Spatial variation of soil CO₂, CH₄ and N₂O fluxes across topographical positions in tropical forests of the Guiana Shield

Short title: GHG soil fluxes in the Guiana shield

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24   **ABSTRACT**

25   The spatial variation of soil greenhouse gas fluxes (GHG; carbon dioxide - CO_2, methane - CH_4

26   and nitrous oxide - N_2O) remain poorly understood in highly complex ecosystems such as

27   tropical forests. We used 240 individual flux measurements of these three GHGs from different

28   soil types, at three topographical positions and in two extreme hydric conditions in the tropical

29   forests of the Guiana shield (French Guiana, South America) to (1) test the effect of

30   topographical positions on GHG fluxes and (2) identify the soil characteristics driving flux

31   variation in these nutrients-poor tropical soils. Surprisingly, none of the three GHG flux rates

32   differed with topographical position. CO_2 effluxes covaried with soil pH, soil water content

33   (SWC), available nitrogen and total phosphorus. The CH_4 fluxes were best explained by

34   variation in SWC, with soils acting as a sink under drier conditions and as a source under wetter

35   conditions. Unexpectedly, our study areas were generally sinks for N_2O and N_2O fluxes were

36   partly explained by total phosphorus and available nitrogen concentrations. This first study

37   describing the spatial variation of soil fluxes of the three main GHGs measured simultaneously

38   in forests of the Guiana Shield lays the foundation for specific studies of the processes

39   underlying the observed patterns.

40

41   **Keywords:** tropical forest, GHG soil fluxes, Guiana Shield, soil characteristics, spatial

42   variation, French Guiana

INTRODUCTION

The rise of greenhouse gas (GHG) concentrations in the atmosphere has been the main driver of recent climate warming on Earth. This increase is attributed mainly to anthropogenic activities, such as deforestation, agricultural practices and the burning of fossil fuels. Most of the atmospheric GHGs are, however, produced or consumed in natural ecosystems, particularly by soil processes. Carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are the three main GHGs in terms of radiative forcing. Special attention has historically been paid to CO_2 because it is present in higher quantities in the atmosphere and CO_2 effluxes are the easiest to measure. Nonetheless, the warming potentials of CH_4 and N_2O molecules are 28- and 265-times greater than CO_2, respectively (on a 100-year basis) and even if their importance has been demonstrated worldwide, determining the magnitude of N_2O and CH_4 fluxes and their driving forces in soils of various ecosystems has recently become one of the most pressing issues in the study of ecosystem GHG balances (Merbold and others 2015). The contribution of CH_4 and N_2O exchange to the total GHG budgets of various ecosystems was estimated from relatively small (Merbold and others 2013 - subalpine grassland; Peichl and others 2014 - temperate pine plantation) to more than 50% (Hörtnagl and Wohlfahrt 2014 - meadow; Zona and others 2013 – poplar plantation).

Soil physical, chemical, and biological characteristics are linked to variation in GHGs emitted from soils which in turn usually display a high degree of spatial and temporal variability (Silver and others 1999; Arias- Navarro and others 2017). Soil GHG fluxes also vary with topography, either directly through dynamics of surface and subsurface water, nutrients, and dissolved organic matter (Fang and others 2009), or indirectly, via differences in soil texture and vegetation (Luizao and others 2004). While CO_2 effluxes from soils are always emissions, N_2O and CH_4 fluxes can shift from sink to source depending on environmental conditions. For these two gases, the static chamber method, commonly used to measure net gas fluxes on the

68   soil surface, cannot differentiate the simultaneously occurring production and consumption

69   within the soil but gives the result of these co-occurring processes.

70   Soil CO_2 efflux is the result of two main sources of CO_2 production in the soil: CO_2

71   respired by living roots and the rhizosphere, and CO_2 respired by heterotrophic microorganism

72   activities during decomposition of fresh litter and soil organic matter (Hanson and others 2000;

73   Janssens and others 2001). Soil temperature exerts a dominant control over the seasonal

74   variation of CO_2 effluxes in temperate forests but is less important in tropical soils where

75   temperatures are particularly high and stable year-round (Smith and others 2003). In contrast,

76   in tropical soils, soil moisture and more generally the variation in precipitation are factors

77   responsible for most of the seasonal variation in soil CO_2 effluxes (Davidson and others 2000b),

78   with generally decreasing fluxes under drier conditions (Davidson and others 2000b; Bonal and

79   others 2008; Rowland and others 2014; Meir and others 2015). Although microbial activity is

80   often limited in dry conditions, very wet conditions can also inhibit CO_2 production in soils by

81   limiting O_2 availability for decomposition processes and gas diffusivity (Davidson and others

82   2000b). While several studies have highlighted significantly higher CO_2 effluxes in lower

83   topographic positions as compared to higher positions (Epron and others 2006; Brito and others

84   2009; Martin and Bolstad 2009; Riveros-Iregui and McGlynn 2009), such patterns are not

85   always consistent (Arias-Navarro and others 2017). This could be due to high spatial

86   heterogeneity in CO_2 effluxes, soil characteristics and nutrient availability in tropical forests.

87   CH_4 production is the result of the obligate relationships between fermentative bacteria

88   and methanogenic archaea. This production primarily takes place in wetland soils (Bartlett and

89   Harriss 1993) but can also occur in upland soils in anaerobic microsites (Silver and others 1999;

90   Teh and others 2005; Liptzin and others 2011). In many parts of tropical forests, especially in

91   lowlands, the soils can remain anoxic, for sometimes long periods, simulating wetland

92   environments and enhancing methane production (Liptzin and others 2011). In well-aerated

93 soils, CH_4 can be oxidized by methanotrophic microorganisms and CH_4 oxidation normally

94 exceeds production, which results in a net CH_4 uptake (Von Fischer and Hedin 2002, 2007). At

95 an annual scale, the soils of tropical forests are generally a net sink for CH_4 (Dutaur and Verchot

96 2007). At fine temporal and spatial scales, the emission or consumption of CH_4 can vary

97 depending on nutrient availability (Veldkamp and others 2013), soil oxygen availability (Silver

98 and others 1999; Teh and others 2005; Liptzin and others 2011), bacterial community

99 composition (Teh and others 2008), soil structure (Teh and Silver 2006) or soil water content

100 (Davidson and others 2008). Similar to CO_2, contrasting evidence suggests either an effect (CH_4

101 uptake in ridges and slopes and emissions in valleys) (Silver and others 1999) or lack of an

102 effect (Reiners and others 1998; Wolf and others 2012) of topographic position on CH_4 fluxes.

