For Biogeosciences

Title

Dynamics and environmental drivers of methane and nitrous oxide fluxes at the soil and ecosystem levels in a wet tropical forest

Authors

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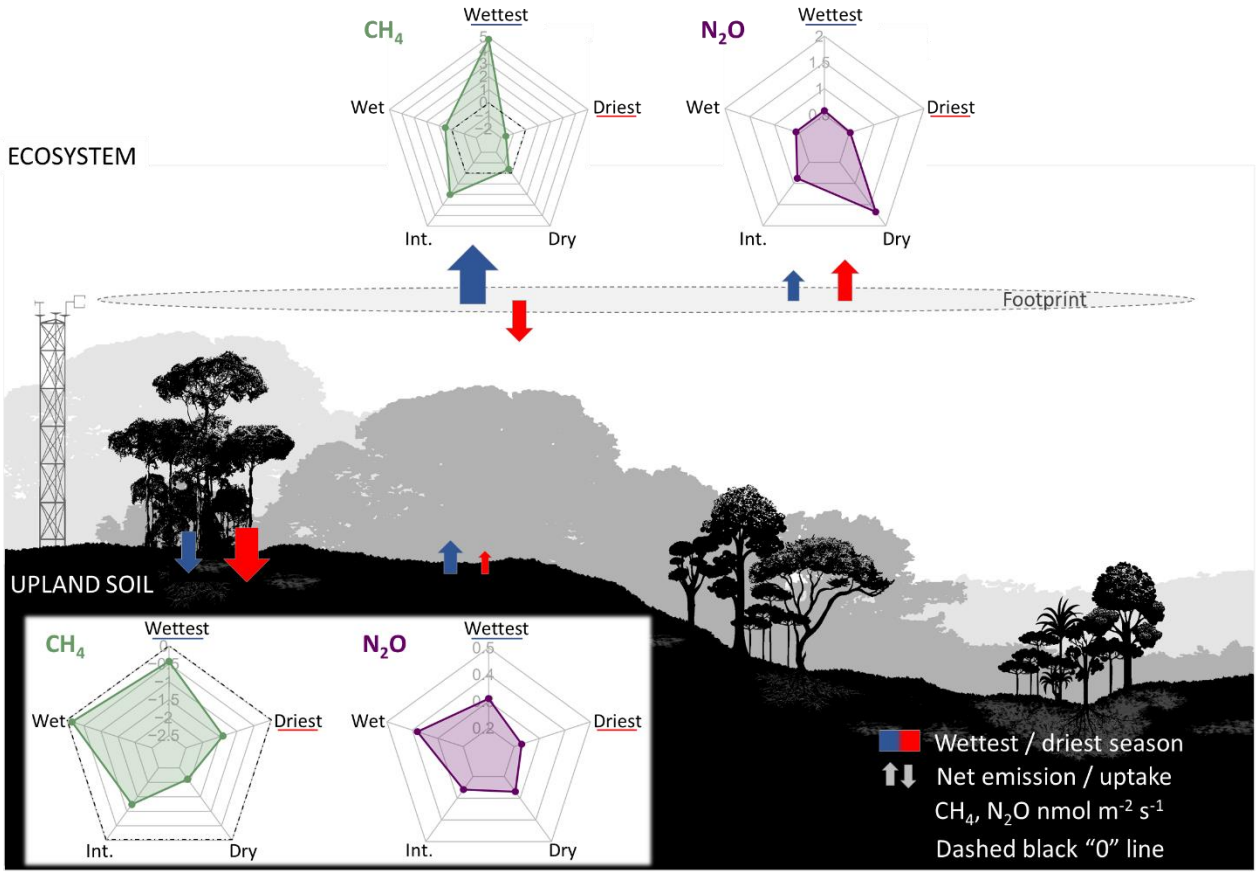
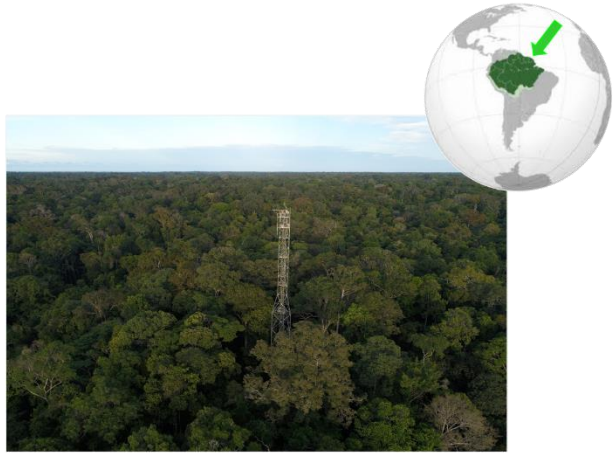
Abstract

Tropical forests are critical for maintaining the global carbon balance and mitigating climate change, yet their exchange of greenhouse gases with the atmosphere remains understudied, particularly for methane (CH_4) and nitrous oxide (N_2O). This study reports on continuous measurements of CH_4 and N_2O fluxes at the ecosystem and soil levels, respectively through eddy covariance and an automated

chamber technique, in a wet tropical forest in French Guiana over a period of 26 months. We studied the magnitude of CH_4 and N_2O fluxes and their drivers (climatic variables) during the driest and wettest seasons. Seasonal ecosystem fluxes showed near-zero net CH_4 uptake during the driest season and emissions during the wettest season that were larger in magnitude than the uptake. Meanwhile, N_2O emissions were of similar magnitudes in both seasons. Upland soils within the footprint of the eddy covariance tower emitted N_2O in both seasons, although these fluxes were particularly small. In contrast, upland soils were characterised by CH_4 uptake. Overall, seasonal ecosystem and soil CH_4 and N_2O fluxes were partially explained by seasonal variations in soil water content, soil temperature and global radiation. The magnitude and sign of the net ecosystem fluxes of CH_4 and N_2O were likely due to outgassing from aboveground biomass and the presence of seasonally flooded areas within the footprint of the eddy covariance system. Further studies of other ecosystem compartments in different forest habitats are needed to better understand the temporal variations in CH_4 and N_2O fluxes in wet tropical forests.



The 26-month study in a wet tropical forest revealed seasonal CH_4 and N_2O fluxes at the ecosystem and soil levels. Daily means of CH_4 and N_2O fluxes were highly variable, changing direction and magnitude on short time scales.



1 Introduction

The lack of knowledge on greenhouse gas fluxes in the tropical forests of the Amazon Basin contributes significantly to the uncertainty in the global greenhouse gas budget, particularly for methane (CH_4) and nitrous oxide (N_2O) (Davidson et al., 2012; Covey et al., 2021), the two most important greenhouse gases in the atmosphere after carbon dioxide (CO_2). Early observations show that tropical forests in the Amazon Basin may contribute disproportionately to global CH_4 and N_2O exchanges compared to other forests (Tian et al., 2015), but considerable uncertainties remain due to the paucity of data and lack of detailed understanding of CH_4 and N_2O cycling at both soil and ecosystem levels in these forests. The role of tropical forest soils is crucial as they can act either as a source or a sink for CH_4 and N_2O (Bouwman et al., 1993). In contrast to the consistent emissions from soil microbial decomposition and root activity for CO_2, anaerobic CH_4-emitting microbes (methanogenic archaea) are dominant in wetland environments, whereas aerobic CH_4-consuming microbes (methanotrophic bacteria) are more abundant in upland soils (Ito and Inatomi, 2012; Welch et al., 2019) where they play the role of CH_4 sinks. For N_2O as well, both emission and uptake can occur in soils. N_2O can be produced by microbes under both anaerobic (via denitrification) and aerobic (via nitrification) conditions (Khalil et al., 2004), although the majority of N_2O production occurs in waterlogged soils (Oertel et al., 2016). On the other hand, soil microbes that are not denitrifiers can reduce N_2O to dinitrogen (Sanford et al., 2012; Jones et al., 2014) to complete the biogeochemical cycle.

Microbial CH_4 and N_2O fluxes in tropical soils are controlled by the complex interplay of multiple environmental and biological factors. The key factors regulating net CH_4 fluxes in tropical soils include redox potential and water table depth (Silver et al., 1999; Teh et al., 2005; von Fischer and Hedin, 2007), plant productivity (Whiting and Chanton, 1993; von Fischer and Hedin, 2007), labile soil organic matter (Wright et al., 2011), competition for carbon substrates among anaerobic microorganisms (Teh and Silver, 2006; von Fischer and Hedin, 2007), temperature (Knox et al., 2021), and the presence of plants that facilitate atmospheric escape (Pangala et al., 2013). The key factors regulating net soil N_2O fluxes in tropical soils include redox potential, soil water content (SWC) or water table depth,

temperature, pH, labile carbon availability and labile nitrogen availability (Groffman et al., 2009). For both CH_4 and N_2O flux dynamics, of all these factors, variations in soil redox conditions, mediated by variations in water table depth, play a particularly important regulatory role in tropical soils (Zhu et al., 2013; Yu et al., 2021) due to the underlying physiology of the microbes that produce and uptake CH_4 and N_2O.

Production and uptake of both CH_4 and N_2O in the soil are highly variable in space (hot spots) and time (hot moments) (Blagodatsky and Smith, 2012). This is because microbial processes are discontinuous (Blagodatsky and Smith, 2012), environmental conditions can change rapidly at short timescales, and the strong seasonality of climate conditions, with pronounced wet and dry seasons, in most tropical forests can significantly affect physical and ecophysiological ecosystem processes, which in turn affect greenhouse gas fluxes. In addition, most published N_2O and CH_4 flux data from tropical ecosystems have been derived from chamber-based measurements at the soil level, often with low spatial and temporal resolutions. Automated soil chambers capture fine-scale temporal variations, including hot moments. However, they represent only a tiny part of the landscape (i.e. a few square metres of soil surface at most) and therefore fail to capture emergent ecosystem properties that may be manifest at larger spatial scales. Moreover, above-ground plant tissues also exchange CH_4 and N_2O with the atmosphere (i.e. produced in the soil and transported in the transpiration stream and/or by diffusion, or produced within the stems), and this cannot be captured by soil chamber measurements alone. This makes chamber approaches insufficient to quantify the magnitude and seasonal pattern of whole-ecosystem greenhouse gas fluxes. Chamber-based measurements also hamper our ability to assess the role of tropical forests in the exchange of CH_4 and N_2O between the atmosphere and the land surface, and induce large uncertainties in our current assessment of the greenhouse gas sink potential of tropical forests.

On the other hand, a combination of soil and ecosystem level measurements can be a powerful tool to reduce the gap between different levels of measurement (e.g. plot to ecosystem) (Lucas-Moffat et al., 2018). Continuous ecosystem-level measurements via the eddy covariance technique provide high

temporal resolution data on mass and energy exchanges at the ecosystem level (Baldocchi, 2014, 2020; Delwiche et al., 2021) and more detailed information on ecosystem functioning at a broader spatial scale than do mere soil measurements, which miss above-ground exchanges and typically, also emissions from wetland areas within the ecosystem (Bonal et al., 2008; Aguilos et al., 2018; Wang et al., 2021; Liu et al., 2022). However, eddy covariance cannot indicate how much different land cover types relatively contribute to the ecosystem's total flux since the measurements integrate high and low frequency flux over time and space. Chamber and eddy covariance-based approaches each have their own strengths and weaknesses; however, taken together, they effectively represent the magnitude of ecosystem fluxes and can help determine the drivers of greenhouse gas flux dynamics (Eugster et al., 2015). We therefore combined these two approaches to test the following assumptions:

- H1: Ecosystem- and soil-level CH_4 and N_2O fluxes vary seasonally in the studied tropical forest, switching between uptake and emission,
- H2: At both the soil and ecosystem levels, soil water content is the primary abiotic driver of these gaseous fluxes during the driest and the wettest seasons.

This study provides, for the first time, a comprehensive assessment of CH_4 and N_2O dynamics at both ecosystem and soil levels based on high-frequency eddy covariance and continuous soil chamber time series over 26 months in a wet tropical forest.

