



- 1 Hot spots, hot moments, and spatiotemporal drivers of soil
- 2 CO₂ flux in temperate peatlands using UAV remote sensing
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Abstract

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CO₂ emissions from peatlands exhibit substantial spatial and temporal variability due to their heterogeneous nature, presenting challenges to identify their underlying drivers and to accurately quantify and model CO2 fluxes. Here, we integrated field measurements with Unmanned Aerial Vehicle (UAV)-based multi-sensor remote sensing to investigate soil respiration across a temperate peatland landscape. Our research addressed two key questions: (1) How do environmental factors control the spatial-temporal distribution of soil respiration across complex landscapes? (2) How do hot spots and hot moments of biogeochemical processes influence landscape-level CO2 fluxes? We find that dynamic variables (i.e., soil temperature and moisture) play significant roles in shaping CO2 flux variations, contributing 43 % to seasonal variability and 29 % to spatial variance, followed by semi-dynamic variables (i.e., NDVI and root biomass) (19 % and 24 %). Relatively static variables (i.e., soil organic carbon (SOC) stock and C/N ratio) have a minimal influence on seasonal variation (2 %) but contribute more to spatial variance (10 %). Additionally, predicting time series of CO2 fluxes is feasible by using key environmental variables (test set: $R^2 = 0.74$, RMSE = 0.57 µmol m⁻² s⁻¹), while UAV remote sensing is an effective tool for mapping daily soil respiration (test set: $R^2 = 0.75$, RMSE = 0.54 µmol m⁻² s⁻¹). By the integration of in-situ high-resolution time-lapse monitoring and spatial mapping, we find that despite occurring in 10 % of the year, hot moments contribute 28 %-31 % of the annual CO₂ fluxes. Meanwhile, hot spots—representing 10 % of the area—account for 20 % of CO2 fluxes across the landscape. Our study demonstrates that integrating UAV-based remote sensing with field surveys improves the understanding of soil respiration mechanisms across timescales in complex landscapes, providing insights into carbon dynamics and supporting peatland conservation and climate change mitigation efforts. Keywords: Peatlands, Soil respiration, Greenhouse gas (CO₂) emission, CO₂ hot spots, CO₂ hot

moments, Multi-sensor UAV remote sensing, Global warming





35 1 Introduction 36 Peatlands are globally distributed ecosystems that store approximately 600 Gt of carbon (Yu et al., 2010), 37 despite covering less than 4 % of the Earth's land surface (Xu et al., 2018). However, rising concerns 38 exist over peatlands shifting from carbon sinks to carbon sources due to the impact of climate change 39 (Dorrepaal et al., 2009; Huang et al., 2021; Hopple et al., 2020), land use/cover conversion (Leifeld et 40 al., 2019; Deshmukh et al., 2021; Prananto et al., 2020), and other disturbances (Wilkinson et al., 2023; 41 Turetsky et al., 2015). In Europe, it has been reported that nearly half of the peatlands are suffering 42 degradation, primarily due to drainage for agricultural or forestry activities (Leifeld et al., 2019; Unep, 43 2022). As a consequence, European peatlands currently emit up to 580 Mt CO2-eq per year across the 44 continent (Unep, 2022). Given the critical role of the peatland ecosystem in the terrestrial carbon cycle, 45 it is therefore important to understand the mechanisms driving carbon fluxes and their responses to 46 climate change and human disturbances. 47 Soil respiration in peatlands is influenced by a combination of biotic and abiotic factors, such as soil 48 temperature and moisture (Treat et al., 2014; Fang and Moncrieff, 2001; Juszczak et al., 2013; Swails et 49 al., 2022; Hoyt et al., 2019; Evans et al., 2021), vegetation and root biomass (Acosta et al., 2017; Wang 50 et al., 2021), and soil organic matter quality (Hoyos-Santillan et al., 2016; Leifeld et al., 2012). CO₂ 51 emissions from peatlands are highly variable over space and time, presenting challenges to accurately 52 quantify and model carbon fluxes. This may partial because peatlands are characterized by a unique 53 microtopography, including features such as soil benches and depressions (Moore et al., 2019). These 54 small-scale variations create differences in hydrology, temperature, biogeochemistry, and vegetation 55 (Harris and Baird, 2019), leading to substantial spatial differences in the factors that control CO2 fluxes 56 and the formation of hot spots with elevated CO₂ emissions (Kelly et al., 2021; Becker et al., 2008; 57 Mcclain et al., 2003; Frei et al., 2012; Kim and Verma, 1992). For instance, the peat surface temperature 58 differences within a 10 m x 10 m plot characterized by hummock and hollow features can be 20°C 59 (Rhoswen et al., 2018). In addition, peatlands experience highly variable weather conditions, which can trigger periods of disproportionately high CO2 fluxes—often referred to as 'hot moments'—in response 60 61 to transient environmental changes, such as sudden shifts in temperature, rainfall events, or fluctuations 62 in the water table (Anthony and Silver, 2023). High CO₂ emissions occur from discrete areas in space





64 fluxes (Anthony and Silver, 2023; Fernandez-Bou et al., 2020). Most studies have examined the 65 mechanisms and contributions of hot spots and hot moments of other greenhouse gases (N2O, CH4) in 66 agricultural and forestry ecosystems (Krichels and Yang, 2019; Anthony and Silver, 2021; Kannenberg 67 et al., 2020; Leon et al., 2014; Fernandez-Bou et al., 2020), while research on CO₂ emission hot spots 68 and hot moments in peatlands remains limited (Anthony and Silver, 2021, 2023). 69 Identifying and quantifying hot spots and hot moments in peatlands is challenging, requiring large-scale, 70 continuous, long-term observations. Currently, most studies on peatland soil respiration rely on point 71 measurements taken at intervals of half a month to one month, primarily during daytime (e.g., Wright et 72 al. (2013); Bubier et al. (2003); Kim and Verma (1992); Danevčič et al. (2010)). This spatial-temporal 73 limitation hinders the effective detection of hot spots and hot moments. Some studies attempted to 74 extrapolate point data using land-use maps (Van Giersbergen et al., 2024; Webster et al., 2008; Mcnamara 75 et al., 2008), but uncertainties in landscape-scale fluxes increase as the number of measurement locations 76 decreases (Arias-Navarro et al., 2017; Wangari et al., 2022; Wangari et al., 2023). While automated 77 chamber systems improve temporal resolution and help capture hot moments (Hoyt et al., 2019; Anthony and Silver, 2023), they are typically limited to a few sampling points, and scaling up is constrained by 78 79 significant resource demands. Eddy covariance towers measure net ecosystem exchange over large areas 80 by recording high-frequency CO2 concentrations and air turbulence, providing insights into temporal 81 variations at the ecosystem level (Rey-Sanchez et al., 2022; Abdalla et al., 2014). However, the 82 underlying controlling factors and mechanisms at the process level are difficult to infer due to the large 83 spatial footprint. In addition, they may not accurately represent the spatial heterogeneity of peatlands 84 (Lees et al., 2018). These limitations highlight the need for complementary approaches to estimate CO₂ 85 fluxes at the landscape scale with methods adapted for heterogeneous peatland ecosystems. 86 Several studies have integrated satellite-based remote sensing datasets with on-site chamber 87 measurements to model landscape-scale CO₂ fluxes (e.g., Junttila et al. (2021); Wangari et al. (2023); 88 Lees et al. (2018); Azevedo et al. (2021)). Remote sensing datasets on topography and vegetation 89 parameters serve as proxies for soil moisture, vegetation cover, and nutrient availability, enabling large-90 scale CO₂ emission estimates within peatlands (Lees et al., 2018). However, this approach is somewhat 91 limited by coarse spatial (10 m to 1 km) and temporal (1 to 16 days) resolutions, which may overlook

