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Complete List of Authors:	<p>Lhosmot, Alexandre; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS</p> <p>Jacotot, Adrien; CNRS, Institut des Sciences de la Terre d'Orléans UMR 7327 Orléans, FR; Institut National de la Recherche en Agriculture, Alimentation et Environnement (INRAE), UMR 1069 SAS</p> <p>Steinmann, Marc; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS</p> <p>Binet, Philippe; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS</p> <p>Toussaint, Marie-Laure; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS</p> <p>Gogo, Sébastien; OSUR, Université de Rennes 1, CNRS</p> <p>Gilbert, Daniel; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS</p> <p>Laggoun-Défarge, Fatima; CNRS, Institut des Sciences de la Terre d'Orléans UMR 7327</p> <p>Coffinet, Sarah; OSUR, Université de Rennes 1, CNRS</p> <p>Bertrand, Guillaume; Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS; Federal University of Paraíba Foundation for Research and Extension Support, Water Resources and Environmental Engineering Laboratory</p>
Key Words:	Peatland ecosystem, Diurnal cycle, Methane flux, Methane oxidation, Temperate ecosystem, eddy-covariance, Sphagnum

Biotic and abiotic control over diurnal CH₄ fluxes in a temperate transitional poor fen ecosystem

Alexandre Lhosmot¹, Adrien Jacotot^{2,3}, Marc Steinmann¹, Philippe Binet¹, Marie-Laure Toussaint¹, Sébastien Gogo⁴, Daniel Gilbert¹, Sarah Coffinet⁴, Fatima Laggoun-Deffarge², and Guillaume Bertrand^{1,5}

¹ Chrono-Environnement, Université de Bourgogne Franche-Comté, UMR6249, CNRS, France

² Institut des Sciences de la Terre d'Orléans (ISTO), Université d'Orléans, UMR7327, CNRS, France.

³ Institut National de la Recherche en Agriculture, Alimentation et Environnement (INRAE), UMR 1069 SAS,

65 rue de Saint-Brieuc, 35042 Rennes, France

⁴ OSUR, Université de Rennes 1, CNRS, France

⁵ Water Resources and Environmental Engineering Laboratory, Federal University of Paraíba, 58051-900 Joao Pessoa, Brazil

Abstract

To understand the variability of methane (CH₄) fluxes between a temperate mid-altitude *Sphagnum*-dominated peatland and the atmosphere, we monitored simultaneously eddy-covariance, hydrometeorological and physical parameters between April 2019 and December 2021. The site was a CH₄ source for the atmosphere, with a cumulative emission of 23.9 ± 0.6 g C m⁻² year⁻¹. At the interannual scale, deeper water table during vegetation growth periods resulted in lower CH₄ fluxes (FCH₄), and reciprocally. Furthermore, the seasonal temperature variation of the anaerobic peat layer was a good predictor for FCH₄. However, while the lowest temperatures occurred between December and February, the lowest FCH₄ were observed between March and May, with around 30 % of negative FCH₄. Indeed, the fastest increase in temperature of the aerobic layer likely stimulated methanotrophy at the expense of methanogenesis. Negative FCH₄, systematically observed at midday, were concurrent with high photon flux densities, latent heat fluxes, and net negative ecosystem CO₂ exchanges, suggesting the control of photosynthesis over CH₄ oxidation. Moreover, our results highlighted marked diurnal cycles with FCH₄ maximal at night and minimal at midday for all seasons. This diurnal cyclicity is in opposition to what is typically known for peatlands dominated by vascular plants. Physical parameters, such as soil surface temperature and sensible heat fluxes, likely contribute to this diurnal FCH₄ cyclicity and require further investigation. Our study thus demonstrates that

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2
3 30 diurnal variations of FCH₄ must be considered before upscaling to seasonal or annual cycles, along
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5 31 with the effect of vegetation on CH₄ transfer and oxidation processes.
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8 32 **Key words:** Peatland ecosystem, Diurnal cycle, Methane flux, Methane oxidation, Sphagnum,
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10
11 33 Temperate ecosystem, eddy-covariance
12
13

14 34 **Highlights:**

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16
17 35 • FCH₄ were lower during daytime and higher at night throughout the year.
18
19 36 • Negative FCH₄ where concomitants with negative NEE.
20
21
22 37 • Diurnal FCH₄ amplitude followed a seasonal trend.
23
24

25 38 **Electronic supplementary material:** Soil-meteorological and piezometers data are available
26
27 39 on Zenodo repository (DOI:10.5281/ZENODO.3763342; DOI: 10.5281/ZENODO.3763766) and also on
28
29 40 the French National Peatland Observatory Service (SNO Tourbières, [https://www.sno-](https://www.sno-tourbieres.cnrs.fr/)
30
31 [tourbieres.cnrs.fr/](https://www.sno-tourbieres.cnrs.fr/)).
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35 42 **Author Contributions:**

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38 43 AL wrote the original draft. AL, AJ and GB participated to the conception of the study, designed
39
40 44 methodology and analyzed data. AJ and MLT acquired eddy-covariance and soil-meteorological data.
41
42
43 45 All authors contributed to the writing and approved the final version of the manuscript.
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1 Introduction

Peatlands host one third of the Earth total soil organic carbon, although they cover only 3 % of the continental surface (Gorham, 1991; Xu and others 2018). These vegetated and waterlogged ecosystems can be considered as biogeochemical and carbon hot spots of the Critical Zone, which is defined as the thin layer of the Earth from the top of the canopy to the unaltered rocks that shelters life and the biogeochemical cycles (Anderson and others 2004; Gaillardet and others 2018). Permanent anaerobic and reduced redox conditions in peatlands limit organic matter degradation and its transformation to carbon dioxide (CO₂), resulting in peatlands being a carbon reservoir that had accumulated over centennial to millennial time scales.

Waterlogged conditions promote the microbial production of methane (CH₄) that is then emitted to the atmosphere and has a radiative power 28 to 34 times greater than CO₂ (Lai 2009; IPCC 2013; Stępniewska and Goraj 2014). The net CH₄ flux to the atmosphere is not only dependent on its production under anoxic conditions, but also on its transfer to the surface. This transfer occurs through molecular diffusion, ebullition or through aerenchymatous tissues (Sebacher and others 1985; Chanton and Dacey 1991; Windsor and others 1992). In parallel, a part of CH₄ may be consumed by methanotrophs in the presence of oxygen, especially in the aerobic surface layer, or in anaerobic conditions through oxidative pathways using different electron acceptor such as nitrate, sulfate or iron (III) (Lai 2009; Smemo and Yavitt 2011; Stępniewska and Goraj 2014; Shi and others 2017). In addition, CH₄ flux (FCH₄) balance results from the interactions of numerous physico-chemical factors such as Water Table Depth (WTD), vegetation cover and temperature (Turetsky and others 2014; Leroy and others 2017; Li and others 2021; Zhang and others 2021). Among these factors, temperature is a key predictor for seasonal CH₄ production in the anaerobic peat layer (Dunfield and others 1993; Long and others 2009; van Winden and others 2012; Stępniewska and Goraj 2014; Knox and others 2021). In contrast, the lowering of the WTD favored by high temperature and evapotranspiration favors oxygenation of the peat column that, in turn, limits CH₄ emissions (Lai 2009; Stępniewska and Goraj

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2
3 71 2014; Bertrand and others 2021). At the diurnal scale, FCH₄ can widely vary in both shape and
4
5 72 amplitude within peatland types and seasons (Nadeau and others 2013; Dooling and others 2018; Knox
6
7 73 and others 2021).

9
10 74 Saunois and others (2020) estimated that over the period 2000-2017 wetlands, at the global
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12 75 scale, including peatlands, contributed 25 to 30 % of the worldwide CH₄ emissions. However, the
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14 76 specific contribution of peatlands to these CH₄ emissions remains uncertain because of the multitude
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16 77 and complexity of controlling parameters to set in the models (Saunois and others 2020; Salmon and
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18 78 others 2021). However, both climatic and land-use change modify hydrometeorological conditions of
19
20 79 peatlands, which do not only impact their distribution, size and vegetation cover, but also potentially
21
22 80 the balance between CH₄ production and oxidation. The heterogeneity of peatland types and sizes
23
24 81 associated to complex interactions between hydrology, carbon cycle and vegetation dynamics make
25
26 82 their response to climate change and anthropogenic disturbances difficult to predict (Loisel and others
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28 83 2021; Riutta and others 2020).

