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

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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

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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 two extreme periods, the driest and wettest seasons. Seasonal ecosystem fluxes showed near-zero net CH_4 uptake during the driest season and emissions occurring during the wettest season that were larger in magnitude than the uptake. Meanwhile, N_2O emissions were of similar magnitudes in both seasons. Some upland soils within the footprint of the eddy covariance tower emitted N_2O in both seasons, although these fluxes were particularly small. None of the measured climatic variables could explain this soil N_2O flux variation. In contrast, the upland soils were characterised by CH_4 uptake. Overall, seasonal ecosystem CH_4 and N_2O fluxes, as well as seasonal upland soil CH_4 fluxes, were partially explained by seasonal variations in soil water content and global radiation. In addition to the upland soil fluxes studied, 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.

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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.

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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 here 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).

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,

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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

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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 flows 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, SWC is the primary abiotic driver of these gaseous fluxes during the driest and 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

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(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 (Fig. S1). 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).

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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 (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 (FGGA, Los Gatos Research, Mountain View, California, USA). 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

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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, and basic environmental and meteorological data. To calculate net ecosystem production and 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, and comparisons between the ecosystem fluxes with and without correction for the storage term showed that the change in the resulting flux was minimal (Figs. S2, S3). Consequently, we assumed that the storage of CH_4 and N_2O was negligible and ignored it in this study. This meant that a larger period of eddy covariance flux measurements could be used (starting in 2016), in addition to the January 2017 - January 2018 period where CH_4 and N_2O storage data were available. Ecosystem fluxes of CH_4 and N_2O were calculated every half-hour (nmol m^{-2} s^{-1}).

2.4 Chamber measurements

In addition to the flux tower and its associated instrumentation, automated static non-steady through-flow 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 (Fig. S1). 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

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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, which 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, the program included two different closure times to account for high and low fluxes, i.e. 2-min and 25-min measurement periods. The equipment is described in more detail 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. Flux values were selected based on the model that provided the best fit and highest determination coefficient (R^2).

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. As an improvement over Courtois et al. (2019), all CH_4 fluxes with R^2 < 0.80 were excluded regardless of the measurement length (i.e. 2-min and 25-min). For N_2O, all short measurements (i.e. 2-min) with R^2 < 0.80 were discarded. In addition, based on the metric proposed

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by Nickerson (2016), we calculated minimum detectable fluxes suitable for high-resolution in situ greenhouse gas measurements as 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. The soil fluxes of CH_4 and N_2O (nmol m^{-2} s^{-1}) were then assigned to the respective half-hours.

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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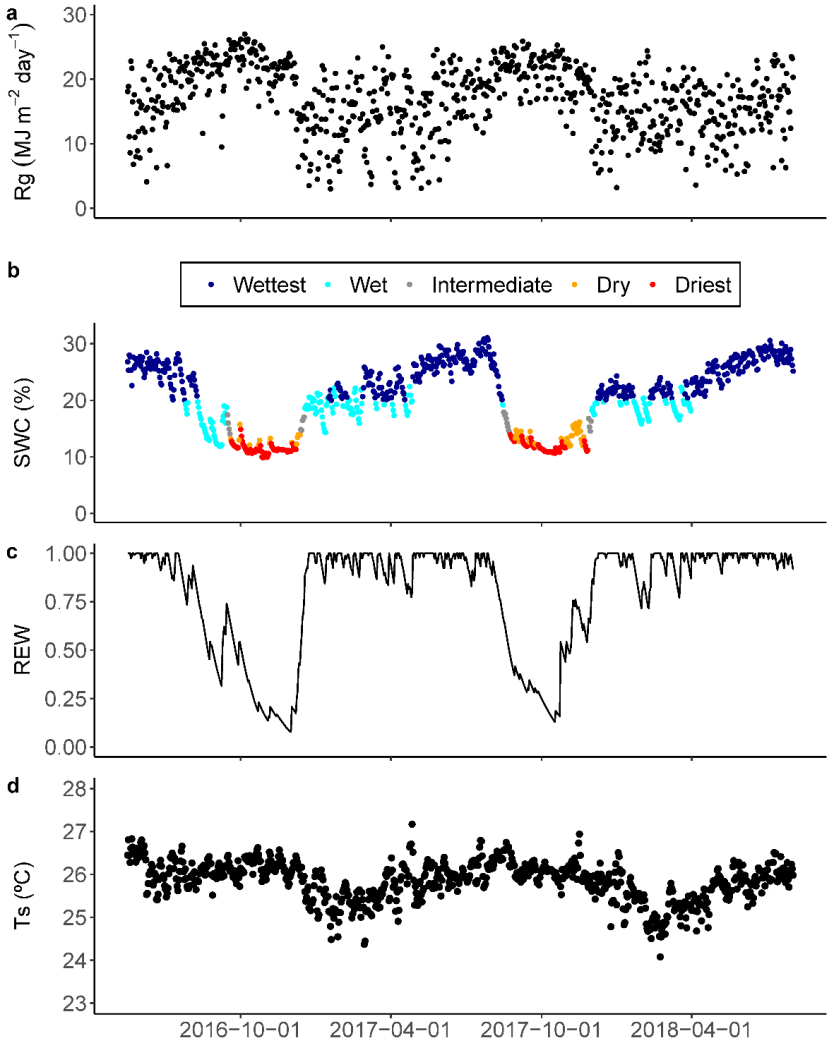

Figure 1. Daily (a) accumulated global radiation (Rg); (b) average soil water content (SWC) at 5 cm in depth during the wet, intermediate and dry seasons, and for two contrasted seasons defined as the wettest (dark blue dots) and the driest (red dots); (c) average relative extractable water (REW) to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

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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).

