1 *For Biogeosciences*

3 **Title**

4 **Dynamics and environmental drivers of methane and nitrous oxide fluxes at**

5 **the soil and ecosystem levels in a wet tropical forest**

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21 **Abstract**

22 Tropical forests are critical for maintaining the global carbon balance and mitigating climate change,

23 yet their exchange of greenhouse gases with the atmosphere remains understudied, particularly for

24 methane (CH_4) and nitrous oxide (N_2O). This study reports on continuous measurements of CH_4 and

25 N_2O fluxes at the ecosystem and soil levels, respectively through eddy covariance and an automated

26 chamber technique, in a wet tropical forest in French Guiana over a period of 26 months. We studied

27 the magnitude of CH_4 and N_2O fluxes and their drivers (climatic variables) during two extreme periods,

28 the driest and wettest seasons. Seasonal ecosystem fluxes showed near-zero net CH_4 uptake during

29 the driest season and emissions occurring during the wettest season that were larger in magnitude

30 than the uptake. Meanwhile, N_2O emissions were of similar magnitudes in both seasons. Some upland

31 soils within the footprint of the eddy covariance tower emitted N_2O in both seasons, although these

32 fluxes were particularly small. ~~None of the measured climatic variables could explain this soil N_2O flux~~

33 ~~variation.~~ In contrast, the upland soils were characterised by CH_4 uptake. Overall, seasonal ecosystem

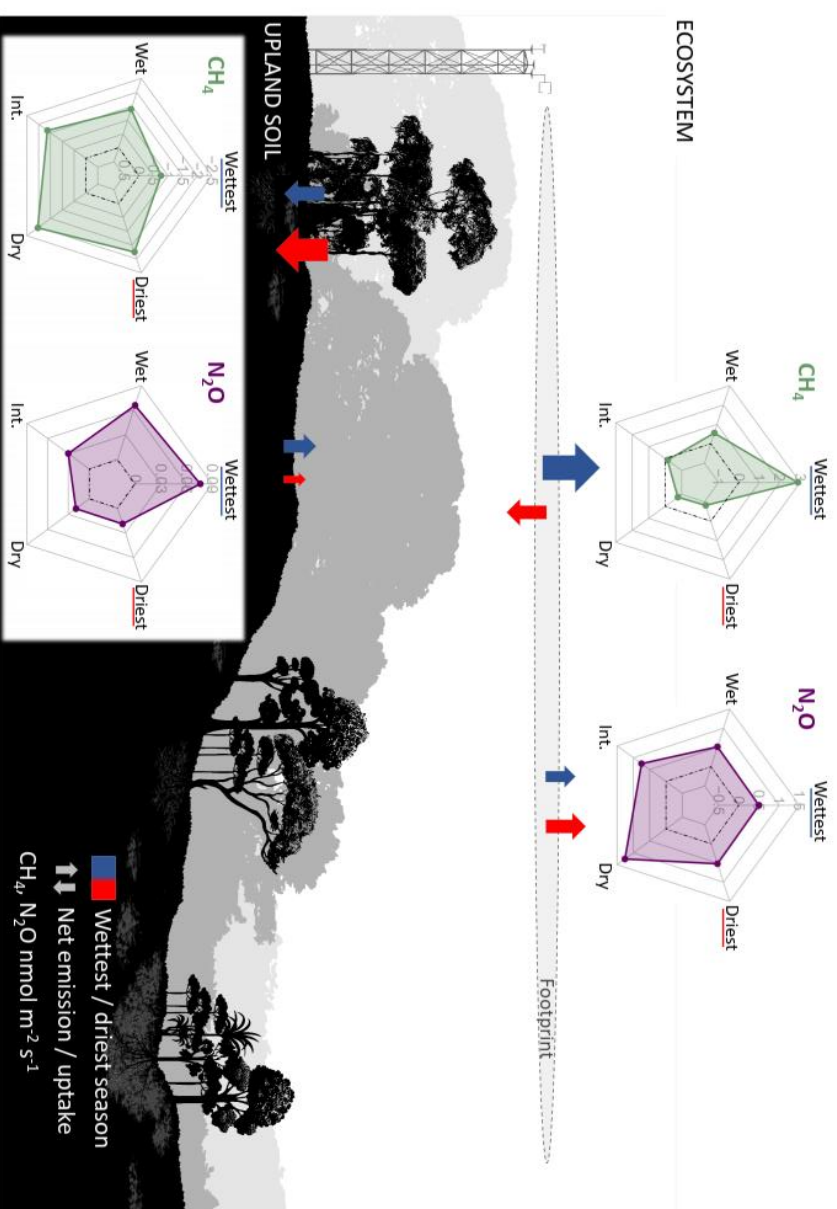
34 CH_4 and N_2O fluxes, as well as seasonal upland soil CH_4 and N_2O fluxes, were partially explained by

35 seasonal variations in soil water content, soil temperature and global radiation. In addition to the

36 upland soil fluxes studied, the magnitude and sign of the net ecosystem fluxes of CH_4 and N_2O were

37 likely due to outgassing from aboveground biomass and the presence of seasonally flooded areas

38 within the footprint of the eddy covariance system. Further studies of other ecosystem compartments

39 in different forest habitats are needed to better understand the temporal variations in CH_4 and N_2O

40 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.

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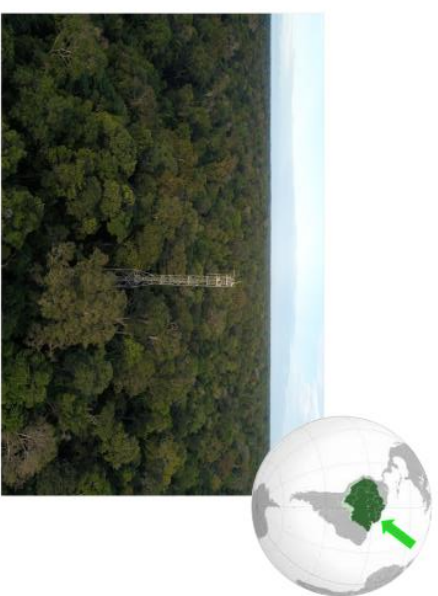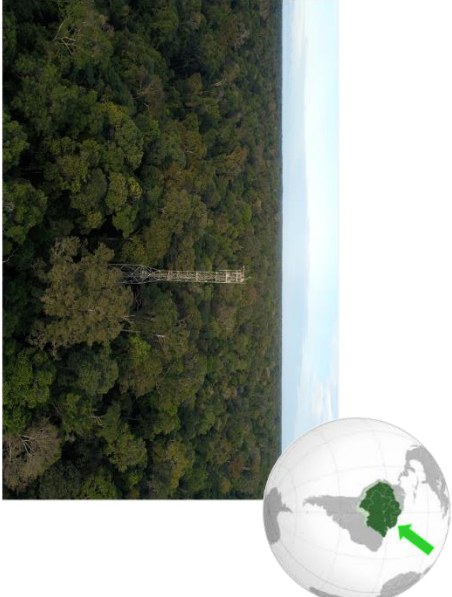
1 Introduction

44 The lack of knowledge on greenhouse gas fluxes in the tropical forests of the Amazon Basin contributes

45 significantly to the uncertainty in the global greenhouse gas budget, particularly for methane (CH_4) and

46 nitrous oxide (N_2O) (Davidson et al., 2012; Covey et al., 2021), the two most important greenhouse

47 gases in the atmosphere after carbon dioxide (CO_2). Early observations show that tropical forests in

48 the Amazon Basin may contribute disproportionately to global CH_4 and N_2O exchanges compared to

49 other forests (Tian et al., 2015), but considerable uncertainties remain due to the paucity of data and

50 lack of detailed understanding of CH_4 and N_2O cycling at both soil and ecosystem levels in these forests.

51 The role of tropical forest soils is crucial here as they can act either as a source or a sink for CH_4 and

52 N_2O (Bouwman et al., 1993). In contrast to the consistent emissions from soil microbial decomposition

53 and root activity for CO_2, anaerobic CH_4-emitting microbes (methanogenic archaea) are dominant in

54 wetland environments, whereas aerobic CH_4-consuming microbes (methanotrophic bacteria) are more

55 abundant in upland soils (Ito and Inatomi, 2012; Welch et al., 2019) where they play the role of CH_4

56 sinks. For N_2O as well, both emission and uptake can occur in soils. N_2O can be produced by microbes

57 under both anaerobic (via denitrification) and aerobic (via nitrification) conditions (Khalil et al., 2004),

58 although the majority of N_2O production occurs in waterlogged soils (Oertel et al., 2016). On the other

59 hand, soil microbes that are not denitrifiers can reduce N_2O to dinitrogen (Sanford et al., 2012; Jones

60 et al., 2014).

61 Microbial CH_4 and N_2O fluxes in tropical soils are controlled by the complex interplay of multiple

62 environmental and biological factors. The key factors regulating net CH_4 fluxes in tropical soils include

63 redox potential and water table depth (Silver et al., 1999; Teh et al., 2005; von Fischer and Hedin,

64 2007), plant productivity (Whiting and Chanton, 1993; von Fischer and Hedin, 2007), labile soil organic

65 matter (Wright et al., 2011), competition for carbon substrates among anaerobic microorganisms (Teh

66 and Silver, 2006; von Fischer and Hedin, 2007), temperature (Knox et al., 2021), and the presence of

67 plants that facilitate atmospheric escape (Pangala et al., 2013). The key factors regulating net soil N_2O

68 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

95 temporal resolution data on mass and energy exchanges at the ecosystem level (Baldocchi, 2014, 2020;

96 Delwiche et al., 2021) and more detailed information on ecosystem functioning at a broader spatial

97 scale than do mere soil measurements, which miss above-ground exchanges and typically, also

98 emissions from wetland areas within the ecosystem (Bonal et al., 2008; Aguilos et al., 2018; Wang et

99 al., 2021; Liu et al., 2022). However, eddy covariance cannot indicate how much different land cover

100 types relatively contribute to the ecosystem's total flux since the measurements integrate high and

101 low frequency flux over time and space. Chamber and eddy covariance-based approaches each have

102 their own strengths and weaknesses; however, taken together, they effectively represent the

103 magnitude of ecosystem fluxes and can help determine the drivers of greenhouse gas flux dynamics

104 (Eugster et al., 2015). We therefore combined these two approaches to test the following assumptions:

105 • H1: Ecosystem- and soil-level CH_4 and N_2O fluxes vary seasonally in the studied tropical forest,

106 switching between uptake and emission,

107 • H2: At both the soil and ecosystem levels, SWC is the primary abiotic driver of these gaseous

108 fluxes during the driest and wettest seasons.

109 This study provides, for the first time, a comprehensive assessment of CH_4 and N_2O dynamics at both

110 ecosystem and soil levels based on high-frequency eddy covariance and continuous soil chamber time

111 series over 26 months in a wet tropical forest.

112

113 **2   Methods**

114 **2.1 Study site**

115 Our research was conducted at the Guyaflux site (5°16'54"N, 52°54'44"W) (Bonal et al., 2008), an ICOS-

116 associated ecosystem station (GF-Guy) located 15 km from the coast and approximately 40 km west of

117 Kourou, in French Guiana, South America. On a decadal time scale, the average annual precipitation at

118 the study site is 3102 ± 70 mm and average annual air temperature is 25.7 ± 0.1 °C (Aguilos et al., 2018).