103   The microbial processes of nitrification and denitrification are the dominant sources of

104 N_2O from the soil (Butterbach-Bahl and others 2013). This occurs during the conversion of

105 NH_4^+ to NO_3^- when ammonia is oxidized in nitrate in the presence of oxygen, and during the

106 conversion of NO_3^- to N_2O or N_2 when nitrate is used as an electron acceptor instead of oxygen

107 (Davidson and Verchot 2000; Hall and others 2004). The relative importance of nitrification as

108 a source of N_2O may depend on the microbial populations involved in ammonia oxidation

109 which in turn can vary with soil pH (Hink and others 2017, Prosser and Nicol 2008). N_2O is

110 emitted during these processes particularly when N availability is high. Production of N_2O,

111 controlled by N availability and soil moisture is commonly found in tropical soils (Davidson

112 and Verchot 2000; van Lent and others 2015). It is generally assumed that denitrification, the

113 electron-transport-linked reduction of nitrogen oxides during respiration of heterotrophic

114 bacteria, is responsible for N_2O consumption (Bremner, 1997). This also occurs in all biomes

115 ranging from the tropics to the poles (Chapuis-Lardy and others 2007; Schlesinger 2013). In

116 addition, nitrifiers also play a role in the consumption of N_2O as they are able to produce N_2

117 from nitrite (NO_2^-). This pathway, called nitrifier denitrification, is now known to proceed from

118   NO_2^- via nitric oxide (NO) and N_2O to N_2 (Schmidt and others 2004). Spatial and temporal

119   variation in N_2O fluxes from the soil are notoriously high and require more understanding of

120   the underlying soil characteristics that may drive N_2O production.

121   Soil temperature and moisture directly control production, consumption and transport

122   of N_2O through effects caused by the metabolic activity of microorganisms, soil aeration and

123   diffusivity (Luo and others 2013). Moreover, other environmental parameters have an effect on

124   N_2O fluxes, such as oxygen availability, nutrient availability and pH of the soil (Weslien and

125   others 2009; Rowlings and others 2012, Yang and others 2017). A recent meta-analysis (van

126   Lent and others 2015) indicates that tropical N_2O and NO fluxes can be expressed as a

127   combination of nitrogen availability and water-filled pore space, even though the predictive

128   power for simulating overall N_2O emissions was low ($R^2 \sim 0.4$). Emissions of N_2O from tropical

129   soils are typically extremely variable in both space and time (Arias-Navarro and others 2017),

130   with transient peaks associated with rain events (Nobre and others 2001; Petitjean and others

131   2015). N_2O fluxes from tropical forests are generally greater during rainy seasons than during

132   dry seasons, a result observed in Amazon (Davidson and others 2004), Central Africa (Rees

133   and others 2006), and in south Chinese forests (Werner and others 2006). Studies reported thus

134   far generally agree that topographical position does have an effect on N_2O emissions with

135   greater N_2O emissions in the valley bottom positions than top hill or midslope positions

136   (Pennock and others 1992; Corre and others 1996; Silver and others 1999; Arias-Navarro and

137   others 2017), yet the soil properties driving these patterns is not clear.

138   French Guiana is located in the Guiana Shield, a part of the Amazonian rainforest that

139   remains one of the largest undisturbed tropical forests in the world (Hansen and others 2013).

140   This tropical region lays on a Precambrian geological substrate that is particularly low in P

141   content compared to the generally younger, nutrient-rich soils of western Amazonia (Hammond

142   2005; Grau and others 2017). While several studies have reported CO_2 effluxes from soils in

143   the Guiana shield (Janssens and others 1998; Epron and others 2006; Bonal and others 2008;

144   Bréchet and others 2011), only one study recently measured N_2O fluxes (Petitjean and others

145   2015) and none, to our knowledge, focused on CH_4. Soil water content and nutrient

146   availabilities vary with topographical position in French Guianese tropical forests (Epron and

147   others 2006; Ferry and others 2010; Stahl and others 2011; Allié and others 2015). This local

148   spatial variation (less than 200 m) creates specific habitats that differ in terms of soil

149   characteristics, aboveground vegetation (Sabatier and others 1997), forest structure (Baraloto

150   and others 2007; Allié and others 2015) and forest dynamics (Ferry and others 2010). Here, we

151   simultaneously measured the three soil GHG fluxes together with soil chemistry and

152   characteristics in two hydrologically contrasting periods (dry and wet conditions) along three

153   topographical positions (top hill, middle slope and bottom slope). Our main objectives were (1)

154   to test whether topographical position has an impact on GHG fluxes and (2) to identify the main

155   environmental drivers of the three GHG fluxes in these nutrient-poor soils.

156

157   **METHODS**

158   *Description of the sites*

159   This study was conducted in French Guiana, which is part of the Guiana Shield, one of three

160   South American cratons (Gibbs and Barron 1993). More specifically, we sampled two sites: the

161   Nouragues research station (Bongers 2001) (04°05′N, 52°40′W) and the Paracou research

162   station (Gourlet-Fleury and others 2004) (04°15′N, 52°55′W) (Figure 1A). Both sites are

163   covered by pristine tropical forest, receive similar mean annual quantities of rainfall (2990 and

164   3041 mm y^{-1} at Nouragues and Paracou, respectively) and have a mean annual air temperature

165   near 25.7 °C (Bongers 2001; Gourlet-Fleury and others 2004). The tropical wet climate of

166   French Guiana is highly seasonal due to the north/south movement of the Inter-Tropical

167   Convergence Zone. This zone brings heavy rains from December to July (wet season) and a

long dry period from August to November (dry season, Supplementary Figure 1). Precipitation

during the dry period is typically <50 mm mo^{-1}. The Nouragues site has sandy soils of variable

depth from a parental material of weathered granite (van der Meer and Bongers 1996). Study

plots at the Paracou site are located on schist soils with veins of pegmatite along a Precambrian

metamorphic formation called the Bonidoro series (Epron and others 2006). The soils at both

sites are characterized as nutrient-poor Acrisols (FAO-ISRIC-ISSS, 1998) (Nachtergaele and

others 2000).

Study plots

For this study, we picked three topographic positions: (1) top of hills (top hill), (2) the middle

of the slopes at intermediate elevation (middle slope) and (3) bottom end of the slopes, at low

elevation, just above the creek (bottom slope) (Table 1). At each site, four plots of 20×20 m per

topographic position were established (distances between plots of 10-200 m) in the vicinity of

long-term undisturbed monitoring plots that have been monitored at both sites for 30 years

(Figure 1). The sand content was higher and the clay contents was lower in the bottom slope

plots than in the top hill and middle slope plots at both sites (Table 1). In each plot, five

Polyvinyl chlorid (PVC) collars 20 cm in diameter were inserted into the soil six months prior

to the first measurement to an average depth of 3.8 cm (± 0.5 cm) in the 20×20 m plot (Figure

1B), for a total of 120 sampling points (2 sites, 3 hill positions, 4 plots per position, 5 points per

plot).

