssaert, S., Abril, G., Andres, R., Bastviken, D. and 33 others (2012) The European land and inland water CO_2, CO, CH_4 and N_2O balance between 2001 and 2005. *Biogeosciences*, 9, 3357–3380. https://doi.org/10.5194/bg-9-3357-2012

Moore, T.R., Dalva, M. (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *Journal of Soil Science*, 44, 651–664. https://doi.org/10.1111/j.1365-2389.1993.tb02330.x

Moore, T.R., Knowles, R. (1989) The influence of water table levels on methane and carbon dioxide emissions from peatland soils. *Canadian Journal of Soil Science*, 69, 33–38. https://doi.org/10.4141/cjss89-004

Morris, P.J., Waddington, J.M., Benscoter, B.W., Turetsky, M.R. (2011) Conceptual frameworks in peatland ecohydrology: looking beyond the two-layered (acrotelm-catotelm) model. *Ecohydrology*, 4, 1–11. https://doi.org/10.1002/eco.191

Morton, P.A., Heinemeyer, A. (2019) Bog breathing: the extent of peat shrinkage and expansion on blanket bogs in relation to water table, heather management and dominant vegetation and its implications for carbon stock assessments. *Wetlands Ecology and Management,* 27, 467–482. https://doi.org/10.1007/s11273-019-09672-5

Nichols, J.E., Peteet, D.M. (2019) Rapid expansion of northern peatlands and doubled estimate of carbon storage. *Nature Geosciences*, 12, 917–921. https://doi.org/10.1038/s41561-019-0454-z

Nugent, K.A., Strachan, I.B., Roulet, N.T., Strack, M., Frolking, S., Helbig, M. (2019) Prompt active restoration of peatlands substantially reduces climate impact. *Environmental Research Letters*, 14, 124030. https://doi.org/10.1088/1748-9326/ab56e6

Oestmann, J., Dettmann, U., Düvel, D., Tiemeyer, B. (2022) Experimental warming increased greenhouse gas emissions of a near-natural peatland and *Sphagnum* farming sites. *Plant and Soil*, 480, 85–104. https://doi.org/10.1007/s11104-022-05561-8

Oudin, L., Hervieu, F., Michel, C., Perrin, C., Andréassian, V., Anctil, F., Loumagne, C. (2005) Which potential evapotranspiration input for a lumped rainfall–runoff model? *Journal of Hydrology*, 303, 290–306. https://doi.org/10.1016/j.jhydrol.2004.08.026

Page, S.E., Baird, A.J. (2016) Peatlands and global change: response and resilience. *Annual Review of Environment and Resources*, 41, 35–57. https://doi.org/10.1146/annurev-environ-110615-085520

Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M., Stringer, L. (2008) *Assessment on Peatlands, Biodiversity and Climate Change: Main Report.* Global Environment Centre, Kuala Lumpur & Wetlands International, Wageningen, 179 pp.

Pearson, M., Penttilä, T., Harjunpää, L., Laiho, R., Laine, J., Sarjala, T., Silvan, K., Silvan, N. (2015) Effects of temperature rise and water-table-level drawdown on greenhouse gas fluxes of boreal sedge fens. *Boreal Environment Research*, 20, 489–505.

Peichl, M., Gažovič, M., Vermeij, I., de Goede, E., Sonnentag, O., Limpens, J., Nilsson, M.B. (2018) Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production. *Scientific Reports*, 8, 8012. https://doi.org/10.1038/s41598-018-26147-4

Perryman, C.R., McCalley, C.K., Ernakovich, J.G., Lamit, L.J., Shorter, J.H., Lilleskov, E., Varner, R.K. (2022) Microtopography matters: belowground CH_4 cycling regulated by differing microbial processes in peatland hummocks and lawns. *Journal of Geophysical Research: Biogeosciences*, 127(8), e2022JG006948. https://doi.org/10.1029/2022JG006948