For eddy covariance and chamber data, the 30 min observations were filtered and flux values outside the 5^{th} - 95^{th} percentile flux range were discarded. 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 calculated daily means for each of the thirteen chambers and retained only the data when at least five observations per chamber per day were recorded. Subsets of values from 1 to 42 for the eddy covariance data and from 1 to 13 for the soil chamber data were then created for each day based on 100 bootstrap iterations. Representative daily means were found for thresholds of 12 minimum observations per day for eddy covariance and 10 for chamber data. 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 from further analyses. 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%, respectively, for CH_4 and N_2O flux data derived from the soil chambers.

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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 dialy 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 our 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

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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).

3 Results

3.1 Environmental seasonality

The Guyaflux site is characterised by an alternating wet and dry season, 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, S4, S5), with seasonal differences particularly evident between the wettest and the driest season (Fig. 3).

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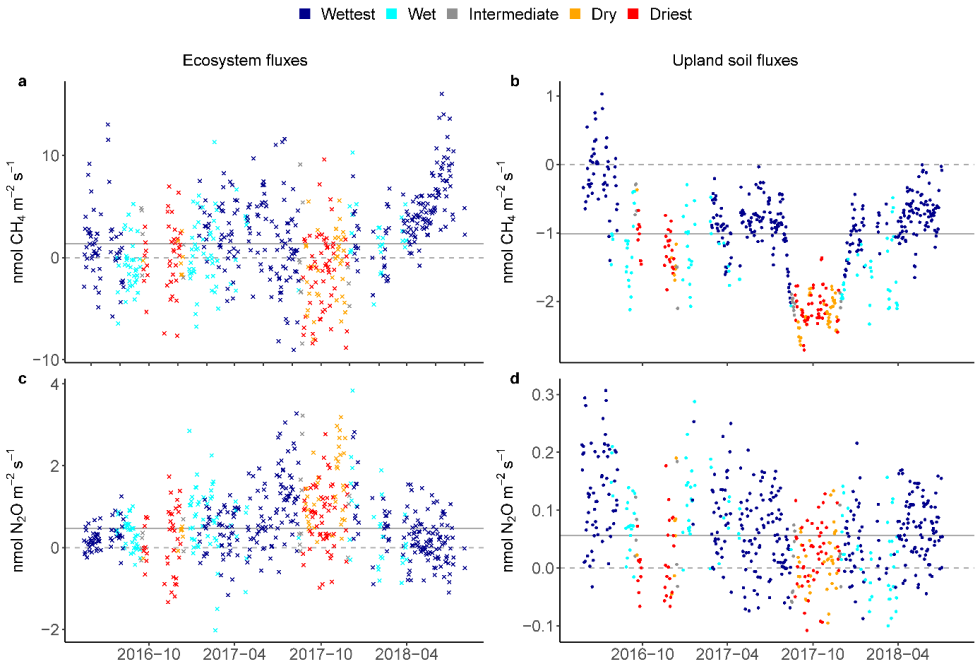

Figure 2. Seasonal courses of average daily ecosystem (crosses on the left) and upland soil (solid dots on the right) fluxes for the wet, intermediate and dry seasons, and for two contrasted seasons defined as the wettest (dark blue dots) and the driest (red dots) for 24-hour CH_4 fluxes (a, b) and N_2O fluxes from 17 May, 2016 to 2 August, 2018 (c, d) in the Guyaflux tropical forest, French Guiana. Positive fluxes (above the dashed grey "0" line) indicate greenhouse gas emissions and negative fluxes (below the "0" line) indicate greenhouse gas uptake; the solid grey line represents the median over the whole period. Note that the scale of the y-axis has been adjusted for each gas and compartment to improve clarity.

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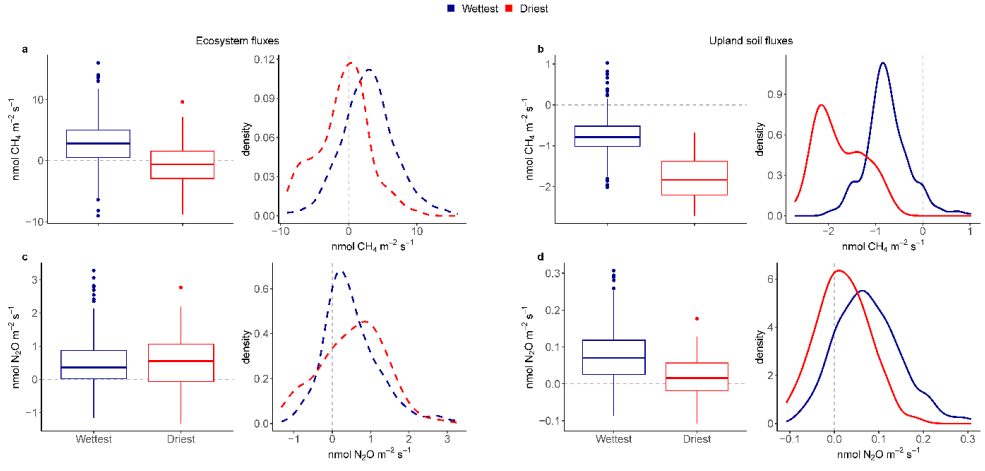

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321 Figure 3. Boxplots and associated density plots of average daily ecosystem fluxes (dashed lines on the
322 left) and upland soil (solid lines on the right) fluxes of 24-hour CH_4 fluxes (a, b) and N_2O fluxes (c, d) for
323 the wettest (blue) and driest (red) seasons, from 17 May, 2016 to 2 August, 2018 in the Guyaflux
324 tropical forest, French Guiana. In the box plots, solid bold lines represent medians, box boundaries
325 mark the 25th and 75th percentiles and whiskers show the 10th and 90th percentiles. Dots mark outliers.
326 In the density plots, positive fluxes on the right side of the dotted "0" line indicate greenhouse gas
327 emissions and negative fluxes on the left side of the "0" line indicate greenhouse gas uptake. All
328 differences among fluxes in the wettest and driest season were statistically significant at $p < 0.05$. See
329 Table 1 for the Kolmogorov-Smirnov test results.