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33 84 In addition, while numerous studies focused on boreal peatlands, the temperate ones remain
34
35 85 understudied, especially temperate montane peatlands (Rosset and others 2019). However,
36
37 86 temperate peatlands might be considered “as ‘ecosystem sentinels’ for climate change, acting as early
38
39 87 warning indicators of climate-carbon feedbacks” as it was proposed by Briones and others (2022).
40
41 88 Beyond, peatland monitoring combining hydrometeorological variables and greenhouse gas (GHG)
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43 89 fluxes in a wide panel of altitude and latitude, vegetation cover and degree of anthropogenic impact
44
45 90 participate to build a robust database. Such a database is essential to evaluate peatland restoration
46
47 91 strategies, that induce, through rewetting, an increase of FCH₄ (Abdalla and others 2016). Monitoring
48
49 92 of GHG fluxes, covering from interannual to diurnal scale including dormant season, is enabled by the
50
51 93 eddy-covariance technique that has been developing over the last 25 years (Morin 2019). Diurnal cycle
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53 94 studies on peatland FCH₄ prove to be important as the majority of FCH₄ are measured only during
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55 95 daytime with the incubation chamber method (Denmead 2008; Dooling and others 2018). Therefore,
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3 96 the comprehension of this diurnal cycle remains a challenge in order to improve annual CH₄ budget of
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5 97 a peatland when only daytime measurements are available (Dooling and others 2018).
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8 98 In this context, this work aims to document current temperate peatland CH₄ dynamic by
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10 99 delineating the biotic and abiotic processes influencing FCH₄. Considering the range of possible
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12 100 constrains over FCH₄, deconvoluting these factors may be helped by long-term and high frequency
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14 101 monitoring. In this perspective, we jointly investigated WTD, soil and air temperatures, Photosynthetic
15
16 102 Photon Flux Density (PPFD), latent and sensible heat fluxes (LE and H), Net Ecosystem CO₂ Exchange
17
18 103 (NEE) and FCH₄ during 2.5 years. This allowed us to address multiannual, seasonal and diurnal CH₄
19
20 104 patterns of a temperate mid-altitude *Sphagnum*-dominated transitional poor fen, located in the Jura
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22 105 Mountains in Eastern France (Forbonnet peatland).
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28 106 **2 Material and Methods**

31 107 **2.1 Study site**

32
33 108 The study was conducted at the Forbonnet peatland, located at a mid-latitude and mid-altitude
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35 109 position (N46.826, E6.1754, 840 m a.s.l.) in the French Jura Mountains within the Frasne-Bouverans
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37 110 peatland complex (~300 ha; Lhosmot and others 2021). The site is one of the four peatlands of the
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39 111 French National Peatland Observatory Service (SNO Tourbières; Gogo and others 2021), being also an
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41 112 observatory of the French research infrastructure of the Critical Zone (OZCAR; Gaillardet and others
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43 113 2018).
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47 114 This ecosystem is located in a karstic syncline made of Jurassic and Cretaceous marls and
48
49 115 limestones, partially covered by glacial impermeable deposits favoring water accumulation and
50
51 116 development of peatlands. The study site corresponds to a *Sphagnum*-dominated peatland (~7 ha)
52
53 117 belonging to a larger peatland complex of around 300 ha that is recognized for its biodiversity (Natura
54
55 118 2000, Ramsar Convention, Regional Natural Reserve). This peatland is supplied in water by (1) local
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57 119 rainfall, (2) lateral flow from the surrounding by topographically higher more mature and wooded
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3 120 peatlands and (3) by localized and intermittent mineralized groundwater from moraines and/or karst
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5 121 system (Lhosmot and others 2021). The upper peat layer remains the most acidic and least mineralized
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7 122 one with pH varying from 4 to 5.5.
8
9

10 123 The climate is temperate with a marked continental influence, straddling between Cfb and Dfb
11
12 124 according to the Köppen-Geiger climate classification (Rubel and others 2017). More particularly, the
13
14 125 site is subjected to contrasted seasons with mean monthly temperatures ranging from 0 °C (December
15
16 126 to February) to 15 °C in July and August while the annual average is ~7 °C (2009-2020). Precipitation
17
18 127 events are regularly distributed over the year with a mean of 135 ± 25 mm month⁻¹ (2009-2019).
19
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21

22 128 Concerning the vegetation, the study area is mainly covered by *Sphagnum spp* mosses.
23
24 129 *Andromeda polifolia*, *Vaccinium oxycoccos*, *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Drosera*
25
26 130 *spp.* and *Calluna vulgaris* are also present. *Pinus uncinata* occurs sparsely around the edges of the
27
28 131 peatland. The micro-topography of the Forbonnet peatland edges features an alternance of hummocks
29
30 132 and hollows supporting a mosaic of vegetation while the center of the system is relatively homogenous
31
32 133 and flat and corresponds to a transitional poor fen (Delarue and others 2011; Buttler and others 2015).
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37 134 2.2 GHG fluxes and auxiliary data measurements

38
39 135 Methane (CH₄), carbon dioxide (CO₂), latent heat flux (LE) and sensible heat flux (H) were
40
41 136 measured with an eddy-covariance (EC) flux tower from the end of April 2019 to December 2021.
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43 137 Localization of the EC is available on the observatory website (Gogo and others 2021) and its footprint
44
45 138 corresponds to the flat transitional poor fen dominated by *Sphagnum* (see Supplementary material 1).
46
47 139 The EC footprint vegetation is dominated by *Sphagnum spp* (~80 %) while vascular plants (mainly
48
49 140 *Eriophorum vaginatum*) represent the rest of the vegetation (Bailly 2017). The EC system included an
50
51 141 open-path CH₄ LI-7700 and an enclosed-path LI-7200/RS (LI-COR Biosciences, USA) to measure
52
53 142 respectively CH₄ and both H₂O and CO₂ concentrations. Wind velocity and direction components as
54
55 143 well as fast temperature readings were provided by a Gill HS-50 3D ultrasonic anemometer (Gill
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3 144 Instruments Limited, UK) placed at 2 m above the soil with a north offset of 220°. All data were sampled
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5 145 at a 20 Hz frequency, and recorded through a LI-7550 Interface Unit (LI-COR Biosciences, USA).
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8 146 Micro-meteorological measurements included PPFD (SKP115 Quantum Sensor, Skye
9
10 147 Instruments Limited, UK), air temperature (T_{Air}) and relative humidity (RH; HMP155A, VAISALA,
11
12 148 Finland). Soil measurements included Water Table Depth (WTD; CS451, Campbell Scientific) at one
13
14 149 location, and temperature (T_{Soil}) at 2, 5, 10, 25 and 60 cm depths. T_{Soil} values at 2 and 5 cm are the
15
16 150 mean of two replicated sensors. Intermediate depth temperatures (5, 10 and 25 cm) showed a gradual
17
18 151 evolution between the 2 and 60 cm depths (see Supplementary material 2). Temperature was also
19
20 152 recorded in a piezometer (T_{Peat}) integrating the complete catotelm profile (40 to 180 cm depth). All
21
22 153 auxiliary data were recorded in a similar environment, beside the EC footprint (~75 m from the EC
23
24 154 station). The data were measured every minute and then 30-min averaged.
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30 155 **2.3 Fluxes calculation**

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32 156 CH_4 , CO_2 , LE and H were calculated using EddyPro version 7.0.6 (LI-COR Biosciences, USA) and
33
34 157 following the methods described by Vitale and others (2020) and references therein. Calculation
35
36 158 included spikes count and removal (Mauder and others 2013), double axis rotation for tilt correction
37
38 159 (Wilczak and others 2001), covariance maximization for time-lag compensation, *in-situ* spectral
39
40 160 correction (Fratini and others 2012), and then 30-min block averaging. Cleaning of FCH4 was
41
42 161 performed using the quality flags qualification of Mauder and Foken (2011) and accordingly, only fluxes
43
44 162 with a flag 0 criterion were kept in the dataset. Cleaning of CO_2 fluxes was performed with the
45
46 163 procedure of Vitale and others (2020) with the RFlux package in its non-ICOS version (Vitale and others
47
48 164 2021). In addition, due to the restricted area of the studied peatland and the location of the EC tower,
49
50 165 only the fluxes recorded with a wind direction between 143-270°N were conserved during the cleaning
51
52 166 procedure. The footprint surface estimation is based on aggregated half-hour measurements from
53
54 167 April 2019 to December 2021 after wind direction filtration and following the method described by
55
56 168 Kljun and others (2015) (Fig. in Supplementary material 1).
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2
3 169 Averaged FCH₄ and CO₂ fluxes were corrected for periods of low friction velocity (u^*) that
4
5 170 frequently appear at night-time. The calculation of the threshold is based on the data, and is thus
6
7 171 specific and different for each dataset. The minimal u^* threshold for accepted fluxes was estimated by
8
9 172 the method of Papale and others (2006) and implemented in the REddyProc algorithm developed by
10
11 173 Wutzler and others (2018). Annual calculated thresholds were 0.043, 0.069 and 0.049 for 2019, 2020
12
13 174 and 2021. Following these results, we decided to take a unique threshold value of 0.075 for the three
14
15 175 measurements years, which is upper than the calculated ones in order to ensure more robustness to
16
17 176 the kept data. All fluxes below this threshold were discarded from the dataset. Finally, the available
18
19 177 CH₄ data covered 22 % of the study period. The data gap in winter 2020-2021 is due to the removal of
20
21 178 the analyzer because of excessive snow cover. In this study a negative flux is defined as a flux from the
22
23 179 atmosphere to the soil, and reciprocally.
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28 180 The daily mean amplitude of FCH₄ (maximum difference of fluxes between day and night) for
29
30 181 each month was calculated as the difference between the mean FCH₄ at night (PPFD < 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$)
31
32 182 and the minimum FCH₄ of the day. Similarly, the daily mean amplitude of temperature in soil was
33
34 183 calculated as the difference between the mean temperature at night (PPFD < 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the
35
36 184 diurnal maximum temperature.
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39