119 The climate is humid tropical and highly seasonal due to the north-south movement of the Inter-

120 Tropical Convergence Zone (ITCZ), which drives regional precipitation. The ITCZ dictates the wet season

121 (from December to July, with rainfall of up to 500 mm month^{-1}) and the long dry season from mid-

122 August (mid-November, with less than 100 mm month^{-1}). In the northernmost part of the Guiana

123 shield, where the study site is located, the topography results in a succession of small elliptical hills

124 from 10 to 40 m asl, with soils classified as nutrient-poor acrisols (IUSS Working Group WRB, 2015).

125 The site is totally surrounded by undisturbed forest, locally characterised by a tree density of about

126 620 trees ha^{-1} (for trees > 10 cm dbh), an average tree height of 35 m, an average tree diameter at

127 breast height (DBH) of 40.1 cm, with emergent trees over 40 m tall, and a tree species richness of about

128 140 species ha^{-1} (Bonal et al., 2008; Aguilos et al., 2018; Daniel et al., 2023).

129

130 **2.2 Tower-based flux measurements**

131 Continuous measurements of the surface-atmosphere exchange of CO_2, H_2O and energy were initiated

132 in 2003 based on the Euroflux methodology (Aubinet et al., 2000) and the eddy covariance approach

133 (Baldocchi, 2003); they have previously been reported and fully documented (Bonal et al., 2008;

134 Aguilos et al., 2018). The Guyaflux flux tower is 55 m high and extends about 20 m beyond the top of

135 the canopy. The putative average footprint of the eddy fluxes from the tower covers approximately 50

136 - 100 ha of undisturbed forest in the direction of the prevailing winds (Bonal et al., 2008; Fang et al.,

137 2024). Within the estimated footprint of the Guyaflux tower, 52% of the area is upland forest, 13% is

138 seasonally flooded forest and the rest (35%) is slope forest. Most of the meteorological and eddy flux

139 sensors are mounted three meters above the top of the tower, and include equipment measuring air

140 temperature and humidity (HMP155, Vaisala, Helsinki, Finland), bulk precipitation (ARG100, EM lmt,

141 Sunderland, UK), wind direction and speed (A05103-5, Young, Traverse City, MI, USA), and global

142 infrared incident and reflected radiation (Rg) (CNR1, Kipp and Zonen, Bohemia, NY, USA). All the

143 meteorological data in the present study were collected at 1-min intervals and compiled as 30-min

144 averages or sums with data loggers (CR23X, CR1000 or CR3000 models; Campbell Scientific Inc., Utah,

145 USA).

146 In 2017, a closed-path fast greenhouse gas analyser (FGGA, Los Gatos Research, Mountain View,

147 California, USA), whose head (gas inlet) was mounted 0.3 m from the head of a 3-D sonic anemometer

148 (R3-50; Gill Instruments, Lymington, UK), was set up at the top of the eddy flux tower to provide eddy

149 covariance measurements of the CH_4 and N_2O fluxes. The FGGA, equipped with a fourth-generation

150 cavity-enhanced laser absorption spectroscopy analyser (DLT-100; Los Gatos Research Inc.), was

151 connected to an external pump (Edwards XDS-35i, Edwards, England, UK) and to a 62 m long PFA inlet

152 tube (4 mm inlet diameter) protected by black foam with a 15 μm filter. All data were sampled at a

153 frequency of 20 Hz with data loggers (model CR3000; Campbell Scientific Inc.).

154 In addition, to take conditions where non-turbulent processes prevail (e.g. calm nights) into account,

155 the eddy covariance measurements were complemented with a vertical profile measurement system

156 to estimate variations in CH_4 and N_2O concentrations at six different heights (i.e. 0.5, 6, 13, 23, 32 and

157 58 m) with a 0.8 L min^{-1} pump connected to a six-line solenoid valve and a closed-path FGGA. The entire

158 system was controlled by a data logger (model CR10X; Campbell Scientific Inc.), which recorded

159 greenhouse gas concentration data every 15 min. The vertical profile system for CH_4 and N_2O was

160 stopped after one year because the storage of the gases was found to be negligible (see below).

161

162 **2.3 Tower-based CH_4 and N_2O flux computation**

163 We used EDDYPRO V6.2.2 (LI-COR Inc.), a software based on a set of standardised post-processing

164 calculations and corrections, to calculate CH_4 and N_2O fluxes from the raw high-frequency eddy

165 covariance data. The parameterization of the software included: a two-dimensional coordinate

166 rotation to set lateral and vertical mean wind speed to zero; a time lag between each scalar and wind

167 speed measurement estimated by covariance maximisation; an empirical frequency correction for

168 high-frequency attenuation; and a Webb-Pearman-Leuning correction for density fluctuations where

169 required, i.e. where concentrations were not measured as mixing ratios. Details of these corrections

170 are given in Aubinet et al. (2012). After the greenhouse gas flux computation, the EDDYPRO output

171 files contained continuous time series for ecosystem-atmosphere greenhouse gas (CH_4 and N_2O) fluxes

172   reported at a 30-min time step (from 17 May, 2016 to 2 August, 2018). The output files also included

173   uncertainties, quality control flags, friction velocity, and basic environmental and meteorological data.

174   To calculate net ecosystem production and uptake, we added the storage term to the turbulent flux

175   measured by the eddy covariance tower. This correction is particularly relevant for CO_2 exchanges in

176   forest ecosystems to reduce the uncertainty of the net flux estimate (Nicolini et al., 2018). However,

177   for the net CH_4 and N_2O fluxes, the relevance of the storage term correction was only marginal. In

178   contrast to CO_2, whose concentrations clearly built up at soil level during low-turbulence conditions,

179   this was not the case for N_2O and CH_4, and comparisons between the ecosystem fluxes with and

180   without correction for the storage term showed that the change in the resulting flux was minimal (Figs.

181   S1, S2). Consequently, we assumed that the storage of CH_4 and N_2O was negligible and ignored it in

182   this study. This meant that a larger period of eddy covariance flux measurements could be used

183   (starting in 2016), in addition to the January 2017 - January 2018 period where CH_4 and N_2O storage

184   data were available. Ecosystem fluxes of CH_4 and N_2O were ~~calculated every~~ half-hourly values in nmol

185   $m^{-2}\ s^{-1}$.

186

187   **2.4 Chamber measurements**

188   In addition to the flux tower and its associated instrumentation, automated ~~static~~ non-steady-state

189   flow-through ~~flow~~ chambers for continuous measurement of soil greenhouse gas fluxes were installed

190   in June 2016 on hypoferralic soils with deep vertical drainage and a very deep water table (~15 m

191   depth), approximately 50 m upwind from the flux tower in some of the upland forest part of the tower

192   footprint. This automated system had two constraints, which when combined, limited the spatial

193   coverage of the soil greenhouse gas flux measurements to the upland forest area: the power supply

194   was only available at the flux tower, and the maximum distance between the automated chambers

195   and the gas analysers was 30 m. Thirteen of the sixteen initial chambers functioned correctly

196   throughout the study period and their data were retained in this study. Briefly, the chambers (LI-8100-

197   104, LI-COR Inc., Lincoln, NE, USA) were mounted on PVC collars (20.3-cm inner diameter; enclosed

198 soil area ~318 cm^2; offset ~4 cm) that were permanently inserted into the soil. The chambers were

199 connected to a multiplexer (LI-8150, LI-COR Inc.), used to program specific measurement cycles, which

200 operated with a cavity ring-down spectroscopy (CRDS) analyser (G2308; Picarro Inc., Santa Clara, CA,

201 USA) to measure CO_2, H_2O and dry air-CH_4 and N_2O concentrations (water corrected concentrations)

202 at 1 Hz. This analyser relied on an external recirculation pump (A0702; Picarro Inc.). The multiplexer

203 program purged the system 15 s before and 45 s after the measurements to flush out the tubing and

204 return to ambient-air greenhouse gas concentrations. A dead band of 60 s avoided potential

205 measurement errors ascribed to pressure changes inside the chamber-tubing-analyser loop following

206 chamber or solenoid valve closure and accounted for time lags. In addition, to maximise the percentage

207 of fluxes that can be detected for N_2O and CH_4 without affecting spatial coverage and temporal

208 resolution, we initially developed a program combining two different closure times. Briefly, each week,

209 four of the initial sixteen chambers were manually set to remain closed for 25 minutes, while the other

210 chambers were set to remain closed for a much shorter period of 2 minutes. This program was rotated

211 across the chambers. The 25-min closure time was a compromise between reliably estimating low N_2O

212 fluxes and ensuring a sufficient number of flux measurements per chamber and per day. The

213 measurement cycle duration was 2.5 hours, providing approximately nine measurements per chamber

214 per day for all gases. Each chamber was therefore measured with the longer closure time for one 7-

215 consecutive-day period per month (4 weeks). More detail of equipment can be found in previous

216 publications (Courtois et al., 2019; Bréchet et al., 2021).~~In addition, the program included two different~~

217 ~~closure times to account for high and low fluxes, i.e. 2-min and 25-min measurement periods. The~~

218 ~~equipment is described in more detail in previous publications (Courtois et al., 2019; Bréchet et al.,~~

219 ~~2021).~~

220

221 **2.5 Chamber-based CH_4 and N_2O flux computation**

222 We used the SOILFLUXPRO software (LI-COR Biosciences) to compute soil greenhouse gas fluxes based

223 on the linear and exponential regression of the change in headspace concentrations over time, the

224 collar area and the system volume, after correction for atmospheric pressure and temperature. Flux

225 values were selected based on the model that provided the best fit and highest determination

226 coefficient (R^2).

227 After calculating the fluxes and implementing our standard soil greenhouse gas QC procedure (Courtois

228 et al., 2019; Bréchet et al., 2021), all CO_2 fluxes with an insufficiently high R^2 (< 0.90), an initial

229 concentration greater than 900 ppm, or a value outside the range of variation from 0.10 to 30 µmol m$^-$

230 ^{2} s^{-1} were discarded for all three gases, based on the assumption that poor-quality CO_2 implied poor-

231 quality values for CH_4 and N_2O. Based on previous work (Courtois et al., 2019), all CH_4 fluxes with R^2 <

232 0.80 were excluded (17% of the total 89380 values). These fluxes were not set to zero, as a low R^2 value

233 does not provide information on the flux value itself. This criterion was inapplicable to N_2O, however,

234 due to the low overall R^2 values, meaning all fluxes were retained for the study. Additionally, we

235 computed the minimum detectable fluxes (MDF) suitable for high-resolution, in situ greenhouse gas

236 measurements, using the metric proposed by Nickerson (2016): 0.040 nmol m^{-2} s^{-1} and 0.002 nmol m$^-$

237 ^{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

238 and 25 min, respectively, for N_2O. This implies that null fluxes were included in the analysis if the flux

239 values for each gas and measurement length fell within the range defined by the corresponding

240 absolute MDF value. After calculating the fluxes and implementing our standard soil greenhouse gas

241 QC procedure (Courtois et al., 2019; Bréchet et al., 2021), all CO_2 fluxes with an insufficiently high R^2 (<

242 0.90), an initial concentration greater than 900 ppm, or a value outside the range of variation from

243 0.10 to 30 µmol m^{-2} s^{-1} were discarded for all three gases, based on the assumption that poor-quality

244 CO_2 implied poor-quality values for CH_4 and N_2O. As an improvement over Courtois et al. (2019), all

245 CH_4 fluxes with R^2 < 0.80 were excluded regardless of the measurement length (i.e. 2-min and 25-min).

246 For N_2O, all short measurements (i.e. 2-min) with R^2 < 0.80 were discarded. In addition, based on the

247 metric proposed by Nickerson (2016), we calculated minimum detectable fluxes suitable for high-

248 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

249 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

250 ~~respectively for N₂O.~~ The soil fluxes of CH$_4$ and N$_2$O were expressed in nmol m^{-2} s^{-1} (unit of soil surface

251 area).

