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

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10

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

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

25

26 **1 Introduction**

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

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

42 In addition to climatic pressure, peatlands can be submitted to anthropic disturbances, and temperate
43 peatlands have been widely transformed by the past into agricultural or forestry lands (Joosten and
44 Clarke, 2002). Drainage that leads to major hydrological disruption is usually a prerequisite before
45 peatland exploitation (Beyer *et al*, 2015). For example, lowering the water table level can change the
46 equilibrium between CO₂ and CH₄ emissions and thus modify the C balance of the ecosystem
47 (Chimner *et al*, 2017). Indeed, increasing the thickness of the oxic layer can lead to (i) higher CO₂
48 fluxes to the atmosphere due to faster decomposition rates of soil organic matter and (ii) lower CH₄
49 fluxes due to the decrease in CH₄ production and/or increase in CH₄ oxidation during its transport to
50 the surface of the soil (Lund *et al*, 2012; Pelletier *et al*, 2007). As a result of both drainage and climatic
51 change, most temperate peatlands are now invaded by vascular plants (Berendse *et al*, 2001; Buttler *et*
52 *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

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

84 **2.2 Carbon fluxes measurements and calculation**

85 In June 2011, 20 stations were set up on the peatland by dividing the area in twenty squares with a grid
86 and choosing randomly one plot (2 m²) within each square (stratified random sampling). This method
87 allowed a homogeneous spatial covering of the studied site (Fig. 1). Fluxes were monthly measured
88 between March 2013 and February 2015 using a semi-cylindrical transparent static chamber equipped
89 (30 cm of diameter, 30 cm height). The chamber was equipped with a HMP 75 sensor (Vaisala Oyj,
90 Vantaa, Finland) to record the temperature and air humidity variations within the chamber during the
91 incubations. In addition, a small fan allowed the air to be homogenized within the chamber (Pumpanen
92 *et al*, 2004). CO₂ fluxes were measured in each of the 20 stations during twenty field campaigns thanks
93 to a CO₂ sensor (GMP 343 model, Vaisala Oyj, Vantaa, Finland) placed inside the chamber. Fluxes
94 were measured at light for Net Ecosystem Exchange (NEE) and with the chamber covered with a light
95 insulating fabric to simulate night conditions and measure the Ecosystem Respiration (ER). Each
96 measurement lasted between 3 to 5 minutes, and the CO₂ concentration inside the chamber was
97 recorded at 5Hz. CH₄ fluxes were measured thanks to the SPIRIT instrument, an Infrared Spectrometer
98 developed by the Laboratory of Physics and Chemistry of Environment and Space, (LPC2E, Orléans,
99 France, Guimbaud *et al*, 2016, 2011; Robert, 2007). For logistical reasons (weight and long start-up
100 time of SPIRIT), CH₄ measurements were only performed during 12 field campaigns and on only 5
101 stations. These measurements regularly required to access to the plots, so, wooden planks was used as
102 mobile pontoons to limits disturbances

103 CO₂ and CH₄ fluxes were then calculated as follow:

$$104 \quad F = \frac{dX}{dt} * \frac{P}{R*T} * \frac{V}{S} \quad (1)$$

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:

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

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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$), b the optimal temperature for a
176 ($^{\circ}\text{C}$), 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 ($^{\circ}\text{C}$), 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 $F_{CH_4-1} = a * e^{(b * T)}$ (12)

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

190 with T the air temperature (°C); a and b the fitted parameters and VI 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 Guette peatland (Binet *et al*, 2013):

194 $F_{DOC} = D * [DOC]$ (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

207 seasonal variability (Fig. 2C). The average WTL manually measured in the 20 stations during the field
208 campaigns showed a similar cyclicity (Fig. 2C) with deeper level during summer (maximum depth of
209 -18 and -10.5 cm in 2013 and 2014, respectively) than during winter. The seasonal variability of
210 vegetation was controlled by the graminoids which started to grow earlier in 2014 (April) than in 2013
211 (May) (Fig. 3). Also, in 2014 the vegetation index (VI) was slightly higher than in 2013, at 0.45 and
212 0.51 respectively.