Soil characteristics

Soil samples for chemical and physical characterization were collected on the same day

as fluxes. A composite soil sample of three soil cores around each sampling point (i.e. collars)

was analyzed. Soil water content (SWC) at a depth of 10 cm and air surface temperature

193 (average of three measurements) were recorded around each collar and on each sampling

194 occasion using a time-domain reflectometer (IMKO-HD2 portable meter fitted with a PICO64

195 probe, Ettlingen, Germany). Soil bulk density to a depth of 5 cm was measured with 100-cm^3

196 cylinders. All other soil characteristics were measured on 0-15 cm top soil at each sampling

197 point (once in the dry period and once in the wet period). Soil pH (KCl) was measured by

198 mixing 10 g of moist soil with 1M KCl in a 1:2.5 ratio. The resulting slurry was stirred for 1h,

199 then allowed to sit for another hour before pH was measured using a pH probe. The amount of

200 total phosphorus (P in ppm) was determined through microwave digestion (CEM, MARS-5) of

201 pulverized soils, previously dried for 48h at 70°C, in trace-metal-free acid (mixture of

202 concentrated HNO_3, HCl and HF). P concentrations in digests were measured on ICP-MS

203 (Optima 4300 DV, Perkin-Elmer, Waltham, USA). The amount of available P (in ppm) was

204 measured by Bray-P acid fluoride extraction (Bray & Kurtz, 1945) of soil dried at 60 °C for 48

205 h, and the resulting solution was analyzed on an iCAP 6300 Duo ICP optical emission

206 spectrometer (Thermo Fisher Scientific). The amount of available nitrogen (N in ppm) was

207 measured by extracting moist soil with 1M KCl, after which the concentrations of NH_4^+ and

208 NO_3^- were determined colorimetrically on a San++ continuous flow analyzer (Skalar Inc,

209 Breda, The Netherlands). The concentrations of NH_4^+ and NO_3^- were summed and treated as a

210 single value during analyses and are reported hereafter as available N. Soil C and N

211 concentrations (in percent) were determined by combustion (Elemental Analyzer, CE

212 Instruments/Thermo Electron, Milan, Italy) coupled with gas chromatography/mass

213 spectrometry (Delta V Advantage, Thermo Fisher Scientific, Cambridge USA). Soil C:N ratios

214 were obtained by dividing C concentrations (percent) by N concentrations (percent).

215

216 *Soil fluxes*

217   Two single-survey sampling campaigns were conducted at each site, one during the dry period

218   (October 2015) and one during the wet period (May 2016) corresponding to the two extreme

219   conditions in soil water content (Supplementary Figure 1) in order to capture the full range of

220   local environment difference. We measured the soil fluxes of CO_2, CH_4 and N_2O during each

221   campaign using opaque (no light allowed) static soil PVC chambers (volume, 0.0026 m^3; area,

222   0.029 m^2, designed in Antwerp laboratory) between 10 am and 2 pm in order to avoid diurnal

223   variability (Teh et al 2014, Yan et al. 2014, Brechet et al. 2011). In total, 240 flux estimations

224   were made during the two sampling campaign (60 sampling points in each forest in the two

225   periods and the two sites). Each sampling point was therefore only measured once in each

226   period. After the chambers were sealed onto the soil collars, four headspace gas samples were

227   collected, one immediately after closure and then at subsequent 10-min intervals. Air samples

228   were taken with a 12-mL syringe whose needle was inserted through a septum in the chamber

229   and then injected into pre-evacuated 12-mL vials (Labco Limited, Ceredigion, UK). To mix the

230   air in the chamber headspace prior to sampling, air was flushed five times with the syringe

231   volume prior to the second, third and fourth air samples in each chamber. The CO_2, CH_4 and

232   N_2O mole fractions in the gas samples were determined by gas chromatography (Trace GC

233   Ultra, Thermo Fisher Scientific, Vienna, Austria) equipped with a vacuum dosing system (S+H

234   Analytics, Germany). Gas samples were filled into a 1 ml sample loop at a pressure of 600

235   mbar. We used a flame ionization detector (FID) with a methanizer for CO_2 and CH_4 detection

236   and a pulsed-discharge detector for N_2O detection.

237   The limits of detection (LoD) of CH_4 and N_2O were calculated from Least-Square

238   Regression data according to the ICH (International Council for Harmonization). We used the

239   "residual standard deviation of the regression line" method between the peak area and

240   concentration of certified standards that were in the range of the detection limit (0.29, 0.54 and

241   0.91 ppm N_2O and 1.01, 2.16 and 4.17 ppm CH_4). We also checked our data for

242 homoscedasticity (i.e., independence of the peak area dispersion from the concentration of the

243 standards). The LoD of the samples was then calculated as 3 times the standard deviation of the

244 residuals divided by the slope of the linear regression of the calibration. For comparison, we

245 also used the "standard deviation of the intercept" method, which yielded LoD values in the

246 same range than the residual method. By using the "residual standard deviation of the regression

247 line" method, we determined the LoD to be 0.116 ppm for N_2O and 0.202 ppm for CH_4 over

248 all standards (n=54). Between different sample batches, the LoD varied only slightly between

249 0.115 and 0.130 ppm for N_2O and between 0.166 and 0.247 ppm for CH_4, respectively.

250 For 17 fluxes measurements (10 in wet period and 7 in dry period), data points were

251 missing either due to problems in the field (i.e. leaks) or during laboratory analyses and these

252 estimations were removed for the three gases. All other fluxes were computed using the HMR

253 package (Pedersen 2010) for the three gases using Linear Regression (LR), or revised

254 Hutchinson/Mosier (HMR) methods following recommendations from Pedersen and others

255 (2010) (70% HMR and 30% LR for CO_2; 55% HMR and 45% LR for CH_4; 65% HMR and

256 35% LR for N_2O). Gas mixing ratios (ppm) were converted by using the Ideal Gas Law to solve

257 for the quantity of gas in the headspace (on a mole or mass basis), normalized by the surface

258 area of each static flux chamber.

259 Calculation of minimum detectable flux (MDF) of N_2O was made with the methodology

260 developed by Parkin and others (2012). The mean concentration (i.e., ambient concentration)

261 of 0.300 ppm of N_2O and the coefficient of variation of 0.05 was defined from values of N_2O

262 at sampling time 0. Minimum detectable flux was ± 8.3 µg N m^{-2} h^{-1}, 27 fluxes (11%) were

263 below the minimum detection limit (MDL) and included in the analysis as null fluxes.

264

265 *Statistical analyses*

266 In order to test the effect of topographical position on GHG fluxes, we performed a linear

267 mixed-effects model (LMM) using topographical position (top hill, middle slope or bottom

268 slope) as fixed explanatory variables and period (dry or wet season conditions) and site (Paracou

269 or Nouragues) as random factor. Variables were transformed as follows: log (flux) for CO_2 and

270 log (flux − min (flux) +1) for CH_4 and N_2O for this analysis. Significance was tested by

271 comparing the null model to a model including topographical positions as fixed factor with a

272 chi-square test.

273 The variations of soil characteristics were assessed with a principal component analysis

274 (PCA) using eight soil variables (Total P, C:N ratio, SWC, air soil surface temperature -

275 Temperature, soil density, soil pH, available P and available N). The spatial segregations of the

276 measurements across period (dry or wet period), site (Paracou or Nouragues) and topographical

277 position (top hill, middle slope or bottom slope) along the two main PCA axes were tested using

278 permutational MANOVA (multivariate analysis of variance).

