Carbon balance and spatial variability of CO₂ and CH₄ fluxes in a *Sphagnum*-dominated peatland in temperate climate

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Abstract. Peatlands are a highly effective natural carbon sink. However, the future of the carbon stored in these ecosystems is still uncertain because of the pressure they undergo. As estimation of the peatland carbon balance shows whether the system functions as carbon sink or source. La Guette peatland is a temperate *Sphagnum*-dominated peatland invaded by vascular plants, mainly *Molinia caerulea*. The studied site was hydrologically disturbed for years by a road crossing its southern part and draining water out of the system. Our aim was to estimate the main carbon fluxes and to calculate the carbon balance at the ecosystem scale. To reach this goal, CO₂ and CH₄ fluxes, DOC content as well as environmental variables were measured monthly for 2 years on 20 plots spread across the site to taking into account spatial variability. The peatland carbon balance was estimated using empirical models. Results showed that the CO₂ fluxes were above 1000 gC m⁻² yr⁻¹. In 2013 and 2014 the peatland was a net C source to the atmosphere with an emission of 220±33 gC m⁻² yr⁻¹. These results provided evidence that restoration should be performed in order to reduce the water losses and favour the *Sphagnum*-dominance of this peatland.

Keywords: CO₂; CH₄; DOC; peatland; ecosystem respiration; gross primary production

1 Introduction

Peatlands are vegetated wetlands that can act as a powerful natural Carbon (C) sink. While they cover only 3% of the emerged lands (Lappalainen, 1996), the C stored in their soils has been estimated to range from 473 to 621 GtC (Yu *et al*, 2010), which represents more than 30% of the C stored in terrestrial soils, estimated between 1500 to 2400 PgC (Ciais *et al*, 2013). Thus, peatlands are of a great importance in the actual context of global changes and their preservation is essential to prevent the C stored in soil to be released to the atmosphere. However, peatlands are mostly located at high latitudes of the northern hemisphere (Strack, 2008) where the greatest climate changes are predicted to occur by the IPCC models (Christensen *et al*, 2013). Under these modified climatic conditions, the behaviour of peatlands in terms of C cycle is still uncertain.

Actually, the C balance in peatlands covers a wide range of C functioning, from sink to source (Beyer and Höper, 2015; Carroll and Crill, 1997; Koehler *et al*, 2011; Vanselow-Algan *et al*, 2015). However, the majority of these estimations were calculated on high latitudes sites, mostly in Northern Europe or in Canada where the winter is cold (Peichl *et al*, 2014; Strack and Zuback, 2013; Trudeau *et al*, 2014; Waddington and Roulet, 2000), even if few studies have been conducted in lower latitudes (below 50°) where warmer climatic conditions prevail (*e.g.* Bortoluzzi *et al*, 2006).

In addition to climatic pressure, peatlands can be submitted to anthropic disturbances, and temperate peatlands have been widely transformed by the past into agricultural or forestry lands (Joosten and Clarke, 2002). Drainage that leads to major hydrological disruption is usually a prerequisite before peatland exploitation (Beyer *et al*, 2015). For example, lowering the water table level can change the equilibrium between CO₂ and CH₄ emissions and thus modify the C balance of the ecosystem (Chimner *et al*, 2017). Indeed, increasing the thickness of the oxic layer can lead to (i) higher CO₂ fluxes to the atmosphere due to faster decomposition rates of soil organic matter and (ii) lower CH₄ fluxes due to the decrease in CH₄ production and/or increase in CH₄ oxidation during its transport to the surface of the soil (Lund *et al*, 2012; Pelletier *et al*, 2007). As a result of both drainage and climatic change, most temperate peatlands are now invaded by vascular plants (Berendse *et al*, 2001; Buttler *et al*, 2015).

53 Invasive vegetation can play a major role in CO₂ and CH₄ emissions by (i) producing litter that is more
54 easily degradable than mosses, (ii) altering the growth of subservient species such as *Sphagnum*
55 mosses, and/or (iii) allowing more CH₄ to be transferred to the atmosphere through the plant
56 aerenchyma (Bubier *et al*, 2007; Francez and Vasander, 1995; Gogo *et al*, 2011; Armstrong et al.,
57 2015). The role of the vegetation on the C fluxes are often related to a comparison between different
58 plant community composition (Ward et al., 2013; Noyce et al., 2014); however only a few of them
59 have attempted to integrate vegetation directly in a C balance model (Bortoluzzi *et al*, 2006; Kandel et
60 al., 2013; Leroy et al., 2019).