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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 some of the 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. Values in bold are different from 0 at p level < 0.05 based on Student's t-test.

	Wettest			Driest		
Fluxes	**Mean**	**SD**	**Median**	**Mean**	**SD**	**Median**
Ecosystem flux ($nmol_{CH4/N2O}$ m^{-2} s^{-1})						
CH_4	2.9	3.9	2.8	-0.8	3.8	-0.6
N_2O	0.5	0.7	0.4	0.5	0.8	0.6
Upland soil flux ($nmol_{CH4/N2O}$ m^{-2} s^{-1})						
CH_4	-0.8	0.5	-0.8	**-1.8**	0.5	-1.8
N_2O	0.1	0.1	0.1	0.0	0.1	0.0

The seasonal pattern of ecosystem N_2O fluxes was less pronounced than for CH_4 (Fig. 2c); the driest season showed only slightly higher emissions than the wettest season (Table 1; Fig. 3c). In contrast to the ecosystem-level fluxes, soil N_2O fluxes in upland areas not only had a more pronounced seasonal pattern, the upland soils also emitted more N_2O during the wettest season than during the driest season, when the average flux was near-zero N_2O (Table 1; Fig. 3d). It is noteworthy that, although there were significant differences between seasons for all fluxes and at both ecosystem and soil levels (Fig. 3), the overall mean flux was significantly different from zero only for soil CH_4 fluxes during the driest season (Table 1). This indicates that the magnitude of the fluxes was very low relative to the large variability among the seasons.

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3.3 Environmental drivers of ecosystem and upland soil greenhouse gas fluxes

Net ecosystem CH_4 fluxes showed that CH_4 emissions decreased with increasing Rg (Fig. 4a), although this negative correlation was statistically significant only during the wettest season (Table 2) when net emissions occasionally switched to net uptakes at highest Rg values (Fig. 4a). Net ecosystem CH_4 fluxes were strongly positively correlated with SWC (Fig. 4b), showing increased CH_4 emissions with increasing SWC, although this correlation too was statistically significant only during the wettest season (Table 2). A weaker, yet statistically significant, correlation was detected between ecosystem CH_4 fluxes and Ts (Table 2).

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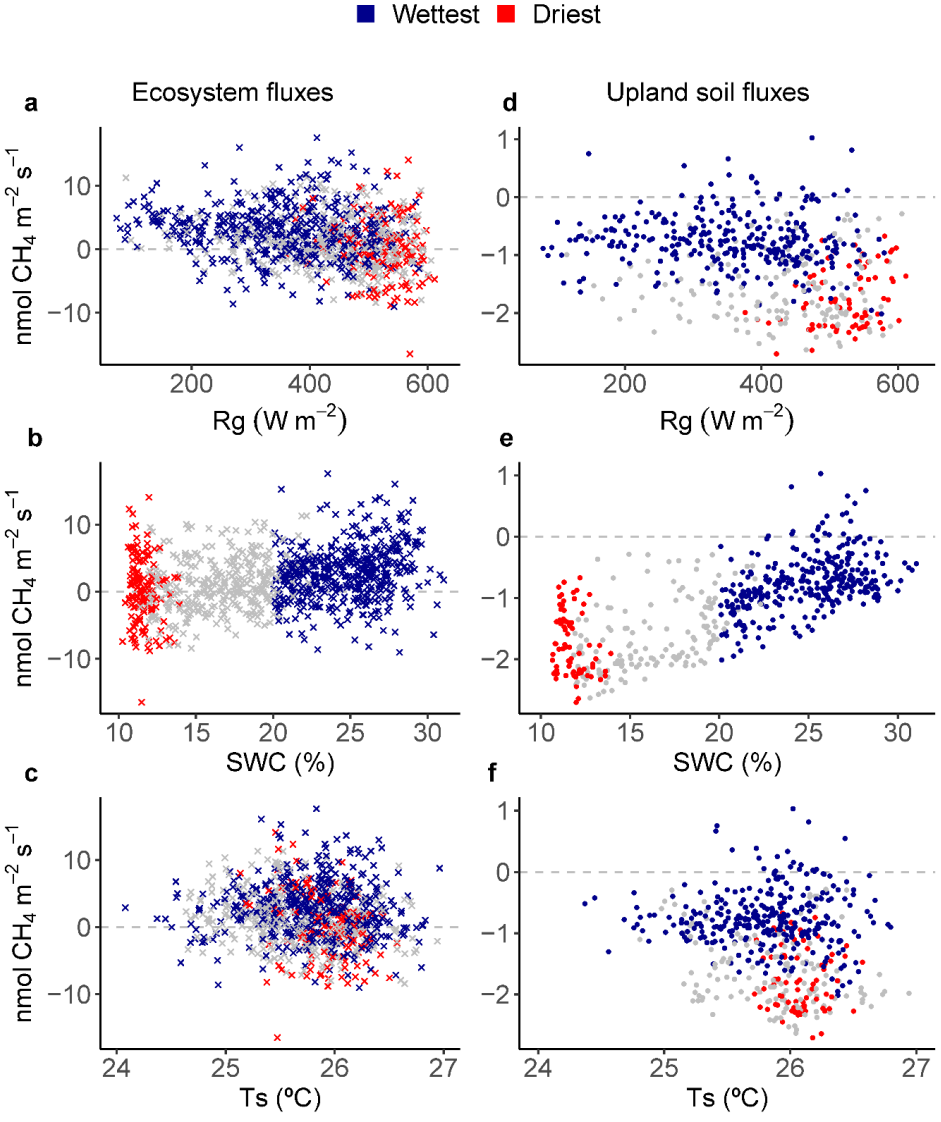