279 We used generalized additive model (GAM) for each gas to identify the best set of

280 variables explaining the variation in the gas fluxes (candidates variables: Total P, C:N ratio,

281 SWC, air soil surface temperature - Temperature, soil density, soil pH, available P and available

282 N). GAMs are semi-parametric extensions of generalized linear models allowing non-linear and

283 non-monotonic relationships between a response and a set of explanatory variables. The form

284 of the predictor function is the principal originality of this method (Fewster and others 2000).

285 The best model (i.e. explaining most of the variation) is selected using Akaikes's information

286 criterion. Once the model best fitting the data is selected, a second step using recursive feature

287 elimination allows for the ranking of variables using their importance in the model. For this,

288 variables were backward selected using recursive feature elimination. Variable importance was

289 then defined as the total reduction in the validation statistic (generalized cross-validation

290 estimate of error) when each predictor's feature is added to the model.

291   All data were processed with R statistical software (R Development Core Team, 2010)

292   using the package HMR (Pedersen and others 2010) for flux computation, the packages ade4

293   (Dray and Dufour 2007) and Momocs (Bonhomme and others 2014) for PCA analysis and

294   permutational MANOVA respectively, the package lme4 (Bates and others 2014) for LMM,

295   the packages mgcv (Wood and Wood 2007) for GAM, , and the package caret (Kuhn 2008) for

296   recursive feature elimination of variables. .

297

298   **RESULTS**

299   *Variation in GHG fluxes*

300   Mean soil CO_2 efflux ranged from 131.9 ± 65.8 mg C m^{-2} h^{-1} in the dry period to 156.4 ± 69.2

301   mg C m^{-2} h^{-1} in the wet period (Figure 2, Supplementary table 1). Soils tended to be sinks of

302   CH_4 in the dry campaign and sources of CH_4 in the wet campaign (mean fluxes of -27.7 ± 129.8

303   µg C m^{-2} h^{-1} in the dry period and 12.0 ± 125.2 µg C m^{-2} h^{-1} in the wet period, Figure 2,

304   Supplementary table 1). Fifty percent of the CH_4 fluxes in the wet period were net emissions,

305   and only 17% were net emissions in the dry period. Mean N_2O fluxes were negative in both

306   campaigns (mean fluxes of -30.7 ± 30.3 µg Nm^{-2} h^{-1} in the dry season and -33.4 ± 47.4 µg N

307   m^{-2} h^{-1} in the wet season, Figure 2, Supplementary table 1). Overall, 98% of the sampling

308   points in the dry season and 95% in the wet season were sinks of N_2O.

309

310   *Topographic positions and soil characteristics*

311   Topographic position (top hill, middle slope, bottom slope) had no effect on any of the three

312   gas fluxes (LMM; CO_2 $\chi^2=1.19$ p=0.55; CH_4 $\chi^2=3.48$ p=0.18; N_2O $\chi^2=0.16$ p=0.92). The PCA

313   classified the environmental variables over all sites into two principal components (PCs), which

314   accounted for 51.4% of variation in the soil characteristics. PC1 (Figure 3A) explained 28.5%

315   of the variance and was correlated positively with soil bulk density and temperature and

316 negatively with available N and total P and. PC2 (Figure 2A) explained 22.9% of the variance

317 and was correlated positively with SWC and negatively with C:N. Soil characteristics in the dry

318 and wet periods are differentiated using these two axes (MANOVA, F=121.54, p<0.001),

319 mostly along the second axis (Figure 3B). Sites are also differentiated using these two axes

320 (MANOVA, F=33.14, p<0.001), mostly along the first axis (Figure 3C). Despite the large

321 overlapping areas in PCA (Figure 3D), MANOVA also indicated that Topographic position can

322 be distinguished using this set of variables (MANOVA, F=34.08, p<0.001).

323

324 *Spatial variation of soil GHG fluxes*

325 The spatial variation in CO_2 efflux was significantly explained by four variables (GAM, SWC

326 > soil pH > available N> Total P, Table 2, Figure 4). These four variables in combination

327 explained 20.7% of the variation. The variation in the CH_4 flux was explained by only one

328 variable (GAM, SWC, Table 2, Figure 4), which explained 4.5% of the variation. The CH_4

329 fluxes were higher in wetter soils (Figure 4). The variation in N_2O flux was explained by two

330 variables (GAM, CN> Total P, Table 2, Figure 4), which explained 9.2% of the variation.

331

332 **DISCUSSION**

333 *CO_2 effluxes did not differ among topographical positions but were partly explained by soil*

334 *physical and chemical characteristics*

335 The soil CO_2 effluxes measured in this study were within the ranges of previous studies in

336 French Guianese forests (Janssens and others 1998; Epron and others 2006; Bonal and others

337 2008; Bréchet and others 2011; Rowland and others 2014). Contrary to previous studies in

338 tropical forest (Brito and others 2009; Martin and Bolstad 2009; Riveros-Iregui and McGlynn

339 2009), even one conducted in French Guiana (Epron and others 2006), soil CO_2 fluxes were not

340 related to topographic position. However, soil characteristics represented by the PCA analysis

341   also did not differ as much at the different topographic positions defined in this study as in other

342   studies, which might explain this contrast. Moreover, in Epron and others (2006), all

343   measurements were made in September, during the dry season only, which might explain the

344   discrepancy between our study and their results. A recent study conducted in tropical areas

345   (Arias-Navarro and others 2017) also did not detect any effect of topographic position on CO_2

346   effluxes despite a very good spatial coverage of the study site. This result is explained by the

347   very large diversity of tree species in tropical forests (as in our two tropical pristine forest, Table

348   1), leading to heterogeneity in the chemical, structural, and functional traits of roots and leaves

349   affecting biogeochemical processes (Hättenschwiler and others 2008; Townsend and others

350   2008) and resulting in a high spatial heterogeneity in soil respiration.

351   SWC and soil pH were the main drivers of soil CO_2 effluxes across topographical positions

352   even if only 20.7% of the variation was explained by the model. In agreement with previous

353   studies conducted in French Guiana (Bonal and others 2008; Rowland and others 2014), we

354   found a positive relationship between SWC and CO_2 effluxes. Soil pH was negatively correlated

355   with soil CO_2 effluxes as found in a previous study (Epron and others 2006) while in temperate

356   areas several studies have highlighted the opposite pattern (Reth and others 2005; Chen and

357   others 2015). This could be due to the relatively low pH (3.9 ± 0.2) of these French Guianese

358   soils. The effect of pH alone is unknown on soil CO_2 effluxes but some studies suggest a

359   combined effect of pH with some others components like clay content and soil organic matter

360   (Epron and others 2006) or via decreased root respiration (Chen and others 2015). Nutrients

361   availability also appears to have an influence on CO_2 effluxes as CO_2 effluxes were positively

362   correlated with available Nitrogen and negatively with total Phosphorus.