2 Methods

2.1 Study site

Our research was conducted at the Guyaflux site (5°16'54"N, 52°54'44"W) (Bonal et al., 2008), an ICOS-associated ecosystem station (GF-Guy) located 15 km from the coast and approximately 40 km west of Kourou, in French Guiana, South America. On a decadal time scale, the average annual precipitation at the study site is 3102 ± 70 mm and average annual air temperature is 25.7 ± 0.1 °C (Aguilos et al., 2018). The climate is humid tropical and highly seasonal due to the north-south movement of the Inter-Tropical Convergence Zone (ITCZ), which drives regional precipitation. The ITCZ dictates the wet season

(from December to July, with rainfall of up to 500 mm month^{-1}) and the long dry season from mid-August (mid-November, with less than 100 mm month^{-1}). In the northernmost part of the Guiana shield, where the study site is located, the topography results in a succession of small elliptical hills from 10 to 40 m asl, with soils classified as nutrient-poor acrisols (IUSS Working Group WRB, 2015). The site is totally surrounded by undisturbed forest, locally characterised by a tree density of about 620 trees ha^{-1} (for trees > 10 cm dbh), an average tree height of 35 m, an average tree diameter at breast height (DBH) of 40.1 cm, with emergent trees over 40 m tall, and a tree species richness of about 140 species ha^{-1} (Bonal et al., 2008; Aguilos et al., 2018; Daniel et al., 2023).

2.2 Tower-based flux measurements

Continuous measurements of the surface-atmosphere exchange of CO_2, H_2O and energy were initiated in 2003 based on the Euroflux methodology (Aubinet et al., 2000) and the eddy covariance approach (Baldocchi, 2003); they have previously been reported and fully documented (Bonal et al., 2008; Aguilos et al., 2018). The Guyaflux flux tower is 55 m high and extends about 20 m beyond the top of the canopy. The putative average footprint of the eddy fluxes from the tower covers approximately 50 - 100 ha of undisturbed forest in the direction of the prevailing winds (Bonal et al., 2008; Fang et al., 2024). Within the estimated footprint of the Guyaflux tower, 52% of the area is upland forest, 13% is seasonally flooded forest and the rest (35%) is slope forest. Most of the meteorological and eddy flux sensors are mounted three meters above the top of the tower and include equipment measuring air temperature and humidity (HMP155, Vaisala, Helsinki, Finland), bulk precipitation (ARG100, EM lmt, Sunderland, UK), wind direction and speed (A05103-5, Young, Traverse City, MI, USA), and global infrared incident and reflected radiation (Rg) (CNR1, Kipp and Zonen, Bohemia, NY, USA). All the meteorological data in the present study were collected at 1-min intervals and compiled as 30-min averages or sums with data loggers (CR23X, CR1000 or CR3000 models; Campbell Scientific Inc., Utah, USA).

In 2017, a closed-path fast greenhouse gas analyser (FGGA, Los Gatos Research, Mountain View, California, USA), whose head (gas inlet) was mounted 0.3 m from the head of a 3-D sonic anemometer (R3-50; Gill Instruments, Lymington, UK), was set up at the top of the eddy flux tower to provide eddy covariance measurements of the CH_4 and N_2O fluxes. The FGGA, equipped with a fourth-generation cavity-enhanced laser absorption spectroscopy analyser (DLT-100; Los Gatos Research Inc.), was connected to an external pump (Edwards XDS-35i, Edwards, England, UK) and to a 62-m long PFA inlet tube (4 mm inlet diameter) protected by black foam with a 15 µm filter. All data were sampled at a frequency of 20 Hz with data loggers (model CR3000; Campbell Scientific Inc.).

In addition, to take conditions where non-turbulent processes prevail (e.g. calm nights) into account, the eddy covariance measurements were complemented with a vertical profile measurement system to estimate variations in CH_4 and N_2O concentrations at six different heights above ground (i.e. 0.5, 6, 13, 23, 32 and 58 m) with a 0.8 L min^{-1} pump connected to a six-line solenoid valve and a closed-path FGGA. The entire system was controlled by a data logger (model CR10X; Campbell Scientific Inc.) which recorded greenhouse gas concentration data every 15 min. The vertical profile system for CH_4 and N_2O was stopped after one year because the storage of the gases was found to be negligible (see below).

2.3 Tower-based CH_4 and N_2O flux computation

We used EDDYPRO V6.2.2 (LI-COR Inc.), a software based on a set of standardised post-processing calculations and corrections, to calculate CH_4 and N_2O fluxes from the raw high-frequency eddy covariance data. The parameterization of the software included: a two-dimensional coordinate rotation to set lateral and vertical mean wind speed to zero; a time lag between each scalar and wind speed measurement estimated by covariance maximisation; an empirical frequency correction for high-frequency attenuation; and a Webb-Pearman-Leuning correction for density fluctuations where required, i.e. where concentrations were not measured as mixing ratios. Details of these corrections are given in Aubinet et al. (2012). After the greenhouse gas flux computation, the EDDYPRO output files contained continuous time series for ecosystem-atmosphere greenhouse gas (CH_4 and N_2O) fluxes

reported at a 30-min time step (from 17 May, 2016 to 2 August, 2018). The output files also included uncertainties, quality control flags, friction velocity.

To calculate net ecosystem production or uptake, we added the storage term to the turbulent flux measured by the eddy covariance tower. This correction is particularly relevant for CO_2 exchanges in forest ecosystems to reduce the uncertainty of the net flux estimate (Nicolini et al., 2018). However, for the net CH_4 and N_2O fluxes, the relevance of the storage term correction was only marginal. In contrast to CO_2, whose concentrations clearly built up at soil level during low-turbulence conditions, this was not the case for N_2O and CH_4 (Figs. S1, S2). Comparisons between ecosystem fluxes with and without correction for the storage term showed that the change in the resulting flux was minimal (Figs. S1, S2). Consequently, we assumed that the storage of CH_4 and N_2O was negligible and we then ignored it in this study. This meant that a larger period of eddy covariance flux measurements could be used in this study (starting in 2016), in addition to the January 2017 - January 2018 period where CH_4 and N_2O storage data were available. Half-hourly ecosystem fluxes of CH_4 and N_2O were expressed in nmol m^{-2} s^{-1} (unit of ground area).

2.4 Chamber measurements

In addition to the flux tower and its associated instrumentation, automated non-steady-state flow-through chambers for continuous measurement of soil greenhouse gas fluxes were installed in June 2016 on hypoferralic soils with deep vertical drainage and a very deep water table (~15 m depth), approximately 50 m upwind from the flux tower in some of the upland forest part of the tower footprint. This automated system had two constraints, which when combined, limited the spatial coverage of the soil greenhouse gas flux measurements to the upland forest area: the power supply was only available at the flux tower, and the maximum distance between the automated chambers and the gas analysers was 30 m. Thirteen of the sixteen initial chambers functioned correctly throughout the study period and their data were retained in this study. Briefly, the chambers (LI-8100-104, LI-COR Inc., Lincoln, NE, USA) were mounted on PVC collars (20.3-cm inner diameter; enclosed

soil area ~318 cm^2; offset ~4 cm) that were permanently inserted into the soil. The chambers were connected to a multiplexer (LI-8150, LI-COR Inc.) used to program specific measurement cycles. It operated with a cavity ring-down spectroscopy (CRDS) analyser (G2308; Picarro Inc., Santa Clara, CA, USA) to measure CO_2, H_2O and dry air-CH_4 and N_2O concentrations (water corrected concentrations) at 1 Hz. This analyser relied on an external recirculation pump (A0702; Picarro Inc.). The multiplexer program purged the system 15 s before and 45 s after the measurements to flush out the tubing and return to ambient-air greenhouse gas concentrations. A dead band of 60 s avoided potential measurement errors ascribed to pressure changes inside the chamber-tubing-analyser loop following chamber or solenoid valve closure and accounted for time lags. In addition, to maximise the percentage of fluxes that can be detected for N_2O and CH_4 without affecting spatial coverage and temporal resolution, we initially developed a program combining two different closure times. Briefly, each week, four of the initial sixteen chambers were manually set to remain closed for 25 minutes, while the other chambers were set to remain closed for a much shorter period of 2 minutes. This program was rotated across the chambers. The 25-min closure time was a compromise between reliably estimating low N_2O fluxes and ensuring a sufficient number of flux measurements per chamber and per day. The measurement cycle duration was 2.5 hours, providing approximately nine measurements per chamber per day for all gases. Each chamber was therefore measured with the longer closure time for one 7-consecutive-day period per month (4 weeks). More detail of equipment can be found in previous publications (Courtois et al., 2019; Bréchet et al., 2021).

2.5 Chamber-based CH_4 and N_2O flux computation

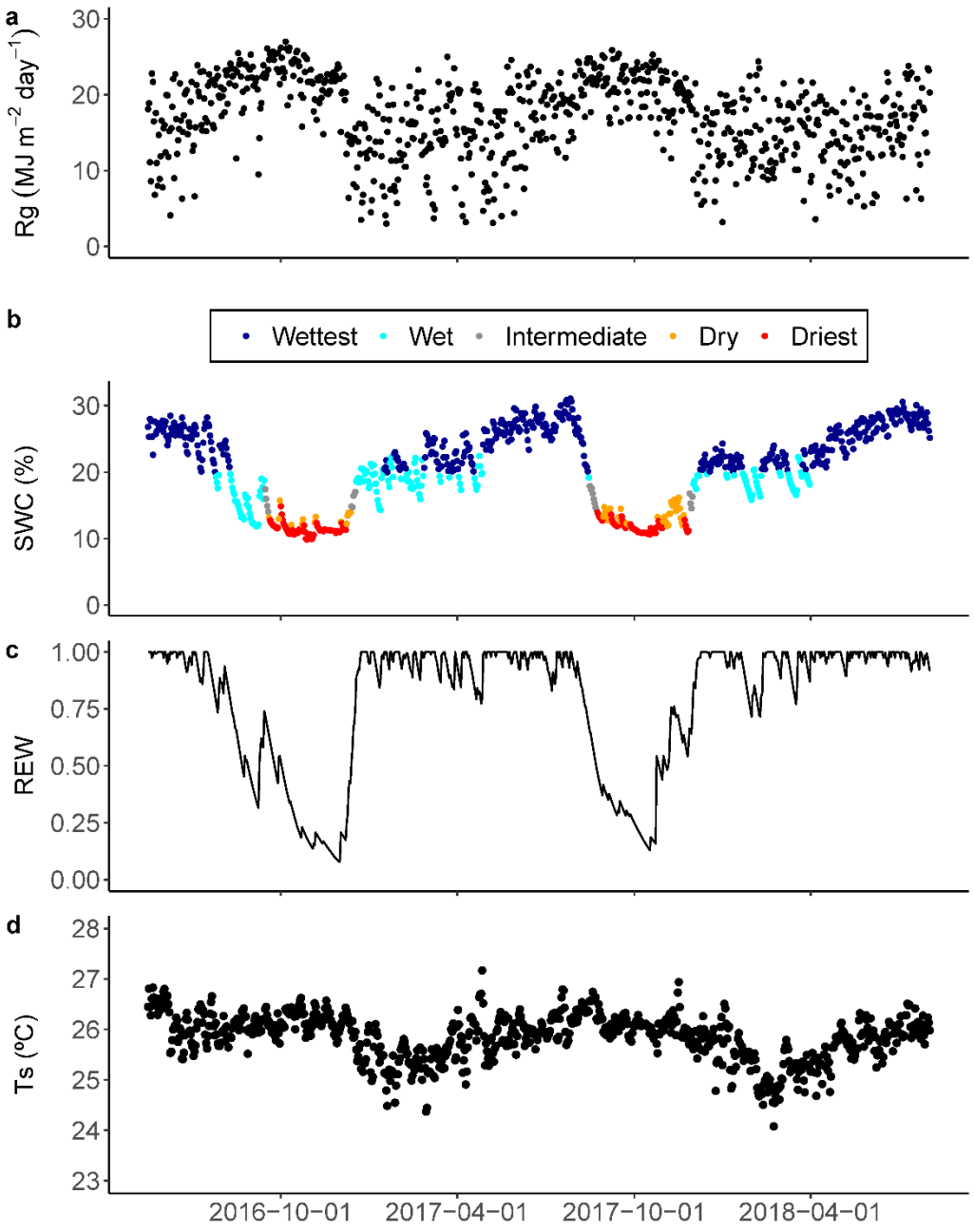
We used the SOILFLUXPRO software (LI-COR Biosciences) to compute soil greenhouse gas fluxes based on the linear and exponential regression of the change in headspace concentrations over time, the collar area and the system volume, after correction for atmospheric pressure and temperature.