61 In this context, the aim of this study was to investigate what is the C-sink function of a disturbed
62 temperate peatland and the mechanisms controlling it. Here, CO₂ fluxes and CH₄ emissions were
63 monthly measured on twenty points distributed homogeneously over a temperate peatland recently
64 invaded by a graminoid plants, *Molinia caerulea*. Then C fluxes measurements were related to biotic
65 and abiotic factors to estimate the annual C budget by using CO₂ and CH₄ models including, or not,
66 vegetation index. Thus, the hypotheses tested were:

- 67 (i) the drainage and the invasion by vascular plants promoted the C emissions and lead the
68 peatland to act as a C source
- 69 (ii) the use of vegetation index into models leads to a better representation of fluxes

70 **2. Materials and methods**

71 **2.1 Description of the La Guette peatland**

72 The study was performed in La Guette peatland, a *Sphagnum* peatland located in France (Neuvy-sur-
73 Barangeon, Cher, N 47°1944, E 2°1704; Fig. 1). It is a transitional poor fen (with a pH between 4 and
74 5 and a conductivity lower than 80 µS m⁻²) with a maximum peat thickness of about 180 cm. Mean
75 annual temperature was 11°C and mean annual rainfall 732 mm for the period 1971–2000 (Gogo et
76 al., 2011). The site is drained in its south part by a road built before 1945 that crosses the peatland. In
77 2009 the drainage ditch of the road was scraped, lowering the output level and consequently increasing
78 the water losses. This hydrological disturbance in addition to a fire (in 1970's) has probably contributed

to the invasion of the site by vascular plants, mainly *Pinus sylvestris*, *Betula* spp. (*Betula verrucosa* and *pubescens*) and *Molinia caerulea*; This *Poaceae* is now invading numerous peatlands in Europe mainly, due to an increase of the nitrogen deposition and drainage (Chambers et al., 1999) and thus at the detriment of the specific peatland species composed of *Sphagnum cuspidatum* and *Sphagnum rubellum*, *Eriophorum angustifolium*, *Erica tetralix* and *Calluna vulgaris*. .

2.2 Carbon fluxes measurements and calculation

In June 2011, 20 stations were set up on the peatland by dividing the area in twenty squares with a grid and choosing randomly one plot (2 m²) within each square (stratified random sampling). This method allowed a homogeneous spatial covering of the studied site (Fig. 1). Fluxes were monthly measured between March 2013 and February 2015 using a semi-cylindrical transparent static chamber equipped (30 cm of diameter, 30 cm height). The chamber was equipped with a HMP 75 sensor (Vaisala Oyj, Vantaa, Finland) to record the temperature and air humidity variations within the chamber during the incubations. In addition, a small fan allowed the air to be homogenized within the chamber (Pumpanen et al, 2004). CO₂ fluxes were measured in each of the 20 stations during twenty field campaigns thanks to a CO₂ sensor (GMP 343 model, Vaisala Oyj, Vantaa, Finland) placed inside the chamber. Fluxes were measured at light for Net Ecosystem Exchange (NEE) and with the chamber covered with a light insulating fabric to simulate night conditions and measure the Ecosystem Respiration (ER). Each measurement lasted between 3 to 5 minutes, and the CO₂ concentration inside the chamber was recorded at 5Hz. CH₄ fluxes were measured thanks to the SPIRIT instrument, an Infrared Spectrometer developed by the Laboratory of Physics and Chemistry of Environment and Space, (LPC2E, Orléans, France, Guimbaud et al, 2016, 2011; Robert, 2007). For logistical reasons (weight and long start-up time of SPIRIT), CH₄ measurements were only performed during 12 field campaigns and on only 5 stations. These measurements regularly required to access to the plots, so, wooden planks was used as mobile pontoons to limits disturbances

CO₂ and CH₄ fluxes were then calculated as follow:

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

105 With F the net gas flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$); dX/dt the gas concentration ($\mu\text{mol mol}^{-1}$) variation during the
 106 incubation time (s); P the atmospheric pressure (Pa); R the ideal gas constant ($8.3144621 \text{ J mol}^{-1} \text{K}^{-1}$);
 107 T the average temperature (K) within the chamber during the incubation; V the total volume of the
 108 system (m^3); and S the chamber surface (0.283 m^2). For CO_2 fluxes, F corresponds to NEE when
 109 measured in light, and to ER when measured in the dark.