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hot spots and hot moments, leading to potential over- or underestimations of CO2 fluxes in heterogeneous peatlands (Kelly et al., 2021; Simpson, 2023). This shortcoming might be overcome by using unmanned aerial vehicles (UAVs) equipped with different kinds of sensors such as Red-Green-Blue (RGB), multispectral, thermal infrared, and Light Detection and Ranging (LiDAR). UAVs offer flexible deployment and capture high-resolution spatiotemporal data (1 cm to 1 m, minutes to months) (Minasny et al., 2019) which makes them particularly suitable for monitoring complex peatland dynamics and detecting hot spots and hot moments. Thus far, UAVs have proven to be reliable tools for peatland applications, including vegetation mapping (Steenvoorden et al., 2023), topographic reconstruction (Harris and Baird, 2019), peat depth and carbon storage estimation (Li et al., 2024), and moisture monitoring (Henrion et al., 2025). In a recent study, Kelly et al. (2021) utilized UAV-derived land surface temperature to estimate ecosystem respiration of a hemi-boreal fen in southern Sweden, and Pajula and Purre (2021) and Walcker et al. (2025) employed UAV-based multispectral vegetation indices to map ecosystem CO2 flux at high resolution. These recent studies demonstrated the great potential of UAVs for linking CO2 fluxes with environmental factors at a very high resolution, although they mainly focused on data from a single sensor. Few studies have explored the fusion of UAV-derived data from multiple sensors for mapping soil respiration across peatland landscapes. In this study, we integrate multi-sensor UAV-based remote sensing with traditional field surveys to investigate soil respiration across a temperate peatland landscape, located in the Belgian Hautes Fagnes. As one of the largest and most ancient peatlands in Western Europe, the Belgian Hautes Fagnes represents an important ecosystem for studying peatland carbon fluxes due to its sensitivity to climate change and hydrological dynamics. Our research addresses two key questions: (1) What controls the nature and strength of the relationship between soil respiration and environmental factors across complex peatland landscapes and across spatial-temporal scales? (2) How do hot spots or hot moments of biogeochemical processes influence landscape-level carbon fluxes? More specifically, our study has three main objectives. First, we aim to identify the factors driving seasonal and spatial variations in soil respiration. Second, we assess the potential for linking environmental factors to CO_2 flux at high spatial and temporal resolutions. Third, we discuss the timing and location of hotspots and hot moments, assessing their contributions to overall CO2 flux budgets.





2 Materials and methods

2.1 Study site

The Belgian Hautes Fagnes plateau, part of the Stavelot-Venn Massif, is located in eastern Belgium (Figure 1a). This elevated landscape experiences a humid climate, with mean annual air temperature and precipitation being approximately 6.7 °C and 1439.4 mm (period: 1971-2000), respectively (Mormal and Tricot, 2004). The peatlands in this region cover an area of 37.50 km², which primarily consist of raised bogs formed since the Late Pleistocene (Frankard et al., 1998). Our study site (50.49 N, 6.05 E; ~0.30 km²) is located in the upper valley of the Hoëgne River peatland region (Figure 1a). The site is characterized by a distinct SE-NW oriented topographic gradient, with a clear transition from a low-relief plateau to steep hillslopes and then to the floodplain of a broad river valley (Sougnez and Vanacker, 2011). The area was drained and planted with spruces in 1914 and 1918. The plantations were progressively cleared between 2000 and 2016; since 2017, the site has been restored through reforestation with native hardwood species such as *Betula pubescens* and *Quercus robur*. Figure 1b shows main vegetation types across this landscape. An observation station of the Royal Meteorological Institute of Belgium (Mont Rigi, 50.51 N, 6.07 E) situated 3.07 km from the study site, records rainfall data every 10 minutes.

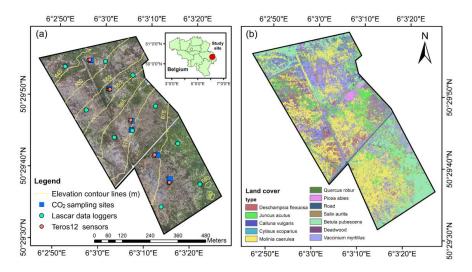


Figure 1. Maps showing the field-sampling locations (a) and land cover types (b) in the study area. Details on the land cover map are provided in our previous work (Li et al., 2024).

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2.2 CO₂ flux measurement campaigns

Soil surface CO₂ flux measurements were conducted at five slope positions along the middle part of the site (Figure 1a). A portable infrared gas analyzer with an automated closed dynamic chamber (LI-8100A system, LI-COR, United States) was used to monitor CO2 fluxes at 33 sites biweekly from December 2022 to March 2024 (Figure S1). At each slope position, six collars (20 cm diameter) were installed randomly, spaced 1-5 meters apart, to capture small-scale spatial variability. While at the shoulder, considering the heterogeneous soil water conditions, six collars were installed in drier areas and another three in wetter areas. All vegetation within the collars was removed. During each campaign, monitoring was conducted between 9:00 and 16:00. At each site, the CO₂ flux (μmol m⁻² s⁻¹) in the chamber was measured for 2.5 minutes per observation. Simultaneously, soil surface temperature (0-10 cm) and volumetric water content (VWC) during each CO2 measurement were recorded using a T-handled type-E thermocouple sensor (8100-201, LI-COR, United States) and a portable five-rod, 0.06 m long frequency domain reflectometry (FDR) probe system (ML2x, Delta-T, United Kingdom), respectively. However, CO2 measurements were not always possible due to technical issues and bad weather conditions, resulting in a total of 666 valid measurements. In addition, a pair of soil CO₂ forced diffusion probes (eosFD, EOSense, United States) were installed near LI-8100A collars from 24 April 2024 to 8 November 2024 (Figure S1). These probes, consisting of a soil node and a reference node, are based on a membrane-based steady-state approach and can measure CO₂ flux every 5 minutes (Risk et al., 2011). During this period, the probes continuously monitored CO₂ flux at different slope positions (Figure S1), resulting in a total of 39476 valid flux measurements.