Figure 4. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC) and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots on the right) CH_4 fluxes for the wettest (blue) and driest (red) seasons, with remaining data in grey, from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. Positive fluxes above the horizontal "0" line indicate CH_4 emissions and negative fluxes below the horizontal "0" line indicate CH_4 uptake.

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Despite the different signs for the net CH_4 flux at ecosystem- and soil levels, relationships comparable with the environmental drivers observed for ecosystem CH_4 fluxes were also found for some of the upland soil: net soil CH_4 uptake increased with increasing Rg (Fig. 4d) and decreased with increasing SWC (Fig. 4e). The correlation between upland soil CH_4 fluxes and Rg was statistically significant in the driest season, while the correlation with SWC was equal and significant in both seasons (wettest and driest, Table 2).

Ecosystem N_2O fluxes showed relatively weak responses to the environmental drivers we investigated (Figs. 5a-c). The statistically significant terms in the model were SWC > Rg >Ts, and only during the wettest season. However, the R^2 of the model was rather low (R^2 = 0.04; Table 2). For the upland soil N_2O fluxes, none of the environmental drivers we investigated explained soil N_2O emissions (Fig. 5; Table 2).

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379 Table 2. Results of generalised additive models (GAM) assessing the relationships between
380 environmental variables, i.e. global radiation (Rg), soil water content (SWC), soil temperature (Ts), and
381 daily mean ecosystem and upland soil CH_4 and N_2O fluxes during the wettest and driest seasons from
382 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. The effective degrees
383 of freedom (edf) and the reference number of degrees of freedom (Ref. df) of the fitted models, with
384 values for each spline term, are shown. Significant terms at p level < 0.05 are shown in bold.

	Fluxes	Best model predictors	R^2	Intercept	Coefficients		F value	p value
					edf	Ref. df		
Ecosystem level								
Daily	CH_4		0.20	0.002				
		Rg: Wettest			0.8	9	0.54	**0.014**
		Rg: Driest			0.6	8	0.19	0.113
		Ts: Wettest			1.7	9	0.62	**0.025**
		Ts: Driest			0.0	9	0.00	0.477
		SWC: Wettest			1.6	9	1.92	**< 0.001**
		SWC: Driest			0.0	6	0.00	0.433
Daily	N_2O		0.04	0.000				
		Rg: Wettest			0.8	9	0.41	**0.026**
		Rg: Driest			0.0	8	0.00	0.772
		Ts: Wettest			1.2	9	0.39	**0.045**
		Ts: Driest			0.3	8	0.05	0.247
		SWC: Wettest			2.2	9	0.93	**0.011**
		SWC: Driest			0.0	6	0.00	0.717
Upland soil level								
Daily	CH_4		0.54	-0.001				
		Rg: Wettest			1.2	9	0.24	0.156
		Rg: Driest			1.5	9	1.24	**0.001**
		Ts: Wettest			0.7	9	0.27	0.057
		Ts: Driest			0.0	9	0.00	0.865
		SWC: Wettest			2.6	9	9.74	**< 0.001**
		SWC: Driest			1.9	7	3.52	**< 0.001**
Daily	N_2O		0.10	0.000				
		Rg: Wettest			0.0	9	0.00	0.419
		Rg: Driest			0.6	8	0.19	0.112
		Ts: Wettest			1.2	9	0.32	0.084
		Ts: Driest			0.0	9	0.00	1.000
		SWC: Wettest			0.0	9	0.00	0.804
		SWC: Driest			0.0	6	0.00	1.000