252

2.6 Tower and chamber flux data analysis

254 In order to include the most complete information possible, we based the study period on the soil flux

255 measurements and included all available data from 17 May, 2016 to 2 August, 2018. This 26-month

256 period included both very dry and very wet seasons (Fig. 1).

257

258
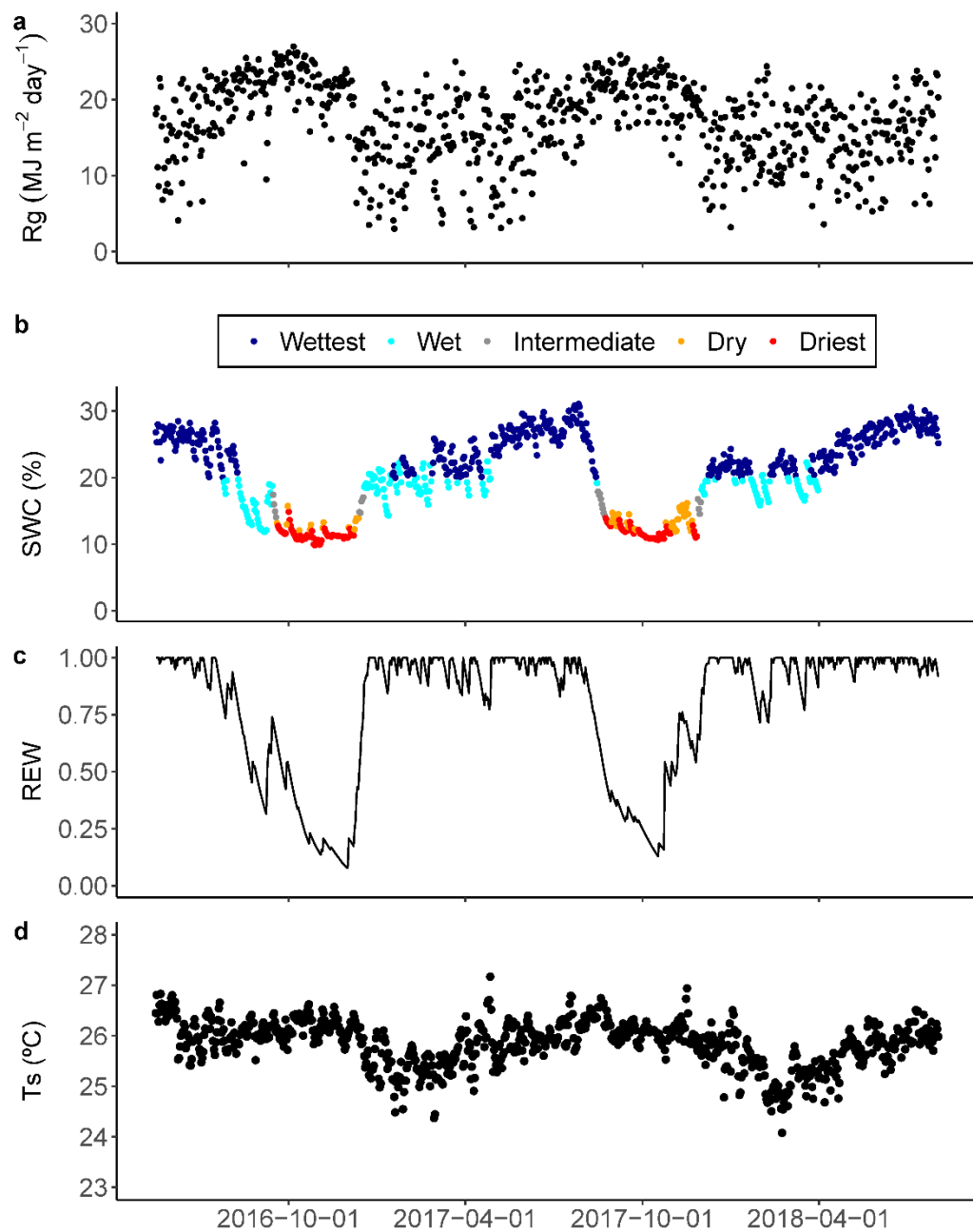
Figure 1. Daily (a) accumulated global radiation (Rg); (b) average soil water content (SWC) at 5 cm in

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.

266   Some flawed data was found (and eliminated) for both eddy covariance and soil chamber

267   measurements. They resulted from particular physical or biological conditions at the sampling point or

268   inside the soil chamber (e.g. wasp nests, disturbance by birds, dust, a branch preventing proper closure

269   of the chamber and causing a leak), or from mechanical issues (e.g. a power cut, soil chamber

270   remaining closed, gas analyser malfunction), which generated gaps in each time series. After flux

271   computation, the eddy covariance data for CH_4 and N_2O were filtered: data below a u* threshold of

272   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

273   to 2) (Mauder and Foken, 2004).

274   ~~For eddy covariance and chamber data, the 30 min observations were filtered and flux values outside~~

275   ~~the 5th - 95th percentile flux range were discarded.~~ To calculate daily averages for greenhouse gas

276   fluxes, we first estimated the optimal number of observations per day necessary to obtain

277   representative daily averages. To do this, we selected a data pool with at least 42 observations per day

278   in the eddy covariance dataset. In the soil chamber dataset, we firstly calculated daily means based on

279   a minimum of five observations for each of the thirteen chambers. Then, for each day, we created

280   subsets of values from 1 to 42 for the eddy covariance data, and from 1 to 13 for the soil chamber data,

281   based on 100 bootstrap iterations. Representative daily means were found for minimum thresholds of

282   12 observations per day for the eddy covariance and 10 chambers per day for the soil flux system.~~To~~

283   ~~calculate daily averages for greenhouse gas fluxes, we first estimated the optimal number of~~

284   ~~observations per day necessary to obtain representative daily averages. To do this, we selected a data~~

285   ~~pool with at least 42 observations per day in the eddy covariance dataset. In the soil chamber dataset,~~

286   ~~we calculated daily means for each of the thirteen chambers and retained only the data when at least~~

287   ~~five observations per chamber per day were recorded. Subsets of values from 1 to 42 for the eddy~~

288   ~~covariance data and from 1 to 13 for the soil chamber data were then created for each day based on~~

289   ~~100 bootstrap iterations. Representative daily means were found for thresholds of 12 minimum~~

290   ~~observations per day for eddy covariance and 10 for chamber data.~~ These tests were performed

291   separately for CH_4 and N_2O and the driest and wettest seasons, giving similar threshold results. Daily

292 means with a number of observations below the corresponding threshold were then discarded from

293 further analyses. After filtering out the non-representative days, the missing daily means for the whole

294 study period represented 27% for both CH_4 and N_2O flux data derived from eddy covariance, and 34%

295 and 30%, respectively, for CH_4 and N_2O flux data derived from the soil chambers.

296

297 **2.7 Environmental measurements**

298 In the vicinity of the tower, we used temperature sensors (CS107; Campbell Scientific Inc., Logan, UT,

299 USA) to measure surface soil temperature (Ts) and frequency domain sensors (CS615 or CS616;

300 Campbell Scientific Inc.) to measure soil volumetric water content (SWC) at a depth of 5 cm. To

301 estimate the daily relative extractable water (REW) for trees from the soil surface to a depth of 3 m,

302 we used a soil water balance model previously validated for tropical forests (Wagner et al., 2011), with

303 daily precipitation, evapotranspiration and solar radiation as input variables. Daily SWC (%), Ts (°C) and

304 REW were defined as the average of the half-hourly flux values over 24 h, while dialy Rg (MJ m^{-2} day^{-1})

305 was the sum of the half-hourly flux values over 24 h.

306 To examine the effect of environmental variables on CH_4 and N_2O fluxes at the ecosystem and soil

307 levels, we extracted data from two contrasting periods, termed "Driest" and "Wettest" (Fig. 1). The

308 driest days occurred at the end of the dry season, when SWC was less than 15% and decreased for at

309 least three consecutive days. The wettest days had a SWC above 20%, corresponding to a REW above

310 0.4, and unlimited available water for trees (Wagner el al., 2011) for more than two consecutive days.

311

312 **2.8 Data analysis**

313 We used the mgcv (Wood and Wood, 2015) and stats packages in R version V3.6.3 (R Core Team, 2020)

314 for our data analyses and ggplot2 for visualisations (Wickham and Wickham, 2016). The significance

315 level for all tests was set at 0.05.

316 We used Kolmogorov-Smirnov tests (ks.test function) to evaluate the effects of contrasting seasons,

317 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 1st - 99th 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 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

344   The ecosystem and soil CH$_4$ and N$_2$O fluxes also displayed some seasonality (Figs. 2, ~~S3~~, ~~S5~~S4), with

345   seasonal differences particularly evident between the wettest and the driest season~~s~~ (Fig. 3).