Premke, K., Attermeyer, K., Augustin, J., Cabezas, A., Casper, P., Deumlich, D., Gelbrecht, J., Gerke, H.H., Gessler, A., Grossart, H., Hilt, S., Hupfer, M., Kalettka, T., Kayler, Z., Lischeid, G., Sommer, M., Zak, D. (2016) The importance of landscape diversity for carbon fluxes at the landscape level: small-scale heterogeneity matters. *WIREs Water*, 3, 601–617. https://doi.org/10.1002/wat2.1147

Price, J.S., Heathwaite, A.L., Baird, A.J. (2003) Hydrological processes in abandoned and restored peatlands: An overview of management approaches. *Wetlands Ecology and Management*, 11, 65–83.

Ratcliffe, J.L., Campbell, D.I., Clarkson, B.R., Wall, A.M., Schipper, L.A. (2019) Water table fluctuations control CO_2 exchange in wet and dry bogs through different mechanisms. *Science of The Total Environment*, 655, 1037–1046. https://doi.org/10.1016/j.scitotenv.2018.11.151

Rubel, F., Brugger, K., Haslinger, K., Auer, I. (2017) The climate of the European Alps: Shift of very high resolution Köppen-Geiger climate zones 1800–2100. *Meteorologische Zeitschrift*, 26, 115–125. https://doi.org/10.1127/metz/2016/0816

Salmon, E., Jégou, F., Guenet, B., Jourdain, L. and 27 others (2022) Assessing methane emissions for northern peatlands in ORCHIDEE-PEAT revision 7020. *Geoscientific Model Development*, 15, 2813–2838. https://doi.org/10.5194/gmd-15-2813-2022

Samaniego, L., Thober, S., Kumar, R., Wanders, N., Rakovec, O., Pan, M., Zink, M., Sheffield, J., Wood, E.F., Marx, A. (2018) Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change*, 8, 421–426. https://doi.org/10.1038/s41558-018-0138-5

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., Zielińska, M., Robroek, B.J.M., Jassey, V.E.J., Buttler, A., Chojnicki, B.H. (2018) The impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in northern Poland. *Wetlands*, 38, 551–563. https://doi.org/10.1007/s13157-018-0999-4

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P., Dosio, A. (2018) Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, 38, 1718–1736. https://doi.org/10.1002/joc.5291

Strakova, P., Niemi, R.M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R. (2011) Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. *Biogeosciences*, 2741–2755. https://doi.org/doi:10.5194/bg-8-2741-2011

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J. and 34 others (2019) Widespread drying of European peatlands in recent centuries. *Nature Geosciences*, 12, 922–928. https://doi.org/10.1038/s41561-019-0462-z

Tanneberger, F., Appulo, L., Ewert, S., Lakner, S., Ó Brolcháin, N., Peters, J., Wichtmann, W. (2021) The power of nature-based solutions: How peatlands can help us to achieve key EU sustainability objectives. *Advanced Sustainable Systems*, 5, 2000146. https://doi.org/10.1002/adsu.202000146

Toussaint, M.-L., Bertrand, G., Lhosmot, A., Gilbert, D., Binet, P., Jacotot, A., Gogo, S., Laggoun-Defarge, F. (2020a) *Soil-Meteorological Dataset Collected at Frasne Peatland (192ha, Jura Mountains, France).* https://doi.org/10.5281/ZENODO.3763342

Toussaint, M.-L., Bertrand, G., Lhosmot, A., Gilbert, D., Binet, P., Gogo, S., Laggoun-Défarge, F. (2020b) *Water Table Depth Dataset Collected at Frasne Peatland (192ha, Jura Mountains, France).*

https://doi.org/10.5281/ZENODO.3763766

Trinder, C.J., Johnson, D., Artz, R.R.E. (2008) Interactions among fungal community structure, litter decomposition and depth of water table in a cutover peatland: Fungi, litter and water table on a cutover peatland. *FEMS Microbiology Ecology*, 64, 433–448. https://doi.org/10.1111/j.1574-6941.2008.00487.x