110 In addition with gas fluxes, dissolved organic carbon (DOC) flux was estimated monthly during the
 111 studied period. Water was sampled at the peatland outlet, filtered at $0.45 \mu\text{m}$ and *in-situ* acidified with
 112 2 drops of H_3PO_4 . The DOC concentration was then determined in the laboratory thank to a TOC-
 113 LCPH analyser (Shimadzu, Kyoto, Japan).

114 **2.2 Monitoring of environmental variables and vegetation cover**

115 Soil-meteorological variables were automatically monitored at a 30-min frequency during the entire
 116 studied period thanks to an automatic station installed on the site in November 2010 (Fig. 1).
 117 Parameters recorded were the total rainfall, net solar radiation, atmospheric pressure, wind direction
 118 and speed, air temperature, relative humidity and soil temperature at -5, -10, -20, and -40 cm depths. In
 119 addition, four automatic piezometer spread into the peatland allowed to record the Water Table Level
 120 (WTL) variations at the ecosystem scale (Binet *et al*, 2013). In addition to automatic measurements,
 121 manual recording of WTL, Photosynthetically Active Radiation (PAR), soil temperatures (-5, -10, -
 122 15, -20, -25, -30, -40, -50, -60, -70, -80, -90, -100 cm depth) and atmospheric pressure were realized
 123 at each measurement campaign.

124 A vegetation Index (VI) was calculated (Eq. 2) by summing the percentage of vegetation cover in each
 125 soil collar following three distinct plant strata: the muscular (*Sphagnum* spp.), herbaceous (*Molinia*
 126 *caerulea* and *Eriophorum augustifolium*), and shrub (*Erica tetralix* and *Calluna vulgaris*) strata
 127 divided by the total potential cover TC ($\text{TC} = n \times 100$, n being the number of vegetation strata
 128 recorded):

$$129 \quad IV = \frac{MS+HS+SS}{TC} \quad (2)$$

130 With MS, HS and SS the percentages of cover of the muscular, herbaceous and shrub strata, and TC
 131 the sum of percentages of the three strata.

132 **2.3 Modelling of high-frequency ER, GPP, F_{CH4} and DOC**

133 The C balance estimation was conducted in 3 successive steps: i) calibration to establish the
 134 relationship between gas fluxes and environmental variables; ii) evaluation to determine the relevance
 135 of these relationships in a broader context; and iii) interpolation to integrate these relationships over
 136 time and to calculate a Net Ecosystem Carbon Balance (Chapin et al, 2006):

$$137 \text{NECB} = \text{GPP} - \text{ER} - \text{F}_{\text{CH}_4} - \text{F}_{\text{DOC}} - \text{F}_{\text{DIC}} - \text{F}_{\text{PC}} - \text{F}_{\text{VOC}} - \text{F}_{\text{CO}} \quad (3)$$

138 with GPP (Gross Primary Production), F_{CH4}, F_{DOC}, F_{DIC}, F_{PC}, F_{COV}, F_{CO}, the fluxes of CH₄, Dissolved
 139 Organic Carbon (DOC), Dissolved Inorganic Carbon (DIC), Particulate Carbon (PC), Volatile Organic
 140 Carbon (VOC) and Carbon Monoxide (CO), respectively. In terms of quantity, the first 4 terms are the
 141 most abundant and were estimated in the present study to calculate the C budget. By convention the
 142 negative sign refers to carbon lost by the ecosystem.