363

364   ***CH_4 fluxes shifted from source under wet conditions to sink under dry conditions***

365   As previously shown for other tropical sites (Reiners and others 1998; Wolf and others 2012),

366   we found no impact of topographic positions on CH_4 fluxes. Soil CH_4 fluxes were correlated

367   with SWC with only 4.5% of the variation explained by this variable. CH_4 fluxes shifted from

368   uptake under dryer conditions to moderate emissions under wet conditions, similar to other

369   tropical forest sites (Keller and Reiners 1994; Keller and others 2005; Davidson and others

370   2008; Teh and others 2014). Increased precipitation is likely to decrease rates of O_2 diffusion

371   into the soil (Silver and others 1999; Teh and others 2005; Liptzin and others 2011), decreasing

372   CH_4 oxidation, and increasing CH_4 emissions. Since no other studies are currently available in

373   the surrounding area and as the temporal coverage of this study is not sufficient to estimate

374   annual budgets from forests of the Guiana Shield, further investigations on soil CH_4 fluxes need

375   to be conducted.

376

377   ***N_2O uptake is linked to C:N ratio and total phosphorus***

378   Surprisingly, most of the N_2O fluxes measured in this study were negative across the

379   topographic positions and between hydric conditions (98% of the total samples). This was

380   unexpected in light of the N-rich, wet conditions of these forests and based on previous results

381   from French Guiana (Petitjean and others 2015) and other tropical soils (Teh and others 2013,

382   2014; van Lent and others 2015; Arias-Navarro and others 2017). The spatial resolution in our

383   study is in line with an extensive survey of N_2O fluxes in Africa (Arias-Navarro and others

384   2017) which suggest that measurements at 78 ± 5 locations per hectare are needed to obtain an

385   estimate of N_2O fluxes within 10% of the true mean (in our study, 5 sampling locations per 400

386   m^2 corresponds to 125 locations per hectare).We did not detect effects of topographic position

387   on the magnitude of the uptake. The mean flux of -32 µg N m^{-2} h^{-1} measured in our study falls

388   within the range of negative N_2O fluxes of -1.4 ng N m^{-2} h^{-1} to - 484 µg N m^{-2} h^{-1} reported in

389   the review by Chapuis-Lardy et al. (2007). More data at a broader spatial and temporal scale

390   are urgently needed to confirm the generality of this pattern and estimate the annual sink

391   capacity of French Guianan soils.

392   The flux of N_2O measured with soil chambers at the soil/atmosphere interface is the

393   result of dynamic production and consumption processes in the soil. This capacity of the soil to

394   act as an N_2O sink is linked to the abundance and phylogenetic diversity of a group of N_2O-

395   reducing microbes (Jones and others 2014). The community composition of these -micro-

396   organisms is influenced by soil properties and in particular by soil stoichiometry (total P and

397   C:N ratio) (Butterbach-Bahl and others 2013). While N_2O fluxes were significantly correlated

398   with soil nutrients, most of the variation in N_2O fluxes remained unexplained in our study (only

399   9.2% of the variation explained by the model).

400   In contrast to other studies in tropical forest soils (Butterbach-Bahl and others 2004;

401   Tang and others 2006; Luo and others 2013), SWC was not linked with N_2O fluxes. This could

402   be mostly due to the fact that we almost only measured N_2O consumption in our study (98% of

403   all sampling points) while other studies report mostly N_2O emission. Moreover, soils with a

404   low water-retention capacity (which is the case for most of the French Guianan soils with high

405   sand content) have limited anaerobic conditions. In addition, competition for NO_3^- between

406   different nitrate-reducing processes under varying moisture conditions (e.g. dissimilatory

407   nitrate reduction to ammonium versus denitrification) may obscure the relationship between

408   soil moisture content and N_2O flux (Morley and Baggs, 2010, Morley et al., 2008). N_2O

409   emissions from tropical soils can be sporadic and transient, e.g. after heavy rains (Breuer and

410   others 2000; Nobre and others 2001), and are characterized by short pulses of emissions

411   associated with higher nitrogen inputs (Bai and others 2014) or high precipitation events

412   (Breuer and others 2000; Nobre and others 2001; Geng and others 2017). Nevertheless, we

413   detected only one high N_2O emission event which could not be linked to a heavy rain, but this

414   study was not designed to capture such a fine level of temporal variation. These transient strong

415 peaks of N_2O emission are likely responsible for the net emission budget of tropical soils

416 highlighted in another study (Nobre and others 2001); a high frequency of N_2O flux

417 measurements is urgently needed to confirm this relationship.

418

419 ***Conclusion and Perspectives***

420 Our study has shed new light on the drivers of the three main GHG fluxes in tropical soils of

421 the Guiana Shield. The fluxes of the three gases did not differ among topographical positions.

422 Nevertheless, we highlighted the significant role of soil physical (SWC) and chemical (pH,

423 Available N, C:N ratio and total P) properties as drivers of soil GHG fluxes even if most of the

424 variation in the three GHG fluxes remains unexplained highlighting again their high spatial

425 variability. Proximate controls on soil fluxes are complex and difficult to elucidate from field

426 measurements alone and more experimental studies are also needed in order to disentangle the

427 effect of different soil characteristics and microbial processes, which result in a modification of

428 soil GHG fluxes. Nitrogen deposition is expected to increase in tropical areas (Penuelas and

429 others 2013) which can induce soil acidification (Tian and Niu 2015) and changes in soil

430 stoichiometry and could impact GHG emissions in the future. Tropical forest soils contribute

431 an estimated 28% to the global CH_4 uptake (Dutaur and Verchot 2007), which is large enough

432 to alter the accumulation of CH_4 in the atmosphere if large changes occur in this sink due to

433 climate change such as increased drought (Brumme and others 1999).

434   Specific studies should be conducted to assess the influence of climatic changes

435 (especially changes in precipitation and an increased occurrence or severity of drought)

436 combined with modifications to soil stoichiometry (mainly by N deposition) on the magnitude

437 of soil GHG fluxes in these poor-nutrient tropical soils over a long period in order to determine

438 (1) the relative frequencies of consumption and emission and (2) the net GHG balance at annual

439 scales.