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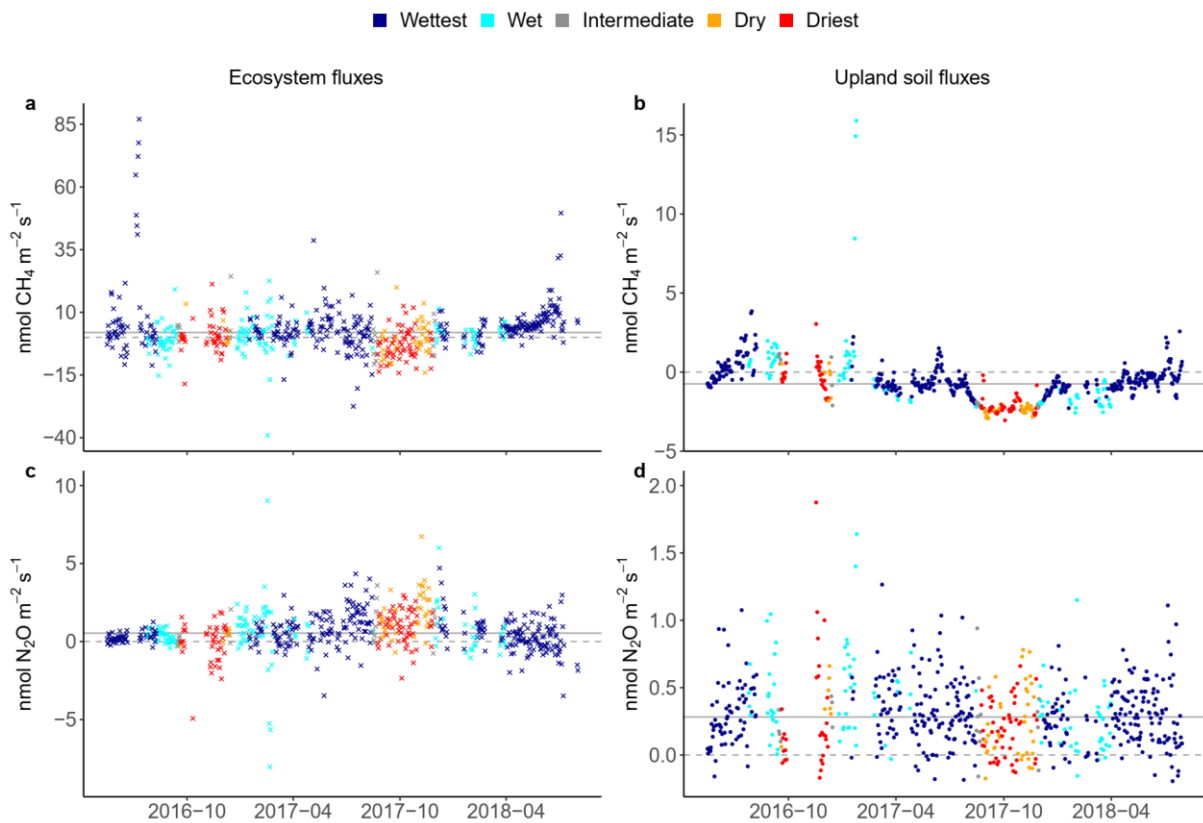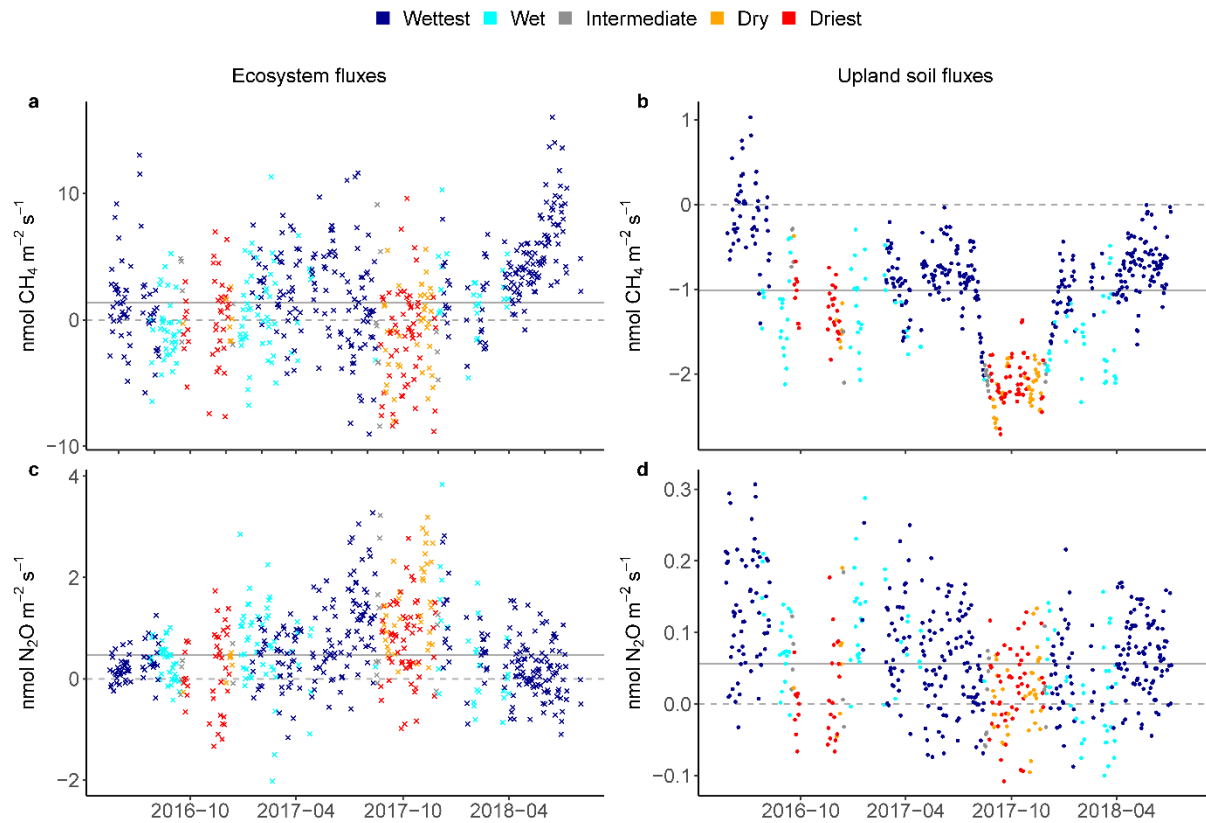
349 Figure 2. Seasonal courses of average daily ecosystem (crosses on the left) and upland soil (solid dots

350 on the right) fluxes for the wet, intermediate and dry seasons, and for two contrasted seasons defined

351 as the wettest (dark blue dots) and the driest (red dots) for 24-hour CH_4 fluxes (a, b) and N_2O fluxes

352 from 17 May, 2016 to 2 August, 2018 (c, d) in the Guyaflux tropical forest, French Guiana. Positive

353 fluxes (above the dashed grey "0" line) indicate greenhouse gas emissions and negative fluxes (below

354 the "0" line) indicate greenhouse gas uptake; the solid grey line represents the median over the whole

355 period. Note that the scale of the y-axis has been adjusted for each gas and compartment to improve

356 clarity. Comparable seasonal courses of the 1st - 99th percentile range of CH_4 and N_2O flux data are

357 shown in Fig. S5.
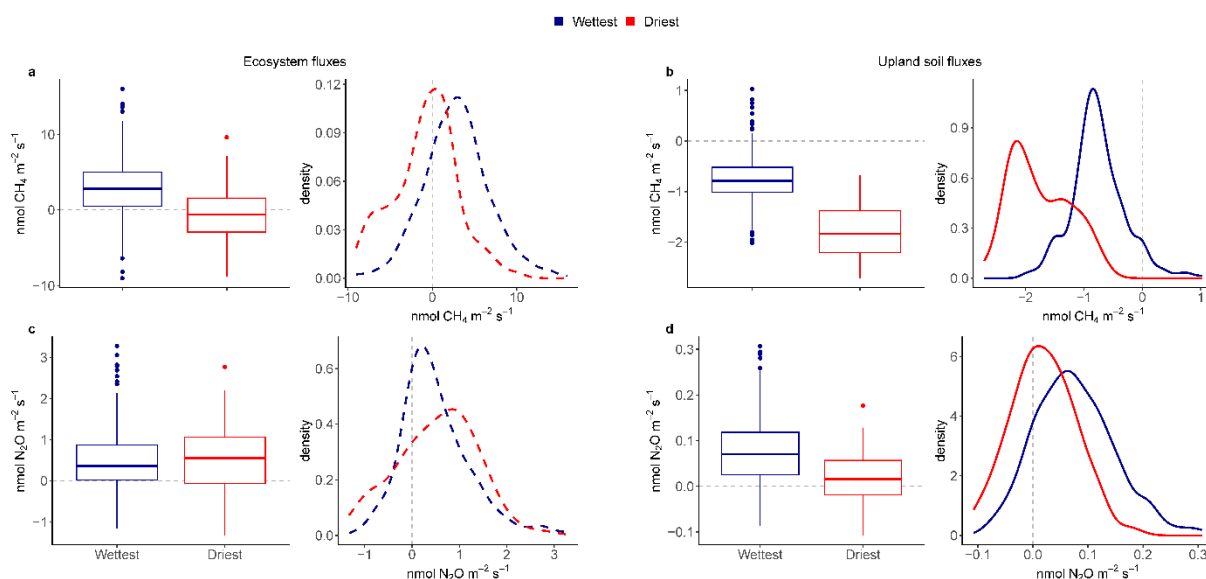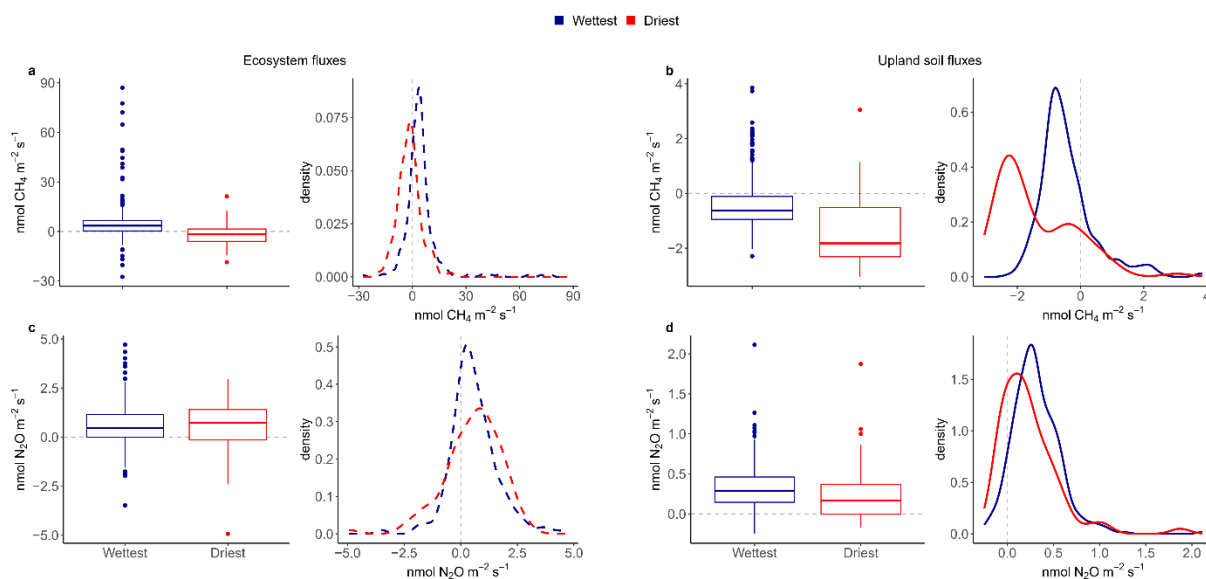
Figure 3. Boxplots and associated density plots of average daily ecosystem fluxes (dashed lines on the left) and upland soil (solid lines on the right) fluxes of 24-hour CH_4 fluxes (a, b) and N_2O fluxes (c, d) for the wettest (blue) and driest (red) seasons, from 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. In the box plots, solid bold lines represent medians, box boundaries mark the 25th and 75th percentiles and whiskers show the 10th and 90th percentiles. Dots mark outliers. In the density plots, positive fluxes on the right side of the dotted "0" line indicate greenhouse gas emissions and negative fluxes on the left side of the "0" line indicate greenhouse gas uptake. All fluxes,

368   except the ecosystem N_2O fluxes (c), exhibited statistically significant differences between the wettest

369   and driest seasons at $p < 0.05$ based on Kolmogorov-Smirnov tests.