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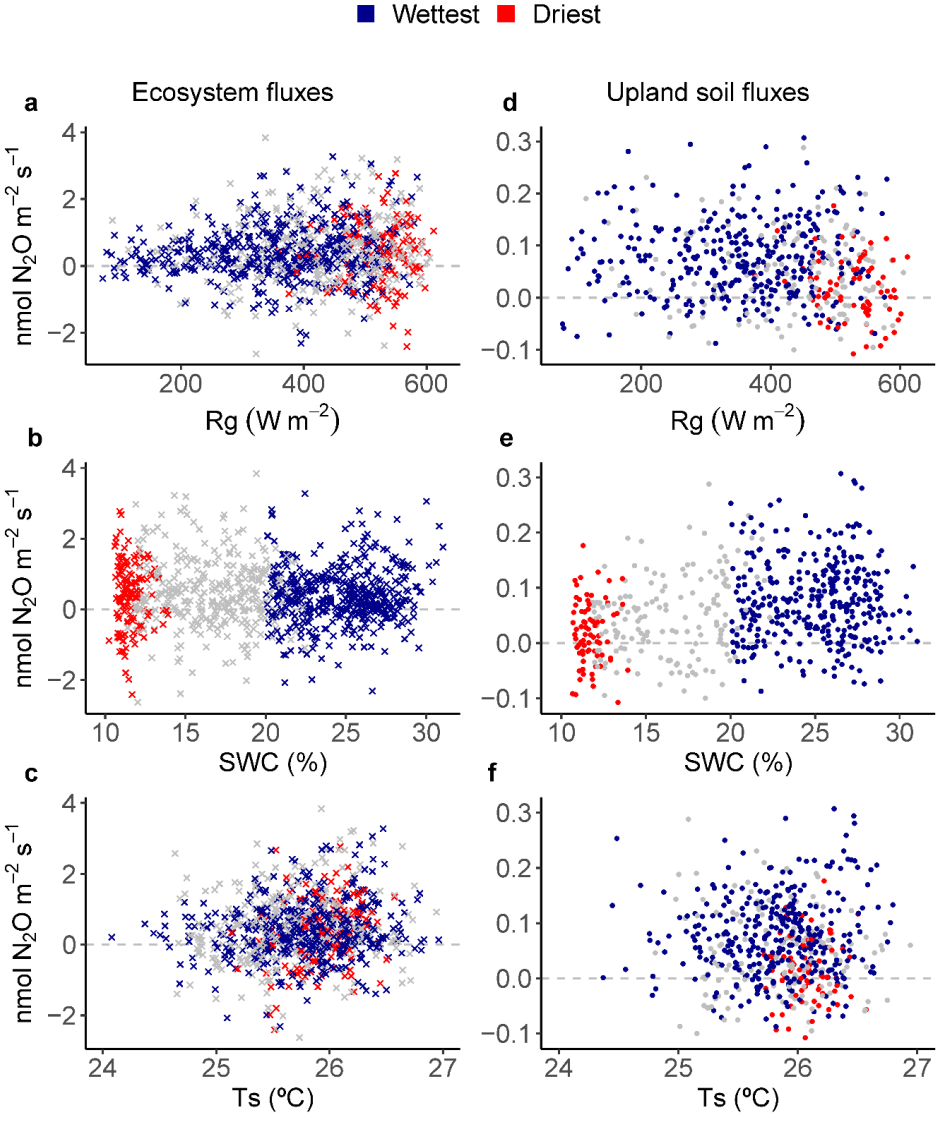

Figure 5. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC) and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots on the right) N_2O fluxes for the wettest (blue) and driest (red) seasons, with remaining data in grey, from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. Positive fluxes above the horizontal "0" line indicate N_2O emissions and negative fluxes below the horizontal "0" line indicate N_2O uptake.

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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 (2.9 ± 3.9 nmolCH_4 m^{-2} s^{-1}; Mean ± SD) dominated during the wettest season, whereas net CH_4 uptake (-0.8 ± 3.8 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 S1). 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 mechanism underlying the large CH_4 emissions during the dry season observed in the Brazilian forests remains 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

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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.

Consistent with H2, the generalised additive models (GAM) revealed that SWC, and to a lesser extent Rg and Ts, were relevant ecosystem CH_4 flux drivers, particularly during the wettest season (Table 2; Figs. 4a-c). It is reasonable to assume that high SWC but relatively low Ts during the wettest season stimulated CH_4 production in most compartments of the ecosystem, not only in the seasonally flooded soils. An increase in SWC at shallow depths may reduce the amount of air-filled pore space in the soil. This reduction may decrease the diffusion of oxygen and CH_4 from the atmosphere through the soil to methanotrophs, resulting in 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 they may partially explain the seasonal trends observed at our site. On the other hand, the statistically significant, albeit weak, relationship between CH_4 emissions and Rg during the wettest season 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. The latter explanation is, however, unlikely because the location of 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

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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 contributed 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 overall net uptake rates of 1.1 ± 0.7 nmolCH_4 m^{-2} s^{-1}, which is higher than 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) but lower than fluxes found in previous studies in tropical plantations and forests in Central and South America (Panama, -13.5 nmolCH_4 m^{-2} s^{-1}, Keller et al., 1990; -19.9 nmolCH_4 m^{-2} s^{-1}, Goreau and de Mello, 1988). CH_4 fluxes at our site ranged seasonally from -0.8 ± 0.5 nmolCH_4 m^{-2} s^{-1} in the wettest season to -1.8 ± 0.5 nmolCH_4 m^{-2} s^{-1} in the driest season (Table S2), supporting H1 and globally corroborating other seasonal studies in tropical forests. In addition, CH_4 flux dynamics in our upland soils were characterised by a large range of variation, but a consistent sign, 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

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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). However, 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).

The best set of meteorological parameters, explaining 53% 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 twice as high in the driest season as in the wettest season. This is consistent with the known dependence of soil CH_4 fluxes on topsoil SWC (Fig. 4e; Tables 1, 3): dryer soil conditions favour soil methanotrophy (Le Mer and Roger, 2001) and wet soils reduce methanotrophic communities and / or their activity (Covey and Megonigal, 2019).

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 0.6 ± 0.8 nmolN_2O m^{-2} s^{-1} (Fig. 3c; Table 1). Though low, this loss of nitrogen (N) from the ecosystem is equivalent to approximately one-fifth of the annual atmospheric N deposition at the site (2.7 kgN_2O-N ha^{-1} yr^{-1} here vs. 13 kgN_2O-N ha^{-1} yr^{-1} in Van Langenhove et al., 2020). 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 very close to the average fluxes

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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 ± 0.8 nmolN_2O m^{-2} s^{-1} and 0.5 ± 0.7 nmolN_2O m^{-2} s^{-1}, in the driest and the wettest seasons, respectively; Table S2), 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 similar 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). Contrary to H2, GAM analyses failed to explain or attribute the observed variations in N_2O fluxes to changes in SWC or other meteorological drivers (R^2 = 0.04, Table 2). 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, we did find statistically significant, though very weak, relationships between ecosystem N_2O fluxes and SWC, Ts and Rg, suggesting 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).