2.3 Temperature and soil moisture monitoring

The temporal evolution of soil temperature and moisture along the middle part was monitored using Teros12 sensors (Meter Group, München, Germany), with two replicates per slope position, spaced 5 meters apart (Figure 1a) (Henrion et al., 2025). These sensors recorded data at a depth of 10 cm from 14 October 2022 to 28 October 2024, every 10 minutes. Between the two replicates of each slope position, a station positioned ~1.4 m above the ground recorded air temperature every ten minutes. Additionally, ten soil temperature data loggers (EL-USB-1-PRO, Lascar, United Kingdom) were installed primarily along two evenly spaced transects parallel to the main slope, at a depth of 10 cm (Figure 1a). These





167 loggers recorded soil temperatures at the same frequency as Teros12 sensors from 21 March 2023 to 8 168 November 2024. 169 2.4 Soil sampling and laboratory analysis 170 After completing all gas sampling campaigns, 33 disturbed soil samples (0-10 cm depth) were collected 171 within LI8100A collars at the five slope positions between 30 July and 15 October 2024. An Emlid Reach 172 RS 2 GPS device with centimeter-level precision was used to record the sampling site locations, using a PPK solution with the Belgian WALCORS network. The samples were stored in a refrigerator until 173 174 laboratory analysis. A subset of the samples was oven-dried at 80 °C for 24 hours (Dettmann et al., 2021), 175 then crushed and ground into a fine powder for soil organic carbon (SOC) and total nitrogen content (TN) 176 analysis (928 Series, LEGO, United States). Roots and litter were removed using tweezers during the 177 pre-processing procedure. We tested the presence of inorganic carbon of each sample by adding one drop 178 of 10 % HCl but found that no inorganic carbon was present in the samples. A subset of fresh samples 179 was used for root biomass analysis. The fresh soil samples were weighed and placed in a 1 mm sieve, 180 then rinsed with water to collect the roots. The washed roots were dried in an oven at 80 °C for 48 hours 181 and then weighed to calculate their dry biomass. 182 2.5 UAV data acquisition and imagery processing 183 During the CO₂ flux monitoring period, we conducted regular UAV flights across the study area to collect 184 high-resolution spatial data (Figure S1). A DJI Matrice 300 RTK was equipped with four different sensors: 185 (i) a Red-Green-Blue (RGB) camera (DJI Zenmuse P1 camera, 35 mm and 45 MP), (ii) a multispectral 186 camera (MicaSense RedEdge-M camera with five discrete spectral bands: blue (475 nm), green (560 nm), 187 red (668 nm), rededge (717 nm), and near-infrared (842 nm), along with a downwelling light sensor), 188 (iii) a LiDAR scanner (DJI Zenmuse L1, integrated with a 20-MP camera with a 1-inch CMOS sensor) 189 and (iv) a thermal infrared camera (TeAX, featuring FLIR Tau2 cores and ThermalCapture hardware). 190 Similar flight patterns and altitudes were used for the UAV missions as in our previous work (Li et al., 191 2024). In total, one RGB and one LiDAR dataset collected on 7 June 2023, were used in this study and 192 ten multispectral and ten thermal datasets collected between 13 April 2023 and 13 May 2024. 193 The raw multispectral images were processed in the Pix4D mapper software (Pix4D S.A., Lausanne,





Switzerland) to generate reflectance maps (resolution: 6 cm) of the five spectral bands of the study area. We calculated the Normalized Difference Vegetation Index (NDVI) across the 10 maps from the monitoring period (Table S1). The raw thermal infrared video streams were converted into RJPG images using ThermoViewer version 3.0.26 (TeAX, 2022). Subsequently, the thermal images were processed with the Pix4D mapper to generate land surface temperature (LST) maps (resolution: 12 cm), which were used for soil temperature mapping (Text S1, Figure S2, Table S2). The RGB photos were processed in DJI Terra V4.0.10 (DJI, 2023) to generate an orthomosaic image with a resolution of 1.26 cm. The raw LiDAR data was processed in DJI Terra to provide a Digital Terrain Model (DTM; .tif file) with a resolution of 15 cm, which was used for generating daily air temperature maps (Text S1) and terrain wetness index (TWI) (Text S2). The variables derived from the four types of images were summarized in Table S1.

2.6 Statistical analysis

All data analyses were conducted in RStudio (v4.1.2). All timestamps in this study were converted to Coordinated Universal Time (UTC) to ensure consistency across datasets. Group differences were assessed by the one-way analysis of variance (ANOVA) using the stats package. When ANOVA detected a significant effect (p < 0.05), Tukey's Honestly Significant Difference (HSD) post-hoc test was performed to determine which groups differed significantly from each other. Pearson correlation analysis was performed using the corrplot package (Murdoch and Chow, 1996). The linear mixed-effects models used to identify factors controlling spatial- temporal variations of CO_2 flux, as well as time series simulation and mapping are introduced below.

2.6.1 Models to explain spatial-temporal variations in CO2 flux

We utilized linear mixed-effects models to assess the impacts of both static and dynamic environmental factors on the spatial and seasonal variability of CO₂ fluxes. This is because mixed models integrate both fixed and random effects, which provide a robust framework for analyzing data with non-independent structures (Pinheiro and Bates, 2000). The model was performed using the *lme4 package* (Bates et al., 2015), with the natural logarithm of CO₂ flux observations as a response. The CO₂ fluxes data are often characterized by extreme values and right-skewed distribution, and a lognormal assumption for CO₂





- 221 fluxes could better account for the influences of extreme values on the overall distribution (Wutzler et
- al., 2020). The mixed-effects models were defined as:

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$$y_{ij} = \beta_0 + \beta_1 x_{ij} + \dots + \beta_p x_{ij} + b_{0j} + b_{1j} z_{ij} + \dots + \epsilon_{ij}$$
 (1)

- 224 Where:
- y_{ij} is the dependent variable (i.e., $\ln (CO_2 \text{ flux})$, unit: $\mu \text{mol m}^{-2} \text{ s}^{-1}$) for observations i in group
- 226 j.

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- 227 $\beta_0, \beta_1, ..., \beta_p$ are fixed-effect coefficients.
- 228 x_{ij} is the fixed-effect variable (independent variable).
- 229 b_{0j} , b_{1j} ,... are random-effect coefficients associated with group j, which account for
- 230 variability across groups.
- 231 z_{ij} is the random-effect variable.
- 232 ϵ_{ij} is the residual error term.
- 233 The fixed-effect predictors were categorized into three groups:
- Static variables: SOC stock, and the ratio of SOC content to nitrogen content (C/N ratio).
- Semi-dynamic variables: root biomass and NDVI.
- Dynamic variables: soil temperature and soil moisture at 0–10 cm depth.