370 Ecosystem CH$_4$ emissions were greater during the wettest season than during the driest season, when

371 net fluxes hovered around zero (Table 1; Fig. 3a). In contrast to the ecosystem-level fluxes, soil CH$_4$

372 fluxes in some of the upland forest were mainly negative, indicating net soil CH$_4$ uptake throughout

373 the year (Fig. 2b), even under varying environmental conditions (Table 1; Fig. 3b). Soil CH$_4$ uptake did

374 decreased significantly in the wettest season compared to the driest season, although the fluxes

375 remained negative overall (i.e. CH$_4$ uptake, Table 1; Fig. 3b).

376

377 Table 1. Mean, standard deviation (SD) and median ecosystem and upland soil CH$_4$ and N$_2$O fluxes for

378 the wettest and driest seasons in the Guyaflux tropical forest, French Guiana. All values are different

379 from 0 at p level < 0.05 based on Student's t-tests.

Fluxes	Wettest			Driest		
	Mean	SD	Median	Mean	SD	Median
Ecosystem flux (nmol$_{CH4/N2O}$ m^{-2} s^{-1})						
CH$_4$	~~2.9~~4.9	~~3.9~~11.2	~~2~~3.85	~~-~~-10.86	~~63.~~84	~~-0~~-1.67
N$_2$O	0.~~5~~6	~~0~~1.70	0.4~~5~~	0.5~~5~~	~~1~~0.38	0.7~~6~~
Upland soil flux (nmol$_{CH4/N2O}$ m^{-2} s^{-1})						
CH$_4$	-0.4~~8~~	0.9~~5~~	-0.6~~8~~	-1.4~~8~~	~~1~~0.25	-1.8
N$_2$O	0.3~~1~~	0.3~~1~~	0.3~~1~~	0.2~~0~~	0.3~~1~~	0.2~~0~~

380

381 The seasonal pattern of ecosystem N$_2$O fluxes was less pronounced than ~~for~~ that of CH$_4$ (Fig. 2c); with

382 similar emission rates observed between the driest and wettest seasons (Table 1; Fig. 3c). In contrast

383 to the ecosystem-level fluxes, soil N$_2$O fluxes in upland areas not only had a more pronounced seasonal

384 pattern, the upland soils also emitted more N$_2$O during the wettest season than during the driest

385 season (Table 1; Fig. 3d). It is noteworthy that all the overall flux means were significantly different

386 from zero (Table 1) and that there were significant differences in fluxes between seasons at both the

387 ecosystem and soil levels, except for N$_2$O fluxes at the ecosystem level (Fig. 3). This suggests that the

388 magnitude of the fluxes was substantial relative to seasonal variability.~~It is noteworthy that, although~~

389 ~~there were significant differences between seasons for all fluxes and at both ecosystem and soil levels~~

390 ~~(Fig. 3), the overall mean flux was significantly different from zero only for soil CH₄ fluxes during the~~

391 ~~driest season (Table 1). This indicates that the magnitude of the fluxes was very low relative to the~~

392 ~~large variability among the seasons.~~

393

394 **3.3 Environmental drivers of ecosystem and upland soil greenhouse gas fluxes**

395 Keeping the 1st - 99th percentile range of the flux data was sufficient to account for the majority of the

396 statistical leverage (Tables 2, S3). This was particularly true for net ecosystem CH_4 fluxes, which showed

397 that CH_4 emissions decreased with increasing Rg (Fig. 4a, S5a, S6a), although this negative correlation

398 was statistically significant only during the wettest season (Table ~~2~~S3) when net emissions occasionally

399 switched to net uptakes at highest Rg values (Fig. 4a, S6a). Net ecosystem CH_4 fluxes were strongly

400 positively correlated with SWC (Fig. 4b, S6b), showing increased CH_4 emissions with increasing SWC,

401 although this correlation too was statistically significant only during the wettest season (Table S3). ~~A~~

402 ~~weaker, yet statistically significant, correlation was detected between ecosystem CH₄ fluxes and Ts~~

403 ~~(Table 2).~~

404
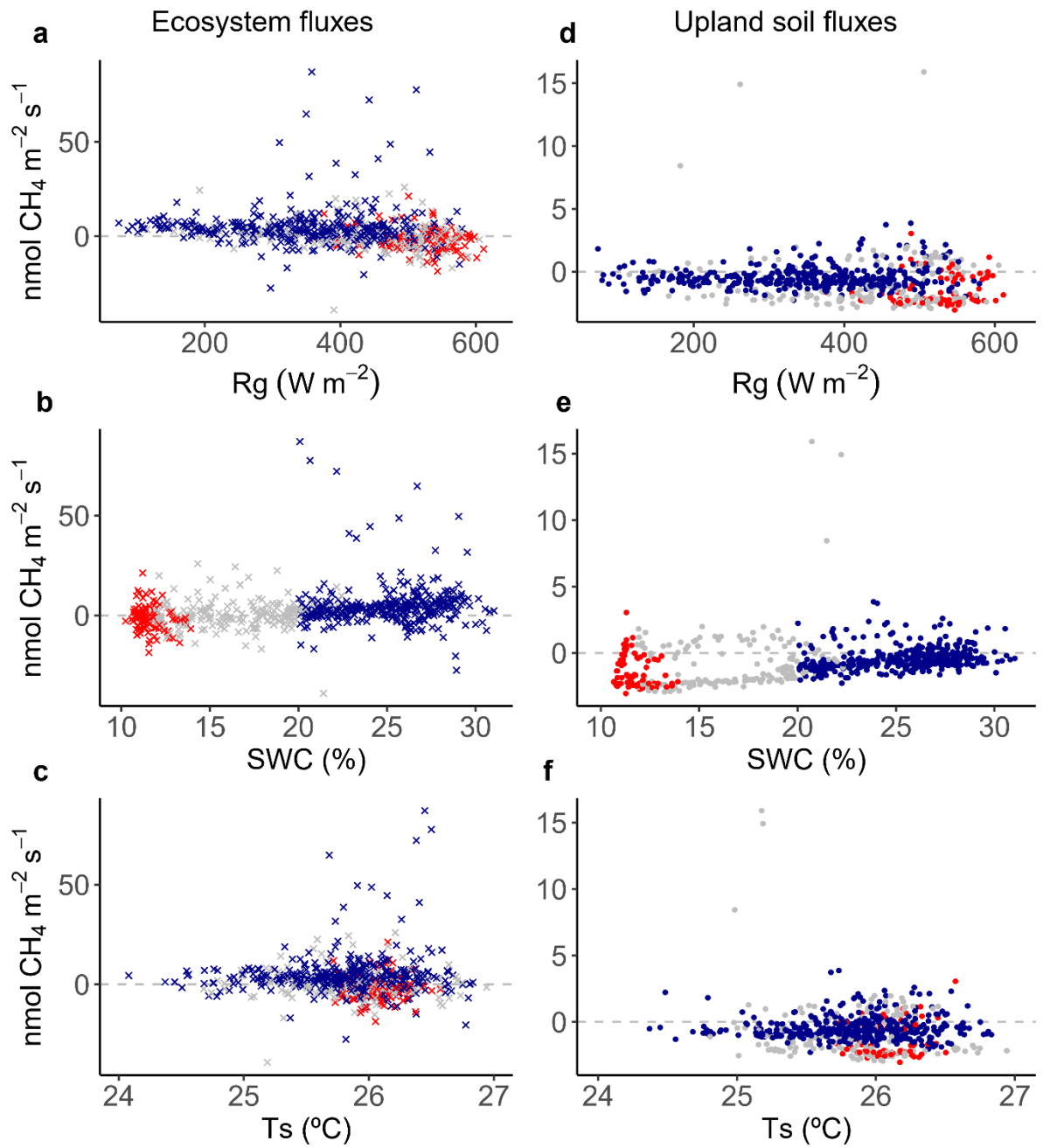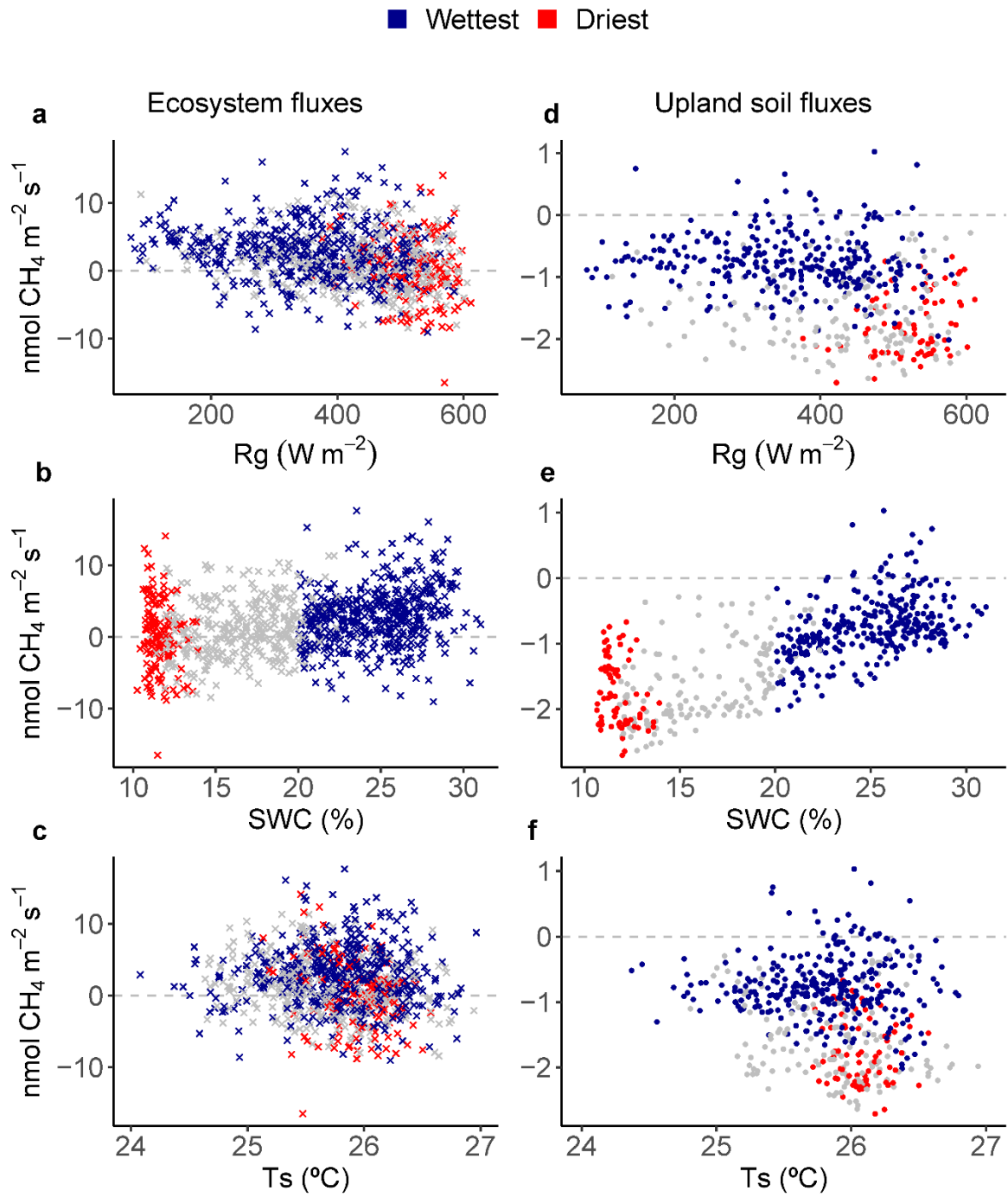
Figure 4. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC) and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots on the right) CH_4 fluxes for the wettest (blue) and driest (red) seasons, with remaining data 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

412 indicate CH_4 uptake. Comparable relationships with the 1st - 99th percentile range of CH_4 flux data are

413 shown in Fig. S6.