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This could indeed counteract the overriding, albeit small, net ecosystem N_2O emissions, suggesting that the proportion of upland versus seasonal 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 upland soils studied were small, averaging 0.1 ± 0.1 nmolN_2O m^{-2} s^{-1} (Table 1, S2), and slightly higher during the wettest season (0.1 ± 0.1 nmolN_2O m^{-2} s^{-1}) compared to the driest season (0.0 ± 0.1 nmolN_2O m^{-2} s^{-1}; Table S2). Our flux values were nine times smaller than those measured with automated chamber systems in a western Kenyan rainforest (0.9 nmolN_2O m^{-2} s^{-1}; Werner et al., 2007), even though the soils in both cases were predominantly N_2O emitters. However, our seasonal N_2O flux observations were within the same order of magnitude as those in two tropical rainforests where soil N_2O emissions measured with manual chambers were lower in the dry season than in the wet season (< 0.20 nmolN_2O m^{-2} s^{-1} and 0.34 nmolN_2O m^{-2} s^{-1}, respectively, in Yu et al., 2021; 0.10 nmolN_2O m^{-2} s^{-1} and 0.49 nmolN_2O m^{-2} s^{-1}, respectively, in Werner et al., 2006).

In contrast to H2, none of our GAMs including meteorological drivers (i.e. SWC, Ts, Rg) predicted the observed seasonal variations in upland soil N_2O fluxes when only the driest and wettest seasons were taken into account (Table 2; Fig. 5). However, when all the seasons were accounted for, an increase in SWC appeared to partially explain the increase in soil N_2O fluxes (Figs. 5e, S5d). Although both nitrification and denitrification can occur simultaneously in various soil microsites (Stevens et al., 1997), N_2O release often occurs on a daily basis in environments with rapidly shifting O_2 availability, which is the case for soils with changing SWC (Davidson, 1992; Fig. 1). Several studies in subtropical and tropical forests have reported significant effects of SWC on tropical soil N_2O fluxes (Kiese and Butterbach-Bahl, 2002; Werner et al., 2006, 2007; Gütlein et al., 2018).

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5 Conclusion

Our long-term monitoring of ecosystem and soil CH_4 and N_2O fluxes over a period of 26 months under contrasting climatic conditions (driest versus wettest seasons) revealed highly variable fluxes that changed direction and amount on short time scales. Although mean daily fluxes were low, N_2O emissions were observed all year long. In contrast, for CH_4, either emission or uptake occurred, depending on the season. As expected, the seasons had a statistically significant effect on ecosystem CH_4 and N_2O fluxes, with CH_4 uptake and higher N_2O emissions during the driest season than during the wettest season. Upland soils exhibited highly variable CH_4 and N_2O fluxes, with an increase in CH_4 uptake and a decrease in N_2O emissions from the wettest to the driest season. The climatic variables we selected explained only a minor part of the seasonal variations in ecosystem CH_4 and N_2O fluxes. At the soil level, none of the climatic variables were significant for seasonal fluxes of N_2O whereas SWC was a strong driver of CH_4 fluxes.

Measurements at the ecosystem and soil levels showed divergent fluxes, probably because soil fluxes represent only one compartment in the whole ecosystem. Furthermore, upland soils (52% of the footprint area) are only one type of soil within the large range of soils found inside the Guyaflux tower footprint. In addition, soil chambers provide integrated fluxes for a much smaller area than does the eddy covariance technique. In order to improve the understanding of seasonal variations in ecosystem CH_4 and N_2O fluxes, our study shows that it is crucial to characterise the fluxes for all existing ecosystem compartments at the same time and to include all the tree components (leaves, stems, branches) and tree species in the forest habitats, not just those on upland soils. However, our study still provides valuable data that, when combined with mechanistic models, may help identify the missing drivers responsible for the seasonal variations in CH_4 and N_2O fluxes in wet tropical forest ecosystems.

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Data availability

All raw data can be provided by the corresponding authors upon request.

Supplement link

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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597

598 **References**

599 Aguilos, M., Hérault, B., Burban, B., Wagner, F., Bonal, D.: What drives long-term variations in carbon
600 flux and balance in a tropical rainforest in French Guiana?, Agric. For. Meteorol., 253–254, 114–
601 123, https://doi.org/10.1016/j.agrformet.2018.02.009, 2018.
602 Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H.,
603 Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K.,
604 Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T.: Estimates of the annual net
605 carbon and water exchange of European forests: the EUROFLUX methodology, Adv. Ecol. Res.,
606 30, 114–175, https://doi.org/10.1016/S0065-2504(08)60018-5, 2000.
607 Aubinet, M., Vesala, T. and Papale, D. eds.: Eddy covariance: a practical guide to measurement and
608 data analysis, Springer Science and Business Media, 2012.
609 Baldocchi, D. D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates
610 of ecosystems: past, present and future, Glob. Chang. Biol., 9, 479–92,
611 https://doi.org/10.1046/j.1365-2486.2003.00629.x, 2003.
612 Baldocchi, D.: Measuring fluxes of trace gases and energy between ecosystems and the atmosphere -
613 the state and future of the eddy covariance method, Glob. Chang. Biol., 20, 3600–9,
614 https://doi.org/10.1111/gcb.12649, 2014.
615 Baldocchi, D. D.: How eddy covariance flux measurements have contributed to our understanding of
616 Global Change Biology, Glob. Chang. Biol., 26, 242–60, https://doi.org/10.1111/gcb.14807, 2020.
617 Bernhardt, E. S., Blaszczak, J. R., Ficken, C. D., Fork, M. L., Kaiser, K. E., Seybold, E. C.: Control points in
618 ecosystems: moving beyond the hot spot hot moment concept, Ecosystems, 20, 665–82,
619 https://doi.org/10.1007/s10021-016-0103-y, 2017.
620 Blagodatsky, S., Smith P.: Soil physics meets soil biology: towards better mechanistic prediction of

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

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.