Estimates for NDVI were extracted from the maps by retrieving the value of the 33 CO₂ flux observation sites and the SOC stock values were extracted from the a local high resolution (0.15 m) SOC stock map (Li et al., 2024). The sites were included as random effects in the seasonal pattern model to account for repeated measurements at the same locations during the monitoring period, whereas slope positions were treated as random effects in the spatial pattern model. Independent variable coefficients, Intraclass Correlation Coefficient (*ICC*), coefficients of determination (*marginal R*² and *conditional R*²), Root Mean Square Error (*RMSE*), and Akaike Information Criterion (*AIC*) were extracted using the *modelsummary package* after running each model. The *ICC* quantifies the proportion of variance explained by a grouping (random) factor in multilevel data; values close to 1 indicate high similarity within groups, while values near 0 suggest that grouping conveys little to no information (Nakagawa et al., 2017; Shrout and Fleiss, 1979). The *marginal R*², represents the variance explained by fixed effects alone, and *conditional R*² represents the variance explained by both fixed and random effects (Pinheiro and Bates, 2000). The





250 multicollinearity in regression analysis, the car package was used to calculate the variance inflation 251 factor (VIF) (Fox and Monette, 1992). 252 2.6.2 Modelling hourly CO₂ flux 253 The mixed-effects model was utilized to simulate the time series of CO₂ fluxes at different slope positions. 254 Here, the slope position was included as random variable, and the natural logarithm of CO2 flux (hourly) 255 was set as a response. We utilized CO2 fluxes data measured by both the LI8100A system and eosFD 256 probes. Specifically, we randomly selected a number of 30 observations from the eosFD probes at each slope position to reduce data redundancy from high-frequency sampling. Afterwards, we applied 257 258 weighting to adjust the remaining imbalance in data density between the high-frequency eosFD 259 monitoring and low-frequency LI8100A measurements, ensuring both data sources contributed 260 proportionally to the model. The independent variables included hourly soil temperature (10 cm depth), 261 volumetric soil moisture (VWC, 10 cm depth), and air temperature (1.4 m height), considering their 262 importance in explaining the seasonal and diurnal patterns of CO₂ flux. 263 As in our previous work (Li et al., 2024), we divided the dataset into a training set (70 %) and a test set 264 (30 %) using K-means clustering to minimize biases that could arise from random sampling (Hair et al., 265 2010). The models were trained on the training set, and the simulation accuracy was validated using the 266 test dataset. The coefficient of determination (R^2) and RMSE were used to assess the quality of the model 267 fit. Finally, we made simulations of the time series of hourly CO2 flux for different slope positions from 268 1 May 2023 to 30 April 2024. Furthermore, we identified CO2 emission hot moments based on the 269 description in Section 2.6.4. 270 2.6.3 Mapping daily CO2 flux 271 The linear mixed-effects model was utilized to map the spatial distribution of daily CO₂ fluxes across the 272 landscape, with daily soil temperature (10 cm depth), corrected daily TWI, and SOC stock being 273 considered as fixed-effect variables and gas sampling sites being included as random variables. The daily 274 CO₂ flux model training, testing procedures, and evaluation of model fit followed the same approach 275 detailed in Section 2.6.2. We then applied the trained model to predict the daily CO₂ flux of the landscape 11

relative importance of each independent variable was obtained using the glmm.hp package. To assess

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276 from 1 May 2023 to 30 April 2024. Additionally, we calculated the mean daily soil CO2 flux maps for 277 each season and the entire year. Based on these predictions, we identified hot spots for each day by the 278 methods described below. 279 2.6.4 Quantifying hot moments and hot spots of CO2 flux 280 In previous studies, percentiles have been used as thresholds for identifying heat waves (e.g., (Meehl and 281 Tebaldi, 2004): 97.5th percentile), soil heat extremes (e.g., García-García et al. (2023): 90th percentile), 282 hot spots of N₂O emissions (e.g., Mason et al. (2017): median plus three times the interquartile range), 283 and hot spots of CO₂ emissions (e.g., Wangari et al. (2023): median plus the interquartile range). In this 284 study, we tested different methods and selected the 90th percentile as the threshold of both hot moments 285 and hot spots to balance capturing extreme CO2 emissions while maintaining a sufficient sample size. To 286 capture the hot moments, we calculated a threshold for each slope position separately using its own dataset. For hot spots, we determined a daily threshold based on each map. 287





3 Results

3.1 Spatial and temporal patterns of CO2 flux

During the monitoring period, the CO₂ emissions show large spatial and seasonal variations across the landscape. The CO₂ fluxes at the summit $(3.16 \pm 3.25 \, \mu \text{mol m}^{-2} \, \text{s}^{-1})$ and shoulder (dry: $2.81 \pm 3.22 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$), wet: $2.33 \pm 2.36 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$) slope positions were significantly higher than that of footslope $(1.25 \pm 1.00 \, \mu \text{mol m}^{-2} \, \text{s}^{-1})$ and backslope $(1.11 \pm 1.03 \, \mu \text{mol m}^{-2} \, \text{s}^{-1})$ (p < 0.05) (Figure 2a). Furthermore, significant differences were observed when grouping the data into three vegetation covers: CO₂ emissions from *Vaccinium myrtillus* were lower than those from *Juncus acutus*, with mean \pm sd values of $1.59 \pm 1.43 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$, and $2.33 \pm 2.36 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$, respectively (Figure 2b) (p < 0.05). However, the CO₂ fluxes under *Molinia caerulea* displayed large variations ($0.02 \sim 20.1 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$), and no significant differences were found compared to the other two vegetation types. The CO₂ flux data indicated large CO₂ emissions from June to September ($3.65 \pm 2.68 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$), which can be 8.11 times higher than that from winter and early spring ($0.45 \pm 0.40 \, \mu \text{mol m}^{-2} \, \text{s}^{-1}$) (Figure 2c). CO₂ emissions in May and October were at a moderate level.