143 The available data were averaged by field campaign to reduce the spatial variability of the fluxes and
 144 then used to produce a high-frequency (1-hour) dataset. For this, the relationship between gas fluxes
 145 and environmental variables was fitted using non-linear regression curves. Robustness of adding a
 146 variable to the models was evaluated following three comparative criteria. First, the adjusted R² (R²_a;
 147 Eq. 4) were used to estimate the proportion of explained variance:

$$148 R_a^2 = 1 - \left(1 - \left(1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2} \right) \right) * \frac{n-1}{n-p-1} \quad (4)$$

149 with R² the traditional R², y the measured data, $\hat{y}$ the modelled data, n the number of observations and
 150 p the number of predictors.

151 Then, the Normalized Root Mean Square Error (NRMSE; Eq. 5) was applied to evaluate the
 152 differences between measured and modelled data points respectively:

$$153 \text{NRMSE} = 100 * \frac{\sqrt{\frac{\sum (y - \bar{y})^2}{n}}}{\bar{y}} \quad (5)$$

154 with $\bar{y}$ the average of the measured data.

155 Finally, the relevance of adding a new variable in the model was estimated by the Akaike Information
 156 Criterion (AIC; Eq. 6; Akaike, 1974; Burnham and Anderson, 2002).

$$157 \quad AIC = -2 \times \log(L) + 2 \times p \quad (6)$$

158 with L the maximum likelihood.

159 The NEE, ER, and CH₄ fluxes were modelled separately and the annual carbon balance was calculated
 160 as the sum of the model interpolations at a 1h time step. This interpolation was done made using (i)
 161 the high frequency measurement values for temperature and (ii) a linear interpolation between the
 162 punctual measurements for vegetation. For all gaseous fluxes two models are presented: one using
 163 temperature as this model is widely used (Ballantyne et al, 2014) and, the other being the best model
 164 estimation using vegetation (Bortoluzzi et al, 2006; Kandel et al, 2013). Evaluation of models 1 and 2
 165 for GPP, ER and FCH₄ was realized using an independent dataset that includes CO₂ and CH₄ fluxes
 166 conducted in the same peatland in 2014 and using similar techniques as in the present study
 167 (unpublished data).

168 For GPP, the saturated GPP (GPP_{sat}) was first calculated following June *et al.* (2004) (Eq. 7), and
 169 secondly by a modified version of the equation that incorporates the vegetation index (Eq. 8):

$$170 \quad GPP_{sat-1} = a * e^{\left(\frac{T-b}{c}\right)^2} \quad (7)$$

$$171 \quad GPP_{sat-2} = (a * VI + d) * e^{\left(\frac{T-b}{c}\right)^2} \quad (8)$$

172 Then, GPP-1 and GPP-2 were calculated using Eq. 9 proposed by Bubier *et al.* (1995) and reused in
 173 many studies (e.g. Bortoluzzi *et al.*, 2006; Worrall *et al.*, 2009):

$$174 \quad GPP = \frac{GPP_{sat} * i * PAR}{GPP_{sat} + i * PAR} \quad (9)$$

175 with a the rate of electron transport at light saturation (μmol m⁻² s⁻¹), b the optimal temperature for a
 176 (°C), and c the difference in temperature from b at which GPP_{sat} equals to e⁻¹ of its value at b (June *et al.*
 177 *et al.*, 2004), T the air temperature (°C), and VI the vegetation index.

178 Concerning ER, the equation proposed by Luo et Zhou (2006) was used for ER-1 and modified with
 179 the integration of the herbaceous strata (HS) for ER-2:

$$180 \quad ER-1 = a * e^{(b * T)} \quad (10)$$

181 $ER-2 = (a * HS + c) * e^{(b * T)}$ (11)
 182 with T the air temperature (°C); a, b and c the fitted parameters and HS the cover of the herbaceous
 183 strata (%).

184 Finally, modelled NEE have been calculated from GPP and ER as $NEE = GPP - RE$. Negative values
 185 of NEE correspond to an emission of carbon from the ecosystem to the atmosphere and positive values
 186 to a fixation of carbon.

187 The two models of CH₄ fluxes were estimated following:

$$188 F_{CH_4-1} = a * e^{(b * T)} \quad (12)$$

$$189 F_{CH_4-2} = a * e^{(b * VI)} \quad (13)$$

190 with T the air temperature (°C); a and b the fitted parameters and IV the vegetation index.