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.

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

647 Covey, K. R., Megonigal, J. P.: Methane production and emissions in trees and forests, New Phytol.,
648 222, 35–51, https://doi.org/10.1111/nph.15624, 2019.
649 Covey, K., Soper, F., Pangala, S., Bernardino, A., Pagliaro, Z., Basso, L., Cassol, H., Fearnside, P.,
650 Navarrete, D., Novoa, S., Sawakuchi, H.: Carbon and beyond: The biogeochemistry of climate in a
651 rapidly changing Amazon, Front. For. Glob. Change., 4, 1–20,
652 https://doi.org/10.3389/ffgc.2021.618401, 2021.
653 Daniel, W., Stahl, C., Burban, B., Goret, J.- Y., Cazal, J., Richter, A., Janssens, I. A., Bréchet, L. M.: Tree
654 stem and soil methane and nitrous oxide fluxes, but not carbon dioxide fluxes, switch sign along
655 a topographic gradient in a tropical forest, Plant Soil, 488, 533–49,
656 https://doi.org/10.1007/s11104-023-05991-y, 2023.
657 Davidson, E.A.: Sources of nitric oxide and nitrous oxide following wetting of dry soil, Soil Sci. Soc. Am.
658 J., 56, 95–102, https://doi.org/10.2136/sssaj1992.03615995005600010015x, 1992.
659 Davidson, E. A., De Araüjo, A. C., Artaxo, P., Balch, J. K., Brown, I. F., Mercedes, M. M., Coe, M. T.,
660 Defries, R. S., Keller, M., Longo, M., Munger, J. W., Schroeder, W., Soares-Filho, B. S., Souza, C.
661 M., Wofsy, S. C., The Amazon basin in transition, Nature, 481, 321–328,
662 https://doi.org/10.1038/nature10717, 2012.
663 Delwiche, K. B., Knox, S. H., Malhotra, A., Fluet-Chouinard, E., McNicol, G., Feron, S., Ouyang, Z., Papale,
664 D., Trotta, C., Canfora, E., Cheah, Y. W.: FLUXNET-CH_4: A global, multi-ecosystem dataset and
665 analysis of methane seasonality from freshwater wetlands, Earth Syst. Sci. Data Discuss., 2021,
666 1–11, https://doi.org/10.5194/essd-13-3607-2021, 2021.
667 Dutaur, L., Verchot, L.V.: A global inventory of the soil CH_4 sink. Global Biogeochem. Cy., 21, 4,
668 https://doi.org/10.1029/2006GB002734, 2007.
669 Epron, D., Bosc, A., Bonal, D., Freycon, V.: Spatial variation of soil respiration across a topographic
670 gradient in a tropical rain forest in French Guiana, J. Trop. Ecol., 22, 565–74,
671 https://doi:10.1017/S0266467406003415, 2006.
672 Eugster, W., Plüss, P.: A fault-tolerant eddy covariance system for measuring CH_4 fluxes, Agric. For.

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

673 Meteorol., 150, 841–51, https://doi.org/10.1016/j.agrformet.2009.12.008, 2010.
674 Eugster, W., Merbold, L.: Eddy covariance for quantifying trace gas fluxes from soils, Soil, 1, 187–205,
675 https://doi.org/10.5194/soil-1-187-2015, 2015.
676 Fang, J., Fang, J., Chen, B., Zhang, H., Dilawar, A., Guo, M. and Liu, S.A.: Assessing spatial
677 representativeness of global flux tower eddy-covariance measurements using data from
678 FLUXNET2015, Sci. Data, 11, 569, https://doi.org/10.1038/s41597-024-03291-3, 2024.
679 von Fischer, J. C., Hedin, L. O.: Controls on soil methane fluxes: Tests of biophysical mechanisms using
680 stable isotope tracers, Global Biogeochem. Cy., 21, 9-Gb2007,
681 https://doi.org/10.1029/2006gb002687, 2007.
682 Gauci, V.: Tree methane exchange in a changing world, Nat. Rev. Earth Environ., 6, 471–483,
683 https://doi.org/10.1038/s43017-025-00692-9, 2025.
684 Gauci, V., Pangala, S. R., Shenkin, A., Barba, J., Bastviken, D., Figueiredo, V., Gomez, C., Enrich-Prast, A.,
685 Sayer, E., Stauffer, T., Welch, B.: Global atmospheric methane uptake by upland tree woody
686 surfaces, Nature, 631, 796–800, https://doi.org/10.1038/s41586-024-07592-w, 2024.
687 Goreau, T. J., De Mello, W. Z.: Tropical deforestation: some effects on atmospheric chemistry, Ambio.,
688 17, 275–281, 1988.
689 Groffman, P. M., Butterbach-Bahl, K., Fulweiler, R. W., Gold, A. J., Morse, J. L., Stander, E. K., Tague, C.,
690 Tonitto, C., Vidon, P.: Challenges to incorporating spatially and temporally explicit phenomena
691 (hotspots and hot moments) in denitrification models, Biogeochemistry, 93, 49–77,
692 https://doi.org/10.1007/s10533-008-9277-5, 2009.
693 Gütlein, A., Gerschlauer, F., Kikoti, I., Kiese, R.: Impacts of climate and land use on N_2O and CH_4 fluxes
694 from tropical ecosystems in the Mt. Kilimanjaro region, Tanzania, Glob. Chang. Biol., 24, 1239–
695 55, https://doi.org/10.1111/gcb.13944, 2018.
696 Ito, A., Inatomi, M.: Use of a process-based model for assessing the methane budgets of global
697 terrestrial ecosystems and evaluation of uncertainty, Biogeosciences, 9, 759–73,
698 https://doi.org/10.5194/bg-9-759-2012, 2012.

