

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 - CO₂, methane - CH₄
26 and nitrous oxide - N₂O) 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. CO₂ effluxes covaried with soil pH, soil water content
33 (SWC), available nitrogen and total phosphorus. The CH₄ 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 N₂O and N₂O 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

43 INTRODUCTION

44 The rise of greenhouse gas (GHG) concentrations in the atmosphere has been the main driver
45 of recent climate warming on Earth. This increase is attributed mainly to anthropogenic
46 activities, such as deforestation, agricultural practices and the burning of fossil fuels. Most of
47 the atmospheric GHGs are, however, produced or consumed in natural ecosystems, particularly
48 by soil processes. Carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) are the three
49 main GHGs in terms of radiative forcing. Special attention has historically been paid to CO₂
50 because it is present in higher quantities in the atmosphere and CO₂ effluxes are the easiest to
51 measure. Nonetheless, the warming potentials of CH₄ and N₂O molecules are 28- and 265-times
52 greater than CO₂, respectively (on a 100-year basis) and even if their importance has been
53 demonstrated worldwide, determining the magnitude of N₂O and CH₄ fluxes and their driving
54 forces in soils of various ecosystems has recently become one of the most pressing issues in the
55 study of ecosystem GHG balances (Merbold and others 2015). The contribution of CH₄ and
56 N₂O exchange to the total GHG budgets of various ecosystems was estimated from relatively
57 small (Merbold and others 2013 - subalpine grassland; Peichl and others 2014 - temperate pine
58 plantation) to more than 50% (Hörtnagl and Wohlfahrt 2014 - meadow; Zona and others 2013
59 – poplar plantation).

60 Soil physical, chemical, and biological characteristics are linked to variation in GHGs
61 emitted from soils which in turn usually display a high degree of spatial and temporal variability
62 (Silver and others 1999; Arias- Navarro and others 2017). Soil GHG fluxes also vary with
63 topography, either directly through dynamics of surface and subsurface water, nutrients, and
64 dissolved organic matter (Fang and others 2009), or indirectly, via differences in soil texture
65 and vegetation (Luizao and others 2004). While CO₂ effluxes from soils are always emissions,
66 N₂O and CH₄ fluxes can shift from sink to source depending on environmental conditions. For
67 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 CO₂ efflux is the result of two main sources of CO₂ production in the soil: CO₂
71 respired by living roots and the rhizosphere, and CO₂ 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 CO₂ 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 CO₂ 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 CO₂ production in soils by
81 limiting O₂ availability for decomposition processes and gas diffusivity (Davidson and others
82 2000b). While several studies have highlighted significantly higher CO₂ 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 CO₂ effluxes, soil characteristics and nutrient availability in tropical forests.

87 CH₄ 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, CH₄ can be oxidized by methanotrophic microorganisms and CH₄ oxidation normally
94 exceeds production, which results in a net CH₄ uptake (Von Fischer and Hedin 2002, 2007). At
95 an annual scale, the soils of tropical forests are generally a net sink for CH₄ (Dutaur and Verchot
96 2007). At fine temporal and spatial scales, the emission or consumption of CH₄ 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 CO₂, contrasting evidence suggests either an effect (CH₄
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 CH₄ fluxes.

103 The microbial processes of nitrification and denitrification are the dominant sources of
104 N₂O from the soil (Butterbach-Bahl and others 2013). This occurs during the conversion of
105 NH₄⁺ to NO₃⁻ when ammonia is oxidized in nitrate in the presence of oxygen, and during the
106 conversion of NO₃⁻ to N₂O or N₂ 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 N₂O 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). N₂O is
110 emitted during these processes particularly when N availability is high. Production of N₂O,
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 N₂O 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 N₂O as they are able to produce N₂
117 from nitrite (NO₂⁻). 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 N₂O fluxes (Petitjean and others
145 2015) and none, to our knowledge, focused on CH₄. 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

168 long dry period from August to November (dry season, Supplementary Figure 1). Precipitation
169 during the dry period is typically $<50 \text{ mm mo}^{-1}$. The Nouragues site has sandy soils of variable
170 depth from a parental material of weathered granite (van der Meer and Bongers 1996). Study
171 plots at the Paracou site are located on schist soils with veins of pegmatite along a Precambrian
172 metamorphic formation called the Bonidoro series (Epron and others 2006). The soils at both
173 sites are characterized as nutrient-poor Acrisols (FAO-ISRIC-ISSS, 1998) (Nachtergaele and
174 others 2000).

175

176 *Study plots*

177 For this study, we picked three topographic positions: (1) top of hills (top hill), (2) the middle
178 of the slopes at intermediate elevation (middle slope) and (3) bottom end of the slopes, at low
179 elevation, just above the creek (bottom slope) (Table 1). At each site, four plots of $20 \times 20 \text{ m}$ per
180 topographic position were established (distances between plots of 10-200 m) in the vicinity of
181 long-term undisturbed monitoring plots that have been monitored at both sites for 30 years
182 (Figure 1). The sand content was higher and the clay contents was lower in the bottom slope
183 plots than in the top hill and middle slope plots at both sites (Table 1). In each plot, five
184 Polyvinyl chlorid (PVC) collars 20 cm in diameter were inserted into the soil six months prior
185 to the first measurement to an average depth of 3.8 cm ($\pm 0.5 \text{ cm}$) in the $20 \times 20 \text{ m}$ plot (Figure
186 1B), for a total of 120 sampling points (2 sites, 3 hill positions, 4 plots per position, 5 points per
187 plot).