After calculating the fluxes and implementing our standard soil greenhouse gas QC procedure (Courtois et al., 2019; Bréchet et al., 2021), all CO_2 fluxes with an insufficiently high R^2 (< 0.90), an initial

concentration greater than 900 ppm, or a value outside the range of variation from 0.10 to 30 µmol m^{-2} s^{-1}, were discarded for all three gases, based on the assumption that poor-quality CO_2 implied poor-quality values for CH_4 and N_2O. Based on previous work (Courtois et al., 2019), all CH_4 fluxes with $R^2 < 0.80$ were excluded (17% of the total 89380 values). These fluxes were not set to zero, as a low R^2 value does not provide information on the flux value itself. This criterion was inapplicable to N_2O, however, due to the low overall R^2 values, meaning all fluxes were retained for the study. Additionally, we computed the minimum detectable fluxes (MDF) suitable for high-resolution, in situ greenhouse gas measurements with the metric proposed by Nickerson (2016): 0.040 nmol m^{-2} s^{-1} and 0.002 nmol m^{-2} s^{-1} for 2 min and 25 min, respectively, for CH_4; and 0.100 nmol m^{-2} s^{-1} and 0.002 nmol m^{-2} s^{-1} for 2 min and 25 min, respectively, for N_2O. This implies that null fluxes were included in the analysis if the flux values for each gas and measurement length fell within the range defined by the corresponding absolute MDF value. The soil fluxes of CH_4 and N_2O were expressed in nmol m^{-2} s^{-1} (unit of soil surface area).

2.6 Tower and chamber flux data analysis

In order to include the most complete information possible, we based the study period on the soil flux measurements and included all available data from 17 May, 2016 to 2 August, 2018. This 26-month period included both very dry and very wet seasons (Fig. 1).



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241 Figure 1. Daily (a) accumulated global radiation (Rg); (b) average soil water content (SWC) at 5 cm in
242 depth during the wet, intermediate and dry seasons, and for two contrasted seasons defined as the
243 wettest (dark blue dots) and the driest (red dots); (c) average relative extractable water (REW) to 3 m
244 in depth based on the water balance model developed by Wagner et al. (2011); and (d) soil
245 temperature (Ts) at 5 cm in depth, from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest,
246 French Guiana. See Sect. 2.7 for details of the methods used to define the “driest” and “wettest”
247 periods with extreme SWC.

Some flawed data was found (and eliminated) for both eddy covariance and soil chamber measurements. They resulted from particular physical or biological conditions at the sampling point or inside the soil chamber (e.g. wasp nests, disturbance by birds, dust, a branch preventing proper closure of the chamber and causing a leak), or from mechanical issues (e.g. a power cut, soil chamber remaining closed, gas analyser malfunction), which generated gaps in each time series. After flux computation, the eddy covariance data for CH_4 and N_2O were filtered: data below a u* threshold of 0.15 m s^{-1} were discarded (Bonal et al., 2008) - as were data with a quality flag of 2 (on a scale from 0 to 2) (Mauder and Foken, 2004).

To calculate daily averages for greenhouse gas fluxes, we first estimated the optimal number of observations per day necessary to obtain representative daily averages. To do this, we selected a data pool with at least 42 observations per day in the eddy covariance dataset. In the soil chamber dataset, we first calculated daily means based on a minimum of five observations for each of the thirteen chambers. Then, for each day, we created subsets of values from 1 to 42 for the eddy covariance data, and from 1 to 13 for the soil chamber data, based on 100 bootstrap iterations. Representative daily means were found for minimum thresholds of 12 observations per day for the eddy covariance and 10 chambers per day for the soil flux system. These tests were performed separately for CH_4 and N_2O and the driest and wettest seasons, giving similar threshold results. Daily means with a number of observations below the corresponding threshold were then discarded. After filtering out the non-representative days, the missing daily means for the whole study period represented 27% for both CH_4 and N_2O flux data derived from eddy covariance and 34% and 30% for CH_4 and N_2O flux data derived from the soil chambers.

2.7 Environmental measurements

In the vicinity of the tower, we used temperature sensors (CS107; Campbell Scientific Inc., Logan, UT, USA) to measure surface soil temperature (Ts) and frequency domain sensors (CS615 or CS616; Campbell Scientific Inc.) to measure soil volumetric water content (SWC) at a depth of 5 cm. To

estimate the daily relative extractable water (REW) for trees from the soil surface to a depth of 3 m, we used a soil water balance model previously validated for tropical forests (Wagner et al., 2011) with daily precipitation, evapotranspiration and solar radiation as input variables. Daily SWC (%), Ts (°C) and REW were defined as the average of the half-hourly flux values over 24 h, while daily Rg (MJ m^{-2} day^{-1}) was the sum of the half-hourly flux values over 24 h.

To examine the effect of environmental variables on CH_4 and N_2O fluxes at the ecosystem and soil levels, we extracted data from two contrasting periods, termed "Driest" and "Wettest" (Fig. 1). The driest days occurred at the end of the dry season, when SWC was less than 15% and decreased for at least three consecutive days. The wettest days had a SWC above 20%, corresponding to a REW above 0.4 and unlimited available water for trees (Wagner el al., 2011) for more than two consecutive days.

2.8 Data analysis

We used the mgcv (Wood and Wood, 2015) and stats packages in R version V3.6.3 (R Core Team, 2020) for the data analyses and ggplot2 for visualisations (Wickham and Wickham, 2016). The significance level for all tests was set at 0.05.

We used Kolmogorov-Smirnov tests (ks.test function) to evaluate the effects of contrasting seasons, specifically the driest and wettest periods, on the distributions of CH_4 and N_2O fluxes at both ecosystem and soil levels. A Student's t-test (t.test function) was used to determine if the greenhouse gas fluxes were statistically different from 0. Generalised additive models (GAM; gam function) were used to assess whether climate variables (i.e. Rg, Ts, SWC) explained the temporal variations in CH_4 and N_2O fluxes at the ecosystem and soil levels. We included the default thin-plate spline smoothing parameter selected by restricted maximum likelihood (REML) and modelled the fluxes of each greenhouse gas as a function of season, climate variables and their interaction. For all GAMs, the "select" option was set to TRUE so that terms could be removed from the GAM during model fitting if they provided no benefit (Wood, 2017). Because of the highly right-skewed nature of the data, particularly for net ecosystem CH_4 fluxes (Fig. 3), similar GAMs were conducted on the 1^{st} - 99^{th} percentile ranges of the data. This

approach mitigated the influence of two episodic CH_4 production events that occurred during the wettest periods (e.g. July 2016 and June 2018; Fig. S5) at the ecosystem level, providing a more representative assessment of the extent to which each environmental variable predicts the fluxes.

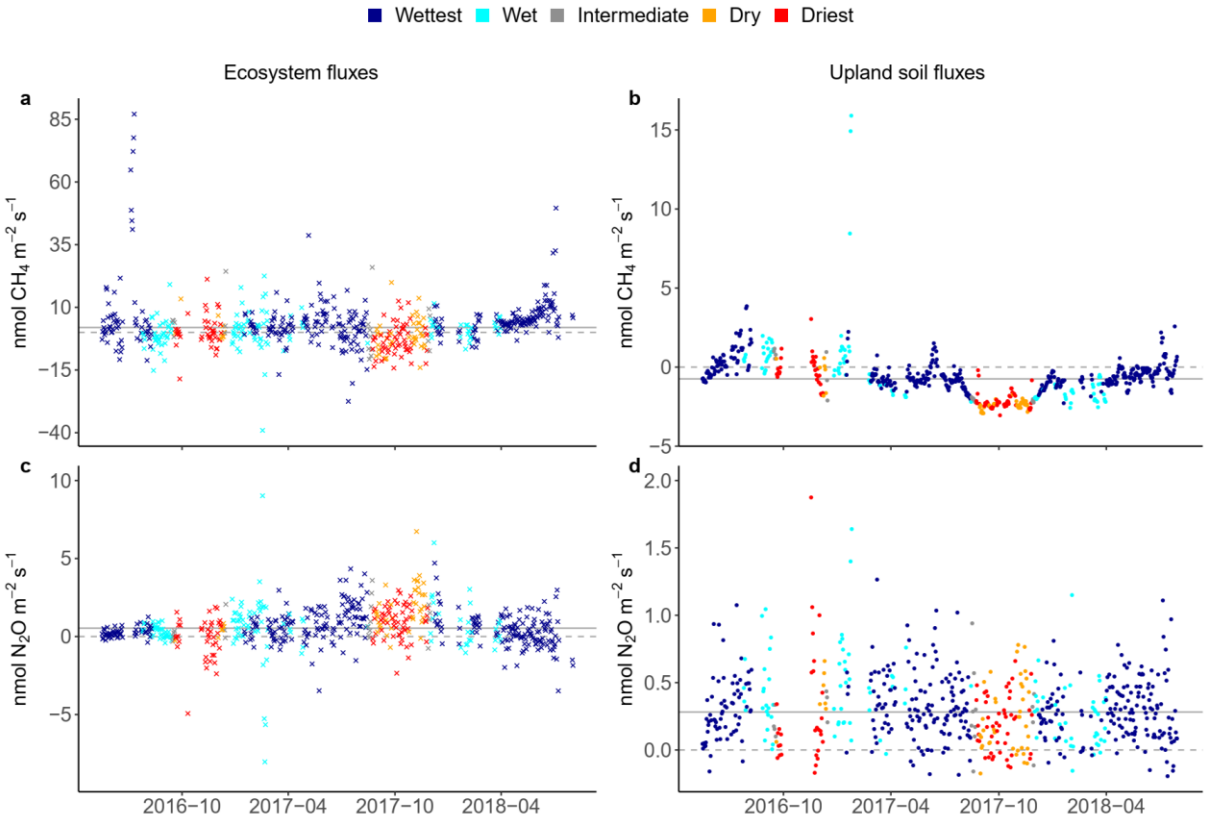
3 Results

3.1 Environmental seasonality

The Guyaflux site is characterised by alternating wet and dry seasons, typical of a wet tropical climate. During the wet season, mean daily global radiation (Rg; Fig. 1a) was at its lowest, while soil water content (SWC; Fig. 1b) was at its highest, accompanied by peak values for relative extractable water (REW; Fig. 1c). In contrast, the dry season had elevated mean daily Rg, minimal SWC and the lowest values of REW. The soil temperature (Ts; Fig. 1d) also exhibited a clear seasonal pattern, albeit weak in absolute values (approximately 2°C), which was influenced by changes in air temperature. During the study period, the driest season (SWC ranging from 9.9% to 15.0%) covered 15.8% of the total study period (128 days), while the wettest season (SWC ranging from 20.0% to 30.0%) covered 55% of the total study period (444 days) and represented near-saturated conditions.

3.2 Greenhouse gas flux seasonality under contrasting environmental conditions

The ecosystem and soil CH_4 and N_2O fluxes also displayed some seasonality (Figs. 2, S3, S4), with seasonal differences particularly evident between the wettest and the driest seasons (Fig. 3).



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321 Figure 2. Seasonal courses of average daily ecosystem (crosses on the left) and upland soil (solid dots
322 on the right) fluxes for the wet, intermediate and dry seasons, and for two contrasted seasons defined
323 as the wettest (dark blue dots) and the driest (red dots) for 24-hour CH_4 fluxes (a, b) and N_2O fluxes
324 from 17 May, 2016 to 2 August, 2018 (c, d) in the Guyaflux tropical forest, French Guiana. Positive
325 fluxes (above the dashed grey "0" line) indicate greenhouse gas emissions and negative fluxes (below
326 the "0" line) indicate greenhouse gas uptake; the solid grey line represents the median over the whole
327 period. Note that the scale of the y-axis has been adjusted for each gas and compartment to improve
328 clarity. Comparable seasonal courses of the 1st - 99th percentile range of CH_4 and N_2O flux data are
329 shown in Fig. S5.