440

454

455   **TABLES**

456

457   **TABLE 1:**

458

	Nouragues			Paracou		
	Top hill	**Middle slope**	**Bottom slope**	**Top hill**	**Middle slope**	**Bottom slope**
Altitude (m)	118.4 ± 1.0	107.0 ± 3.0	103.5 ± 1.4	72.9 ± 2.9	48.5 ± 8.4	23.9 ± 0.05
Number of species (sp ha^{-1})	178	180	164	131	120	136
Stand density (>10 cm DBH) (tree ha^{-1})	532	564	573	678	580	578
Basal area (m² ha^{-1})	36	32.9	33	34.2	32.7	28.6
Soil density (g cm^{-3})	0.78 ± 0.02	0.91 ± 0.03	0.94 ± 0.04	1.12 ± 0.05	1.03 ± 0.02	1.16 ± 0.03
Sand content (%)	22.49 ± 4.77	53.07 ± 6.22	63.65 ± 2.15	76.23 ± 3.51	63.01 ± 3.51	76.81 ± 2.09
Clay content (%)	42.85 ± 1.99	25.94 ± 3.40	18.3 ± 1.19	9.28 ± 0.35	17.76 ± 2.28	8.65 ± 1.27

459

460

461 **Table 2:**

	CO_2		CH_4		N_2O	
	F	**p-value**	**F**	**p-value**	**F**	**p-value**
pH	**1.385**	**<0.001**	0.000	0.611	0.086	0.195
Density	0.086	0.174	0.000	1.000	0.042	0.220
Temperature	0.000	0.776	0.155	0.126	0.000	1.000
SWC	**2.117**	**<0.001**	**0.667**	**0.006**	0.314	0.061
Available N	**0.711**	**0.015**	0.000	1.000	0.000	0.451
Available P	0.147	0.119	0.000	0.537	0.000	1.000
C:N	0.027	0.262	0.000	1.000	**1.311**	**0.001**
P	**0.359**	**0.031**	0.162	0.133	**0.346**	**0.039**

462

463

TABLE LEGENDS

465

466 **Table 1:** Environmental characteristics of each topographical position (top hill, middle slope

467 and bottom slope) at two tropical forest site sites (Nouragues and Paracou). Values are means

468 ± standard errors (N=4). Percentages of sand and clay contents were determined for a composite

469 sample from each topographical position at each site, so only one value is available for each

470 topographical position.

471

472 **Table 2:** Results from GAM analysis. Significant p-values are highlighted in bold.

FIGURE CAPTIONS

474

475 **Figure 1: Site locations and experimental design.** (A) Location of the two study sites

476 (Paracou and Nouragues) in French Guiana. The insert shows the location of French Guiana in

477 South America. (B) Experimental set-up of the five sampling points (collars) in each 20×20 m

478 plot (gray). Location of the 12 plots by topographical position (top hill, blue; middle slope,

479 green and bottom slope, red) at the Nouragues site (C) and the Paracou site (D) near the long-

480 term undisturbed monitoring plots (yellow).

481

482 **Figure 2: Variation of GHGs fluxes among topographical positions.** Boxplot of (A) CO_2,

483 (B) CH_4 and (C) N_2O by topographical position (T - top hill in blue; M - middle slope in green

484 and B - bottom slope in red) for each site (Paracou – PAR; Nouragues – NOU) and each

485 campaign (DRY – Dry period; WET – Wet period).

486

487 **Figure 3: Principal component analysis of the soil variables**. (A) Circular correlation plots

488 of PC1 and PC2. (B) Projections of the water condition classes (dry period, orange; wet period,

489 brown) on PC1 and PC2. (C) Projections of the site classes (Nouragues, light gray; Paracou,

490 dark gray) on PC1 and PC2. (D) Projections of the topographical position (T, top hill, blue; M,

491 middle slope, green and B, bottom slope, red) on PC1 and PC2 These two axes explain 51.4%

492 of the variation in soil characteristics (28.5% for PC1, 22.9% for PC2 and 15.71% for PC3).

493

494 **Figure 4: Variable importance.** Importance of the variables (P - Total P, C:N, SWC, Temp -

495 Temperature, Dens - density, pH, Av. P - Available P and Av. N - Available N) to the variation

496 in the fluxes of (A) CO_2, (B) CH_4 and (C) N_2O. This value is computed as the total reduction
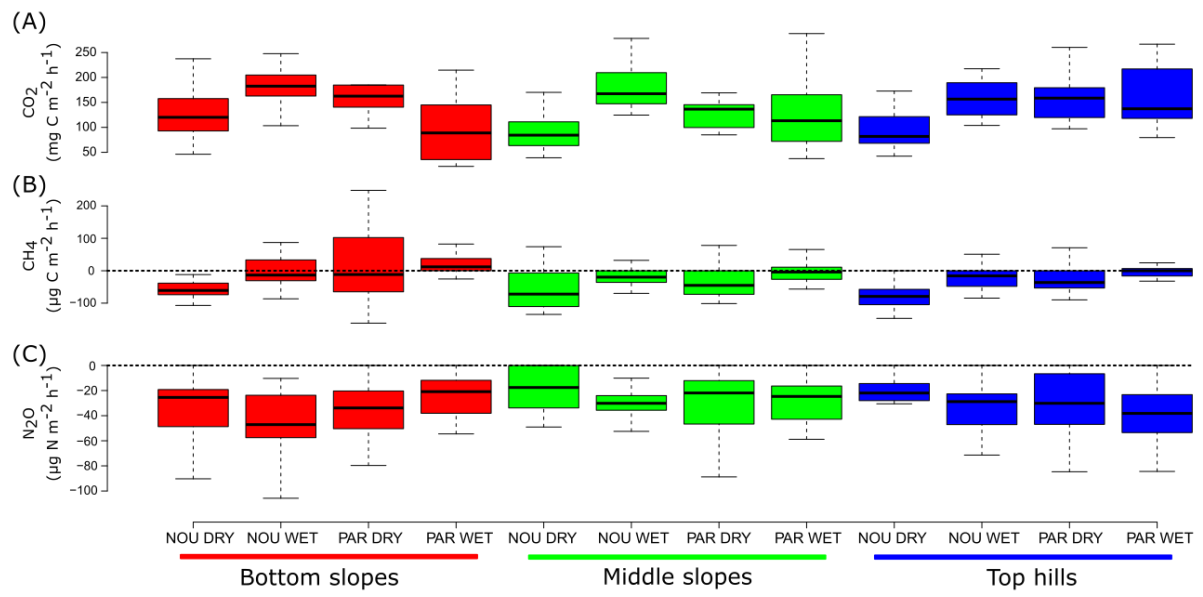
497   in the validation statistic (generalized cross-validation estimate of error) when each predictor's