414 Despite the different signs for the net CH_4 flux at ecosystem- and soil levels, relationships comparable

415 with the environmental drivers observed for ecosystem CH_4 fluxes were also found for some of the

416 upland soil: net soil CH_4 uptake increased with increasing Rg (Fig. 4d, S6d) and decreased with

417 increasing SWC (Fig. 4e, S6e). While statistically significant terms were found during the driest season

418 (i.e. Ts > Rg > SWC), the strongest relationship was observed with SWC during the wettest season (Table

419 2).~~The correlation between upland soil CH_4 fluxes and Rg was statistically significant in the driest~~

420 ~~season, while the correlation with SWC was equal and significant in both seasons (wettest and driest,~~

421 ~~Table 2).~~

422 Ecosystem N_2O fluxes only showed ~~relatively weak~~a significant response to SWC during the wettest

423 season ~~the environmental drivers we investigated~~ (Figs. 5~~a -c~~b). ~~The statistically significant terms in the~~

424 ~~model were SWC > Rg >Ts, and only during the wettest season.~~ However, the R^2 of the model was

425 rather low (R^2 = 0.04; Table 2). The best results for upland soil N_2O fluxes were found with Ts and Rg,

426 but only during the driest season~~For the upland soil N_2O fluxes, (none of the environmental drivers we~~

427 ~~investigated explained soil N_2O emissions (~~Fig. 5; Table 2).

428

 Table 2. Results of generalised additive models (GAM) assessing the relationships between

430 environmental variables, i.e. global radiation (Rg), soil water content (SWC), soil temperature (Ts), and

431 daily mean ecosystem and upland soil CH_4 and N_2O fluxes during the wettest and driest seasons from

432 17 May, 2016 to 2 August, 2018 in the Guyaflux tropical forest, French Guiana. The effective degrees

433 of freedom (edf) and the reference number of degrees of freedom (Ref. df) of the fitted models, with

434 values for each spline term, are shown. Significant terms at p level < 0.05 are shown in bold.

435 Comparable GAM results with the 1st - 99th percentile ranges of CH_4 and N_2O fluxes are shown in Table

436 S3.

	Fluxes	Best model predictors	R^2	Intercept	Coefficients		F value	p value
					edf	Ref. df		
Ecosystem level								
Daily	CH_4		0.~~200~~7	~~0~~4.~~0097~~52				
		Rg: Wettest			0.~~8~~0	9	0.~~540~~0	0.~~0147~~43
		Rg: Driest			0.~~6~~3	8	0.~~190~~5	0.~~1132~~40
		Ts: Wettest			1.~~7~~0	9	0.~~623~~3	0.~~0250~~56
		Ts: Driest			0.0	9	0.00	0.~~4776~~50
		SWC: Wettest			~~0~~1.60	9	~~0~~1.~~920~~0	<~~0.~~996
		SWC: Driest			0.~~0~~5	6	0.~~00~~14	0.~~4331~~74
Daily	N_2O		0.04	~~0~~1.~~0000~~90				
		Rg: Wettest			0.~~8~~5	9	0.~~41~~13	0.~~0261~~26
		Rg: Driest			0.~~5~~0	8	0.~~00~~17	0.~~7721~~28
		Ts: Wettest			~~0~~1.28	9	0.~~391~~9	0.~~0451~~09
		Ts: Driest			0.~~3~~0	~~9~~8	0.~~050~~0	0.~~2478~~25
		SWC: Wettest			2.~~2~~3	9	~~0~~1.~~933~~3	**0.~~0110~~02**
		SWC: Driest			0.0	6	0.00	0.~~357~~17
Upland soil level								
Daily	CH_4		0.~~542~~2	-0.~~001~~602				
		Rg: Wettest			1.~~2~~4	9	0.~~246~~1	**0.~~1560~~17**
		Rg: Driest			1.~~5~~1	9	~~1~~0.~~246~~1	**0.~~0010~~12**
		Ts: Wettest			0.~~7~~4	9	0.~~270~~7	0.~~0571~~89
		Ts: Driest			~~0~~2.05	9	~~0~~1.~~009~~1	**< 0.001**~~0.865~~
		SWC: Wettest			~~2~~1.60	9	~~9~~2.~~748~~2	**< 0.001**

				Factor				
				SWC: Driest	1.~~9~~6	7	~~3~~0.5~~2~~65	≤ **0.00~~10~~1 4**
Daily	N$_2$O	0.10	0.~~000~~313					
				Rg: Wettest	0.0	9	0.00	1~~0.4~~190 00
				Rg: Driest	0.~~9~~6	~~7~~8	0.~~19~~99	**0.~~11~~200 5**
				Ts: Wettest	~~0~~1.~~2~~0	9	0.3~~2~~00	0.~~08~~445 6
				Ts: Driest	~~4~~0.06	9	~~03.00~~95	≤ **0.001~~1.0 00~~**
				SWC: Wettest	0.0	9	0.00	0.~~80~~479 0
				SWC: Driest	0.~~0~~2	~~5~~6	0.~~00~~05	~~10.000~~2 61

437
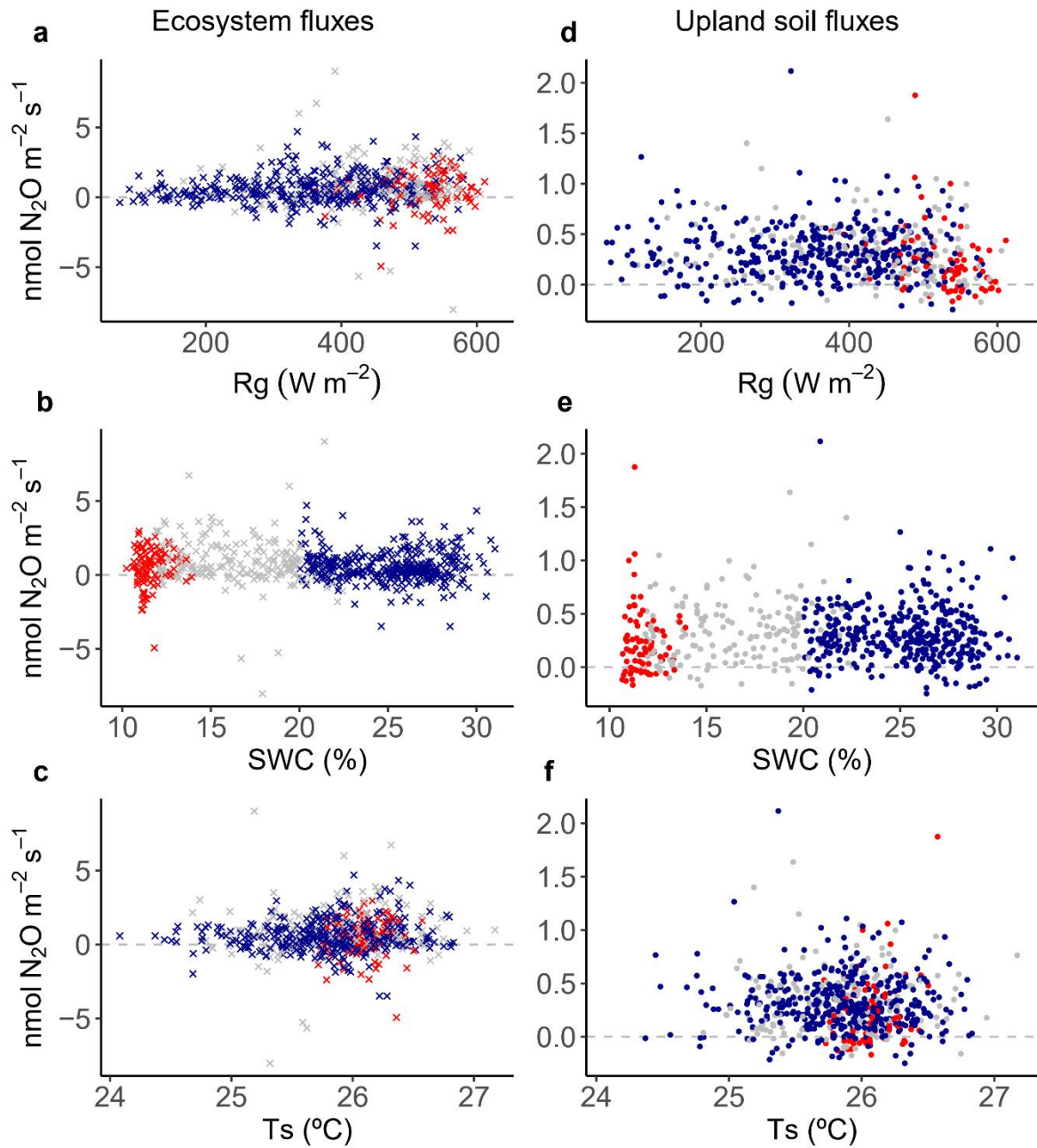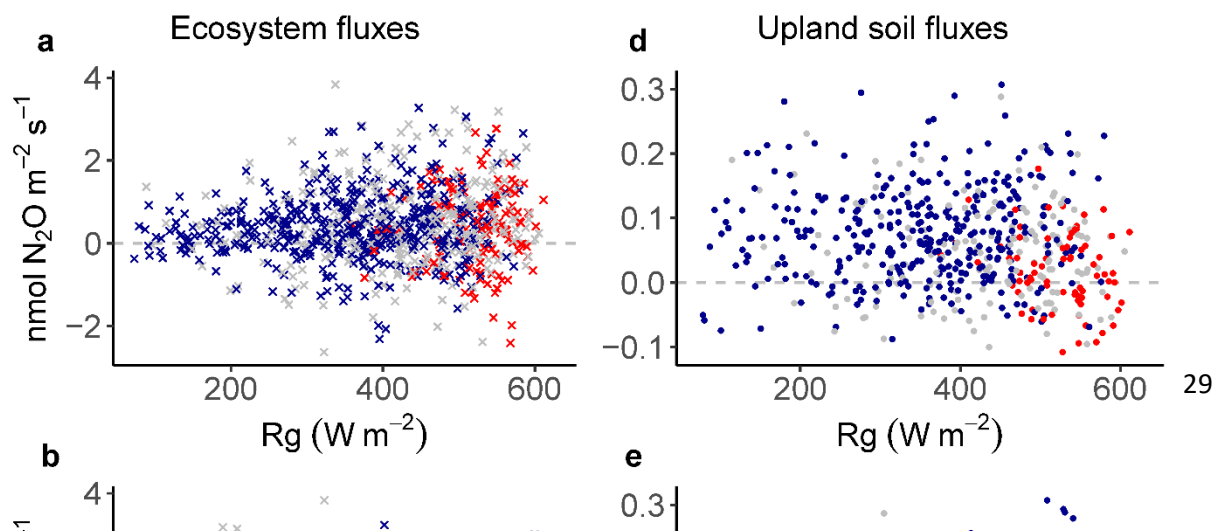
Figure 5. Relationships between environmental drivers (global radiation (Rg), soil water content (SWC) and soil temperature (Ts)) and daily average ecosystem (crosses on the left) and upland soil (solid dots on the right) N_2O fluxes for the wettest (blue) and driest (red) seasons, with remaining data 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. Comparable relationships with the 1st - 99th percentile range of N_2O flux data are 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 (24.9 9 ± 311.9 2 $nmolCH_4$ m^{-2} s^{-1}; Mean ± SD) dominated during the wettest season, whereas net CH_4 uptake (-01.8 6 ± 36.8 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 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