191 High frequency of DOC fluxes (F_{DOC}) have been extrapolated using the monthly measured
 192 concentrations of DOC and an estimation of the water quantities leaving the ecosystem (D) using a
 193 hydrological model specifically calibrated for the La Gnette peatland (Binet *et al*, 2013):

$$194 F_{DOC} = D * [DOC] \quad (14)$$

195 **2.5 Spatial variability of CO₂ fluxes**

196 To estimate the spatial variability of the CO₂ fluxes, the best models were also calibrated for each of
 197 the 20 plots individually. Hence the model parameters R²_a and NRMSE were estimated for each
 198 measurement point as well as the annual CO₂ flux.

199 **3. Results**

200 **3.1 Environmental monitoring**

201 Variations of air temperature, rainfall, and water table level are presented in Fig. 2. Between 2011 and
 202 2015 the mean annual air temperature measured by the meteorological station varied between 9.5 and
 203 11.5°C (Fig. 2A), with a high seasonal variability. In addition, average air temperature measured in
 204 the 20 stations during the field campaigns ranged from 6 to 32°C. Total rainfall recorded on the site
 205 for 2014 and 2015 were quite similar with 935 and 940 mm, respectively (Fig. 2B). The WTL measured
 206 by the automatic piezometers ranged between -17.5 and -0.1 cm during the studied period, with clear

seasonal variability (Fig. 2C). The average WTL manually measured in the 20 stations during the field campaigns showed a similar cyclicity (Fig. 2C) with deeper level during summer (maximum depth of -18 and -10.5 cm in 2013 and 2014, respectively) than during winter. The seasonal variability of vegetation was controlled by the graminoids which started to grow earlier in 2014 (April) than in 2013 (May) (Fig. 3). Also, in 2014 the vegetation index (VI) was slightly higher than in 2013, at 0.45 and 0.51 respectively.

3.2 CO₂, CH₄ and DOC fluxes

Results of CO₂ fluxes (NEE, ER and calculated GPP) are presented in Fig. 2. CO₂ fluxes (GPP and ER) showed a clear seasonal trend with a maximum in summer. In 2013 the GPP averaged maximum occurred at the end of July reaching $12.80 \pm 4.91 \mu\text{mol m}^{-2} \text{s}^{-1}$ and ER $9.43 \pm 3.48 \mu\text{mol m}^{-2} \text{s}^{-1}$, with the maximum of both variables reached at the end of July (Fig. 2A and B). In 2014 the GPP and ER averaged maxima were reached earlier, in June with $13.16 \pm 4.70 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $7.83 \pm 2.55 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively (Fig. 2A and B). Averages values of GPP for 2013 and 2014 were 7.12 ± 5.19 and $6.56 \pm 4.72 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively. For ER, the average values were, for 2013 and 2014, 4.27 ± 3.16 and $3.63 \pm 2.56 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 4 A and B). Mean values of NEE for 2013 and 2014 were 2.85 ± 3.05 and $2.93 \pm 2.77 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 4 C). In comparison to CO₂, CH₄ emissions showed a lower magnitude with fluxes below $0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$. A clear difference was also visible between 2013 and 2014 respectively (Fig. 5). In 2013 CH₄ average fluxes were $0.04 \pm 0.03 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas they reached $0.10 \pm 0.08 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2014. For both years, the average DOC concentrations measured at the outlet of the peatland were $18.5 \pm 7.7 \text{ mg L}^{-1}$. Thus, the average cumulated flux of DOC leaving the peatland for 2013 and 2014 was $12 \pm 1 \text{ gC m}^{-2} \text{yr}^{-1}$ (8 ± 1 and $16 \pm 1 \text{ gC m}^{-2} \text{yr}^{-1}$ in 2013 and 2014, respectively).