40 185 To estimate the annual FCH₄ budget, FCH₄ were gap-filled from 2019 to 2021 using the Random
41
42 186 Forest (RF) method with T_{soil} , WTD, PPFD, and u^* as input predictors. Although no standardized gap-
43
44 187 filling method currently exists concerning CH₄ (Knox and others 2019), mostly due to its dependence
45
46 188 to many environmental drivers, Kim et al., (2020) recently showed a high performance of random
47
48 189 forest algorithms (RF).
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52 53 190 **2.4 Statistical analyses**

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55 191 Linear regressions and statistical analyses were realized using the SciPy library in python
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57 192 language (Jones and others 2001). Difference of annual and monthly means WTD were compared with
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60

193 the non-parametric Mann Whitney U test as the main data were not normally distributed. All
194 uncertainties given in the manuscript correspond to the standard deviation.

195 3 Results

196 3.1 Environmental variables

197 Monthly T_{Air} and T_{Soil} at 2 cm depth ($T_{\text{soil-2cm}}$) showed similar variations with lowest values in
198 January ($\sim 0^{\circ}\text{C}$) and peaks in July for 2020 and June for 2021 (respectively ~ 16 and $\sim 18^{\circ}\text{C}$, Fig. 1A). For
199 T_{Soil} at 60 cm depth ($T_{\text{soil-60cm}}$), the seasonal peak was offset in August and the seasonal amplitude
200 ($\sim 13^{\circ}\text{C}$) was lower than for $T_{\text{soil-2cm}}$ ($\sim 17^{\circ}\text{C}$, Fig. 1A). The mean monthly peat water temperature
201 recorded in a piezometer (T_{Peat}) at 40 to 180 cm depth varied between 4.4 and 13.5 $^{\circ}\text{C}$. For T_{Air} the
202 values ranged between -1 and 17 $^{\circ}\text{C}$, for $T_{\text{soil-2cm}}$ between 0.4 and 18.1 $^{\circ}\text{C}$, and for $T_{\text{soil-60cm}}$
203 between 2.9 and 15.6 $^{\circ}\text{C}$. T_{Peat} reached its seasonal peak at the end of August (Fig. 1A). PPFD showed
204 seasonal trends similar to T_{Air} with highest values in July ($2300 \mu\text{mol m}^{-2} \text{s}^{-1}$) and lowest values in winter
205 ($< 800 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 1B).

206 At the diurnal scale, PPFD, T_{Air} , and T_{Soil} were highest during the day. PPFD reached its
207 maximum between 1 and 3 pm. T_{Air} and $T_{\text{soil-2cm}}$ reached maximum values between 3 and 5 pm,
208 whereas $T_{\text{soil-60cm}}$ was highest between 11 pm and 2 am. The amplitude of T_{Soil} decreased with depth
209 and remained, similarly to T_{Peat} , close to zero at 60 cm depth, reflecting the thermic inertia of peat
210 (McKenzie and others 2007). The daily amplitude of T_{Soil} at 2 and 5 cm depth was highest from April to
211 September and considerably lower for the rest of the year (at 2 cm from 3.2 to 10.1 $^{\circ}\text{C}$, mean = 6.5 $^{\circ}\text{C}$;
212 at 5 cm from 1.9 to 5.5 $^{\circ}\text{C}$, mean = 3.9 $^{\circ}\text{C}$, Fig. 2). For deeper levels (10, 25 and 60 cm), the daily mean
213 amplitude did not exceed 2.2 $^{\circ}\text{C}$ (mean = 1 $^{\circ}\text{C}$).

214 WTD remained at an average of -0.12 ± 0.07 m (Fig. 1C, daily mean values). Seasonal variations
215 featured greater depths from July to September in 2019, 2020 and 2021 (respectively -0.21 ± 0.04 , -

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2
3 216 0.24 ± 0.04 and -0.10 ± 0.04) and shallower depths in winter (from -10 cm to occasional positive values).
4
5 217 WTD in 2021 (-0.9 ± 0.05 m) was significantly higher than in 2019 (-0.11 ± 0.07 m, p -value < 0.05) and
6
7 218 2020 (-0.13 ± 0.08 m, p -value < 0.05). The monthly mean WTD compared year to year show that for
8
9 219 May, July, August and September the WTD was significantly higher in 2021 than in the two others years
10
11
12 220 (p -value < 0.05).

13
14
15 221 Seasonal variability of NEE showed lower amplitude from November to March, where the
16
17 222 majority of half-hour fluxes ranged from -4 to +4 $\mu\text{mol s}^{-1} \text{m}^{-2}$. Mean monthly NEE for this period ranged
18
19 223 from 0 to +1 $\mu\text{mol s}^{-1} \text{m}^{-2}$. Higher NEE amplitude was measured in July-August months. Half-hour NEE
20
21 224 ranged from approximatively -13 to +10 $\mu\text{mol s}^{-1} \text{m}^{-2}$ and mean monthly NEE reached -5 $\mu\text{mol s}^{-1} \text{m}^{-2}$
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23
24 225 (Fig. 1D).

27 226 3.2 CH₄ fluxes

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29
30 227 Along the two and a half years covered by the EC measurements (April 2019 to December
31
32 228 2021), measured mean daily FCH₄ were 57.5 ± 41 $\text{nmol m}^{-2} \text{s}^{-1}$. Annual budget from gap-filled data for
33
34 229 2019, 2020 and 2021 was respectively 23.4, 23.5 and 24.8 $\text{g C m}^{-2} \text{year}^{-1}$. Seasonal variation of FCH₄
35
36 230 was similar for the whole period of study (Fig. 1E). Highest monthly average FCH₄ were recorded in
37
38 231 July and August (respectively from 92.5 to 122 with a mean of 106 $\text{nmol m}^{-2} \text{s}^{-1}$ and from 76.2 to 147.4
39
40 232 with a mean of 101.2 $\text{nmol m}^{-2} \text{s}^{-1}$) while lowest FCH₄ occurred in early spring (March and April monthly
41
42 233 average, respectively 13 to 14.8 and 4.8 to 16.1 $\text{nmol m}^{-2} \text{s}^{-1}$). Regarding the half-hour values, negative
43
44 234 FCH₄ were most frequent between March and May, representing in average 30.8 ± 8.5 % of the half
45
46 235 hour measurements. In February, negative FCH₄ were more variable, comprised between 5.7 % and
47
48 236 28.8 % of measured FCH₄ in 2020 and 2021, respectively. In contrast, for all other months, negative
49
50 237 FCH₄ only represented 1.1 ± 1.5 % of measured FCH₄. In addition, the diurnal FCH₄ showed lowest
51
52 238 values during daytime (11am-3pm) for all month of the year (Fig. 3). Amplitude of this cycle was the
53
54 239 highest in spring and summer (103.9 ± 21 $\text{nmol m}^{-2} \text{s}^{-1}$) and the lowest from October to January (47.1
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240 $\pm 20 \text{ nmol m}^{-2} \text{ s}^{-1}$; Fig. 2). Diurnal FCH₄ amplitude at the end of winter (February and March) was $75 \pm$
241 $29 \text{ nmol m}^{-2} \text{ s}^{-1}$.