464   larger CH_4 source during the driest season (64.1 and 88.3 $nmolCH_4$ m^{-2} s^{-1}, respectively; Carmo et al.,

465   2006), while the Guyaflux forest switched from a CH_4 source during the wet periods to a small sink

466   during the dry ones. Ecosystem CH_4 fluxes are driven by a combination of plant, microbial and abiotic

467   processes, which are mediated by both living and dead plants, and can explain episodic bursts (Eugster

468   and Plüss, 2010; Covey and Megonigal, 2019). The mechanism underlying the large CH_4 emissions

469   during the dry season observed in the Brazilian forests remains unknown, but the authors suggest that

470   it may have been connected to the anaerobic decay of waterlogged wood, undrained soil patches or

471   the waterlogged cavities of tank bromeliads. Concomitantly, drought-induced reduced oxidation in the

472   soil surface layer may have exacerbated the net CH_4 emissions. Contrary to Carmo et al. (2006), Sakabe

473   et al. (2018) found a seasonal pattern similar to the one we observed in our study where the eddy

474   covariance technique was applied. Although the flux values they found had a higher range of variation

475   (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

476   most likely due to the different ecosystem they studied, an Indonesian tropical peat swamp forest.

477   Surprisingly, in contrast to~~Consistent with~~ H2, the generalised additive models (GAM) revealed that

478   none of the environmental variables studied, including SWC~~, and to a lesser extent Rg and Ts~~, were

479   relevant drivers of ecosystem CH_4 flux ~~drivers, particularly during the wettest season~~ (Table 2; Figs. 4a-

480   c). However, a similar statistical analysis of the remaining 1st - 99th percentile range of data revealed a

481   significant effect of various environmental drivers (Table S3). While these findings indicate that the

482   models are relatively sensitive to extreme flux values, further explanation may be suggested. Indeed,

483   a significant increase in SWC in the wettest season could stimulate CH_4 production in most

484   compartments of the ecosystem, not only in the seasonally flooded soils~~It is reasonable to assume that~~

485   ~~high SWC but relatively low Ts during the wettest season stimulated CH_4 production in most~~

486   ~~compartments of the ecosystem, not only in the seasonally flooded soils~~. At shallow depths, a higher

487   SWC may reduce the amount of air-filled pore space, thereby decreasing the diffusion of oxygen and

488   CH_4 from the atmosphere through the soil to methanotrophs. As a result, there may be a decrease in

489   net uptake or an increase in net emissions, if production exceeds uptake (Wang et al., 2013). ~~An~~

490 ~~increase in SWC at shallow depths may reduce the amount of air-filled pore space in the soil. This~~

491 ~~reduction may decrease the diffusion of oxygen and CH₄ from the atmosphere through the soil to~~

492 ~~methanotrophs, resulting in a decrease in net uptake or an increase in net emissions, if production~~

493 ~~exceeds uptake (Wang et al., 2013).~~ Such processes may occur in all the soil types within the footprint

494 of the eddy flux tower (see Sect. 4.1.2)~~,~~ and ~~they~~ may ~~partially~~ explain some of the seasonal trends

495 observed at our site. ~~On~~ Using the same ~~other hand~~ range of data (excluding episodic CH₄ peaks in July

496 2016 and June 2018)~~,~~ ~~the~~ a statistically significant~~,~~ ~~albeit weak,~~ relationship was found between CH₄

497 emissions and Rg during the wettest season (Table S3). This could occur if the occasional high light

498 intensity (Fig. 1a) is sufficient to stimulate plant-mediated CH₄ transport through sap flow, and / or if

499 the measured forest area has more seasonally flooded areas than upland forest. However, the latter

500 explanation is mitigated by the fact that the Guyaflux tower ~~The latter explanation is, however, unlikely~~

501 ~~because the location of the Guyaflux tower~~ (~300 m from the seasonally flooded area) was specifically

502 chosen to guarantee consistent types of ecosystem flux observations regardless of the season and of

503 associated changes in wind direction and atmospheric stability. Further research is needed to clarify

504 the correlation between Rg and net CH₄ flux. Increased fluxes in the flooded areas and anaerobic

505 microsites, rather than seasonal changes in the footprint, probably explain part of the observed

506 seasonal variations.

507 Disentangling the drivers of net CH₄ fluxes is further complicated by aboveground processes that also

508 contribute to CH₄ emissions and uptake in forest ecosystems. Soil-produced CH₄ dissolved in water can

509 indeed be taken up by roots, transported through the xylem stream in the stem, branches and leaves,

510 and then released into the atmosphere, thus bypassing the oxidation processes in the shallow soil

511 layers. As such, the highest CH₄ emissions from trees have been found in waterlogged soils, for

512 example, in wetland and riparian forests (Pangala et al., 2013; Covey and Megonigal, 2019; Gauci et

513 al., 2025). However, recent studies have shown that tree compartments (i.e. stems, branches, and

514 leaves) can also consume CH₄, particularly in free-draining upland soils (Gauci et al., 2024). At our study

515 site, both stem CH₄ emission and uptake were observed within the footprint of the Guyaflux tower

516   (Bréchet et al., 2021, 2025; Daniel et al., 2023). Although these fluxes were weak, they may contribute

517   to the seasonal variations in ecosystem CH_4 exchanges (Bréchet et al., 2021, 2025; Daniel et al., 2023).

518

519   4.1.2 Seasonal variations in upland soil CH_4 fluxes: trends and drivers

520   The upland soils studied within the tower footprint were active consumers of atmospheric CH_4 (Fig.

521   3b), with an overall net uptake rates of ~~10.1~~ 7 ± ~~01.7~~ 5 $nmolCH_4$ m^{-2} s^{-1} (or 1.0 $mgCH_4$ m^{-2} d^{-1}), ~~,~~ which is

522   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},

523   Dutaur and Verchot, 2007). Our results were also close to those of an Australian tropical rainforest (-

524   0.8 $mgCH_4$ m^{-2} d^{-1}, Butterbach-Bahl et al., 2004), but higher (i.e. lower uptake) than those of a Kenyan

525   rainforest (ranging from -2.8 to -1.3 $mgCH_4$ m^{-2} d^{-1}, Werner et al., 2007), with both studies using

526   automated chamber systems. ~~higher than the global average for tropical forests (-0.7 $nmolCH_4$ m^{-2} s^{-1}~~

527   ~~or -2.5 $kgCH_4$-C ha^{-1} yr^{-1}, Dutaur and Verchot, 2007) but lower than fluxes found in previous studies in~~

528   ~~tropical plantations and forests in Central and South America (Panama, -13.5 $nmolCH_4$ m^{-2} s^{-1}, Keller et~~

529   ~~al., 1990; -19.9 $nmolCH_4$ m^{-2} s^{-1}, Goreau and de Mello, 1988).~~ CH_4 fluxes at our site ranged seasonally

530   from -0.~~48~~ ± 0.~~5~~ 9 $nmolCH_4$ m^{-2} s^{-1} in the wettest season to -1.~~8~~ 4 ± ~~01.5~~ 2 $nmolCH_4$ m^{-2} s^{-1} in the driest

531   season (Table 1~~S2~~), supporting H1 and globally corroborating other seasonal studies in tropical forests.

532   ~~In addition, CH_4 flux dynamics in our upland soils were characterised by a large range of variation,~~ The

533   sign of the upland soil CH_4 fluxes were ~~but a~~ consistent ~~sign,~~ between the driest and wettest seasons.

534   A study conducted in a seasonal tropical forest in China with static chambers showed a comparable

535   seasonal pattern for soils: they acted mainly as CH_4 consumers, with an uptake rate of 0.7 ± 0.0

536   $nmolCH_4$ 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

537   decreased by approximately 50% after the first rainfall events and the associated increases in SWC.

538   Another study carried out with the static chamber technique near the Guyaflux forest and in similar

539   environmental conditions reported that upland soils consumed 1.0 ± 3.2 $nmolCH_4$ m^{-2} s^{-1} during the dry

540   season (Courtois et al., 2018). Yet, those soils become slight emitters during the wet season (0.1 ± 0.9

541   $nmolCH_4$ 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

542 dry and wet seasons, respectively; Courtois et al., 2018). Although meaningful, these comparisons

543 between studies should be interpreted with great caution because the measurement techniques

544 differed (i.e. automated in our study versus manual chambers in the other studies) as well as study

545 duration (i.e. months versus years). In addition, CH_4 flux dynamics in our upland soils were

546 characterised by a large range of variation. Microtopographic and edaphic heterogeneity may have

547 caused some chamber locations to remain aerobic in surface horizons, even during the wettest season.

548 This may explain their year-round CH_4-uptake, albeit reduced during the wettest season. Other

549 locations, in contrast, may have become anaerobic during the wet season, disabling methanotrophs to

550 oxidize the produced CH_4 and eliciting a switch to net CH_4 emissions.

551 From the GAMs, the best set of climatic variables, explaining ~~53~~22% of the seasonal variation in CH_4

552 fluxes from upland soils, were SWC, Ts and Rg (Table 2), consistent with H2. We observed a net upland

553 soil CH_4 uptake during both the driest and the wettest seasons; CH_4 emissions occurred only on a few

554 days during the wettest season (Fig. 2b). This can likely be explained by the soil characteristics at our

555 site where upland soils were hypoferralic acrisols, characterised by deep vertical drainage (Epron et

556 al., 2006). It is likely that these well aerated soils provided the aerobic conditions for methanotrophic

557 CH_4 oxidation (Smith et al., 2003). The seasonal variations in net CH_4 fluxes were strong (Fig. 3b), with

558 a net soil CH_4 uptake more than ~~twice as~~three times high~~er~~ in the driest season than in the wettest

559 season. This is consistent with the known dependence of soil CH_4 fluxes on topsoil SWC (Fig. 4e, S6e;

560 Tables 1, 3): dryer soil conditions favour soil methanotrophy (Le Mer and Roger, 2001), whereas ~~and~~

561 wet~~ter~~ soil conditions reduce methanotrophic communities and / or their activity (Covey and

562 Megonigal, 2019). In addition, the significant influence of Ts on soil CH_4 uptake may be attributed to

563 the temperature sensitivity of the underlying enzymatic process. However, at elevated temperatures

564 (> 15 °C), such as in tropical forests, gas diffusion limitations and drought effects may supersede

565 temperature responses (Steinkamp et al., 2001). The significant relationships between Rg and upland

566 soil CH_4 fluxes are still unclear. Yet when the combined effects of changes in SWC and Ts were

567 considered, the explanatory power of the GAM with regard to soil CH_4 flux variations remained low.