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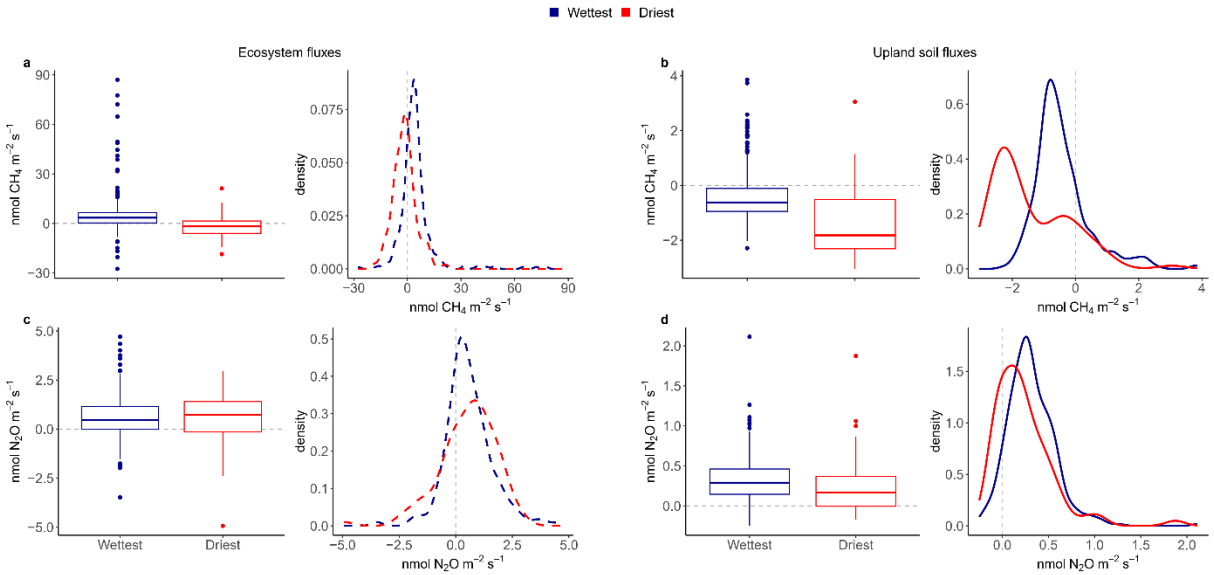


331 Figure 3. Boxplots and associated density plots of average daily ecosystem fluxes (dashed lines on the
332 left) and upland soil (solid lines on the right) fluxes of 24-hour CH_4 fluxes (a, b) and N_2O fluxes (c, d) for
333 the wettest (blue) and driest (red) seasons, from 17 May, 2016 to 2 August, 2018 in the Guyaflux
334 tropical forest, French Guiana. In the box plots, solid bold lines represent medians, box boundaries
335 mark the 25th and 75th percentiles and whiskers show the 10th and 90th percentiles. Dots mark outliers.
336 In the density plots, positive fluxes on the right side of the dotted "0" line indicate greenhouse gas
337 emissions and negative fluxes on the left side of the "0" line indicate greenhouse gas uptake. All fluxes,
338 except the ecosystem N_2O fluxes (c), exhibited statistically significant differences between the wettest
339 and driest seasons at $p < 0.05$ based on Kolmogorov-Smirnov tests.

Ecosystem CH_4 emissions were greater during the wettest season than during the driest season, when net fluxes hovered around zero (Table 1; Fig. 3a). In contrast to the ecosystem-level fluxes, soil CH_4 fluxes in the studied upland forest were mainly negative, indicating net soil CH_4 uptake throughout the year (Fig. 2b), even under varying environmental conditions (Table 1; Fig. 3b). Soil CH_4 uptake did decreased significantly in the wettest season compared to the driest season, although the fluxes remained negative overall (i.e. CH_4 uptake, Table 1; Fig. 3b).

Table 1. Mean, standard deviation (SD) and median ecosystem and upland soil CH_4 and N_2O fluxes for the wettest and driest seasons in the Guyaflux tropical forest, French Guiana. All values are different from 0 at p level < 0.05 based on Student's t-tests.

	Wettest			Driest		
Fluxes	**Mean**	**SD**	**Median**	**Mean**	**SD**	**Median**
Ecosystem flux ($nmol_{CH4/N2O}$ m^{-2} s^{-1})						
CH_4	4.9	11.2	3.5	-1.6	6.4	-1.7
N_2O	0.6	1.0	0.5	0.5	1.3	0.7
Upland soil flux ($nmol_{CH4/N2O}$ m^{-2} s^{-1})						
CH_4	-0.4	0.9	-0.6	-1.4	1.2	-1.8
N_2O	0.3	0.3	0.3	0.2	0.3	0.2

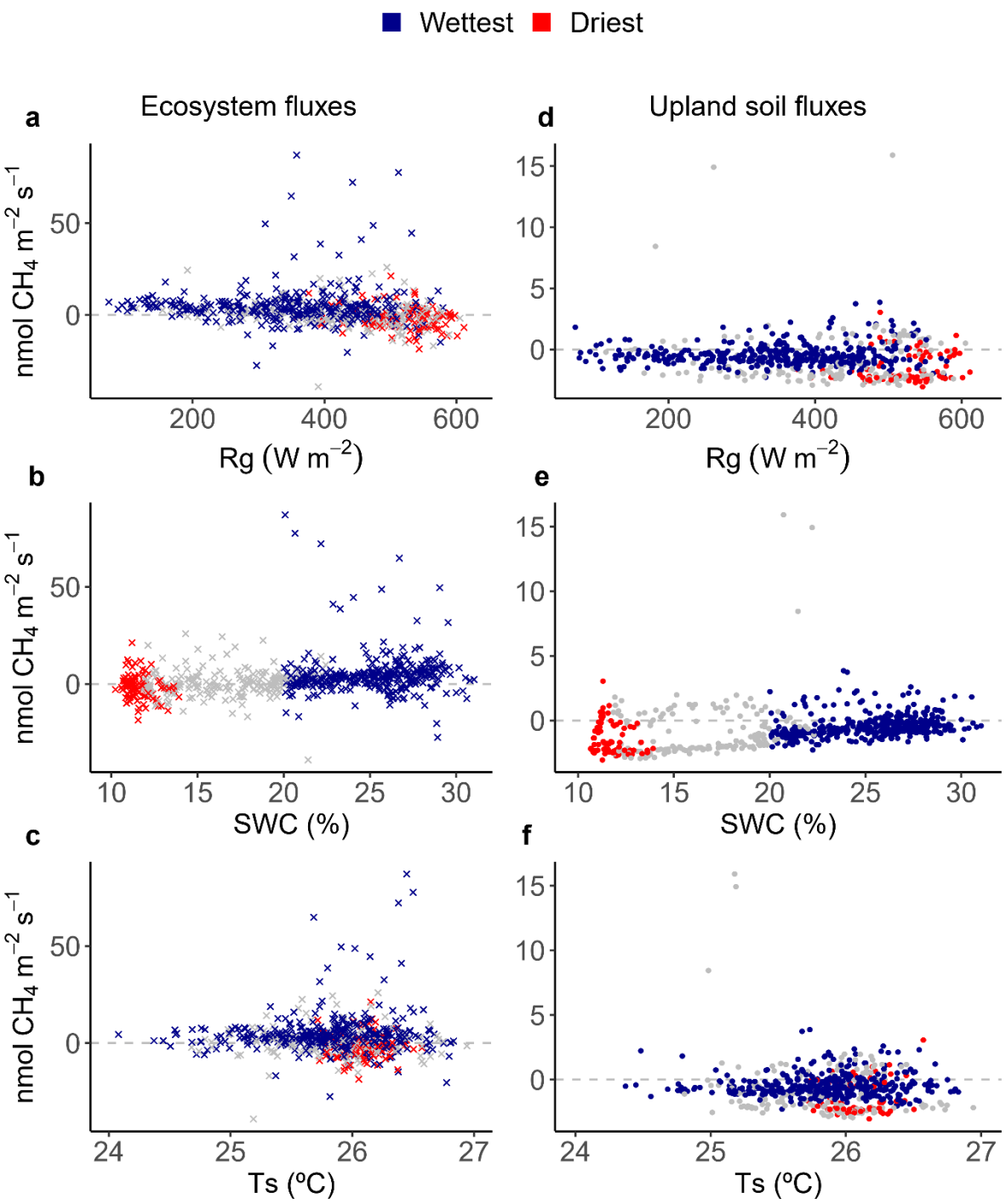
The seasonal pattern of ecosystem N_2O fluxes was less pronounced than that of CH_4 (Fig. 2c). Similar emission rates were observed during the driest and the wettest seasons (Table 1; Fig. 3c). In contrast to the ecosystem-level fluxes, soil N_2O fluxes in the studied upland forest not only had a more pronounced seasonal pattern, but these soils also emitted more N_2O during the wettest season than during the driest season (Table 1; Fig. 3d). It is noteworthy that all the overall flux means were significantly different from zero (Table 1) and that there were significant differences in fluxes between seasons at both the ecosystem and soil levels, except for N_2O fluxes at the ecosystem level (Fig. 3). This suggests that the magnitude of the fluxes was large compared to the seasonal variations.

359

360 **3.3 Environmental drivers of ecosystem and upland soil greenhouse gas fluxes**

361 Keeping the 1st - 99th percentile range of the flux data was sufficient to account for the majority of the
362 statistical leverage (Tables 2, S3). This was particularly true for net ecosystem CH_4 fluxes, which showed
363 that CH_4 emissions decreased with increasing Rg (Fig. 4a, S5a, S6a), although this negative correlation
364 was statistically significant only during the wettest season (Table S3) when net emissions occasionally
365 switched to net uptakes at highest Rg values (Fig. 4a, S6a). Net ecosystem CH_4 fluxes were strongly
366 positively correlated with SWC (Fig. 4b, S6b), showing increased CH_4 emissions with increasing SWC,
367 although this correlation was statistically significant only during the wettest season (Table S3).

368



369 Figure 4. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC)
370 and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots
371 on the right) CH_4 fluxes for the wettest (blue) and driest (red) seasons, with remaining data in grey,
372 from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. Positive fluxes
373 above the horizontal "0" line indicate CH_4 emissions and negative fluxes below the horizontal "0" line
374 indicate CH_4 uptake. Comparable relationships with the 1st - 99th percentile range of CH_4 flux data are
375 shown in Fig. S6.

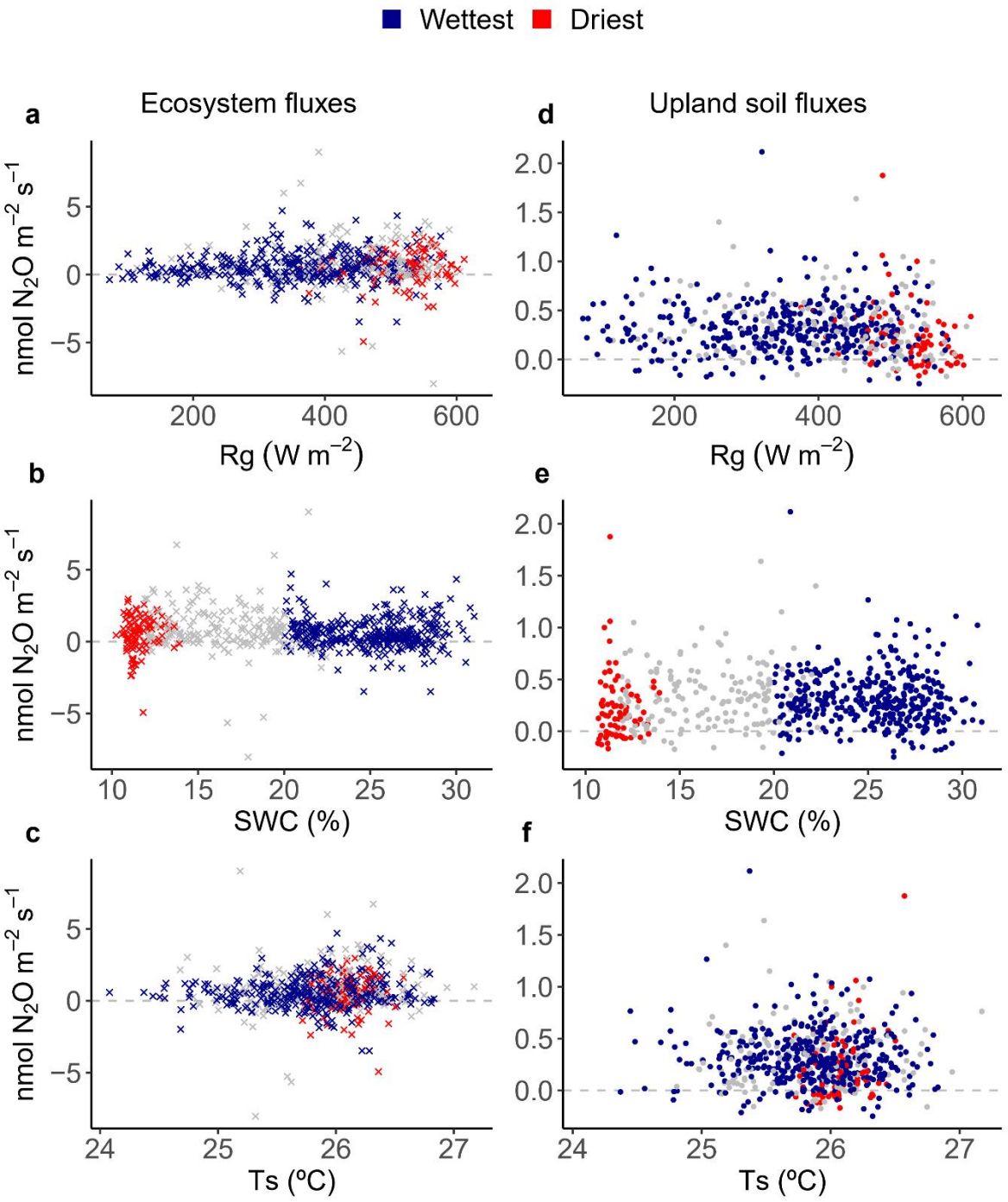
376 Even though the signs of the net CH_4 flux were different at the ecosystem and soil levels, comparable
377 relationships between CH_4 fluxes and the environmental drivers were observed for the studied upland
378 soils as for the ecosystem : net soil CH_4 uptake increased with increasing Rg (Fig. 4d, S6d) and decreased
379 with increasing SWC (Fig. 4e, S6e). Statistically significant terms were found during the driest season
380 (i.e. Ts > Rg > SWC). However, the strongest relationship was observed with SWC during the wettest
381 season (Table 2).