242 3.3 Environmental control on FCH₄

243 At the seasonal scale, monthly WTD showed complex relationships with monthly mean FCH₄
244 with a large variation of FCH₄ (from 15 to 140 $\text{nmol m}^{-2} \text{ s}^{-1}$) in a restricted WTD range of variation (-
245 0.13 to -0.07 m), corresponding to 25 % of the monthly WTD amplitude observed in our dataset (Fig.
246 4). Nevertheless, a positive relationship between WTD and FCH₄ was detectable, but only for selected
247 seasons. Positive relationships can be observed for the July-September and December-May periods
248 where linear regressions were determined (Fig. 4, respectively R^2 equal to 0.61 and 0.33 and p -value <
249 0.05). In addition, the link between WTD and FCH₄ stood out by focusing on interannual cycles. For
250 the July-September period mean FCH₄ was higher in 2021, corresponding to the wettest summer
251 (FCH₄ = $122.6 \pm 20 \text{ nmol m}^{-2} \text{ s}^{-1}$ / WTD = $-0.10 \pm 0.05 \text{ m}$), than for the drier summers of 2019 and 2020
252 (FCH₄ = 86.5 ± 12 and $75.4 \pm 14 \text{ nmol m}^{-2} \text{ s}^{-1}$, respectively; WTD = -0.21 ± 0.04 and $-0.24 \pm 0.04 \text{ m}$ with
253 a drop at -0.31 m, respectively; Fig. 1C and E).

254 In order to better understand the diurnal FCH₄ variations over the season, we decomposed
255 the diurnal FCH₄ between the monthly mean FCH₄ at night (FCH₄-night) and the monthly mean of the
256 daytime minimum (FCH₄-min-day). These two variables were plotted against the Tsoil-25cm that is
257 considered as a proxy for seasonal CH₄ production variations (Fig. 5, Ueyama and others 2020). Fig. 5A
258 shows that the FCH₄-night was positively correlated with the Tsoil-25cm (exponential relation, $R^2 =$
259 0.86 , p -value < 0.05). In contrast, the relation between the FCH₄-min-day and the Tsoil-25cm showed
260 a complex pattern with a seasonal hysteresis, *e.g.* lower values in spring (-20 to $-50 \text{ nmol m}^{-2} \text{ s}^{-1}$) than
261 in autumn (20 to $30 \text{ nmol m}^{-2} \text{ s}^{-1}$, Fig. 5B) for similar temperature (~ 5 - $10 \text{ }^\circ\text{C}$). As a result of FCH₄-night
262 and FCH₄-day-min dynamic, the monthly diurnal amplitude of FCH₄ also followed a hysteresis for
263 similar Tsoil-25cm, *e.g.* greater values during the end of winter and spring than during autumn and

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3 264 early winter (Fig. 5C). This result indicates that temperature of saturated peat is not able to fully explain
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5 265 the seasonal variation of FCH4-min-day.
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8 266 Diurnal pattern of temperature (from air to soil 60 cm depth) was synchronous with FCH4
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10 267 despite a lag time from 2 to 12 hours between the daily minimum FCH4 (coming first) and the daily
11
12 268 peak of T_{air} and $T_{\text{soil-60cm}}$, respectively. Both the mean diurnal amplitude of FCH4 and $T_{\text{soil-2cm}}$
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15 269 followed the same seasonal trend (Fig. 2).
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18 270 Diurnal FCH4 was also synchronous with PPFD, NEE, LE and H for all months of the year with
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20 271 daily peaks at mid-day (Figs. 3, 6, 7 and 8). FCH4 was positively correlated to NEE and negatively
21
22 272 correlated to PPFD, LE and H. Highest FCH4 occurred at nighttime and concomitant with null PPFD and
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24 273 LE, negative H and positive NEE. The linear regressions between NEE and LE variables and FCH4 where
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26 274 the most significant from March to May with R^2 between 0.61 and 0.85 for NEE and 0.59 and 0.77 for
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28 275 LE (Figs. 6 and 7). For H and FCH4 relationship, the linear regression was as strong in February ($R^2 =$
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30 276 0.89) as in March to May (R^2 between 0.83 and 0.93, Fig. 8).
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35 277 4 Discussion

38 278 4.1 FCH4 budget and daily FCH4 dynamics

41 279 FCH4 recorded in the Forbonnet between 2019 and 2021 indicated that the site acted as an
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43 280 annual net source of CH_4 to the atmosphere with an annual average budget of $23.9 \pm 0.6 \text{ g C m}^{-2}$, in the
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45 281 high range of those reported by Abdalla and others (2016) for northern peatlands ($\text{N}40$ to 70° ; 95% CI
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47 282 of $7.6\text{--}15.7 \text{ g C m}^{-2}$ and mean of $12 \pm 21 \text{ g C m}^{-2}$). Abdalla and others (2016) found that CH_4 emissions
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49 283 from fen ecosystems were significantly higher than those from bog, consistent with the significant
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51 284 emissions recorded at the Forbonnet. In addition, despite the site being located in a mountainous
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53 285 environment (840 m a.s.l.), the high CH_4 emissions were more consistent with its temperate location
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55 286 ($\text{N}47^\circ$, mean annual $T_{\text{air}} = 7^\circ\text{C}$). For instance, Ueyama and others (2020) found, in a temperate bog
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57 287 ($\text{N}43^\circ$, 16 m a.s.l) with comparable annual air temperature (mean = $7.2 \pm 0.6^\circ\text{C}$), annual CH_4 emissions
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288 between 13 and 19 gC m⁻². Beyond latitudinal and climatic influences, FCH₄ budget seems therefore
289 highly site-dependent (Abdalla and others 2016).

290 Along the two and a half years of study, FCH₄ presented a diurnal cycle with higher values at
291 night, and lower values during the day, the minimum being reached around noon (Fig. 3). This result is
292 consistent with other temperate and boreal peatlands that showed similar shape of FCH₄ diurnal cycle
293 (Yavitt and others 1990; Mikkilä and others 1995; Waddington and others 1996; Dooling and others
294 2018; Ueyama and others 2020). However, Nadeau and others (2013), in a boreal bog, or Greenup and
295 others (2000) in a temperate bog, did not find such a clear daily variation. Beyond, Long and others
296 (2009), focusing on summer periods in a boreal fen, measured no diurnal variations in June while the
297 July month (peak of growing season) showed higher FCH₄ in daytime of about 20 nmol s⁻¹ m⁻².
298 Consistent with this diurnal pattern, Knox and others (2021) observed distinct daytime/nighttime FCH₄
299 in 12 peatlands (four fen, four marshes, three rice paddies, one swamp and one bog) from the FLUXNET
300 network dataset. These contrasted observations highlight the need to better constraint the variables
301 controlling the diurnal FCH₄ cycles in peatlands at various temporal scales. In particular, the shape of
302 the diurnal cycle measured in this work highlights the need to distinct processes that may decrease
303 FCH₄ during daytime to those that may contrariwise increase nighttime FCH₄. In this perspective, we
304 discuss in the following, the possible role of hydrological, thermal and photosynthetic processes on
305 FCH₄.

4.2 WTD influence on FCH₄

307 The respective thickness of the shallower aerobic and the deeper anaerobic peat layers is
308 driven by the WTD variations (Sundh and others 1995; Turetsky and others 2008). In the present study,
309 WTD, remained at an average of -0.12 m, with occasional and relatively limited seasonal variations
310 (minimum of -0.29, -0.31 and -0.18 m depths in the summers of 2019, 2020 and 2021, respectively,
311 Fig. 1C). In parallel, at the interannual scale, FCH₄ is positively correlated with WTD. This is illustrated
312 in summer (July to September) during which both WTD and FCH₄ were significantly higher in 2021 than

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3 313 in 2019 and 2020 (p -value < 0.05). Christensen and others (2003) and Knox and others (2021) suggested
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5 314 that CH₄ emission response to WTD variations mainly occurs for large WTD drops like those occurring
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7 315 during extreme events like drought. Consequently, as the WTD cannot fully explain the FCH₄ variability
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9
10 316 at seasonal scale, one must consider others seasonal processes such as thermal conditions and
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12 317 photosynthetic activity cycles.

16 318 **4.3 Temperature influence on microbiological and physical controls on** 17 18 319 **FCH₄**

20 320 Seasonal variations in CH₄ emissions at the Forbonnet featured higher emissions in summer,
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22
23 321 and lower fluxes during the remaining part of the year, similar to emission variability observed in
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25 322 temperate-boreal peatlands exhibiting a distinct seasonal pattern of temperature (Lai 2009; Ueyama
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27 323 and others 2020; Knox and others 2021) (Fig. 1A-E). However, the lowest and punctually even negative
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29 324 FCH₄ occurred during spring while they were expected to occur during winter, when T_{soil} in the
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31 325 anaerobic peat layer is at its minimum, hence limiting biological activity (Fig. 1A-E, Dunfield and others
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33
34 326 1993; van Winden and others 2012).