498   feature is added to the model. Significant variables in GAMs are indicated by an asterisk.
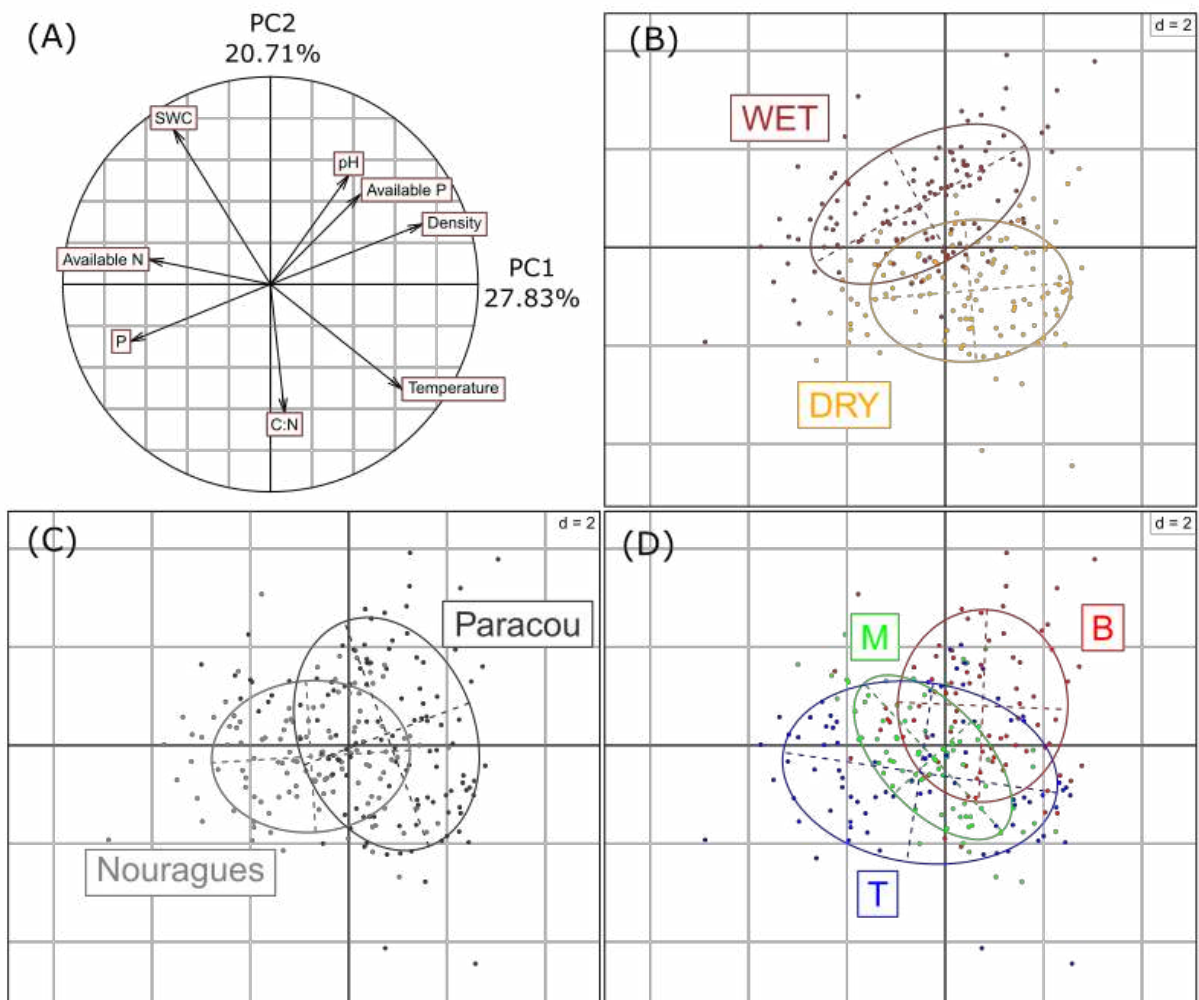
499