3.3 Model selection

Comparisons between modelled and measured values of ER, GPP and CH₄, using models 1 and 2 during calibration and evaluation are presented in Fig. 6. During models' calibration, incorporation of vegetation in the ER model (leading to ER-2) improved the representation of ER, yielded to a higher

R^2 and a lower NRMSE than without vegetation (ER-1, Fig. 6A and Table 1). However, the difference between ER-1 and ER-2 is low but the AIC, which decreased from 47 to 35, confirmed this observation (Table 1). ER was estimated to 1286 ± 231 and 1261 ± 164 gC m⁻² yr⁻¹ for ER-1 and ER-2, respectively. Concerning GPP, GPP-2 realized a higher R^2_a score, a lower NRMSE, and a lower AIC compared to GPP-1 (Fig. 6C and Table 1). Resulting cumulated fluxes were 1290 ± 400 and 1070 ± 203 gC m⁻² yr⁻¹ for GPP-1 and GPP-2. For CH₄, only CH₄-2 (including vegetation) that showed a satisfying result (Fig. 6E and Table 1) was used to estimate the CH₄ cumulated fluxes. Evaluation of the GPP models showed high NRMSE values with 47 and 58 % for GPP-1 and GPP-2 respectively (Fig. 6D and Table 1). CH₄ evaluation led to even higher NRMSE values with 68 % for F_{CH₄}-2. R^2_a negative values due to the use of non-linear regression were here irrelevant (Fig. 6F and Table 1). On the contrary, the ER models led to high R^2_a and low NRMSE values with ER-2 performing better than ER-1: R^2_a values increased from 0.16 to 0.59 and NRMSE values decreased from 35 to 23 % (Fig. 6E and Table 1).

3.4 Calculation of Net Ecosystem Carbon Balance (NECB)

NECB (estimated here as GPP-ER-F_{CH₄}-F_{DOC}) was calculated first without inclusion of vegetation in the model (GPP-1, ER-1) and then with vegetation (GPP-2, ER-2), at the exception of the calculation of CH₄ for which only the model with vegetation was used (CH₄-2). Whether model 1 or 2 was used, the NECB showed that the peatland was a source of carbon to the atmosphere in 2013 and 2014 with -26 gC m⁻² yr⁻¹ and -220 gC m⁻² yr⁻¹ for model 1 or 2, respectively (Table 2). The high difference in the estimation of NECB was principally due to the GPP estimations (Table 1). In addition, NECB was higher in 2013 than in 2014 (Table 2). NECB was mainly driven by CO₂ fluxes as CH₄ and DOC fluxes are two orders of magnitude lower. However, in terms of the Global Warming Potential (GWP), CH₄ fluxes are not negligible with CH₄ having a GWP 34 times higher than CO₂ for the 100-year time horizon (Myhre *et al.*, 2013).

3.4 Spatial variability

The calibration of ER-2 and GPP-2 on each measurement plot enabled the spatial variability of the CO₂ fluxes on the site to be estimated. For ER-2, the R^2_a of the individual plots were above 0.5 (with

the exception of measurement plot n°10) and the NRMSE values were below 50% (Fig. 7). The model parameter variations ranged from 0 to 0.015 for a, from 0.035 to 0.11 for b, and from 0.18 to 1.03 for c. For GPP-2 the R^2_a were above 0.5 and the NRMSE values between 20 and 60% (with the exception of point n°10). Model parameters for GPP-2 showed higher variations: between -6.1 and 66 for a, 23.9 and 90.4 for b, 6.2 and 60.0 for c and -10.7 and 27.1 for d (Fig. 8). For both measurement years, cumulated GPP fluxes ranged from 511 to 1420 gC m⁻² yr⁻¹, with most values around 1100 gC m⁻² yr⁻¹ and an average of 1052±238 gC m⁻² yr⁻¹. For ER, the cumulated fluxes ranged from 842 to 2363 gC m⁻² yr⁻¹ with an average of 1215±362 gC m⁻² yr⁻¹ (Fig. 7 and 8).