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37 327 As FCH₄ results from the balance between methanogenesis and methanotrophy, negative
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39 328 values are expected to occur when CH₄ oxidation surpasses its production. Hence, considering the
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41 329 acrotelm-catotelm model (Ingram 1978), relevant at the Forbonnet (Bertrand and others 2021;
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43 330 Lhosmot and others 2021), this suggests that the peat profile may, at the seasonal scale, be
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45
46 331 conceptualized as a two stacked biogeochemical reactor with reverse carbon dynamics due to
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48 332 contrasted redox conditions. First, the deep (catotelmic) anaerobic peat is expected to support CH₄
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50 333 production in reduced conditions (Granberg and others 1997; Stępniewska and Goraj, 2014). This is
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52 334 consistent with a CH₄ production highlighted at the Forbonnet by Lhosmot and others (2022) (under
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54 335 review) based on the observed $\delta^{13}\text{C}$ enrichment of the dissolved inorganic carbon in the catotelmic
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57 336 compartment. Second, the superficial, *i.e.* acrotelmic, peat layer is expected to support CH₄ oxidation
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59 337 due to a more variable waterlogging column favoring oxic conditions that shelter methanotrophs
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3 338 (Andersen and others 2013). This vertical delineation implies that the superficial methanotrophic peat
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5 339 reactor is stronger than the deep methanogenic reactor earlier in spring, due to progressive warming
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7 340 of the peat column from the surface (McKenzie and others 2007). Reversely, in autumn, the catotelm
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9 341 exhibits higher temperatures than the surface as the superficial peat progressively cools down and the
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11 342 deep peat CH₄ production is expected to exceed the superficial CH₄ oxidation (Fig. 1A-E).

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15 343 This two stacked biogeochemical reactor model agrees with the observed seasonal FCH₄ cycle
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17 344 (Fig. 1E) and can be deepened by focusing on the dynamics of nocturnal and daily CH₄ separately (Fig.
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19 345 5 A-B-C). Hysteresis for FCH₄-day-min suggests that surface and aerobic control on FCH₄ occurred in
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21 346 addition to deep and anaerobic temperature (25 cm depth) seasonal variation. The impact of
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23 347 day/nighttime surface temperature variation on superficial processes is generally less clear than at the
24
25 348 seasonal scale. Indeed, diurnal soil temperature and FCH₄ showed positive or negative correlations
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27 349 depending on the considered peatlands (Shannon and others 1996; Long and others 2009; Knox and
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29 350 others 2021). These contrasted observations suggest the combination of a range of processes at the
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31 351 diurnal scale that we propose to review under the light of the observed dynamics at the Forbonnet
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33 352 peatland.

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38 353 First, the diurnal cycle of T_{soil} could play a role on methanotrophs as it is well-established that
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40 354 temperature controls microbial activity (Andersen and others 2013). Lower temperature at night is
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42 355 expected to limit surface methanotrophy (Mikkilä and others 1995). However, the daily peak of
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44 356 surface T_{soil} occurred between three to five hours after the daily minimum FCH₄, suggesting that in
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46 357 addition to surface temperature other processes control daytime FCH₄ cycle. In contrast, as
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48 358 temperature at depth below 25 cm showed very limited diurnal variations (on average lower than
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50 359 0.1°C), this may favor a constant CH₄ production at the diurnal scale. Therefore, at the diurnal cycle,
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52 360 catotelmic thermal stability and superficial thermal variations likely favor constant methanogenesis
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54 361 and variable methanotrophy.

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3 362 Second, we observed a negative and significant linear regression between FCH4 and H (Fig. 8),
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5 363 the highest H values occurring during nighttime. Koebisch and others (2015) and Godwin and others
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7 364 (2013) reported that as far as the radiation heat maintains the water thermal stratification, this would
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9 365 favor CH₄ trapping below the surface. In contrast, at night, water releases sensible heat leading to
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11 366 convective mixing and associated CH₄ emissions. Therefore, the diurnal variation of the vertical
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13 367 thermal gradient can increase nighttime FCH4 due to changing physical conditions controlling CH₄
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15 368 transfer.

20 369 4.4 A photosynthesis control over FCH4?

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23 370 The diurnal FCH4 variability also showed a positive relationship with NEE. Notably, we
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25 371 observed an outstanding co-occurrence of negative NEE and FCH4 at daytime (Fig. 6). This suggests
26
27 372 that plant activity may significantly influence CH₄ balance. Plant influence was previously reported
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29 373 (Greenup and others 2000; Dooling and others 2018; Knox and others 2021). Nevertheless, a great
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31 374 range of peatland FCH4 evaluation such as those reported by Long and others (2009), Knox and others
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33 375 (2021) or Rey-Sanchez and others (2019) rather highlight greater FCH4 at daytime and interpreted this
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35 376 pattern as the effect of vascular plant aerenchymatous tissues favoring CH₄ transfer to the
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37 377 atmosphere. They also found that LE, a proxy of plant activity and of CH₄ transport through plant
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39 378 tissues (Knox and others 2021), is positively correlated to FCH4.

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43 379 Even though such a process is not detectable in our study as FCH4 was lower during the day
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45 380 and negatively correlated with LE (Fig. 7), it is not excluded that the presence of vascular plants
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47 381 participates to FCH4 diurnal cycle. Vascular plant photosynthesis produces labile organic matter, *e.g.*
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49 382 acetate, that is transferred through the root system and used as substrate for methanogenesis (Rovira
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51 383 1969; Whiting and others 1991; Ström and others 2003; Leroy and others 2017; Waldo and others
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53 384 2019; Mitra and others 2020). Various studies showed that these root exudates are transformed into
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55 385 CH₄ within 24 hours (Ström and others 2003; Mitra and others 2020; Knox and others 2021). This is
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57 386 consistent with the diurnal FCH4 observed in our study. However, this time lag may be variable and
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2
3 387 dependent of plant species (Ström and others 2003). While Knox and others (2021) showed a lag time
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5 388 from one to four hours between the peak of green primary production (GPP) and the peak of CH₄
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7 389 emissions, King and Reeburgh (2002) and Ström and others (2003) showed that CH₄ emitted from root
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9 390 exudates began after two hours and may reach a peak between three and seven days.

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13 391 In contrast to a possible positive role of photosynthesis on nighttime FCH₄, but presumably
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15 392 limited because of the low abundance of vascular plant, plant photosynthetic activity may limit
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17 393 daytime FCH₄ as oxygen (O₂) penetration depth within the peat column increases during daytime (King
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19 394 1990; Nedwell and Watson 1995; Frenzel and Karofeld 2000). This photosynthetic O₂ may then be used
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21 395 by methanotrophs to oxidize CH₄. In peatlands where vascular plants are not dominant such as at the
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23 396 Forbonnet, various organisms are known to be purveyors of O₂ by photosynthesis, essentially mosses,
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25 397 phototrophs (*e.g.* microalgae, cyanobacteria) and mixotrophic protists (*e.g.* ciliates) (Hamard and
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27 398 others 2021). Therefore, extrinsic microbial photosynthetic activity could be an important source of O₂
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29 399 in the superficial peat pore water and contribute to limit daytime FCH₄. This hypothesis is reinforced
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31 400 by Song and others (2016) who showed at the Forbonnet that the first centimeters of *Sphagnum* were
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33 401 mainly covered by mixotrophs, and that phototrophs accounted for 19 % of the microbial biomass.
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35 402 More generally, Hamard and others (2021) estimated that approximately 10 % of the peatland's net
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37 403 primary O₂ production is due to this extrinsic superficial microbial photosynthesis. In addition, CH₄ may
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39 404 be directly oxidized within *Sphagnum* hyaline cells, where endosymbiotic methanotrophs were found
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41 405 to be active in both submerged or aerated conditions, providing up to 20 % of the carbon used by the
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43 406 host plant (Kostka and others 2016; Raghoebarsing and others 2005). Consistently, Parmentier and
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45 407 others (2011) found in a Siberian peatland that this intrinsic symbiosis may result in a decline of 50 %
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47 408 of CH₄ emissions in a *Sphagnum* dominated area compared to an area without *Sphagnum* based on
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49 409 chamber measurements operated during one summer. Similar results were recently found in
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51 410 mesocosm experiments showing the positive effect of photosynthesis on CH₄ oxidation by *Sphagnum*
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53 411 (Kox and others 2020). As a result, at the Forbonnet, it is therefore hypothesized that the
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55 412 photosynthesis has a twofold impact on FCH₄. Firstly, a limiting constraint on FCH₄ associated with
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3 413 *Sphagnum* and mixotroph photosynthesis coupled to CH₄ oxidation and, secondly, a nighttime FCH₄
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5 414 increase associated with root exudates production of substrates for methanogenesis.
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8 415 At the seasonal scale, the relationship between FCH₄ and both NEE and LE was the strongest
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10 416 at the end of winter and spring (March to May, Figs. 6 and 7), suggesting a stronger photosynthetic
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12 417 control at that period. Accordingly, Campbell and Rydin (2019) and Moore and others (2006) showed
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14 418 that *Sphagnum* mosses stay photosynthetically active in winter and that the increase of photosynthesis
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16 419 at spring is initiated by bryophytes, respectively. In the same perspective, Korrensalo and others (2017)
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18 420 reported that *Sphagnum* photosynthesis was the highest during spring in an ombrotrophic peatland
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20 421 located in southern Finland. In addition, from March to May the period is generally wetter than the
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22 422 following summer (Fig. 1C). The photosynthesis derived O₂ might then be the overriding factor
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24 423 controlling O₂ availability and therefore CH₄ oxidation. Consistent with a greater spring activity,
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26 424 summer and autumn months featured a weaker relationship between FCH₄ and both NEE and LE.
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28 425 During summer, hot, dry and high PPDF conditions can induce photoinhibition of plants and in
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30 426 particular of *Sphagnum* whose primary production respond negatively to a decrease of the volumetric
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32 427 water content and increase of soil temperature (Murray and others 1993; Bragazza 2008; Norby and
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34 428 others 2019). Considering these elements, it is expected that *Sphagnum* photosynthesis and associated
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36 429 role on CH₄ dynamic becomes more impacted by the increase of droughts and heatwaves frequency
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38 430 and intensity related to climate change (IPCC 2022).
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45 431 **4.5 Toward a conceptual model of FCH₄ dynamic**