500

501   **FIGURE 1**
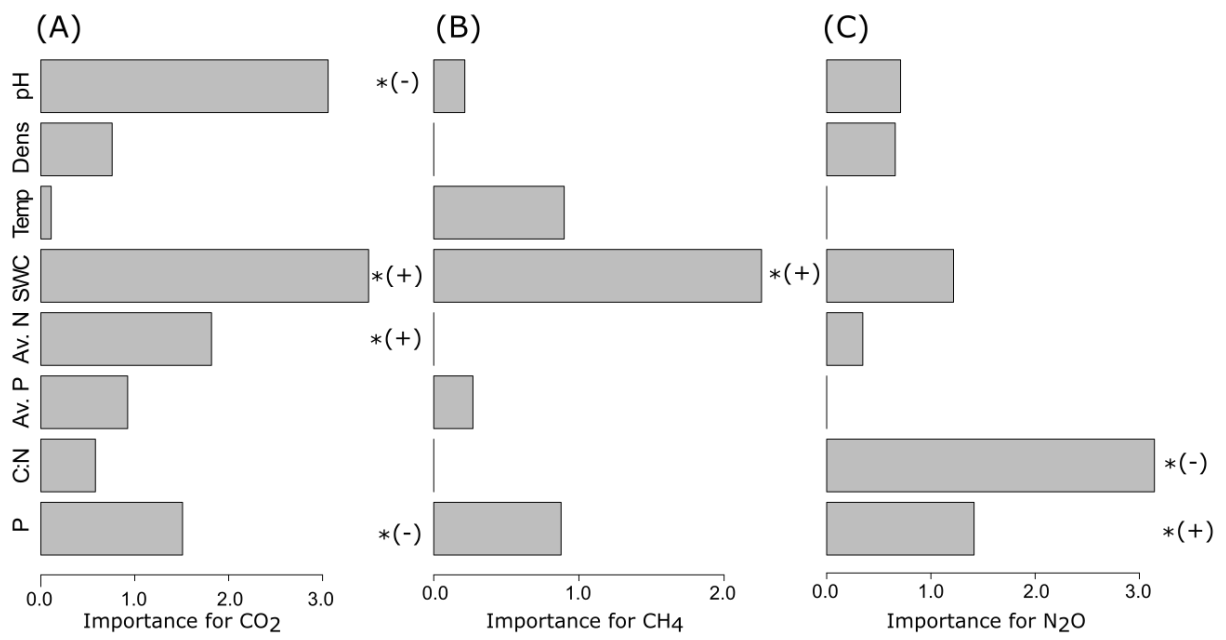

502
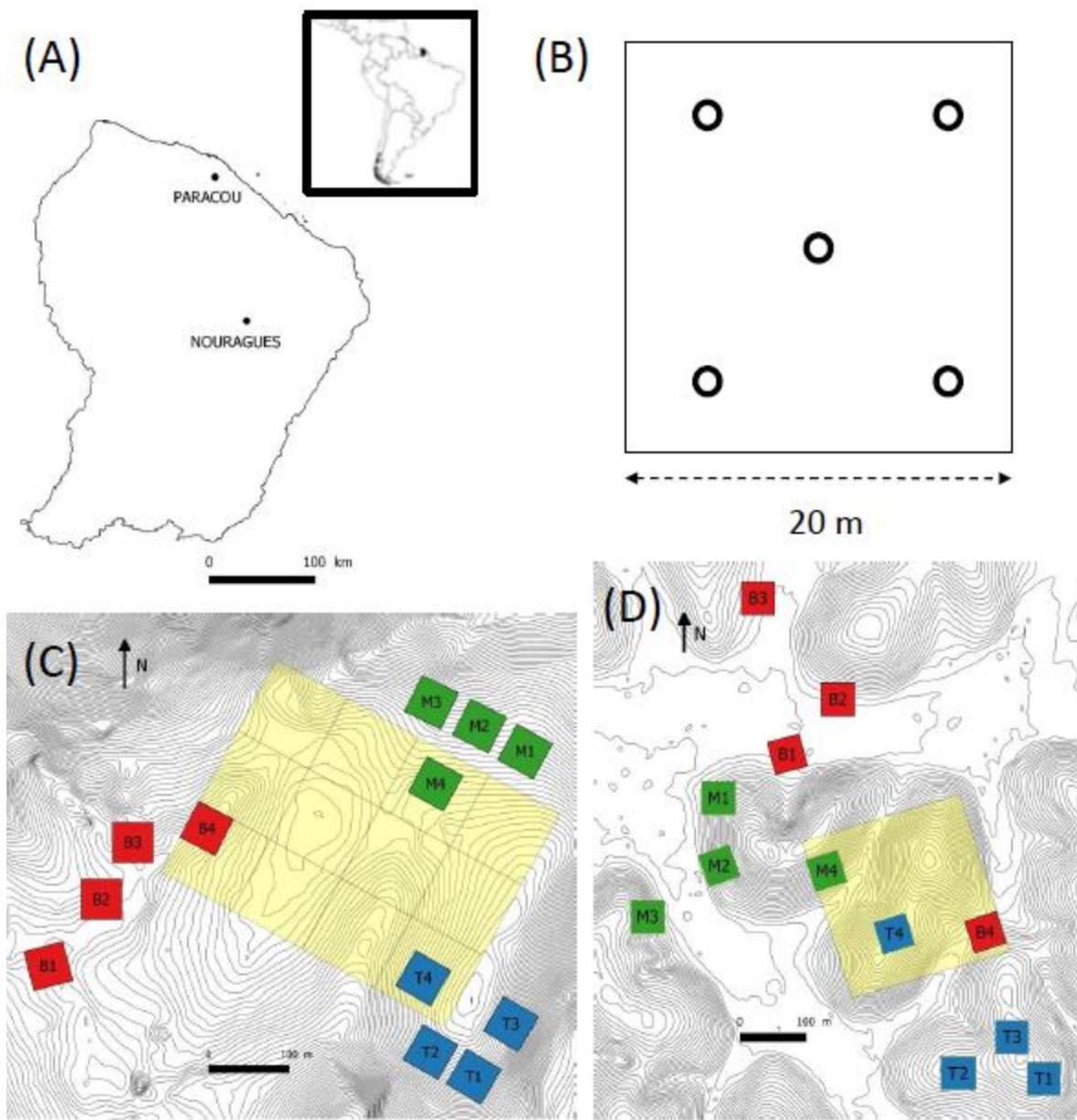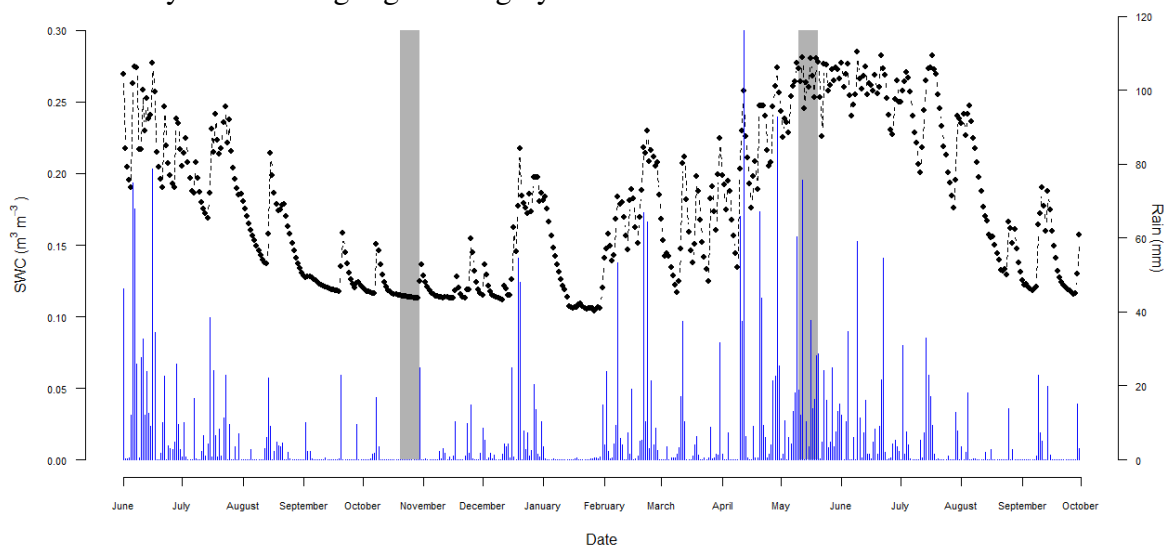
503 **FIGURE 2**

504

505

506

507   **FIGURE 3**

510 **FIGURE 4**

511

513 **Supplementary Figure 1:** Soil water content (in $m^3 m^{-3}$ in black) and rain (in mm in blue) at
514 one site (Paracou) from June 1st 2015 to September 30th 2016. Sampling occasions in October
515 2015 and May 2016 are highlighted in grey.

516
517
518 **Supplementary Table 1:** Means ± standard errors (N=4) of the three GHG fluxes by site
519 (Nouragues and Paracou) and topographical position (T, top hill; M, middle slope and B, bottom
520 slope) for the dry and wet periods. Negative fluxes (consumption) are highlighted in bold.
521

		Nouragues				Paracou				Total
		T	M	B	All	T	M	B	All	
DRY	**CO₂** (mg C m⁻² h⁻¹)	92.6 ± 34.4	89.9 ± 37.8.9	131.0 ± 64.2.4	104.7 ± 50.5	165.2 ± 50.2	131.7 ± 34.3	189.6 ± 96.8	161.7 ± 68.0	131.9 ± 65.8
	CH₄ (µg C m⁻² h⁻¹)	**-64.0** ± 69.7	6.6 ± 237.9	**-49.9** ± 50.1	**-35.8** ± 146.8	**-44.0** ± 139.7	**-19.9** ± 79.5	6.6 ± 103.7	**-19.1** ± 109.3	**-27.7** ± 129.8
	N₂O (µg N m⁻² h⁻¹)	**-20.4** ± 15.0	**-20.1** ± 17.4	**-32.5** ± 21.6	**-25.0** ± 19.1	**-31.2** ± 27.5	**-41.4** ± 54.5	**-35.7** ± 21.8	**-36.1** ± 37.2	**-30.7** ± 30.3
WET	**CO₂** (mg C m⁻² h⁻¹)	159.6 ± 36.5	191.7 ± 66.5	188.8 ± 50.2	180.1 ± 54.0	161.6 ± 62.9	138.3 ± 88.7	94.8 ± 57.4	131.0 ± 75.1	156.4 ± 69.3
	CH₄ (µg C m⁻² h⁻¹)	**-19.9** ± 70.3	43.2 ± 274.0	9.4 ± 64.9	15.0 ± 171.1	3.7 ± 40.1	**-1.9** ± 41.2	23.9 ± 34.6	8.9 ± 39.5	12.0 ± 125.2
	N₂O (µg N m⁻² h⁻¹)	**-30.7** ± 30.9	**-31.9** ± 15.5	**-55.4** ± 47.6	**-39.1** ± 35.0	**-49.7** ± 49.8	**-19.3** ± 45.1	**-18.0** ± 70.9	**-19.8** ± 26.0	**-33.4** ± 47.4

522

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