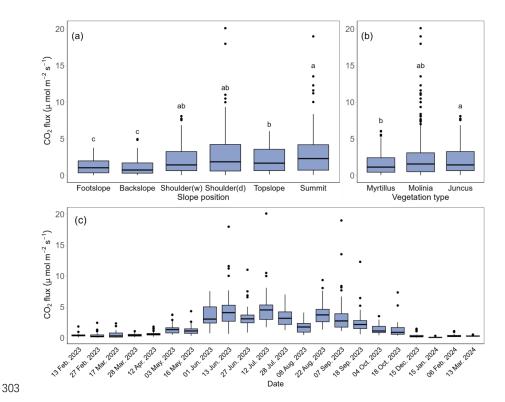


Figure 2. Boxplot of CO₂ flux (μmol m⁻² s⁻¹) across different slope positions (a), vegetation types (b), and sampling dates (c), using data from the LI8100 A system recorded between 2023-02-13 and 2024-03-13. (a), CO₂ flux data of each box were from all dates, and Shoulder (w) and Shoulder (d) indicate shoulder wet and shoulder dry areas, respectively. (b), CO₂ flux data of each box were from all dates, and Myrtillus, Molinia and Juncus indicate *Vaccinium myrtillus*, *Molinia caerulea* and *Juncus acutus*, respectively. (c), CO₂ flux data of each box were from all slope positions. The edges of each box represent the first quartile (Q1) and third quartile (Q3), while the line inside the box indicates the median CO₂ flux. Whiskers extend from the box to the smallest and largest values within 1.5 times the interquartile range, and points outside the whiskers are considered extreme values. The *ANOVA* and *HSD* post-hoc tests were performed within slope positions and vegetation types, with boxes sharing the same letters indicating no significant difference.

3.2 Factors contributing to spatial-temporal variability

Three types of environmental factors explain 64 % of the observed seasonal variance in CO₂ emissions, with contributions of 33 % from soil temperature, 10 % from VWC, 19 % from vegetation (i.e., NDVI,





root biomass), 2 % from relatively static factors (i.e., SOC stock, C/N ratio), and 6 % from random effects (i.e., 33 sampling sites) (Table 1). This suggests that long-term stable environmental factors have minimal direct influence on seasonal CO₂ flux patterns. Interestingly, the contribution of these relatively stable factors is nearly 11 times higher in explaining overall spatial variations, although soil temperature is still the dominant factor (Table 1). The low *ICC* values in both spatial and seasonal models highlight significant small-scale heterogeneity in soil respiration.

Table 1. Coefficients and relative contributions of three types of input variables (static, semi-dynamic, dynamic) of mixed linear regression models for modelling CO₂ flux. Random effects were evaluated by *ICC* and model performance was evaluated by *Marginal R*², *Conditional R*², and *RMSE*.

	Input variables		Seasonal patterns	Spatial patterns	
Fixed effects:	Static	SOC stock	0.003	-0.003	
coefficient		(t ha ⁻¹)	(1 %)	(0.06 %)	
(contribution)		C/N ratio	0.05	0.07*	
			(1 %)	(10 %)	
	Semi	root biomass	0.06	0.09*	
	dynamic	(g 100g ⁻¹)	(0.36 %)	(12 %)	
		NDVI	0.90***	-3.35**	
			(18 %)	(12 %)	
	Dynamic	Soil temp.	0.12***	0.39***	
		(°C)	(33 %)	(18 %)	
		VWC	-0.77***	-1.37**	
		$(cm^3 cm^{-3})$	(10 %)	(11 %)	
Random effects	ICC		0.18	0.06	
	(contribution)		(6 %)	(3 %)	
Model	Marginal R ²		0.64	0.63	
performance	Conditional R ²		0.70	0.66	
	AIC		1386.00	50.10	
	RMSE		0.64	0.25	

Note. Significance level: *** p < 0.001, ** p < 0.01, * p < 0.05. All CO₂ fluxes (unit: μ mol m⁻² s⁻¹), soil temperature, and VWC data for spatial and seasonal patterns was from the LI8100 A system. To investigate the factors controlling spatial variations of CO₂ flux, we calculated the mean values of CO₂ flux, NDVI, soil temperature, and VWC of each site during the monitoring time.





3.3 Continuous hourly time series of CO2 flux and hot moments

Three dynamic variables (i.e., soil temp., VWC, air temp.) were taken into account to predict the time series of hourly CO₂ flux at different slope positions. These input variables were selected due to their influential roles in explaining the diurnal (Figure S3) and seasonal fluctuations of CO₂ emissions. As shown in Table 2, the temporal model yielded a robust performance in both training and testing dataset, achieving *R*² and *RMSE* values of 0.86 and 0.39 μmol m⁻² s⁻¹ and 0.74 and 0.57 μmol m⁻² s⁻¹, respectively.

Table 2. Model performance for simulating time series of hourly CO₂ flux (unit: μmol m⁻² s⁻¹) and mapping daily CO₂ flux (unit: μmol m⁻² s⁻¹) across the landscape.

Models	Training dataset		Testing dataset	
Models	RMSE	R^2	RMSE	R^2
Temporal model	0.39	0.86	0.57	0.74
Spatial model	0.50	0.81	0.54	0.75

Note. Temporal model used the natural logarithm of CO₂ flux data from LI8100 A and eosFD probes, whereas spatial model used the natural logarithm of CO₂ flux data only from LI8100 A.

The modelled CO₂ emissions at all slope positions display a clear seasonal trend, with higher CO₂ fluxes from June to September and lower estimates in other months, in line with the observed fluxes shown in brown dots (Figures 3c-3h). The total CO₂ fluxes (Table 3) at the summit (19.50 t ha⁻¹) and the shoulder (dry: 19.47 t ha⁻¹, wet: 16.31 t ha⁻¹) slope positions were higher than that of topslope (14.45 t ha⁻¹), followed by footslope (13.94 t ha⁻¹) and backslope (11.54 t ha⁻¹) (Table 3), consistent with the spatial patterns of our observations (Figure 3a). However, the modelled mean ± sd CO₂ fluxes at all slope positions (Table 3) were lower than measured CO₂ fluxes by the LI8100 A system. This is because the measurements were taken during the daytime when fluxes were higher (Figure 2), whereas the modeled values represent the average of both daytime and nighttime fluxes. Most hot moments occurred from June to September 2023, whereas few hot moments were observed from late July to the early August (Figures 3c-3h). Although these hot moments of different slope positions only accounted for 10 % across the year, they could contribute 28 %-31 % to the annual total CO₂ emissions (Table 3).