568   This suggests that other factors, such as substrate availability, soil aeration, gas diffusivity and

569   microbial processes, may significantly control the temporal dynamics of CH_4 fluxes at our study site.

570

571   **4.2 Ecosystem and upland soil-N_2O fluxes**

572   4.2.1 Seasonal variations in ecosystem N_2O fluxes: trends and drivers

573   The measurements at the Guyaflux wet-tropical-forest site revealed very low N_2O fluxes, with an

574   average net emission of 0.7~~6~~ ± ~~1~~0.3~~8~~ $nmolN_2O$ m^{-2} s^{-1} (Fig. 3c; Table S2~~1~~). Though low, this loss of

575   nitrogen (N) from the ecosystem is equivalent to approximately one-~~fifth~~ fourth of the annual

576   atmospheric N deposition at the site (3~~2.7~~1 kgN_2O-N ha^{-1} yr^{-1} here ~~vs~~versus~~.~~ 13 kgN_2O-N ha^{-1} yr^{-1} in

577   Van Langenhove et al., 2020b). Compared to other publications on forest ecosystem N_2O fluxes from

578   studies based on eddy covariance techniques, net ecosystem N_2O fluxes at our study site were ~~very~~

579   ~~close~~similar to the average fluxes reported by Stiegler et al. (2023) for a regularly-fertilised Indonesian

580   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

581   those reported by Mander et al. (2021) for a temperate riparian deciduous forest (0.1 $nmolN_2O$ m^{-2} s^{-1}

582   or 87.3 mgN_2O-N m^{-2} for the September 2017 - December 2019 period).

583   Measured ecosystem-level N_2O fluxes at the Guyaflux site were highly variable, but overall showed

584   little seasonal variation (means of 0.~~5~~5 ± ~~0~~1.8~~3~~ $nmolN_2O$ m^{-2} s^{-1} and 0.~~5~~6 ± ~~0~~1.~~7~~0 $nmolN_2O$ m^{-2} s^{-1}, in

585   the driest and the wettest seasons, respectively; Table 1~~S2~~), partially supporting H1. These

586   observations fall within the range of net ecosystem N_2O exchanges measured by eddy covariance

587   reported in an oil palm plantation in Indonesia, with ~~similar~~ comparable mean N_2O emissions of 0.7

588     $nmolN_2O$ m^{-2} s^{-1} for both the dry and wet seasons (Stiegler et al., 2023). Once again, this comparison

589   must be interpreted with extreme caution even though both studies used the eddy covariance

590   technique as the ecosystems and seasons concerned were different (a tropical oil palm plantation with

591   strong seasons versus a primary wet tropical forest).

592   As with CH_4 fluxes, the temporal variability of the N_2O fluxes was very high (Fig. 2c). ~~Contrary~~ Although

593   the explanatory power of the relationships was poor (R^2 = 0.04, Table 2), the GAM analyses supported

594   H2 by attributing some of the variations in N_2O fluxes to changes in SWC. ~~to H2, GAM analyses failed~~

595   ~~to explain or attribute the observed variations in N₂O fluxes to changes in SWC or other meteorological~~

596   ~~drivers (R² = 0.04, Table 2).~~ Furthermore, daily mean ecosystem N_2O fluxes switched signs and changed

597   in order of magnitude on short time scales, most likely because these fluxes are controlled by

598   discontinuous microbial processes (Blagodatsky and Smith, 2012). Yet, although there were no

599   seasonal differences, ~~we did find~~the statistically significant, ~~though very weak,~~ relationships between

600   ecosystem N_2O fluxes and SWC~~, Ts and Rg, suggesting~~ suggested that the wettest season may provide

601   favourable conditions for soil bacterial N_2O production and plant-mediated N_2O transport, which could

602   contribute to higher net N_2O emissions at the ecosystem level (Stiegler et al., 2023). It is worth noting

603   that the extent to which trees mediate N_2O emissions is still uncertain; at Guyaflux, within the tower

604   footprint, tree stems in the seasonally flooded forest emit N_2O while those in the upland forest absorb

605   N_2O (Daniel et al., 2023). Other studies at Guyaflux and in a lowland tropical rain forest in the Réunion

606   Islands reported that tree stems can absorb N_2O through as yet unknown mechanisms (Bréchet et al.,

607   2021, 2025; Machacova et al., 2021). This could indeed counteract the overriding, albeit small, net

608   ecosystem N_2O emissions, suggesting that the proportion of upland versus seasonally flooded areas

609   should be taken into account.

610

611   4.2.2 Seasonal variations in upland soil N_2O fluxes: trends and drivers

612   In support of H1, N_2O fluxes recorded for the upland soils studied were small, averaging 0.3~~1~~ ± 0.3~~1~~

613     $nmolN_2O$ m^{-2} s^{-1} (Table ~~1,~~ S2), ~~and~~ but ~~slightly~~ significantly higher during the wettest season (0.3~~1~~ ±

614   0.3~~1~~ $nmolN_2O$ m^{-2} s^{-1}) compared to the driest season (0.2~~0~~ ± 0.3~~1~~ $nmolN_2O$ m^{-2} s^{-1}; Table 1~~S2~~).

615   Our average flux value, 15.6 μgN_2O-N m^{-2} h^{-1}, was nearly 3 time smaller than those reported for ~~an~~ a

616   Kenyan rainforest (42.9 μgN_2O-N m^{-2} h^{-1}, Werner et al., 2007) and about 1.5 time smaller than those

617   found for an Australian tropical rainforest (25.6 μgN_2O-N m^{-2} h^{-1}, Butterbach-Bahl et al., 2004), even

618   though the soils in both cases were predominantly N_2O emitters and all measurements were

619   performed ~~Our flux values were nine times smaller than those measured~~ with automated chamber

620 systems ~~in a western Kenyan rainforest (0.9 nmolN$_2$O m^{-2} s^{-1}; Werner et al., 2007), even though the~~

621 ~~soils in both cases were predominantly N$_2$O emitters~~. However, our seasonal N$_2$O flux observations

622 were within the same order of magnitude as those in two tropical rainforests where soil N$_2$O emissions

623 measured with manual chambers were lower in the dry season than in the wet season (< 0.20 nmolN$_2$O

624 m^{-2} s^{-1} and 0.34 nmolN$_2$O m^{-2} s^{-1}, respectively, Yu et al., 2021; 0.10 nmolN$_2$O m^{-2} s^{-1} and 0.49 nmolN$_2$O

625 m^{-2} s^{-1}, respectively, Werner et al., 2006). In addition, net N$_2$O uptake was observed in the upland soil

626 at our site, a phenomenon that has rarely been reported in tropical forests. Previous observations at

627 the Guyaflux site revealed soil N$_2$O uptake and showed that, although these fluxes were low, they were

628 primarily recorded over short measurement periods (2 minutes instead of 25 minutes; Courtois et al.,

629 2019). The very low flux detection limit of our instrument (G2308; Picarro) may explain why net uptake

630 fluxes were frequently measured. Since N$_2$O uptake rates are typically small, setups with a high MDF,

631 which are usually employed in remote areas such as tropical rainforests, are often unable to detect

632 these small uptake fluxes. Regarding the seasonal pattern, we suspect that during the wet season,

633 when conditions are ideal for both litter mineralisation and heterotrophic N$_2$ fixation (Van Langenhove

634 et al., 2020a), as well as denitrification, N$_2$O production typically exceeds consumption. During the dry

635 season, however, the drier conditions in the topsoil favour N$_2$O uptake, enabling microbial

636 communities to consume all the N$_2$O produced on average.

637 Unlike H2, ~~none of our~~the GAM~~s~~, including climatic ~~meteorological drivers~~ variables, ~~(i.e. SWC, Ts, Rg)~~

638 could only partially ~~predicted~~ predict the observed seasonal variations in upland soil N$_2$O fluxes, ~~when~~

639 ~~only the driest and wettest seasons were taken into account~~ with Ts and Rg as drivers (Table 2; Fig. 5).

640 This was even more unexpected as it only occurred during the driest season (Table 2), when low SWC

641 occurred alongside high and stable Ts and Rg (Fig. 1b, d, a, respectively). Previous studies have

642 observed an exponential increase in soil N$_2$O fluxes with Ts (Schindlbacher et al., 2004; Smith et al.,

643 2003), which can be explained by the temperature sensitivity of the underlying enzymatic processes.

644 However, Ts at our tropical site did not vary greatly (Fig. 1d). In addition, the significant relationships

645 between Rg and the upland soil N$_2$O fluxes are still unclear. Although these relationships were

significant, their explanatory power was rather poor (R^2 = 0.10), suggesting that other controlling

variables such as N and carbon availability (Morley and Baggs, 2010), or microbial community dynamics

(Regan et al., 2011), may also substantially influence the temporal dynamics of N_2O fluxes. This

emphasised the potential for both synergistic and antagonistic effects of key environmental drivers

(e.g. Ts, SWC) on regulating variables, highlighting the complexity of predicting seasonal variations in

N_2O flux in upland tropical forest soils.

~~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).~~

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. At the ecosystem level, mean daily fluxes were

low, but~~Although mean daily fluxes were low,~~ N_2O emissions were observed all-year-round, whereas

~~all year long. In contrast, for~~ CH_4 emissions or uptake depended on the season. ~~As expected,~~

~~t~~Seasonality was statistically significant for~~he seasons had a statistically significant effect on ecosystem~~

CH_4 ~~and N_2O fluxes~~, with ~~CH_4~~ uptake mainly occurring ~~and higher N_2O emissions~~ during the driest

season ~~than~~ compared to ~~during~~ the wettest season. At the soil level, ~~Upland soils exhibited highly~~

~~variable~~ CH_4 and N_2O fluxes were highly variable, with statistically significant~~an~~ increase in CH_4 uptake

and ~~a~~ decrease in N_2O emissions from the wettest to the driest season. The selected climatic variables

~~we selected~~ explained only a minor part of the seasonal variations in ecosystem ~~CH_4 and~~ N_2O fluxes

and were highly dependent on the selected ecosystem CH_4 fluxes. The best results were found when the effects of changes in SWC and Ts were considered, although the explanatory power of the models with regard to seasonal variations in soil CH_4 and N_2O fuxes was at most 20%. ~~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 of the whole ecosystem. Furthermore, upland soils (52% of the footprint area) are just one type of the wide variety of soils found within ~~the large range of soils found inside~~ the Guyaflux tower footprint. Soil chambers also provide integrated fluxes for a much smaller area than does the eddy covariance technique, which collects data from integrated processes across various forest habitats, soil types, tree species, hydrological conditions, and topographical positions. To improve the understanding of seasonal variations in ecosystem CH_4 and N_2O fluxes, it is crucial to characterise the fluxes in all existing ecosystem compartments simultaneously, ~~at the same time and to~~ including all tree components (leaves, stems, branches) and ~~tree~~ species in the forest habitats, not just those on upland soils. ~~However, o~~Our study still provides valuable data ~~that~~which, when combined with mechanistic models, could help to identify the missing drivers responsible for the seasonal variations in CH_4 and N_2O fluxes in wet tropical forest ecosystems.

Data availability

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

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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