4. Discussion

4.1 Rationale behind the high C fluxes recorded and the C source functioning

CO₂ fluxes measured at La Guette peatland were above 1000 gC m⁻² yr⁻¹ for the GPP and the ER, whatever the model used. These fluxes were high compared to those of boreal peatlands. Trudeau *et al.* (2014) and Peichl *et al.* (2014) found GPP and ER fluxes between 100 and 500 gC m⁻² yr⁻¹ approximately for sites located in Quebec, Canada and in Northern Sweden respectively. However, these large fluxes were close to those found for sites with a high Mean Annual Temperature (MAT). For instance, Beyer and Höper (2015) found for a site with similar vegetation (*Molinia caerulea*, *Eriophorum augustifolium*, *Sphagnum* spp.) and with a MAT of 8.6°C, GPP fluxes between 534 and 1058 gC m⁻² yr⁻¹ and ER fluxes between 420 and 1052 gC m⁻² yr⁻¹. Thus, the large fluxes measured in La Guette peatland can be related to the relatively warmer climate compared to peatlands at higher latitudes. However, a MAT alone cannot explain why the system functioned as a source of C as other studies have shown that peatlands with a MAT above 8°C can still be a C sink. For instance, Koehler *et al.* (2011) estimated an uptake of -29.7 gC m⁻² yr⁻¹ in an Atlantic blanket bog with a MAT of 10.6°C for a 6-year average (2003-2008). The water table drawdown favours oxic reactions in a thicker soil layer, thus it is often adduced to explain the sources of C in peatlands. During the two years of measurements, La Guette peatland experienced favourable hydrological conditions due to heavy rainfall leading to high water table levels (Bernard-Jannin *et al.*, 2018). In spite of this, the system

functioned as a source to the atmosphere. Moreover, these high water table levels was spatially and temporally similar during the time course of the experiment (2013-2014, two exceptionally wet years), which did not allow to include this factor during the modelling processes. Higher variation of the water table depth could have brought to use equations with this parameters as Luan et al. (2015) to explain the GPP or Leroy et al. (2019) to model the CO₂ and CH₄ emissions. Nevertheless, inclusion of environmental parameters have to be considered up to their contribution to the models and to the models parsimony (Baird et al., 2019).

This C source function if the La Guette peatland is now also shown thanks to an Eddy-covariance tower and this with C fluxes similar as reported here (Jacotot et al., in prep). The main hypothesis concerning the mechanisms behind the C source function of the La Guette is linked to recent invasion of the site by *Molinia caerulea*, which is suspected to modify the C dynamic of the ecosystem. The observed C flux intensities and losses are often related to the plant community of the peatland. Vascular plants have higher gaseous C fluxes than bryophytes in poor fens (Leroy et al., 2019; Rydin and Jeglum, 2013) and a shift in peatland plant communities, especially those reducing *Sphagnum* dominance in favor of vascular vegetation, is expected to have significant effects on carbon storage (Dieleman et al., 2015). Now, the site is almost entirely invaded by vascular plants, especially *Molinia caerulea* in the graminoid strata (Gogo et al., 2011). The occurrence of this plant can stimulate the C uptake compared to *Sphagnum* peatland (Leroy et al., 2019). However it also significantly increase the ER respiration and CH₄ emissions through different physiological, phenological, and ecological traits (Gogo et al., 2011; Leroy et al., 2019). The ratio GPP/ER should be further assessed, especially in the context of interaction between different functional types (D'Angelo, 2015)

4.2 Implication of taking vegetation into account in the C budget estimation

The plants functional type often explained large of variation of the CO₂ and CH₄ fluxes (Armstrong et al., 2015). In this way, it was thus important to include the vegetation in our models, especially with the occurrence of *Molina caerulea*. Indeed, this species shows a high growth variability during the growing season (e.g. number of leaves, leave length) that could impact the C fluxes (more leaves, more GPP). However, its integration into models is seldom carried out (Bortoluzzi et al., 2006; Görres et al.,

2014), probably because of the difficulty in measuring the pertinent variables (leaf area index, leaves number). Including vegetation in models has led to a better representation of CO₂ fluxes. These results were in accordance with Bortoluzzi *et al.* (2006) who also found a lower NRMSE when vegetation was included in the model. Another way to take the vegetation into account is to use the Ratio Vegetation Index (RVI), which is a measurement of incoming and reflected radiation. This method was used by Görres *et al.* (2014) and led to an improvement for GPP modelling but not for ER. However, such an improvement using the RVI for ER modelling was found by Kandel *et al.* (2013) on a cultivated fen peatland in Denmark. Although the calibration of the model was as good for ER as for GPP, evaluation of the models presented more contrasted results since only ER-2 showed a high R^2_a and a low NRMSE. For F_{CH₄}-2 the evaluation revealed that the interpretation of the model outputs should be limited to the current study and could not be used to extrapolate fluxes for other times and spaces. Nevertheless, as hypothesis, model evaluations indicated that the inclusion of vegetation increased the model's capability to represent CO₂ fluxes.