382 Ecosystem N_2O fluxes only showed a significant response to SWC during the wettest season (Figs. 5b).
383 However, the R^2 of the model was very low (R^2 = 0.04; Table 2). The best results for upland soil N_2O
384 fluxes were found with Ts and Rg, but only during the driest season (Fig. 5; Table 2).

385

Table 2. Results of generalised additive models (GAM) assessing the relationships between environmental variables, i.e. global radiation (Rg), soil water content (SWC), soil temperature (Ts), and daily mean ecosystem and upland soil CH_4 and N_2O fluxes during the wettest and driest seasons from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. The effective degrees of freedom (edf) and the reference number of degrees of freedom (Ref. df) of the fitted models, with values for each spline term, are shown. Significant terms at p level < 0.05 are shown in bold. Comparable GAM results with the 1st - 99th percentile ranges of CH_4 and N_2O fluxes are shown in Table S3.

	Fluxes	Best model predictors	R^2	Intercept	Coefficients		F value	p value
					edf	Ref. df		
Ecosystem level								
Daily	CH_4		0.07	4.975				
		Rg: Wettest			0.0	9	0.00	0.743
		Rg: Driest			0.3	8	0.05	0.240
		Ts: Wettest			1.0	9	0.33	0.056
		Ts: Driest			0.0	9	0.00	0.650
		SWC: Wettest			0.0	9	0.00	0.996
		SWC: Driest			0.5	6	0.14	0.174
Daily	N_2O		0.04	1.090				
		Rg: Wettest			0.5	9	0.13	0.126
		Rg: Driest			0.5	8	0.17	0.128
		Ts: Wettest			0.8	9	0.19	0.109
		Ts: Driest			0.0	9	0.00	0.825
		SWC: Wettest			2.3	9	1.33	**0.002**
		SWC: Driest			0.0	6	0.00	0.357
Upland soil level								
Daily	CH_4		0.22	-0.602				
		Rg: Wettest			1.4	9	0.61	**0.017**
		Rg: Driest			1.1	9	0.61	**0.012**
		Ts: Wettest			0.4	9	0.07	0.189
		Ts: Driest			2.5	9	1.91	**< 0.001**
		SWC: Wettest			1.0	9	2.82	**< 0.001**
		SWC: Driest			1.6	7	0.65	**0.014**
Daily	N_2O		0.10	0.313				
		Rg: Wettest			0.0	9	0.00	1.000
		Rg: Driest			0.9	7	0.99	**0.005**
		Ts: Wettest			0.0	9	0.00	0.456
		Ts: Driest			4.6	9	3.95	**< 0.001**
		SWC: Wettest			0.0	9	0.00	0.790
		SWC: Driest			0.2	5	0.05	0.261



395 Figure 5. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC)
396 and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots
397 on the right) N_2O fluxes for the wettest (blue) and driest (red) seasons, with remaining data in grey,
398 from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. Positive fluxes
399 above the horizontal "0" line indicate N_2O emissions and negative fluxes below the horizontal "0" line
400 indicate N_2O uptake. Comparable relationships with the 1st - 99th percentile range of N_2O flux data are
401 shown in Fig. S7.

4 Discussion

To our knowledge, this is the first study to report on simultaneous ecosystem and upland soil CH_4 and N_2O flux observations in a wet tropical forest over a period of more than two years (Fig. 2). This study provides a unique opportunity to investigate the dynamics and environmental drivers of CH_4 and N_2O fluxes in these ecosystems.

4.1 Ecosystem and upland soil-CH_4 fluxes

4.1.1 Seasonal variations in ecosystem CH_4 fluxes: trends and drivers

Our long-term monitoring of eddy covariance CH_4 fluxes above the Guyaflux forest canopy showed high temporal variability, with changes in the sign (net emission or uptake) and amount of the ecosystem fluxes observed over short time scales, supporting hypothesis H1 (Fig. 2). Net CH_4 emission rates (4.9 ± 11.2 nmolCH_4 m^{-2} s^{-1}; Mean ± SD) dominated during the wettest season, whereas net CH_4 uptake (-1.6 ± 6.4 nmolCH_4 m^{-2} s^{-1}) was more common during the driest season, although large temporal variations occurred throughout the study seasons (Figs. 2-3, Table 1). Much higher wet-season net fluxes had previously been found in two Brazilian tropical forests, Manaus and Sinop (62.3 and 34.6 nmolCH_4 m^{-2} s^{-1}, respectively; Carmo et al., 2006), though the studies were based on canopy air samples and a modelling approach. Surprisingly, these Brazilian forests acted as an even larger CH_4 source during the driest season (64.1 and 88.3 nmolCH_4 m^{-2} s^{-1}, respectively; Carmo et al., 2006), while the Guyaflux forest switched from a CH_4 source during the wet periods to a small sink during the dry ones. Ecosystem CH_4 fluxes are driven by a combination of plant, microbial and abiotic processes, which are mediated by both living and dead plants and can explain episodic bursts (Eugster and Plüss, 2010; Covey and Megonigal, 2019). The mechanisms underlying the large CH_4 emissions during the dry season observed in the Brazilian forests remain unknown, but the authors suggest that it may have been connected to the anaerobic decay of waterlogged wood, undrained soil patches or the waterlogged cavities of tank bromeliads. Concomitantly, drought-induced reduced oxidation in the soil

surface layer may have exacerbated the net CH_4 emissions. Contrary to Carmo et al. (2006), Sakabe et al. (2018) found a seasonal pattern similar to the one we observed in our study where the eddy covariance technique was applied. Although the flux values they found had a higher range of variation (10.3 nmolCH_4 m^{-2} s^{-1} versus -8.5 nmolCH_4 m^{-2} s^{-1}, respectively, in the wet and dry seasons), this was most likely due to the different ecosystem they studied, an Indonesian tropical peat swamp forest.

Surprisingly, in contrast to H2, the generalised additive models (GAM) revealed that none of the environmental variables studied, including SWC, were relevant drivers of ecosystem CH_4 flux (Table 2; Figs. 4a-c). However, a similar statistical analysis of the remaining 1^{st} - 99^{th} percentile range of data revealed a significant effect of various environmental drivers (Table S3). While these findings indicate that the models are relatively sensitive to extreme flux values, further explanation may be suggested. Indeed, a significant increase in SWC in the wettest season could stimulate CH_4 production in most compartments of the ecosystem, not only in the seasonally flooded soils. At shallow depths, a higher SWC may reduce the amount of air-filled pore space, thereby decreasing the diffusion of oxygen and CH_4 from the atmosphere through the soil to methanotrophs. As a result, there may be a decrease in net uptake or an increase in net emissions if production exceeds uptake (Wang et al., 2013). Such processes may occur in all the soil types within the footprint of the eddy flux tower (see Sect. 4.1.2) and may explain some of the seasonal trends observed at our site. Using the same range of data (excluding episodic CH_4 peaks in July 2016 and June 2018), a statistically significant relationship was found between CH_4 emissions and Rg during the wettest season (Table S3). This could occur if the occasional high light intensity (Fig. 1a) is sufficient to stimulate plant-mediated CH_4 transport through sap flow, and / or if the measured forest area has more seasonally flooded areas than upland forest. However, the latter explanation is mitigated by the fact that the Guyaflux tower (~300 m from the seasonally flooded area) was specifically chosen to guarantee consistent types of ecosystem flux observations regardless of the season and of associated changes in wind direction and atmospheric stability. Further research is needed to clarify the correlation between Rg and net CH_4 flux. Increased

fluxes in the flooded areas and anaerobic microsites, rather than seasonal changes in the footprint, probably explain part of the observed seasonal variations.

Disentangling the drivers of net CH_4 fluxes is further complicated by aboveground processes that also contribute to CH_4 emissions and uptake in forest ecosystems. Soil-produced CH_4 dissolved in water can indeed be taken up by roots, transported through the xylem stream in the stem, branches and leaves, and then released into the atmosphere, thus bypassing the oxidation processes in the shallow soil layers. As such, the highest CH_4 emissions from trees have been found in waterlogged soils, for example, in wetland and riparian forests (Pangala et al., 2013; Covey and Megonigal, 2019; Gauci et al., 2025). However, recent studies have shown that tree compartments (i.e. stems, branches, and leaves) can also consume CH_4, particularly in free-draining upland soils (Gauci et al., 2024). At our study site, both stem CH_4 emission and uptake were observed within the footprint of the Guyaflux tower (Bréchet et al., 2021, 2025; Daniel et al., 2023). Although these fluxes were weak, they may contribute to the seasonal variations in ecosystem CH_4 exchanges (Bréchet et al., 2021, 2025; Daniel et al., 2023).

4.1.2 Seasonal variations in upland soil CH_4 fluxes: trends and drivers

The upland soils studied within the tower footprint were active consumers of atmospheric CH_4 (Fig. 3b), with an overall net uptake rates of 0.7 ± 1.5 nmolCH_4 m^{-2} s^{-1} (or 1.0 mgCH_4 m^{-2} d^{-1}), which is consistent with the global average for tropical forests (-0.7 nmolCH_4 m^{-2} s^{-1} or -2.5 kgCH_4-C ha^{-1} yr^{-1}, Dutaur and Verchot, 2007). Our results were also close to those of an Australian tropical rainforest (-0.8 mgCH_4 m^{-2} d^{-1}, Butterbach-Bahl et al., 2004), but higher (i.e. lower uptake) than those of a Kenyan rainforest (ranging from -2.8 to -1.3 mgCH_4 m^{-2} d^{-1}, Werner et al., 2007), with both studies using automated chamber systems. CH_4 fluxes at our site ranged seasonally from -0.4 ± 0.9 nmolCH_4 m^{-2} s^{-1} in the wettest season to -1.4 ± 1.2 nmolCH_4 m^{-2} s^{-1} in the driest season (Table 1), supporting H1 and globally corroborating other seasonal studies in tropical forests. The sign of the upland soil CH_4 fluxes were consistent between the driest and wettest seasons. A study conducted in a seasonal tropical forest in China with static chambers showed a comparable seasonal pattern for soils: they acted mainly

as CH_4 consumers, with an uptake rate of 0.7 ± 0.0 nmolCH_4 m^{-2} s^{-1} (or 29.5 ± 0.3 μgCH_4-C m^{-2} h^{-1}; Werner et al., 2006) during the dry period. The uptake decreased by approximately 50% after the first rainfall events and the associated increases in SWC. Another study carried out with the static chamber technique near the Guyaflux forest and in similar environmental conditions reported that upland soils consumed 1.0 ± 3.2 nmolCH_4 m^{-2} s^{-1} during the dry season (Courtois et al., 2018). Yet, those soils become slight emitters during the wet season (0.1 ± 0.9 nmolCH_4 m^{-2} s^{-1}; corresponding to -44.0 ± 139.7 μgCH_4-C m^{-2} h^{-1} and 3.7 ± 40.1 μgCH_4-C m^{-2} h^{-1} for the dry and wet seasons, respectively; Courtois et al., 2018). Although meaningful, these comparisons between studies should be interpreted with great caution because the measurement techniques differed (i.e. automated in our study versus manual chambers in the other studies) as well as study duration (i.e. months versus years). In addition, CH_4 flux dynamics in our upland soils were characterised by a large range of variation. Microtopographic and edaphic heterogeneity may have caused some chamber locations to remain aerobic in surface horizons, even during the wettest season. This may explain their year-round CH_4-uptake, albeit reduced during the wettest season. Other locations, in contrast, may have become anaerobic during the wet season, disabling methanotrophs to oxidize the produced CH_4 and eliciting a switch to net CH_4 emissions.