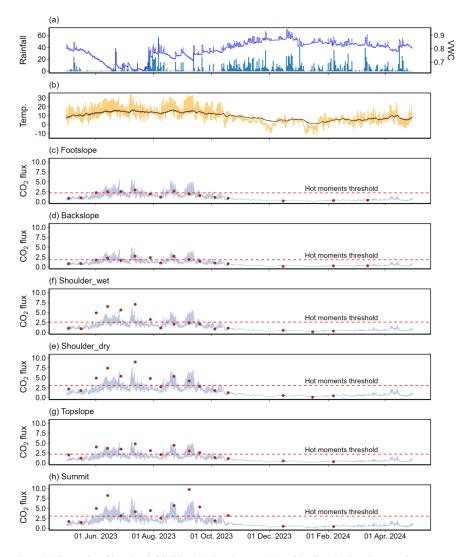


Figure 3. Time series of hourly rainfall (blue bar), hourly mean VWC (blue line) (a), hourly mean air temperature (orange line) and soil temperature (black line) (b), modelled hourly CO₂ flux (purple lines) and in-situ measurements (brown dots) at different slope positions (c-h). Rainfall (unit: mm) data was from the nearby meteorological observation station. The VWC (unit: cm³ cm⁻³) and soil temperature (unit: °C) were mean values from five slope positions monitored by Teros12 sensors at a depth of 10 cm. Air temperatures (unit: °C) were mean values from 5 stations at 1.4 m height above ground. Measured CO₂ fluxes (unit: μmol m⁻² s⁻¹) were from the LI8100A system.





Table 3. Summary of modelled mean ± sd CO₂ fluxes, thresholds for identifying hot moments, total CO₂ flux, and the contribution of hot moments to total flux at different slope positions.

Slope position	Footslope	Backslope	Shoulder	Shoulder	Topslope	Summit
			wet	dry		
$Mean \pm sd \ CO_2 \ flux$	1.00 ± 0.91	0.83 ± 0.73	1.21 ± 0.99	1.44 ± 1.22	1.04 ± 0.86	1.41 ± 1.22
(µmol m ⁻² s ⁻¹)						
Total CO2 flux	13.94	11.54	16.31	19.47	14.45	19.50
(t ha-1)						
Threshold	2.22	1.80	2.55	3.07	2.19	3.04
(µmol m ⁻² s ⁻¹)						
Contribution	30.74 %	30.31 %	28.99 %	28.41 %	28.91 %	29.93 %
of hot moments						

3.4 Daily CO₂ flux maps and hot spots

A linear mixed-effects model was utilized to map daily CO₂ flux from 1 May 2023 to 30 April 2024, incorporating soil temperature, corrected TWI, and SOC stock as predictors due to their significant role in explaining the spatial-seasonal variability of CO₂ flux and their availability as spatial data. The mapping model yielded robust performance metrics (Table 2), with R^2 and RMSE values of 0.81 and 0.50 μ mol m⁻² s⁻¹ in the training dataset, and 0.75 and 0.54 μ mol m⁻² s⁻¹ in the test dataset, respectively.

Consistent with our observations, the modelled soil respiration also displayed substantial spatial-temporal heterogeneity (Figures 4a-4d). More specifically, the mean CO_2 fluxes ranged from 0.17 µmol m^{-2} s^{-1} to 10.80 µmol m^{-2} s^{-1} in spring (Figure 4a), 0.36 µmol m^{-2} s^{-1} to 30.60 µmol m^{-2} s^{-1} in summer (Figure 4b), 0.18 µmol m^{-2} s^{-1} to 14.87 µmol m^{-2} s^{-1} in autumn (Figure 4c), and 0.04 µmol m^{-2} s^{-1} to 2.24 µmol m^{-2} s^{-1} in winter (Figure 4d). Many modelled mean CO_2 fluxes at the footslope and backslope (elevation < 660 m) remained below 2 µmol m^{-2} s^{-1} (Figure 4e). In contrast, the modelled CO_2 emissions remained higher throughout the year at the shoulder (660 m \leq elevation \leq 670 m) and east of summit (elevation > 675 m) with high vegetation cover. About 10 % of the area were identified as hot spots, with a high frequency of hot spots occurring in these regions, while the locations of sporadic hot spots varied over time (Figure 4f). Overall, the landscape emitted approximately 24.34 t ha⁻¹ CO_2 to the atmosphere during the simulation period, with 19.63 % \pm 0.57 % of the CO_2 fluxes coming from the hot spots.





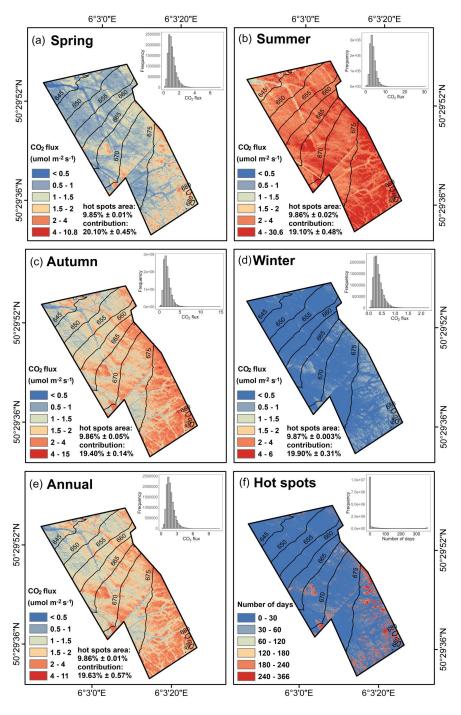


Figure 4. Maps of modelled mean daily CO_2 flux (μ mol m^{-2} s^{-1}) in four seasons (a, b, c, d), throughout the year (e),

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383 hot spots area proportion and CO_2 flux contribution from the hot spots of each season and across the year are

384 summarized in the corresponding maps.





4 Discussion

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4.1 Drivers of spatiotemporal heterogeneity in CO₂ emission

Consistent with prior temperate peatland studies (Juszczak et al., 2013; Wilson et al., 2015; Danevčič et al., 2010; Swails et al., 2022), our results indicate that seasonal variations in soil CO2 flux across the landscape are highly related to soil temperature, which could account for 33 % of the seasonal variability (Table 1). In contrast to tropical peatlands, where precipitation or water table fluctuations often dominate CO₂ flux dynamics (Hoyt et al., 2019; Cobb et al., 2017), our observations reveal that temperature exhibits distinct seasonal patterns (Figure 3b), which in turn drive fluctuations in soil respiration throughout the year (Figure 2c). Moreover, spatial heterogeneity in soil temperature further shaped landscape-scale CO₂ emission patterns (Table 1). For instance, the south-facing summit slopes, which receive more solar radiation in the daytime, consistently show higher CO₂ fluxes (Figure 2a). Conversely, the north-facing footslope and backslope, situated on the windward side, experience lower temperatures, resulting in generally lower soil respiration rates throughout the observation period (Figure 2a). While temperature is the dominant driver, soil water content influences oxygen availability within the peat profile, thereby regulating microbial decomposition and CO₂ production (Hatala et al., 2012; Knox et al., 2015; Zou et al., 2022; Huang et al., 2021; Deshmukh et al., 2021). For example, Knox et al. (2015) demonstrated that a declining water table caused by drainage increases oxygen penetration into the peat, resulting in higher CO2 flux compared to restored peatlands. In our study case, the CO2 fluxes were slightly higher in drier shoulder positions compared to wetter areas (Figure 2a), and VWC accounted for approximately 10 % of the spatial-seasonal variance in CO2 fluxes (Table 1). The monthly/biweekly NDVI is the second-most influential predictor for CO₂ seasonal fluctuations (Table 1), as NDVI reveals vegetation phenology during the monitoring period. In the spatial-pattern model, the contribution from root biomass becomes more substantial, together with mean NDVI explaining 24 % of spatial variance. These findings align with previous studies that vegetation mediates soil respiration through root respiration, exudates, litter inputs, and rhizosphere priming effects (Acosta et al., 2017; Wang et al., 2015a; Walker et al., 2016; Jovani-Sancho et al., 2021; Bragazza et al., 2013). In our study, the CO2 fluxes of dwarf shrubs (i.e., Vaccinium myrtillus) were significantly lower than those in Juncus acutus-dominated areas (Figure 2b), likely due to the lower root biomass of dwarf shrubs