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

699 IUSS Working Group WRB: World reference base for soil resources 2014, update 2015. International
700 soil classification system for naming soils and creating legends for soil maps, World Soil Resources
701 Reports No. 106. FAO, Rome (2015), 2015.
702 Jones, C. M., Spor, A., Brennan, F. P., Breuil, M. C., Bru, D., Lemanceau, P., Griffiths, B., Hallin, S.,
703 Philippot, L.: Recently identified microbial guild mediates soil N_2O sink capacity, Nat. Clim.
704 Change, 4, 801–5, https://doi.org/10.1038/nclimate2301, 2014.
705 Keller, M., Mitre, M. E., Stallard, R. F.: Consumption of atmospheric methane in soils of central Panama:
706 effects of agricultural development, Global Biogeochem. Cy., 4, 21–27,
707 https://doi.org/10.1029/GB004i001p00021, 1990.
708 Khalil, K., Mary, B., Renault, P.: Nitrous oxide production by nitrification and denitrification in soil
709 aggregates as affected by O_2 concentration, Soil Biol. Biochem., 36, 687–99,
710 https://doi.org/10.1016/j.soilbio.2004.01.004, 2004.
711 Kiese, R., Butterbach-Bahl, K.: N_2O and CO_2 emissions from three different tropical forest sites in the
712 wet tropics of Queensland, Australia, Soil Biol. Biochem., 34, 975–87,
713 https://doi.org/10.1016/S0038-0717(02)00031-7, 2002.
714 Knox, S. H., Bansal, S., McNicol, G., Schafer, K., Sturtevant, C., Ueyama, M., Valach, A. C., Baldocchi, D.,
715 Delwiche, K., Desai, A. R., Euskirchen, E., et al.: Identifying dominant environmental predictors of
716 freshwater wetland methane fluxes across diurnal to seasonal time scales, Glob. Chang. Biol., 27,
717 3582–604, https://doi.org/10.1111/gcb.15661, 2021.
718 Le Mer, J., Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review,
719 Eur. J. Soil Biol., 37, 25–50, https://doi.org/10.1016/S1164-5563(01)01067-6, 2001.
720 Liu, Z., Li, H., Wu, F., Wang, H., Chen, H., Zhu, Q., Yang, G., Liu, W., Chen, D., Li, Y., Peng, C.:
721 Quantification of ecosystem-scale methane sinks observed in a tropical rainforest in Hainan,
722 China, Land, 11, 154, https://doi.org/10.3390/land11020154, 2022.
723 Lucas-Moffat, A. M., Huth, V., Augustin, J., Brummer, C., Herbst, M., Kutsch, W. L.: Towards pairing plot
724 and field scale measurements in managed ecosystems: Using eddy covariance to cross-validate

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

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.

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.

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,

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

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.

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.

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.

Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J., Rey, A.: Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes, Eur. J. soil sci., 54, 779–91, https://doi.org/10.1046/j.1351-0754.2003.0567.x, 2003.

Stevens, R. J., Laughlin, R. J., Burns, L. C., Arah, J. R., Hood, R. C.: Measuring the contributions of nitrification and denitrification to the flux of nitrous oxide from soil, Soil Biol. Biochem., 29, 139–51, https://doi.org/10.1016/S0038-0717(96)00303-3, 1997.

Stiegler, C., Koebsch, F., Ali, A. A., June, T., Veldkamp, E., Corre, M. D., Koks, J., Tjoa, A., Knohl, A.: Temporal variation in nitrous oxide (N_2O) fluxes from an oil palm plantation in Indonesia: An ecosystem-scale analysis, GCB Bioenergy, 15, 1221–39, https://doi.org/10.1111/gcbb.13088, 2023.

The, Y. A., Silver, W. L., Conrad, M. E.: Oxygen effects on methane production and oxidation in humid tropical forest soils, Glob. Chang. Biol., 11, 1283–1297, https://doi.org/10.1111/j.1365-2486.2005.00983.x, 2005.

The, Y. A., Silver, W. L.: Effects of soil structure destruction on methane production and carbon

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

partitioning between methanogenic pathways in tropical rain forest soils, J. Geophys. Res. G: Biogeosciences, 111, G1, https://doi.org/10.1029/2005JG000020, 2006.

Tian, H., Chen, G., Lu, C., Xu, X., Ren, W., Zhang, B., Banger, K., Tao, B., Pan, S., Liu, M., Zhang, C.: Global methane and nitrous oxide emissions from terrestrial ecosystems due to multiple environmental changes, Ecosyst. Health Sustain., 1, 1–20, https://doi.org/10.1890/EHS14-0015.1, 2015.

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.: 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, 2020.

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.-

https://doi.org/10.5194/egusphere-2025-3501
Preprint. Discussion started: 7 August 2025

803 Atmos., 112, D3, https://doi.org/10.1029/2006JD007388, 2007.

804 Wickham, H., Wickham, H.: Getting Started with ggplot2. ggplot2: Elegant graphics for data analysis,
805 11–31, 2016.

806 Whiting, G. J., Chanton, J. P.: Primary production control of methane emission from wetlands, Nature,
807 364, 794–5, https://doi.org/10.1038/364794a0, 1993.

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

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

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

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

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