From the GAMs, the best set of climatic variables, which explained 22% of the seasonal variation in CH_4 fluxes from upland soils, were SWC, Ts and Rg (Table 2), consistent with H2. We observed a net upland soil CH_4 uptake during both the driest and the wettest seasons; CH_4 emissions occurred only on a few days during the wettest season (Fig. 2b). This can likely be explained by the soil characteristics at our site where upland soils were hypoferralic acrisols, characterised by deep vertical drainage (Epron et al., 2006). It is likely that these well aerated soils provided the aerobic conditions for methanotrophic CH_4 oxidation (Smith et al., 2003). The seasonal variations in net CH_4 fluxes were strong (Fig. 3b), with a net soil CH_4 uptake more than three times higher in the driest season than in the wettest season. This is consistent with the known dependence of soil CH_4 fluxes on topsoil SWC (Fig. 4e, S6e; Tables 1, 3): dryer soil conditions favour soil methanotrophy (Le Mer and Roger, 2001), whereas wetter soil

conditions reduce methanotrophic communities and / or their activity (Covey and Megonigal, 2019). In addition, the significant influence of Ts on soil CH_4 uptake may be attributed to the temperature sensitivity of the underlying enzymatic process. However, at elevated temperatures (> 15 °C), such as in tropical forests, gas diffusion limitations and drought effects may supersede temperature responses (Steinkamp et al., 2001). The significant relationships between Rg and upland soil CH_4 fluxes are still unclear. Yet when the combined effects of changes in SWC and Ts were considered, the explanatory power of the GAM with regard to soil CH_4 flux variations remained low. This suggests that other factors, such as substrate availability, soil aeration, gas diffusivity and microbial processes, may significantly control the temporal dynamics of CH_4 fluxes at our study site.

4.2 Ecosystem and upland soil-N_2O fluxes

4.2.1 Seasonal variations in ecosystem N_2O fluxes: trends and drivers

The measurements at the Guyaflux wet-tropical-forest site revealed very low N_2O fluxes, with an average net emission of 0.7 ± 1.3 nmolN_2O m^{-2} s^{-1} (Fig. 3c; Table S2). Though low, this loss of nitrogen (N) from the ecosystem is equivalent to approximately one-fourth of the annual atmospheric N deposition at the site (3.1 kgN_2O-N ha^{-1} yr^{-1} here versus 13 kgN_2O-N ha^{-1} yr^{-1} in Van Langenhove et al., 2020b). Compared to other publications on forest ecosystem N_2O fluxes from studies based on eddy covariance techniques, net ecosystem N_2O fluxes at our study site were similar to the average fluxes reported by Stiegler et al. (2023) for a regularly-fertilised Indonesian oil palm plantation (0.7 ± 0.0 nmolN_2O m^{-2} s^{-1} or 0.32 ± 0.003 gN_2O-N m^{-2} yr^{-1}) but much higher than those reported by Mander et al. (2021) for a temperate riparian deciduous forest (0.1 nmolN_2O m^{-2} s^{-1} or 87.3 mgN_2O-N m^{-2} for the September 2017 - December 2019 period).

Measured ecosystem-level N_2O fluxes at the Guyaflux site were highly variable, but overall showed little seasonal variation (means of 0.5 ± 1.3 nmolN_2O m^{-2} s^{-1} and 0.6 ± 1.0 nmolN_2O m^{-2} s^{-1}, in the driest and the wettest seasons, respectively; Table 1), partially supporting H1. These observations fall within the range of net ecosystem N_2O exchanges measured by eddy covariance reported in an oil palm

plantation in Indonesia, with comparable mean N_2O emissions of 0.7 nmolN_2O m^{-2} s^{-1} for both the dry and wet seasons (Stiegler et al., 2023). Once again, this comparison must be interpreted with extreme caution even though both studies used the eddy covariance technique as the ecosystems and seasons concerned were different (a tropical oil palm plantation with strong seasons versus a primary wet tropical forest).

As with CH_4 fluxes, the temporal variability of the N_2O fluxes was very high (Fig. 2c). Although the explanatory power of the relationships was poor (R^2 = 0.04, Table 2), the GAM analyses supported H2 by attributing some of the variations in N_2O fluxes to changes in SWC. Furthermore, daily mean ecosystem N_2O fluxes switched signs and changed in order of magnitude on short time scales, most likely because these fluxes are controlled by discontinuous microbial processes (Blagodatsky and Smith, 2012). Yet, although there were no seasonal differences, the statistically significant relationships between ecosystem N_2O fluxes and SWC suggested that the wettest season may provide favourable conditions for soil bacterial N_2O production and plant-mediated N_2O transport, which could contribute to higher net N_2O emissions at the ecosystem level (Stiegler et al., 2023). It is worth noting that the extent to which trees mediate N_2O emissions is still uncertain; at Guyaflux, within the tower footprint, tree stems in the seasonally flooded forest emit N_2O while those in the upland forest absorb N_2O (Daniel et al., 2023). Other studies at Guyaflux and in a lowland tropical rain forest in the Réunion Islands reported that tree stems can absorb N_2O through as yet unknown mechanisms (Bréchet et al., 2021, 2025; Machacova et al., 2021). This could indeed counteract the overriding, albeit small, net ecosystem N_2O emissions, suggesting that the proportion of upland versus seasonally flooded areas should be taken into account.

4.2.2 Seasonal variations in upland soil N_2O fluxes: trends and drivers

In support of H1, N_2O fluxes recorded for the studied upland soils were small, averaging 0.3 ± 0.3 nmolN_2O m^{-2} s^{-1} (Table S2), but significantly higher during the wettest season (0.3 ± 0.3 nmolN_2O m^{-2} s^{-1}) compared to the driest season (0.2 ± 0.3 nmolN_2O m^{-2} s^{-1}; Table 1).

557 Our average flux value, 15.6 $\mu gN_2O\text{-}N\ m^{-2}\ h^{-1}$, was nearly 3 times smaller than those reported for a
558 Kenyan rainforest (42.9 $\mu gN_2O\text{-}N\ m^{-2}\ h^{-1}$, Werner et al., 2007) and about 1.5 times smaller than those
559 found for an Australian tropical rainforest (25.6 $\mu gN_2O\text{-}N\ m^{-2}\ h^{-1}$, Butterbach-Bahl et al., 2004), even
560 though the soils in both cases were predominantly N_2O emitters and all measurements were
561 performed with automated chamber systems. However, our seasonal N_2O flux observations were
562 within the same order of magnitude as those in two tropical rainforests where soil N_2O emissions
563 measured with manual chambers were lower in the dry season than in the wet season (< 0.20 $nmolN_2O$
564 $m^{-2}\ s^{-1}$ and 0.34 $nmolN_2O\ m^{-2}\ s^{-1}$, respectively, Yu et al., 2021; 0.10 $nmolN_2O\ m^{-2}\ s^{-1}$ and 0.49 $nmolN_2O$
565 $m^{-2}\ s^{-1}$, respectively, Werner et al., 2006). In addition, net N_2O uptake was observed in the studied
566 upland soil, a phenomenon that has rarely been reported in tropical forests. Previous observations at
567 the Guyaflux site revealed soil N_2O uptake and showed that, although these fluxes were low, they were
568 primarily recorded over short measurement periods (2 minutes instead of 25 minutes; Courtois et al.,
569 2019). The very low flux detection limit of our instrument (G2308; Picarro) may explain why net uptake
570 fluxes were frequently measured. Since N_2O uptake rates are typically small, setups with a high MDF,
571 which are usually employed in remote areas such as tropical rainforests, are often unable to detect
572 these small uptake fluxes. Regarding the seasonal pattern, we suspect that during the wet season,
573 when conditions are ideal for both litter mineralisation and heterotrophic N_2 fixation (Van Langenhove
574 et al., 2020a), as well as denitrification, N_2O production typically exceeds consumption. During the dry
575 season, however, the drier conditions in the topsoil favour N_2O uptake, enabling microbial
576 communities to consume all the N_2O produced on average.
577 Unlike H2, the GAMs, including climatic variables, could only partially predict the observed seasonal
578 variations in upland soil N_2O fluxes, with Ts and Rg as drivers (Table 2; Fig. 5). This was even more
579 unexpected as it only occurred during the driest season (Table 2), when low SWC occurred alongside
580 high and stable Ts and Rg (Fig. 1b, d, a, respectively). Previous studies have observed an exponential
581 increase in soil N_2O fluxes with Ts (Schindlbacher et al., 2004; Smith et al., 2003), which can be
582 explained by the temperature sensitivity of the underlying enzymatic processes. However, Ts at our

583 tropical site did not vary greatly (Fig. 1d). In addition, the significant relationships between Rg and the
584 upland soil N_2O fluxes are still unclear. Although these relationships were significant, their explanatory
585 power was poor ($R^2 = 0.10$), suggesting that other controlling variables such as N and carbon availability
586 (Morley and Baggs, 2010), or microbial community dynamics (Regan et al., 2011), may also
587 substantially influence the temporal dynamics of N_2O fluxes. This emphasised the potential for both
588 synergistic and antagonistic effects of key environmental drivers (e.g. Ts, SWC) on regulating variables,
589 highlighting the complexity of predicting seasonal variations in N_2O flux in upland tropical forest soils.
590

591 ## 5 Conclusion

592 Our long-term monitoring of ecosystem and soil CH_4 and N_2O fluxes over a period of 26 months under
593 contrasting climatic conditions revealed highly variable fluxes that changed direction and amount on
594 short time scales and between the driest and the wettest seasons. At the ecosystem level, mean daily
595 CH_4 and N_2O fluxes were low, but N_2O emissions were observed all-year-round, whereas CH_4 emissions
596 or uptake depended on the season. Seasonality was statistically significant for CH_4, with uptake mainly
597 occurring during the driest season compared to the wettest season. For the upland soil we studied,
598 CH_4 and N_2O fluxes were highly variable, with statistically significant increase in CH_4 uptake and
599 decrease in N_2O emissions from the wettest to the driest season. Overall, the selected climatic
600 variables only explained a minor part of the seasonal variations in net ecosystem greenhouse gas
601 fluxes. In addition, the results of the relationships for CH_4 depended on the selected ecosystem flux
602 values. The best results were found when the effects of changes in SWC and Ts were considered,
603 although the explanatory power of the models with regard to seasonal variations in soil CH_4 and N_2O
604 fluxes was at most 20%.
605 Measurements at the ecosystem and soil levels showed divergent fluxes, probably because studied
606 upland soil fluxes represent only one compartment of the whole ecosystem. Furthermore, upland soils
607 (52% of the footprint area) are just one type of the wide variety of soils found within the footprint of
608 the Guyaflux tower. Soil chambers also provide integrated fluxes for a much smaller area than does

609 the eddy covariance technique, which collects data from integrated processes across various forest
610 habitats, soil types, tree species, hydrological conditions, and topographical positions. To improve the
611 understanding of seasonal variations in ecosystem CH_4 and N_2O fluxes, it is crucial to characterise the
612 fluxes in all existing ecosystem compartments simultaneously, including all tree components (leaves,
613 stems, branches) and species in the forest habitats, not just those on upland soils. Our study still
614 provides valuable data which, when combined with mechanistic models, could help to identify the
615 missing drivers responsible for the seasonal variations in CH_4 and N_2O fluxes in wet tropical forest
616 ecosystems.
617

Data availability

The datasets analysed during the current study are available at the Zenodo repository (Bréchet et al., 2025): https://doi.org/10.5281/zenodo.17535314, and are also available from the corresponding author upon request.