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soil compared to Sphagnum/herbs (Bragazza et al., 2013; Wang et al., 2015a), which further constrains microbial activity and CO2 production. In addition, vegetation cover may indirectly influence soil respiration by regulating surface microclimate conditions such as humidity and temperature (Nichols, 1998; Stoy et al., 2012). As shown in Table 1, the SOC stock and C/N ratio have limited explanatory power for the seasonal variability of CO₂ flux, in line with findings of Danevčič et al. (2010). However, when analyzing drivers of average soil CO2 flux rate across the entire monitoring period, the importance of C/N ratio increased nearly 11 times (Table 1). This likely reflects how long-term averaging integrates short-term dynamic variability, thereby amplifying the role of spatial heterogeneity mediated by the C/N ratio. Prior studies suggesting that the quality of organic material, rather than its quantity, primarily regulates CO2 fluxes in peatlands (Hoyos-Santillan et al., 2016; Leifeld et al., 2012). Specifically, the soil C/N ratio is known to regulate microbial community functionality and respiration intensity (Leifeld et al., 2020; Briones et al., 2014; Ishikura et al., 2018; Wang et al., 2015b). 4.2 CO₂ emission hot moments and hot spots: identification, implications, and importance 4.2.1 Temporal analysis and hot moments During past decades, efforts have been made to model CO2 flux over time based on its relationship with environmental factors such as hydrology, temperature, substrate quality, microbial community, and vegetation (Hoyt et al., 2019; Junttila et al., 2021; Schubert et al., 2010; Rowson et al., 2012; Abdalla et al., 2014; Farmer et al., 2011; Anthony and Silver, 2021). In our study, diurnal cycles of CO2 fluxes are closely related to air temperature (Figure S3), while soil temperature and moisture are important factors in explaining the seasonal patterns of CO₂ flux (Table 1). Hence, the three dynamic environment variables

(Table S3). Furthermore, it has been shown that dwarf shrubs in northern peatlands produce high-

phenolic litter with higher resistance to breakdown and introduce more water-soluble phenolics into the

were incorporated into the model to simulate the hourly CO2 flux across the entire monitoring period.

Overall, the temporal model demonstrated robust performance in both the training and testing datasets

(Table 2) and effectively captured seasonal and diurnal trends at most sites (Figures 3c-3h). However,

the modelled peak values are lower than the observations at shoulder and summit slope positions (Figures





440 3f, 3e, 3h), which may be partially due to the limited number of high-value observations in these areas. 441 Consequently, the model is more influenced by the more frequent lower CO₂ fluxes, leading to an overall 442 underestimation of the peak. In addition, two types of gas analyzers were employed to monitor CO2 flux 443 with different sampling frequency and time: the LI-8100A sensor was used biweekly or monthly to 444 capture seasonal trends, while eosFD probes collected data every five minutes to track diurnal 445 fluctuations. The integration of these datasets for modelling temporal dynamics improved estimation 446 accuracy but might also introduce uncertainties into the model. 447 Anthony and Silver (2023) demonstrated that identifying hot moments of CO2 flux in peatland requires 448 intensive continuous measurements, while as an alternative, our robust simulation of hourly CO2 flux 449 enabled the identification of hot moments in a complex landscape. We found that most of these hot 450 moments occurred during the summer and early autumn seasons (Figure 3c-3h), in agreement with our 451 in-situ observations (Figure 2c). The frequent high CO2 emissions in June and July can be attributed to 452 the low precipitation, decreased soil moisture, and high temperatures (Figure 3a-3b). However, few hot 453 moments were captured during late July and early August due to the heavy rainfall events (Figure 3a). 454 This absence may be attributed to the fact that intense rainfall led to lower temperatures and increased 455 soil moisture (Figures 3a, 3b), thereby suppressing microbial and root respiration (Hoyt et al., 2019). 456 Following this period, CO₂ emissions reached values that exceeded the 'hot moments' threshold in mid-457 August, aligning with declining rainfall and rising temperatures (Figures 3c-3h). The hot moments 458 observed in September are linked to seasonal fluctuations in precipitation and temperature (Figures 459 3a,3b). 460 Similar to the findings of Anthony and Silver (2021) and Kannenberg et al. (2020), these hot moments 461 accounted for approximately 10 % throughout the year, while they contributed significantly to the annual 462 total CO₂ emissions (28 %-31 %; Table 3), highlighting the important role of short-term high-emission 463 events in the overall carbon emission. Therefore, missing hot moments may lead to significant 464 underestimates of total peat soil respiration budgets. Despite continuous automated chamber or eddy 465 covariance measurements that are ideal for capturing hot moments of CO2 emissions (Anthony and Silver, 466 2023; Hoyt et al., 2019; Anthony and Silver, 2021), long-term continuous monitoring is still labor-467 intensive and cost-prohibitive in many locations within the complex peatland ecosystems. Given that we

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observed a concentration of hot moments in the summer and autumn, we recommend increasing monitoring frequency during these seasons for temperate peatlands. This strategy would help capture carbon emission dynamics more effectively, reduce uncertainties in annual carbon flux estimates, and provide more representative peatland CO₂ flux data.