46 432 The discussion proposed in the previous sections allows delineating an updated conceptual
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48 433 model synthesizing the biotic and abiotic controls on FCH₄ in *Sphagnum*-dominated peatlands (Fig. 9).
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50 434 First, it was shown in the section 4.2 that interannual variation of WTD is negatively correlated to FCH₄
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52 435 and controls the sizes of the aerobic and anaerobic peat layers. Second, at the seasonal scale (section
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54 436 4.3), the mean nocturnal FCH₄ variability is tightly linked to the anaerobic soil temperature (25 cm
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56 437 depth), suggesting a seasonal control over CH₄ production (Fig. 5A). However, due to the thermic
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3 438 inertia of peat, the fastest increase of peat temperature in the aerobic layer at the end of the winter
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5 439 stimulates methanotrophic activity at the expense of methanogenic activity. This allows to explain the
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7 440 high density of negative FCH₄ from March to May. Then, in addition to the above-mentioned abiotic
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9 441 controls, the links of photosynthesis indicators (PPFD, LE, NEE) with diurnal and seasonal FCH₄, and
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11 442 especially its limitation (sections 4.4), suggest that, photosynthesis associated to *Sphagnum* and
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13 443 microbiological activity might be conceptualized as a third compartment partially driving FCH₄ through
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15 444 its own dynamic.
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20 445 **5 Conclusions and perspectives**

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22 446 This work investigated temporal variabilities of FCH₄ between a temperate and mid- altitude
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24 447 transitional mire and the atmosphere through eddy-covariance measurements during two and half
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26 448 consecutive years. The site was an annual source of CH₄ whose emissions were controlled by a range
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28 449 of parameters respectively acting predominantly at contrasted time scales. In particular, our work
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30 450 highlights an outstanding role of photosynthesis activating daytime methanotrophy that clearly
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32 451 contrasts with sites where aerenchymatous plants dominated and where greater daytime FCH₄ are
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34 452 common.
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39 453 In addition, the majority of diurnal FCH₄ found in literature were measured only in summer
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41 454 months or during the growing season. Here we measured the diurnal FCH₄ including the dormant stage
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43 455 of vegetation and evidenced complex seasonal variations. Thus, the proposed conceptual model is (Fig.
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45 456 9), to our knowledge, the first one to introduce a multi-temporal frame for the FCH₄ dynamics at the
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47 457 ecosystem scale in a temperate *Sphagnum* dominated transitional poor fen.
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50 458 In this framework and in order to better understand the CH₄ balance variability of peatlands,
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52 459 this model especially highlights the further need to (1) study both daytime and nighttime FCH₄ to
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54 460 improve CH₄ annual budget estimations and CH₄ peatland modeling at global scale (as suggested by
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56 461 Dooling and others 2018), and (2) to investigate and quantify the possible concurrent controls of
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58 462 microbiological and thermal stability over CH₄ emissions. In addition to the abiotic and biotic controls
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3 463 delineated in this study, such investigations could provide further drivers to constrains the future
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5 464 trajectories of *Sphagnum*-dominated peatlands under increasing climate changes.
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10
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33 477 manuscript.
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42 479 **7 Data availability**

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44 480 Soil-meteorological and piezometers data are available on Zenodo repository
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46 481 ([DOI:10.5281/ZENODO.3763342](https://doi.org/10.5281/ZENODO.3763342); [DOI: 10.5281/ZENODO.3763766](https://doi.org/10.5281/ZENODO.3763766)). Detailed data are available upon
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48 482 request.
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52 483 **8 Conflict of Interest**

53
54 484 The authors declare that they have no conflict of interest.
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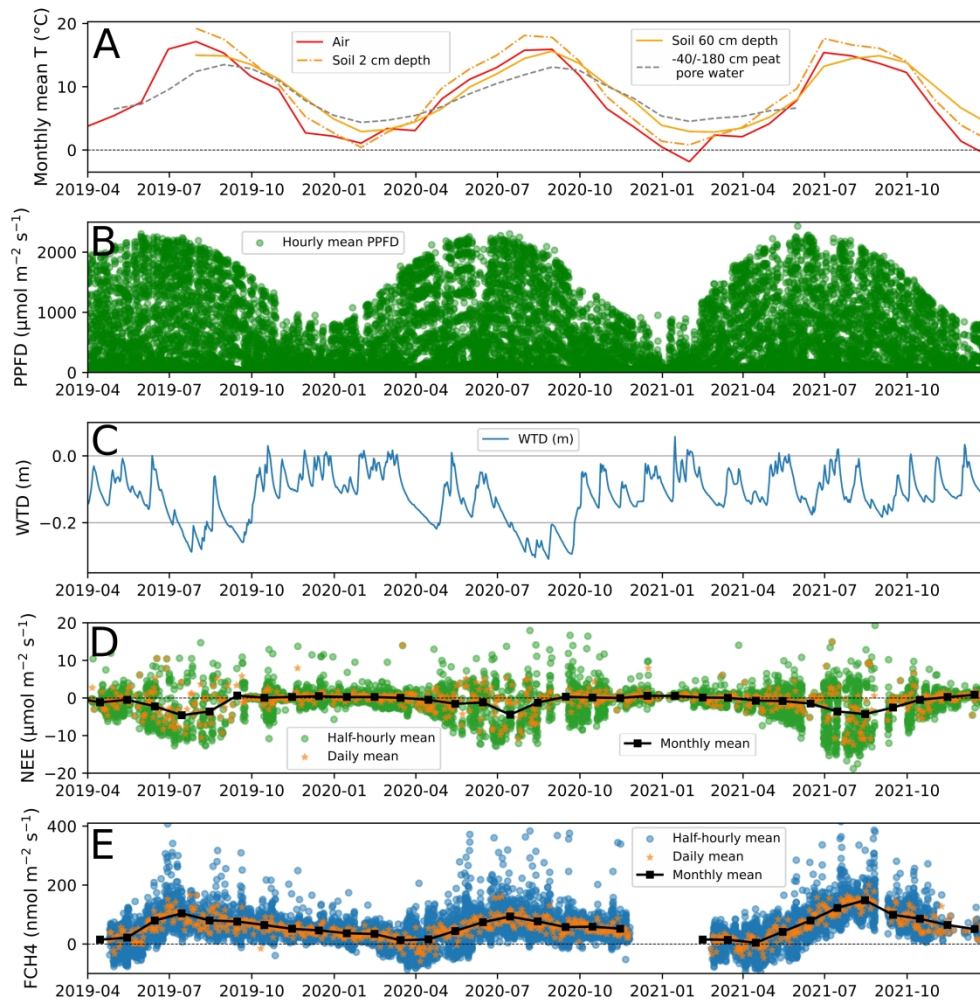
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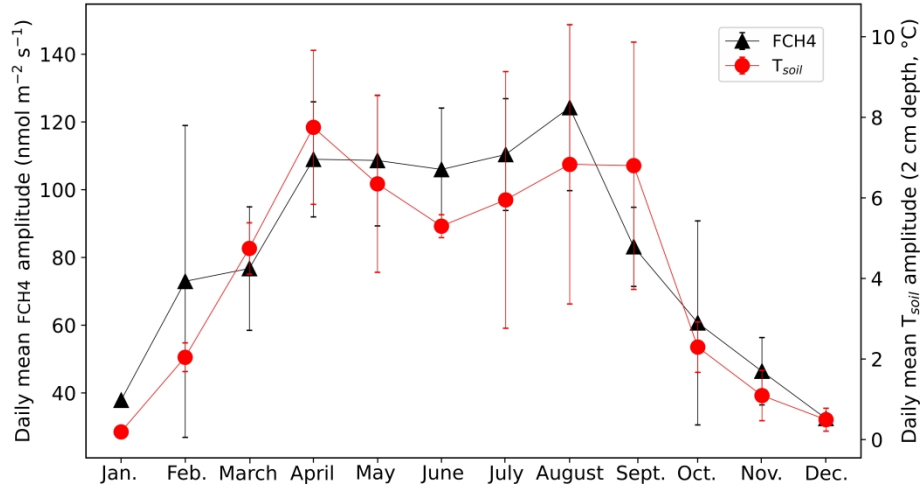
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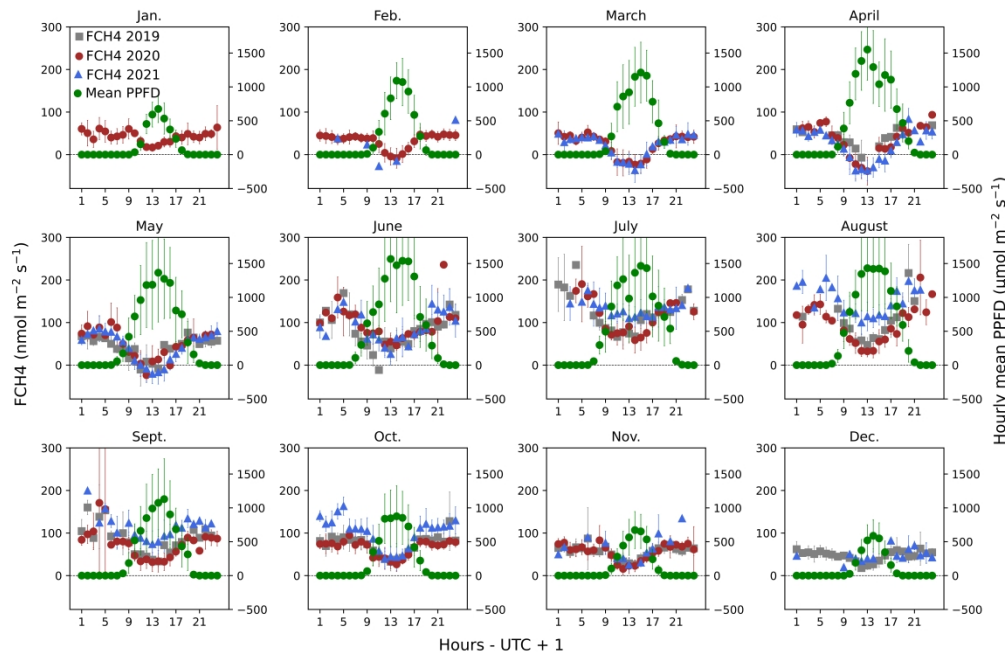
A- Monthly mean temperature measured in different compartments of the ecosystem ($^{\circ}\text{C}$). For T_{soil} only the 2 and 60 cm depths are plotted in Figure 1 to keep figures readable, for intermediate depths, see Supplementary data. B- Hourly PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$). C- Daily mean WTD (m). D- Half-hourly, daily, and monthly NEE measured by eddy covariance ($\mu\text{mol m}^{-2} \text{s}^{-1}$). The horizontal dashed line indicates the zero value. E- Half hourly, daily, and monthly FCH₄ measured by eddy covariance ($\text{nmol m}^{-2} \text{s}^{-1}$). The horizontal dashed line indicates the zero value, highlighting the negative FCH₄.