Supplement link

The supplement related to this article is available online at…

Author contributions

LMB, MI, CS, DB, IAJ conceived the ideas and designed the methodology; LMB and BB collected the data; LMB and MI performed quality control checks on the data and analysed the data; IAJ and RBJ obtained the funding; LMB led the writing of the manuscript and all authors contributed to the manuscript and gave final approval for submission.

Competing interests

The authors declare that they have no conflict of interest.

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References

Aguilos, M., Hérault, B., Burban, B., Wagner, F., Bonal, D.: What drives long-term variations in carbon flux and balance in a tropical rainforest in French Guiana? Agric. For. Meteorol., 253–254, 114–123, https://doi.org/10.1016/j.agrformet.2018.02.009, 2018.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T.: Estimates of the annual net carbon and water exchange of European forests: the EUROFLUX methodology, Adv. Ecol. Res., 30, 114–175, https://doi.org/10.1016/S0065-2504(08)60018-5, 2000.

Aubinet, M., Vesala, T. and Papale, D. eds.: Eddy covariance: a practical guide to measurement and data analysis, Springer Science and Business Media, 2012.

Baldocchi, D. D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future, Glob. Chang. Biol., 9, 479–92, https://doi.org/10.1046/j.1365-2486.2003.00629.x, 2003.

Baldocchi, D.: Measuring fluxes of trace gases and energy between ecosystems and the atmosphere - the state and future of the eddy covariance method, Glob. Chang. Biol., 20, 3600–9, https://doi.org/10.1111/gcb.12649, 2014.

Baldocchi, D. D.: How eddy covariance flux measurements have contributed to our understanding of Global Change Biology, Glob. Chang. Biol., 26, 242–60, https://doi.org/10.1111/gcb.14807, 2020.

Bernhardt, E. S., Blaszczak, J. R., Ficken, C. D., Fork, M. L., Kaiser, K. E., Seybold, E. C.: Control points in

ecosystems: moving beyond the hot spot hot moment concept, Ecosystems, 20, 665–82, https://doi.org/10.1007/s10021-016-0103-y, 2017.

Blagodatsky, S., Smith P.: Soil physics meets soil biology: towards better mechanistic prediction of greenhouse gas emissions from soil, Soil Biol. Biochem., 47, 78–92, https://doi.org/10.1016/j.soilbio.2011.12.015, 2012.

Bonal, D., Bosc, A., Ponton, S., Goret, J.- Y., Burban, B. T., Gross, P., Bonnefond, J. M., Elbers, J., Longdoz, B., Epron, D., Guehl, J. M., Granier, A.: Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana, Glob. Chang. Biol., 14, 1917–1933, https://doi.org/10.1111/j.1365-2486.2008.01610.x, 2008.

Bouwman, A. F., Fung, I., Matthews, E., John, J.: Global analysis of the potential for N_2O production in natural soils, Global Biogeochem. Cy., 7, 557–597, https://doi.org/10.1029/93GB01186, 1993.

Bréchet, L. M., Daniel, W., Stahl, C., Burban, B., Goret, J.- Y., Salomón, R. L., Janssens, I. A.: Simultaneous tree stem and soil greenhouse gas (CO_2, CH_4, N_2O) flux measurements: a novel design for continuous monitoring towards improving flux estimates and temporal resolution, New Phytol., 230, 2487–500, https://doi.org/10.1111/nph.17352, 2021.

Bréchet, L. M., Salomón, R. L., Machacova, K., Stahl, C., Burban, B., Goret, J.- Y., Steppe, K., Bonal, D., Janssens, I. A.: Insights into the subdaily variations in methane, nitrous oxide and carbon dioxide fluxes from upland tropical tree stems, New Phytol., 245, 2451–2466, https://doi.org/10.1111/nph.20401, 2025.

Butterbach-Bahl, K., Kock, M., Willibald, G., Hewett, B., Buhagiar, S., Papen, H., Kiese, R.: Temporal variations of fluxes of NO, NO_2, N_2O, CO_2, and CH_4 in a tropical rain forest ecosystem, Global Biogeochem. Cy.,, 18, 3, https://doi.org/10.1029/2004GB002243, 2004.

Carmo, J. B., Keller, M., Dias, J. D., Camargo, P. B., Crill, P.: A source of methane from upland forests in the Brazilian Amazon, Geophys. Res. Lett., 33, 4, https://doi.org/10.1029/2005GL025436, 2006.

Courtois, E. A., Stahl, C., Van den Berge, J., Bréchet, L., Van Langenhove, L., Richter, A., Urbina, I., Soong, J. L., Penuelas, J., Janssens, I. A.: Spatial variation of soil CO_2, CH_4 and N_2O fluxes across

topographical positions in tropical forests of the guiana shield, Ecosystems, 21, 1445–58, https://doi.org/10.1007/s10021-018-0232-6, 2018.

Courtois, E. A., Stahl, C., Burban, B., Van den Berge, J., Berveiller, D., Bréchet, L., Soong, J. L., Arriga, N., Peñuelas, J., Janssens, I. A.: Automatic high-frequency measurements of full soil greenhouse gas fluxes in a tropical forest, Biogeosciences, 16, 785–96, https://doi.org/10.5194/bg-16-785-2019, 2019.

Covey, K. R., Megonigal, J. P.: Methane production and emissions in trees and forests, New Phytol., 222, 35–51, https://doi.org/10.1111/nph.15624, 2019.

Covey, K., Soper, F., Pangala, S., Bernardino, A., Pagliaro, Z., Basso, L., Cassol, H., Fearnside, P., Navarrete, D., Novoa, S., Sawakuchi, H.: Carbon and beyond: The biogeochemistry of climate in a rapidly changing Amazon, Front. For. Glob. Change., 4, 1–20, https://doi.org/10.3389/ffgc.2021.618401, 2021.

Daniel, W., Stahl, C., Burban, B., Goret, J.- Y., Cazal, J., Richter, A., Janssens, I. A., Bréchet, L. M.: Tree stem and soil methane and nitrous oxide fluxes, but not carbon dioxide fluxes, switch sign along a topographic gradient in a tropical forest, Plant Soil, 488, 533–49, https://doi.org/10.1007/s11104-023-05991-y, 2023.

Davidson, E.A.: Sources of nitric oxide and nitrous oxide following wetting of dry soil, Soil Sci. Soc. Am. J., 56, 95–102, https://doi.org/10.2136/sssaj1992.03615995005600010015x, 1992.

Davidson, E. A., De Araüjo, A. C., Artaxo, P., Balch, J. K., Brown, I. F., Mercedes, M. M., Coe, M. T., Defries, R. S., Keller, M., Longo, M., Munger, J. W., Schroeder, W., Soares-Filho, B. S., Souza, C. M., Wofsy, S. C., The Amazon basin in transition, Nature, 481, 321–328, https://doi.org/10.1038/nature10717, 2012.

Delwiche, K. B., Knox, S. H., Malhotra, A., Fluet-Chouinard, E., McNicol, G., Feron, S., Ouyang, Z., Papale, D., Trotta, C., Canfora, E., Cheah, Y. W.: FLUXNET-CH_4: A global, multi-ecosystem dataset and analysis of methane seasonality from freshwater wetlands, Earth Syst. Sci. Data Discuss., 2021, 1–11, https://doi.org/10.5194/essd-13-3607-2021, 2021.

Dutaur, L., Verchot, L.V.: A global inventory of the soil CH_4 sink. Global Biogeochem. Cy., 21, 4, https://doi.org/10.1029/2006GB002734, 2007.

Epron, D., Bosc, A., Bonal, D., Freycon, V.: Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana, J. Trop. Ecol., 22, 565–74, https://doi:10.1017/S0266467406003415, 2006.

Eugster, W., Plüss, P.: A fault-tolerant eddy covariance system for measuring CH_4 fluxes, Agric. For. Meteorol., 150, 841–51, https://doi.org/10.1016/j.agrformet.2009.12.008, 2010.

Eugster, W., Merbold, L.: Eddy covariance for quantifying trace gas fluxes from soils, Soil, 1, 187–205, https://doi.org/10.5194/soil-1-187-2015, 2015.

Fang, J., Fang, J., Chen, B., Zhang, H., Dilawar, A., Guo, M. and Liu, S.A.: Assessing spatial representativeness of global flux tower eddy-covariance measurements using data from FLUXNET2015, Sci. Data, 11, 569, https://doi.org/10.1038/s41597-024-03291-3, 2024.

von Fischer, J. C., Hedin, L. O.: Controls on soil methane fluxes: Tests of biophysical mechanisms using stable isotope tracers, Global Biogeochem. Cy., 21, 9-Gb2007, https://doi.org/10.1029/2006gb002687, 2007.

Gauci, V.: Tree methane exchange in a changing world, Nat. Rev. Earth Environ., 6, 471–483, https://doi.org/10.1038/s43017-025-00692-9, 2025.

Gauci, V., Pangala, S. R., Shenkin, A., Barba, J., Bastviken, D., Figueiredo, V., Gomez, C., Enrich-Prast, A., Sayer, E., Stauffer, T., Welch, B.: Global atmospheric methane uptake by upland tree woody surfaces, Nature, 631, 796–800, https://doi.org/10.1038/s41586-024-07592-w, 2024.

Groffman, P. M., Butterbach-Bahl, K., Fulweiler, R. W., Gold, A. J., Morse, J. L., Stander, E. K., Tague, C., Tonitto, C., Vidon, P.: Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models, Biogeochemistry, 93, 49–77, https://doi.org/10.1007/s10533-008-9277-5, 2009.

Gütlein, A., Gerschlauer, F., Kikoti, I., Kiese, R.: Impacts of climate and land use on N_2O and CH_4 fluxes from tropical ecosystems in the Mt. Kilimanjaro region, Tanzania, Glob. Chang. Biol., 24, 1239–

748 55, https://doi.org/10.1111/gcb.13944, 2018.
749 Ito, A., Inatomi, M.: Use of a process-based model for assessing the methane budgets of global
750 terrestrial ecosystems and evaluation of uncertainty, Biogeosciences, 9, 759–73,
751 https://doi.org/10.5194/bg-9-759-2012, 2012.
752 IUSS Working Group WRB: World reference base for soil resources 2014, update 2015. International
753 soil classification system for naming soils and creating legends for soil maps, World Soil Resources
754 Reports No. 106. FAO, Rome (2015), 2015.
755 Jones, C. M., Spor, A., Brennan, F. P., Breuil, M. C., Bru, D., Lemanceau, P., Griffiths, B., Hallin, S.,
756 Philippot, L.: Recently identified microbial guild mediates soil N_2O sink capacity, Nat. Clim.
757 Change, 4, 801–5, https://doi.org/10.1038/nclimate2301, 2014.
758 Khalil, K., Mary, B., Renault, P.: Nitrous oxide production by nitrification and denitrification in soil
759 aggregates as affected by O_2 concentration, Soil Biol. Biochem., 36, 687–99,
760 https://doi.org/10.1016/j.soilbio.2004.01.004, 2004.
761 Kiese, R., Butterbach-Bahl, K.: N_2O and CO_2 emissions from three different tropical forest sites in the
762 wet tropics of Queensland, Australia, Soil Biol. Biochem., 34, 975–87,
763 https://doi.org/10.1016/S0038-0717(02)00031-7, 2002.
764 Knox, S. H., Bansal, S., McNicol, G., Schafer, K., Sturtevant, C., Ueyama, M., Valach, A. C., Baldocchi, D.,
765 Delwiche, K., Desai, A. R., Euskirchen, E., et al.: Identifying dominant environmental predictors of
766 freshwater wetland methane fluxes across diurnal to seasonal time scales, Glob. Chang. Biol., 27,
767 3582–604, https://doi.org/10.1111/gcb.15661, 2021.
768 Le Mer, J., Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review,
769 Eur. J. Soil Biol., 37, 25–50, https://doi.org/10.1016/S1164-5563(01)01067-6, 2001.
770 Liu, Z., Li, H., Wu, F., Wang, H., Chen, H., Zhu, Q., Yang, G., Liu, W., Chen, D., Li, Y., Peng, C.:
771 Quantification of ecosystem-scale methane sinks observed in a tropical rainforest in Hainan,
772 China, Land, 11, 154, https://doi.org/10.3390/land11020154, 2022.
773 Lucas-Moffat, A. M., Huth, V., Augustin, J., Brummer, C., Herbst, M., Kutsch, W. L.: Towards pairing plot

and field scale measurements in managed ecosystems: Using eddy covariance to cross-validate CO_2 fluxes modeled from manual chamber campaigns, Agric. For. Meteorol., 256, 362–378, https://doi.org/10.1016/j.agrformet.2018.01.023, 2018.