213 **3.2 CO₂, CH₄ and DOC fluxes**

214 Results of CO₂ fluxes (NEE, ER and calculated GPP) are presented in Fig. 2. CO₂ fluxes (GPP and
215 ER) showed a clear seasonal trend with a maximum in summer. In 2013 the GPP averaged maximum
216 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
217 maximum of both variables reached at the end of July (Fig. 2A and B). In 2014 the GPP and ER
218 averaged maxima were reached earlier, in June with $13.16 \pm 4.70 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $7.83 \pm 2.55 \mu\text{mol m}^{-2}$
219 s^{-1} respectively (Fig. 2A and B). Averages values of GPP for 2013 and 2014 were 7.12 ± 5.19 and
220 $6.56 \pm 4.72 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively. For ER, the average values were, for 2013 and 2014, 4.27 ± 3.16
221 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
222 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
223 emissions showed a lower magnitude with fluxes below $0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$. A clear difference was also
224 visible between 2013 and 2014 respectively (Fig. 5). In 2013 CH₄ average fluxes were $0.04 \pm 0.03 \mu\text{mol}$
225 $\text{m}^{-2} \text{s}^{-1}$, whereas they reached $0.10 \pm 0.08 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2014. For both years, the average DOC
226 concentrations measured at the outlet of the peatland were $18.5 \pm 7.7 \text{ mg L}^{-1}$. Thus, the average
227 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 ± 1
228 $\text{gC m}^{-2} \text{ yr}^{-1}$ in 2013 and 2014, respectively).

229 **3.3 Model selection**

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

233 R^2 and a lower NRMSE than without vegetation (ER-1, Fig. 6A and Table 1). However, the difference
234 between ER-1 and ER-2 is low but the AIC, which decreased from 47 to 35, confirmed this observation
235 (Table 1). ER was estimated to 1286 ± 231 and 1261 ± 164 $\text{gC m}^{-2} \text{yr}^{-1}$ for ER-1 and ER-2, respectively.
236 Concerning GPP, GPP-2 realized a higher R^2_a score, a lower NRMSE, and a lower AIC compared to
237 GPP-1 (Fig. 6C and Table 1). Resulting cumulated fluxes were 1290 ± 400 and 1070 ± 203 $\text{gC m}^{-2} \text{yr}^{-1}$
238 for GPP-1 and GPP-2. For CH_4 , only CH_4 -2 (including vegetation) that showed a satisfying result (Fig.
239 6E and Table 1) was used to estimate the CH_4 cumulated fluxes. Evaluation of the GPP models showed
240 high NRMSE values with 47 and 58 % for GPP-1 and GPP-2 respectively (Fig. 6D and Table 1). CH_4
241 evaluation led to even higher NRMSE values with 68 % for F_{CH_4} -2. R^2_a negative values due to the use
242 of non-linear regression were here irrelevant (Fig. 6F and Table 1). On the contrary, the ER models
243 led to high R^2_a and low NRMSE values with ER-2 performing better than ER-1: R^2_a values increased
244 from 0.16 to 0.59 and NRMSE values decreased from 35 to 23 % (Fig. 6E and Table 1).

245 **3.4 Calculation of Net Ecosystem Carbon Balance (NECB)**

246 NECB (estimated here as $\text{GPP} - \text{ER} - F_{\text{CH}_4} - F_{\text{DOC}}$) was calculated first without inclusion of vegetation in
247 the model (GPP-1, ER-1) and then with vegetation (GPP-2, ER-2), at the exception of the calculation
248 of CH_4 for which only the model with vegetation was used (CH_4 -2). Whether model 1 or 2 was used,
249 the NECB showed that the peatland was a source of carbon to the atmosphere in 2013 and 2014 with
250 -26 $\text{gC m}^{-2} \text{yr}^{-1}$ and -220 $\text{gC m}^{-2} \text{yr}^{-1}$ for model 1 or 2, respectively (Table 2). The high difference in
251 the estimation of NECB was principally due to the GPP estimations (Table 1). In addition, NECB was
252 higher in 2013 than in 2014 (Table 2). NECB was mainly driven by CO_2 fluxes as CH_4 and DOC fluxes
253 are two orders of magnitude lower. However, in terms of the Global Warming Potential (GWP), CH_4
254 fluxes are not negligible with CH_4 having a GWP 34 times higher than CO_2 for the 100-year time
255 horizon (Myhre *et al.*, 2013).