382x387mm (236 x 236 DPI)



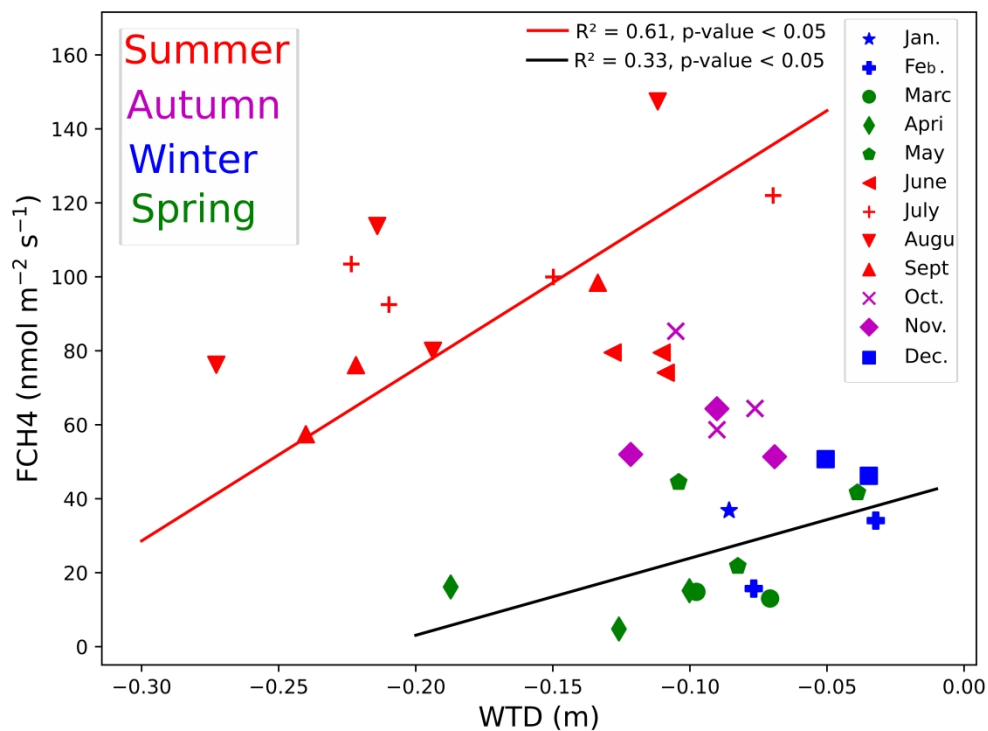
Monthly mean daily amplitude of FCH4 (nmol m⁻² s⁻¹) and soil temperature (°C, 2 cm depth). The vertical error bar corresponds to the standard deviation.

619x371mm (236 x 236 DPI)



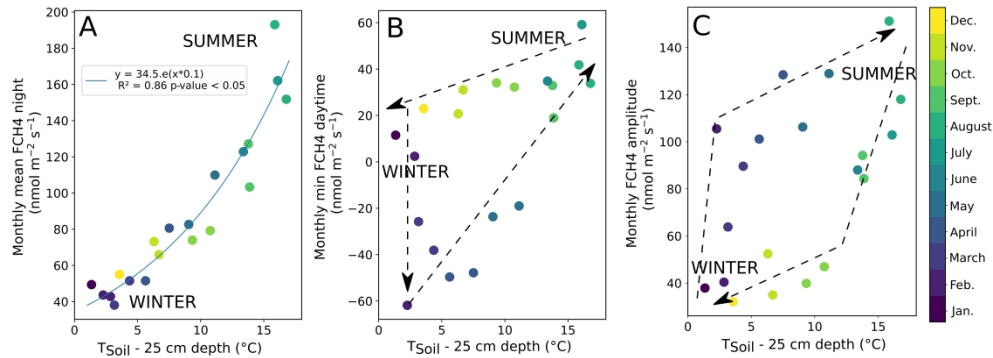
FCH₄ and PPFD for each month of the year (nmol and $\mu\text{mol m}^{-2} \text{s}^{-1}$). The vertical error bar represents the standard deviation. The data presented are hourly averages. The horizontal dashed line indicates the zero value.

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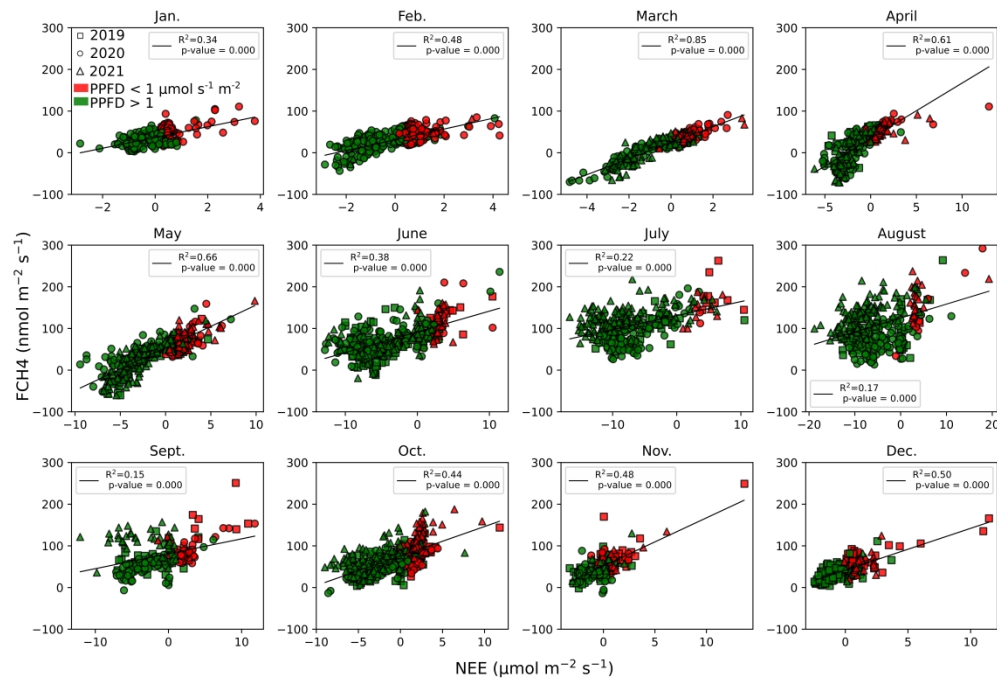
Scatter plot showing FCH₄ (nmol m⁻² s⁻¹) function of WTD (monthly mean). The marker color indicates the season and the marker symbol the month of the year. The red linear regression ($R^2 = 0.61$, $p\text{-value} < 0.05$) was calculated for months from July to September. The black linear regression ($R^2 = 0.33$, $p\text{-value} < 0.05$) was calculated for months from January to May.