Tuittila, E.-S., Vasander, H., Laine, J. (2004) Sensitivity of C sequestration in reintroduced *Sphagnum* to water-level variation in a cutaway peatland. *Restoration Ecology*, 12, 483–493. https://doi.org/10.1111/j.1061-2971.2004.00280.x

Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkkinen, K., Moore, T.R., Myers-Smith, I.H., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N., Tuittila, E.-S., Waddington, J.M., White, J.R., Wickland, K.P., Wilmking, M. (2014) A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Global Change Biology*, 20, 2183–2197. https://doi.org/10.1111/gcb.12580

Ueyama, M., Yazaki, T., Hirano, T., Futakuchi, Y., Okamura, M. (2020) Environmental controls on methane fluxes in a cool temperate bog. *Agricultural and Forest Meteorology*, 281, 107852. https://doi.org/10.1016/j.agrformet.2019.107852

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

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., Moore, P.A. (2015) Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8, 113–127. https://doi.org/10.1002/eco.1493

Walker, A.P., Carter, K.R., Gu, L., Hanson, P.J., Malhotra, A., Norby, R.J., Sebestyen, S.D., Wullschleger, S.D., Weston, D.J. (2017) Biophysical drivers of seasonal variability in *Sphagnum* gross primary production in a northern temperate bog. *Journal of Geophysical Research: Biogeosciences*, 122, 1078–1097. https://doi.org/10.1002/2016JG003711

Wang, M(iaorun)., Liu, H., Lennartz, B. (2021) Small-scale spatial variability of hydro-physical properties of natural and degraded peat soils. *Geoderma*, 399, 115123. https://doi.org/10.1016/j.geoderma.2021.115123

Wang, M(ing)., Han, Y., Xu, Z., Wang, S., Jiang, M., Wang, G. (2021) Hummock-hollow micro-topography affects soil enzyme activity by creating environmental heterogeneity in the sedge-dominated peatlands of the Changbai Mountains, China. *Ecological Indicators*, 121, 107187. https://doi.org/10.1016/j.ecolind.2020. 107187

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, R.D. (2013) Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, 16, 1285–1293. https://doi.org/10.1111/ele.12167

Wheeler, B.D., Proctor, M.C.F. (2000) Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology*, 88, 187–203. https://doi.org/10.1046/j.1365-2745.2000.00455.x

Williams, T.G., Flanagan, L.B. (1996) Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*. *Oecologia*, 108, 38–46. https://doi.org/10.1007/BF00333212

Xu, J., Morris, P.J., Liu, J., Holden, J. (2018) PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *CATENA*, 160, 134–140. https://doi.org/10.1016/j.catena.2017.09.010

Yu, Z. (2011) Holocene carbon flux histories of the world's peatlands: Global carbon-cycle implications. *The Holocene*, 21, 761–774. https://doi.org/10.1177/0959683610386982

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J. (2010) Global peatland dynamics since the last glacial maximum: Global peatlands since the LGM. *Geophysical Research Letters*, 37, L13402. https://doi.org/10.1029/2010GL043584

Zak, D., McInnes, R.J. (2022) A call for refining the peatland restoration strategy in Europe. *Journal of Applied Ecology*, 59, 2698–2704. https://doi.org/10.1111/1365-2664.14261

Submitted 05 Jul 2024, final revision 05 Feb 2025
Editor: Gerald Jurasinski

Authors for correspondence:
PhD Alexandre Lhosmot, Département de Géographie, Université de Montréal, QC, Montréal, campus MIL 1375, ave Thérèse-Lavoie-Roux, Canada. E-mail: alexandrelhosmot@gmail.com
Associate Professor Guillaume Bertrand, Chrono-Environnement, Université Marie et Louis Pasteur, UMR6249, CNRS, 4 place Tharradin, 25200 Montbéliard, France. E-mail: guillaume.bertrand2@univ-fcomte.fr