4.3 The DOC exports

The quantities of DOC exported by La Gnette peatland are in the same order of magnitude of those present in the literature (e.g. Waddington and Roulet, 2000; Worrall., 2009) but have a low impact on C balance compared to CO₂ fluxes. The doubling of the DOC flux observed in 2014 compared to 2013 is linked to a greater quantity of water leaving the bog with similar DOC contents. At the same time, the average water table measured in 2014 is slightly higher than that measured in 2013 and precipitation is of the same order of magnitude (Fig. 2).

4.4 ER and GPP spatial variability

Calibration of the individual CO₂ fluxes at the 20 measurement points showed a large range of cumulated flux estimation (Fig. 7 and 8). Nonetheless, the average of these fluxes was coherent with those estimated at the ecosystem scale with the average of the 20 points: 1215 vs. 1261 gC m⁻² yr⁻¹ and 1052 vs. 1070 for ER and GPP respectively (Table 1). The ER estimates are very close for the two years, which is consistent with the relatively similar water table also observed. The difference in air

338 temperature between 2013 and 2014 (9.1 and 10.1 °C respectively) is not sufficient to observe a
339 significant difference. The order of magnitude of the spatial variability was the same between ER and
340 GPP estimated within one site (this study) and ER and GPP estimated in different sites by Jacobs *et*
341 *al.* (2007). For ER, the spatial variability found within La Guette peatland was also larger than the
342 inter-annual variability measured by Beyer *et al.* (2015), in which the difference between the maximum
343 and minimum annual fluxes was 429 gC m⁻² yr⁻¹ on a temperate fen used as grassland. With the
344 acquired data, no patterns have been found between the location of the points and the model parameters
345 or with the measured environmental variables that would enable this spatial variability to be linked to
346 specific local environmental conditions. Indeed, this variability does not seem geographically
347 distributed or related to gradient of environmental parameters with spatial and temporal similarity of
348 the air temperature and water table levels. However, a first approach by grouping points per vegetation
349 classes (with dominance of the muscular, herbaceous or shrubs strata) shows promising results in order
350 to explain this spatial variability (D'Angelo, 2015).

351 **Conclusions**

352 In this study we have shown that despite high water table levels, La Guette peatland acted as a C source
353 to the atmosphere for the 2 years of measurements, in 2013 and 2014. This was partly explained by
354 the high mean annual temperatures that led to large fluxes. However, it is probable that the site history
355 also played a significant role: after several dry years, the peatland was just starting to refill during the
356 2 measurement years, probably leading to air trapped in the porosity that favoured oxic organic matter
357 degradation. Longer observations are needed to catch the long-term dynamics in terms of hydrological
358 cycle and site history leading to hysteresis effects. The vegetation had a significant effect when
359 included in ER models despite the difficulty in monitoring the vegetation profile without disturbances.
360 However, such an effect was not as clear for the GPP models. As a result, the ER models had a narrower
361 range of estimations (more precise when vegetation is included) than the GPP ones, indicating that ER
362 models seem more reliable. As a result, this study advocates the inclusion of vegetation in models,
363 even in a simplistic way. These results also emphasize the importance of model evaluation as it

364 outcomes may be quite different from the calibration and this even for models with very well-fitted
365 parameters. Accessing these differences might help to estimate the interpretative power of such models
366 in a broader context. Finally, the estimations of the CO₂ fluxes on the 20 measurement points showed
367 a large spatial variability. The order of magnitude of this variability estimated on one site was the same
368 as those reported between different sites. More studies are needed to better quantify the spatial
369 variability within a site, and to allow a better estimation of the uncertainty of the greenhouse gas budget
370 estimated at larger scales.

371

372 **Author contribution.**

373 BD, SG and FLD designed the experiment

374 BD, SG, CG, FL and FLM collected data

375 BD, SG, CG, FL and FLM performed model simulations and data analysis

376 BD and FL prepared the manuscript with contributions from all co-authors

377 AJ and RZ reviewed and corrected the manuscript

378

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