256 **3.4 Spatial variability**

257 The calibration of ER-2 and GPP-2 on each measurement plot enabled the spatial variability of the
258 CO_2 fluxes on the site to be estimated. For ER-2, the R^2_a of the individual plots were above 0.5 (with

259 the exception of measurement plot n°10) and the NRMSE values were below 50% (Fig. 7). The model
260 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
261 c. For GPP-2 the R^2_a were above 0.5 and the NRMSE values between 20 and 60% (with the exception
262 of point n°10). Model parameters for GPP-2 showed higher variations: between -6.1 and 66 for a, 23.9
263 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,
264 cumulated GPP fluxes ranged from 511 to 1420 $\text{gC m}^{-2} \text{yr}^{-1}$, with most values around 1100 $\text{gC m}^{-2} \text{yr}^{-1}$
265 and an average of $1052 \pm 238 \text{ gC m}^{-2} \text{yr}^{-1}$. For ER, the cumulated fluxes ranged from 842 to 2363 gC
266 $\text{m}^{-2} \text{yr}^{-1}$ with an average of $1215 \pm 362 \text{ gC m}^{-2} \text{yr}^{-1}$ (Fig. 7 and 8).

267 **4. Discussion**

268 **4.1 Rationale behind the high C fluxes recorded and the C source functioning**

269 CO_2 fluxes measured at La Guette peatland were above 1000 $\text{gC m}^{-2} \text{yr}^{-1}$ for the GPP and the ER,
270 whatever the model used. These fluxes were high compared to those of boreal peatlands. Trudeau *et*
271 *al.* (2014) and Peichl *et al.* (2014) found GPP and ER fluxes between 100 and 500 $\text{gC m}^{-2} \text{yr}^{-1}$
272 approximately for sites located in Quebec, Canada and in Northern Sweden respectively. However,
273 these large fluxes were close to those found for sites with a high Mean Annual Temperature (MAT).
274 For instance, Beyer and Höper (2015) found for a site with similar vegetation (*Molinia caerulea*,
275 *Eriophorum augustifolium*, *Sphagnum* spp.) and with a MAT of 8.6°C, GPP fluxes between 534 and
276 1058 $\text{gC m}^{-2} \text{yr}^{-1}$ and ER fluxes between 420 and 1052 $\text{gC m}^{-2} \text{yr}^{-1}$. Thus, the large fluxes measured in
277 La Guette peatland can be related to the relatively warmer climate compared to peatlands at higher
278 latitudes. However, a MAT alone cannot explain why the system functioned as a source of C as other
279 studies have shown that peatlands with a MAT above 8°C can still be a C sink. For instance, Koehler
280 *et al.* (2011) estimated an uptake of $-29.7 \text{ gC m}^{-2} \text{yr}^{-1}$ in an Atlantic blanket bog with a MAT of 10.6°C
281 for a 6-year average (2003-2008). The water table drawdown favours oxic reactions in a thicker soil
282 layer, thus it is often adduced to explain the sources of C in peatlands. During the two years of
283 measurements, La Guette peatland experienced favourable hydrological conditions due to heavy
284 rainfall leading to high water table levels (Bernard-Jannin *et al.*, 2018). In spite of this, the system

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

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

306 **4.2 Implication of taking vegetation into account in the C budget estimation**

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

312 2014), probably because of the difficulty in measuring the pertinent variables (leaf area index, leaves
313 number). Including vegetation in models has led to a better representation of CO₂ fluxes. These results
314 were in accordance with Bortoluzzi *et al.* (2006) who also found a lower NRMSE when vegetation
315 was included in the model. Another way to take the vegetation into account is to use the Ratio
316 Vegetation Index (RVI), which is a measurement of incoming and reflected radiation. This method
317 was used by Görres *et al.* (2014) and led to an improvement for GPP modelling but not for ER.
318 However, such an improvement using the RVI for ER modelling was found by Kandel *et al.* (2013)
319 on a cultivated fen peatland in Denmark. Although the calibration of the model was as good for ER as
320 for GPP, evaluation of the models presented more contrasted results since only ER-2 showed a high
321 R^2_a and a low NRMSE. For F_{CH₄-2} the evaluation revealed that the interpretation of the model outputs
322 should be limited to the current study and could not be used to extrapolate fluxes for other times and
323 spaces. Nevertheless, as hypothesis, model evaluations indicated that the inclusion of vegetation
324 increased the model's capability to represent CO₂ fluxes.

325 **4.3 The DOC exports**

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

332 **4.4 ER and GPP spatial variability**

333 Calibration of the individual CO₂ fluxes at the 20 measurement points showed a large range of
334 cumulated flux estimation (Fig. 7 and 8). Nonetheless, the average of these fluxes was coherent with
335 those estimated at the ecosystem scale with the average of the 20 points: 1215 vs. 1261 gC m⁻² yr⁻¹ and
336 1052 vs. 1070 for ER and GPP respectively (Table 1). The ER estimates are very close for the two
337 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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