Luo, G. J., Kiese, R., Wolf, B., Butterbach-Bahl, K.: Effects of soil temperature and moisture on methane uptake and nitrous oxide emissions across three different ecosystem types, Biogeosciences, 10, 3205–19, https://bg.copernicus.org/articles/10/3205/2013, 2013.

Machacova, K., Bäck, J., Vanhatalo, A., Halmeenmäki, E., Kolari, P., Mammarella, I., Pumpanen, J., Acosta, M., Urban, O., Pihlatie, M.: Pinus sylvestris as a missing source of nitrous oxide and methane in boreal forest, Sci. Rep., 6, 23410, https://doi.org/10.1038/s41598-017-13781-7, 2016.

Machacova, K., Borak, L., Agyei, T., Schindler, T., Soosaar, K., Mander, Ü., Ah-Peng, C.: Trees as net sinks for methane (CH_4) and nitrous oxide (N_2O) in the lowland tropical rain forest on volcanic Réunion Island, New Phytol., 229, 1983–94, https://doi.org/10.1111/nph.17002, 2021.

Mander, Ü., Krasnova, A., Escuer-Gatius, J., Espenberg, M., Schindler, T., Machacova, K., Pärn, J., Maddison, M., Megonigal, J. P., Pihlatie, M., Kasak, K.: Forest canopy mitigates soil N_2O emission during hot moments, npj Clim. Atmos. Sci., 4, 39, https://doi.org/10.1038/s41612-021-00194-7, 2021.

Mauder, M., Foken, T.: Documentation and instruction manual of the eddy covariance software package TK2, Universität Bayreuth, Abt. Mikrometeorologie, Arbeitsergebnisse 26:44 pp. Internet, ISSN 1614–8926, 2004.

Morley, N., Baggs, E. M.: Carbon and oxygen controls on N_2O and N_2 production during nitrate reduction, Soil Biol. Biochem., 42, 1864–1871, https://doi.org/10.1016/j.soilbio.2010.07.008, 2010.

Nickerson, N.: Evaluating gas emission measurements using Minimum Detectable Flux (MDF), Eosense Inc., Dartmouth, Nova Scotia, Canada, 2016.

Nicolini, G., Aubinet, M., Feigenwinter, C., Heinesch, B., Lindroth, A., Mamadou, O., Moderow, U.,

Mölder, M., Montagnani, L., Rebmann, C., Papale, D., Impact of CO_2 storage flux sampling uncertainty on net ecosystem exchange measured by eddy covariance, Agric. For. Meteorol., 248, 228–239, https://doi.org/10.1016/j.agrformet.2017.09.025, 2018.

Oertel, C., Matschullat, J., Zurba, K., Zimmermann, F., Erasmi, S.: Greenhouse gas emissions from soils—A review, Geochem., 76, 327–52, https://doi.org/10.1016/j.chemer.2016.04.002, 2016.

Pangala, S. R., Moore, S., Hornibrook, E. R., Gauci, V.: Trees are major conduits for methane egress from tropical forested wetlands, New Phytol., 197, 524–31, https://doi.org/10.1111/nph.12031, 2013.

Pitz, S., Megonigal, J. P.: Temperate forest methane sink diminished by tree emissions, New Phytol., 214, 1432–9, https://doi.org/10.1111/nph.14559, 2017.

Regan, K., Kammann, C., Hartung, K., Lenhart, K., Müller, C., Philippot, L., Kandeler, E., and Marhan, S.: Can differences in microbial abundances help explain enhanced N_2O emissions in a permanent grassland under elevated atmospheric CO_2?, Glob. Change Biol., 17, 3176–3186, https://doi.org/10.1111/j.1365-2486.2011.02470.x, 2011.

Sakabe, A., Itoh, M., Hirano, T., Kusin, K.: Ecosystem-scale methane flux in tropical peat swamp forest in Indonesia, Glob. Chang. Biol., 24, 5123–36, https://doi.org/10.1111/gcb.14410, 2018.

Sanford, R. A., Wagner, D. D., Wu, Q., Chee-Sanford, J. C., Thomas, S. H., Cruz-García, C., Rodríguez, G., Massol-Deyá, A., Krishnani, K. K., Ritalahti, K. M., Nissen, S.: Unexpected nondenitrifier nitrous oxide reductase gene diversity and abundance in soils, Proc. Natl. Acad. Sci., 109, 19709–14, https://doi.org/10.1073/pnas.1211238109, 2012.

Schindlbacher, A., Zechmeister-Boltenstern, S., ButterbachBahl, K.: Effects of soil moisture and temperature on NO, NO2, and N2O emissions from European forest soils, J. Geophys. Res.,109, D17302, https://doi.org/10.1029/2004JD004590, 2004.

Silver, W. L., Lugo, A., Keller, M.: Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils, Biogeochemistry, 44, 301–328, https://doi.org/10.1007/BF00996995, 1999.

826 Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J., Rey, A.: Exchange of greenhouse gases
827 between soil and atmosphere: interactions of soil physical factors and biological processes, Eur.
828 J. soil sci., 54, 779–91, https://doi.org/10.1111/ejss.12539, 2003.
829 Steinkamp, R., Butterbach-Bahl, K., Papen, H.: Methane oxidation by soils of an N limited and N
830 fertilized spruce forest in the Black Forest, Germany, Soil Biol. Biochem., 33, 145–153,
831 https://doi.org/10.1016/S0038-0717(00)00124-3, 2001.
832 Stevens, R. J., Laughlin, R. J., Burns, L. C., Arah, J. R., Hood, R. C.: Measuring the contributions of
833 nitrification and denitrification to the flux of nitrous oxide from soil, Soil Biol. Biochem., 29, 139–
834 51, https://doi.org/10.1016/S0038-0717(96)00303-3, 1997.
835 Stiegler, C., Koebsch, F., Ali, A. A., June, T., Veldkamp, E., Corre, M. D., Koks, J., Tjoa, A., Knohl, A.:
836 Temporal variation in nitrous oxide (N_2O) fluxes from an oil palm plantation in Indonesia: An
837 ecosystem-scale analysis, GCB Bioenergy, 15, 1221–39, https://doi.org/10.1111/gcbb.13088,
838 2023.
839 The, Y. A., Silver, W. L., Conrad, M. E.: Oxygen effects on methane production and oxidation in humid
840 tropical forest soils, Glob. Chang. Biol., 11, 1283–1297, https://doi.org/10.1111/j.1365-
841 2486.2005.00983.x, 2005.
842 The, Y. A., Silver, W. L.: Effects of soil structure destruction on methane production and carbon
843 partitioning between methanogenic pathways in tropical rain forest soils, J. Geophys. Res. G:
844 Biogeosciences, 111, G1, https://doi.org/10.1029/2005JG000020, 2006.
845 Tian, H., Chen, G., Lu, C., Xu, X., Ren, W., Zhang, B., Banger, K., Tao, B., Pan, S., Liu, M., Zhang, C.: Global
846 methane and nitrous oxide emissions from terrestrial ecosystems due to multiple environmental
847 changes, Ecosyst. Health Sustain., 1, 1–20, https://doi.org/10.1890/EHS14-0015.1, 2015.
848 Van Langenhove, L., Depaepe, T., Vicca, S., van den Berge, J., Stahl, C., Courtois, E. A., Weedon, J.,
849 Urbina, I., Grau, O., Asensio, D., Peñuelas, J., Boeckx, P., Richter, A., Van Der Straeten, D.,
850 Janssens, I. A.: Regulation of nitrogen fixation from free-living organisms in soil and leaf litter of
851 two tropical forests of the Guiana shield, Plant Soil, 450, 93–110.

https://doi.org/10.1007/s11104-019-04012-1, 2020a.

Van Langenhove, L., Verryckt, L. T., Bréchet, L., Courtois, E. A., Stahl, C., Hofhansl, F., Bauters, M., Sardans, J., Boeckx, P., Fransen, E., Peñuelas, J., Janssens, I. A.: Atmospheric deposition of elements and its relevance for nutrient budgets of tropical forests, Biogeochemistry, 149, 175–93, https://doi.org/10.1007/s10533-020-00673-8, 2020b.

Wagner, F., Hérault, B., Stahl, C., Bonal, D., Rossi, V.: Modeling water availability for trees in tropical forests, Agric. For. Meteorol., 151, 1202–13, https://doi.org/10.1016/j.agrformet.2011.04.012, 2011.

Wang, Z. P., Chang, S. X., Chen, H., Han, X. G.: Widespread non-microbial methane production by organic compounds and the impact of environmental stresses, Earth-Sci. Rev., 127, 193–202, https://doi.org/10.1016/j.fuel.2015.12.074, 2013.

Wang, H., Li, H., Liu, Z., Lv, J., Song, X., Li, Q., Jiang, H., Peng, C.: Observed methane uptake and emissions at the ecosystem scale and environmental controls in a subtropical forest, Land, 10, 975, https://doi.org/10.3390/land10090975, 2021.

Welch, B., Gauci, V., Sayer, E. J.: Tree stem bases are sources of CH_4 and N_2O in a tropical forest on upland soil during the dry to wet season transition, Glob. Chang. Biol., 25, 361–72, https://doi.org/10.1111/gcb.14498, 2019.

Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R., Butterbach-Bahl, K.: N_2O, CH_4 and CO_2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China, Plant Soil, 289, 335–53, https://doi.org/10.1007/s11104-006-9143-y, 2006.

Werner, C., Kiese, R., Butterbach-Bahl, K.: Soil-atmosphere exchange of N_2O, CH_4, and CO_2 and controlling environmental factors for tropical rain forest sites in western Kenya, J. Geophys. Res.-Atmos., 112, D3, https://doi.org/10.1029/2006JD007388, 2007.

Wickham, H., Wickham, H.: Getting Started with ggplot2. ggplot2: Elegant graphics for data analysis, 11–31, 2016.

Whiting, G. J., Chanton, J. P.: Primary production control of methane emission from wetlands, Nature,

364, 794–5, https://doi.org/10.1038/364794a0, 1993.

Wright, E. L., Black, C. R., Cheesman, A. W., Drage, T., Large, D., Turner, B. L., Sjoegersten, S.: Contribution of subsurface peat to CO_2 and CH_4 fluxes in a neotropical peatland, Glob. Chang. Biol., 17, 2867–81, https://doi.org/10.1111/j.1365-2486.2011.02448.x, 2011.

Wood, S., Wood, M. S.: Package "mgcv". R package version, 1:729, 2015.

Wood, S. N.: Generalized additive models: an introduction with R. chapman and hall/CRC, Boca Raton., Pp 496, https://doi.org/10.1201/9781315370279, 2017.

Yu, L., Zhu, J., Ji, H., Bai, X., Lin, Y., Zhang, Y., Sha, L., Liu, Y., Song, Q., Dörsch, P., Mulder, J.: Topography-related controls on N_2O emission and CH_4 uptake in a tropical rainforest catchment, Sci. Total Environ., 775, 145616, https://doi.org/10.1016/j.scitotenv.2021.145616, 2021.

Zhu, J., Mulder, J., Wu, L.P., Meng, X. X., Wang, Y. H., Dörsch, P.: Spatial and temporal variability of N_2O emissions in a subtropical forest catchment in China, Biogeosciences, 10, 1309–21, https://doi.org/10.5194/bg-10-1309-2013, 2013.