4.2.2 Spatial analysis of CO2 fluxes and hot spots

Our mapping of CO₂ flux across the landscape yielded a model performance of $R^2 = 0.75$ and RMSE =0.54 µmol m⁻² s⁻¹ for the test dataset (Table 2). This can be attributed to the incorporation of key environmental factors that drive the spatiotemporal heterogeneity of soil respiration into the model inputs. These factors - including soil temperature, corrected TWI, and SOC stock - can be directly obtained through multi-sensor UAV remote sensing or estimated using high spatiotemporal resolution data. Previous studies upscaled spatial carbon fluxes using area-weighted methods, extrapolating point data from CO2 chamber flux measurements to adjacent or larger areas based on land cover maps (Van Giersbergen et al., 2024; Webster et al., 2008; Leon et al., 2014). However, this approach can lead to over- or underestimation (Wangari et al., 2023; Leifeld and Menichetti, 2018), because our findings reveal that even within the same vegetation cover, such as Molinia caerulea, CO2 emissions exhibit significant spatial-temporal variability (Figure 2b). In recent years, spatial upscaling of CO2 fluxes has increasingly relied on satellite-based remote sensing data (e.g., Junttila et al. (2021); Wangari et al. (2023); Zhang et al. (2020); Azevedo et al. (2021); Huang et al. (2015). While this method covers larger areas, it is often constrained by coarse temporal and spatial resolutions. The peatland ecosystem is characterized by great temporal and spatial heterogeneity at small scales, and ignoring these variations can introduce significant uncertainties in CO2 emission estimates. Our study demonstrates that high-resolution UAV remote sensing imagery, with fine temporal and spatial scales, could effectively upscale CO2 fluxes from point measurements across a heterogeneous landscape, thereby reducing uncertainties in spatial predictions of CO2 fluxes. Furthermore, the high-resolution CO₂ flux maps allowed for the identification of hot spot areas across the landscape. We found that most of the hot spots occurred at the shoulder areas where soil moisture was relatively lower and to the east of the summit which is covered by dense vegetation (Figure 1b,

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496 temperature, moisture, water table depth, vegetation type, and substrate quality, is likely driving these 497 differences (Anthony and Silver, 2023; Kuzyakov and Blagodatskaya, 2015; Mcnamara et al., 2008). For 498 instance, the tree-covered areas at the summit contribute substantial root respiration, which may, in turn, 499 trigger the formation of consistent hot pots throughout the year. Besides, litterfall beneath trees insulates 500 the peat soil and provides an abundant resource for microbial activity. 501 High-emission events from hot spots play a crucial role in overall CO₂ fluxes (Anthony and Silver, 2023), 502 hence, neglecting these areas could lead to substantial underestimation of peatland carbon emissions. In 503 our study, although less than 10 % of area was identified as hot spots, their CO2 flux contribution 504 accounted for nearly 20 % across the year (Figure 4). However, research specifically focusing on 505 peatland CO₂ emission hot spots remains limited (Anthony and Silver, 2023), despite increased 506 exploration of greenhouse gas emission hot spots in other ecosystems (e.g., agricultural field (Krichels 507 and Yang, 2019; Rey-Sanchez et al., 2022; Leifeld et al., 2020); wetland (Rey-Sanchez et al., 2022); 508 water-limited Mediterranean ecosystem (Leon et al., 2014); forest (Wangari et al., 2023)). Hence, to 509 improve the accuracy of CO2 spatial budgeting for peatlands, there is a need for enhanced high-resolution 510 dynamic monitoring of hot spot areas (Becker et al., 2008). Our study demonstrates the great potential 511 of UAV technology for peatland hot spot identification and quantification, offering new insights into 512 studying soil respiration within heterogeneous ecosystems as well as optimizing peatland management 513 and CO2 emission reduction strategies.





5 Conclusion

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In this study, we monitored the dynamics of peatland surface and subsurface environments using both field surveys and multi-sensor UAVs at high spatial-temporal resolution. We investigated the influence of dynamic and static environmental factors on soil respiration rates across different scales, thereby enhancing our understanding of peatland carbon cycling. Additionally, we simulated CO2 flux with high spatial-temporal resolution by integrating field measurements and UAV data. These reliable modelling allow us to identify and quantify CO2 emission hot spots and hot moments across the landscape. To summarize, the main findings of our study are as follows: (1) Soil respiration rates vary significantly across space and time, influenced by both dynamic and relatively static environmental factors at different scales. Temperature is the primary driver of CO₂ flux variations, explaining 33 % CO2 seasonal variability and 18 % spatial variability. Soil moisture negatively affects both seasonal and spatial variations, accounting for 10 % - 11 % of the variance. Semidynamic factors (i.e., NDVI and root biomass) contribute 19 % to seasonal variability and 24 % to spatial variability. While relative static factors (i.e., the C/N and SOC stock) have little impact on the seasonal CO₂ flux variability, the contribution of the C/N ratio increases nearly 11 times for spatial variability. (2) Predicting temporal series of hourly CO₂ flux can be effectively achieved (test set: $R^2 = 0.74$, RMSE = 0.57 µmol m⁻² s⁻¹) by considering its relationship with key environmental variables such as air temperature, soil temperature and soil moisture, all of which are relatively straightforward to monitor. These reliable time series data provide a foundation for capturing respiration pulses occurring over short periods, with hot moments primarily occurring in summer and early autumn. (3) The UAV remote sensing data can yield robust spatial mapping of soil respiration rates across heterogeneous landscapes, with RMSE and R2 values of 0.54 µmol m-2 s-1 and 0.75 in the test dataset, respectively. These high-resolution CO2 flux maps enable us to locate hot spots. (4) Despite representing 10 % of time within one year, CO₂ fluxes from hot moments contribute 28 %-31 % to the overall CO₂ flux budgets. Approximately 10 % areas are identified as hot spots, while contributing 19.63 $\% \pm 0.57$ % of total CO₂ fluxes. The locations of high-frequency hot spots remain consistent, while the locations of sporadic hot spots vary over time.





542 Code and data availability 543 Code and data will be made available on request. 544 545 CRediT authorship contribution statement 546 YL: Writing - original draft, Visualization, Investigation, Formal analysis, Conceptualization. MH: 547 Writing - review & editing, Investigation. AM: Writing - review & editing. SL: Writing - review & editing, Funding acquisition, Conceptualization. SO: Writing - review & editing, Funding acquisition, 548 549 Conceptualization. VV: Writing - review & editing, Funding acquisition, Conceptualization. FJ: Writing 550 - review & editing, Funding acquisition, Supervision, Conceptualization. KVO: Writing - review & 551 editing, Investigation, Funding acquisition, Supervision, Conceptualization. 552 553 **Declaration of Competing Interest** 554 The authors declare that they do not have any commercial or associative interest that represents a conflict 555 of interest in connection with the work submitted. 556 557 Acknowledgements 558 Yanfei Li wishes to thank the joint grant from China Scholarship Council and UCLouvain (No. 559 202106380030). Kristof Van Oost, Sophie Opfergelt, and Sébastien Lambot are supported by the Fonds 560 de la Recherche Scientifique (FNRS). The authors would like to thank the Département de la Nature et 561 des Forêts (DNF) and Joël Verdin for giving access to the study site. The authors would like to thank 562 Dylan Vellut for his assistance with soil respiration measurements and UAV campaigns. 563 564 Financial support 565 This work is an Action de Recherche Concertée, n° 21/26-119, funded by the Communauté française 566 de Belgique.





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