769x573mm (236 x 236 DPI)



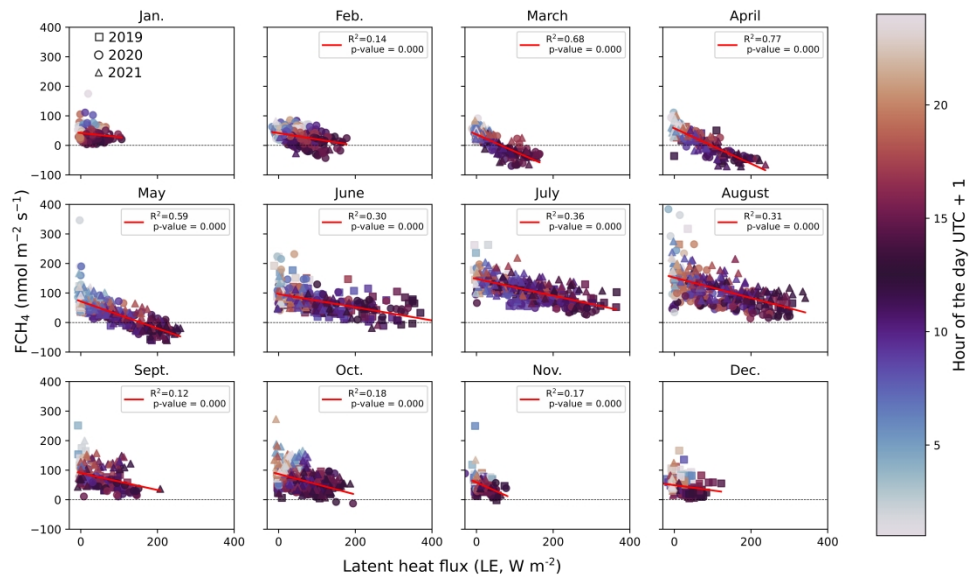
Scatter plots showing the relation between decomposed parts of the diurnal FCH₄ cycle and temperature at 25 cm depth ($T_{\text{Soil-25cm}}$). $T_{\text{Soil-25cm}}$ was recorded from August 2019 to November 2021. Markers correspond to monthly averages. The color bar indicates the month of the year. The dashed arrows highlight the seasonal pattern of these variables and in particular the hysteresis. A: The vertical axis is the average FCH₄ during the night (PPFD below 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ /sup). B: The vertical axis is the average minimum FCH₄ of the day. C: The vertical axis is the average daily amplitude of FCH₄.

1133x418mm (236 x 236 DPI)



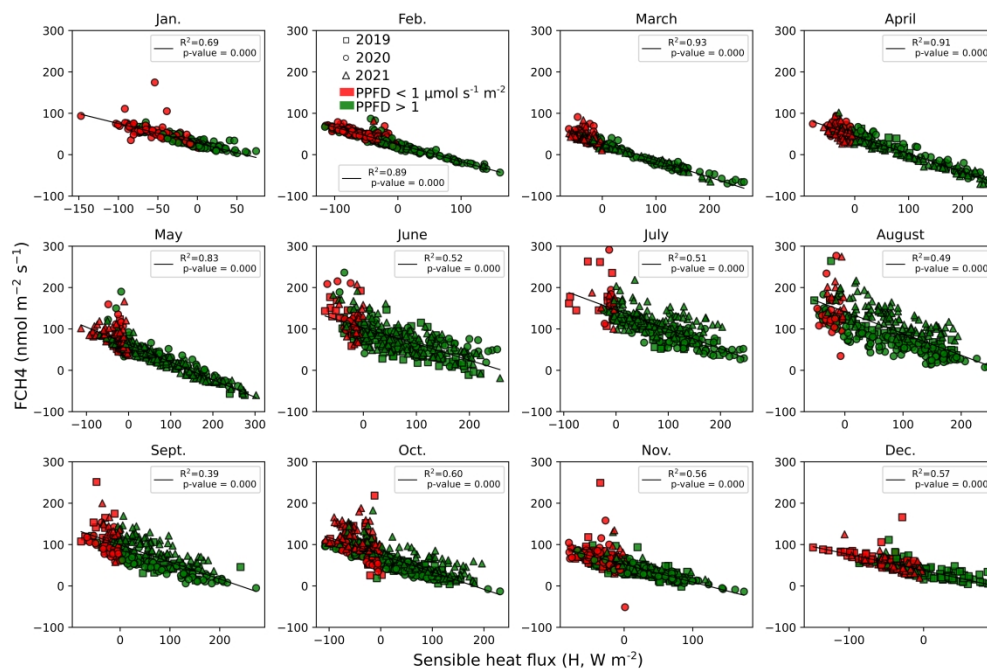
FCH₄ function of Net CO₂ Ecosystem Exchange (NEE) grouped by each month of the year (nmol and $\mu\text{mol m}^{-2} \text{s}^{-1}$ respectively). The data presented are half-hourly averages. The red color corresponds to conditions with PPFD below $1 \mu\text{mol m}^{-2} \text{s}^{-1}$. Reciprocally, the green color corresponds to conditions with PPFD higher than $1 \mu\text{mol m}^{-2} \text{s}^{-1}$. The black line is a linear regression including all points of the subplot.

747x514mm (236 x 236 DPI)



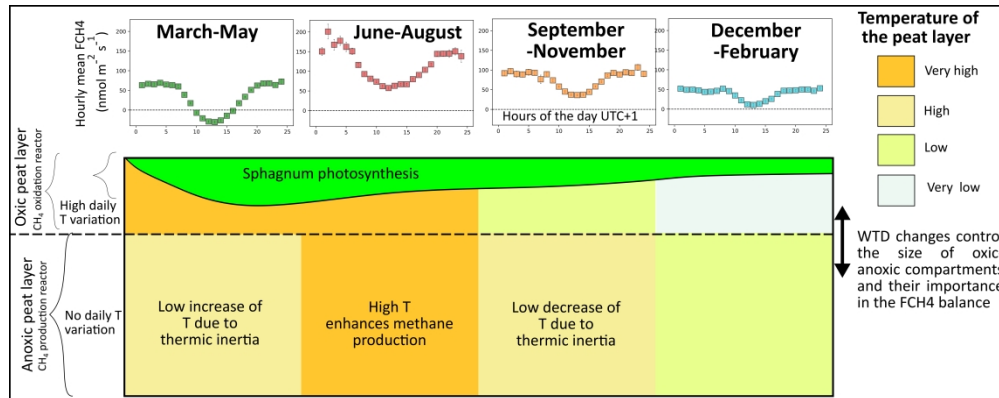
FCH₄ function of latent heat flux (LE) grouped by each month of the year ($\text{nmol m}^{-2} \text{s}^{-1}$ and W m^{-2} respectively). The data presented are half-hourly averages. The color code refers to the hour (UTC + 1) of the measurement. The red line is a linear regression including all points of the subplot. The horizontal dashed line indicates the zero value, highlighting the negative FCH₄.

760x443mm (236 x 236 DPI)



FCH4 function of sensible heat flux (H) grouped by each month of the year (nmol m⁻² s⁻¹ and W m⁻² respectively). The data presented are half-hourly averages. The red color corresponds to conditions with PPFD below 1 μmol m⁻² s⁻¹. Reciprocally, the green color corresponds to conditions with PPFD higher than 1 μmol m⁻² s⁻¹. The black line is a linear regression including all points of the subplot.

752x501mm (236 x 236 DPI)



Conceptual model showing CH₄ dynamic according to biotic and abiotic seasonal and diurnal variations.

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