188

189 *Soil characteristics*

190 Soil samples for chemical and physical characterization were collected on the same day
191 as fluxes. A composite soil sample of three soil cores around each sampling point (i.e. collars)
192 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-cm³
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 HNO₃, 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 NH₄⁺ and
208 NO₃⁻ were determined colorimetrically on a San++ continuous flow analyzer (Skalar Inc,
209 Breda, The Netherlands). The concentrations of NH₄⁺ and NO₃⁻ 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 CO₂, CH₄ and N₂O during each
221 campaign using opaque (no light allowed) static soil PVC chambers (volume, 0.0026 m³; area,
222 0.029 m², 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 CO₂, CH₄ and
232 N₂O 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 CO₂ and CH₄ detection
236 and a pulsed-discharge detector for N₂O detection.

237 The limits of detection (LoD) of CH₄ and N₂O 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 N₂O and 1.01, 2.16 and 4.17 ppm CH₄). 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 N₂O and 0.202 ppm for CH₄ over
248 all standards (n=54). Between different sample batches, the LoD varied only slightly between
249 0.115 and 0.130 ppm for N₂O and between 0.166 and 0.247 ppm for CH₄, 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 CO₂; 55% HMR and 45% LR for CH₄; 65% HMR and
256 35% LR for N₂O). 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 N₂O 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 N₂O and the coefficient of variation of 0.05 was defined from values of N₂O
262 at sampling time 0. Minimum detectable flux was $\pm 8.3 \mu\text{g N m}^{-2} \text{ h}^{-1}$, 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: $\log(\text{flux})$ for CO_2 and
270 $\log(\text{flux} - \min(\text{flux}) + 1)$ 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 Akaike'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 CO₂ 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 CH₄ in the dry campaign and sources of CH₄ 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 CH₄ fluxes in the wet period were net emissions,
305 and only 17% were net emissions in the dry period. Mean N₂O fluxes were negative in both
306 campaigns (mean fluxes of -30.7 ± 30.3 µg N m⁻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 N₂O.

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; CO₂ $\chi^2=1.19$ p=0.55; CH₄ $\chi^2=3.48$ p=0.18; N₂O $\chi^2=0.16$ 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 CO₂ 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 CH₄ flux was explained by only one
328 variable (GAM, SWC, Table 2, Figure 4), which explained 4.5% of the variation. The CH₄
329 fluxes were higher in wetter soils (Figure 4). The variation in N₂O 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 *CO₂ effluxes did not differ among topographical positions but were partly explained by soil* 334 *physical and chemical characteristics*

335 The soil CO₂ 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 CO₂ 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 CO₂
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 CO₂ 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 CO₂ effluxes. Soil pH was negatively correlated
355 with soil CO₂ 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 CO₂ 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 CO₂ effluxes as CO₂ effluxes were positively
362 correlated with available Nitrogen and negatively with total Phosphorus.

363

364 *CH₄ 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 CH₄ fluxes. Soil CH₄ fluxes were correlated
367 with SWC with only 4.5% of the variation explained by this variable. CH₄ 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 O₂ diffusion
371 into the soil (Silver and others 1999; Teh and others 2005; Liptzin and others 2011), decreasing
372 CH₄ oxidation, and increasing CH₄ 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 CH₄ fluxes need
375 to be conducted.

376

377 *N₂O uptake is linked to C:N ratio and total phosphorus*

378 Surprisingly, most of the N₂O 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 N₂O 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 N₂O fluxes within 10% of the true mean (in our study, 5 sampling locations per 400
386 m² 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 $-32 \mu\text{g N m}^{-2} \text{h}^{-1}$ measured in our study falls
388 within the range of negative N₂O fluxes of $-1.4 \text{ ng N m}^{-2} \text{h}^{-1}$ to $-484 \mu\text{g N m}^{-2} \text{h}^{-1}$ 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 N₂O 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 N₂O sink is linked to the abundance and phylogenetic diversity of a group of N₂O-
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 N₂O fluxes were significantly correlated
398 with soil nutrients, most of the variation in N₂O 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 N₂O fluxes. This could
402 be mostly due to the fact that we almost only measured N₂O consumption in our study (98% of
403 all sampling points) while other studies report mostly N₂O 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 NO₃⁻ 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 N₂O flux (Morley and Baggs, 2010, Morley et al., 2008). N₂O
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 N₂O 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 N₂O 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 N₂O 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 CH₄ uptake (Dutaur and Verchot 2007), which is large enough
432 to alter the accumulation of CH₄ 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

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452 identification and characterization of each topographical position and to Margarethe Watzka
453 for the gas analyses.

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 ₂ O	
	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

464 **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 \pm 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.

473 **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) CO₂,
483 (B) CH₄ and (C) N₂O 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).

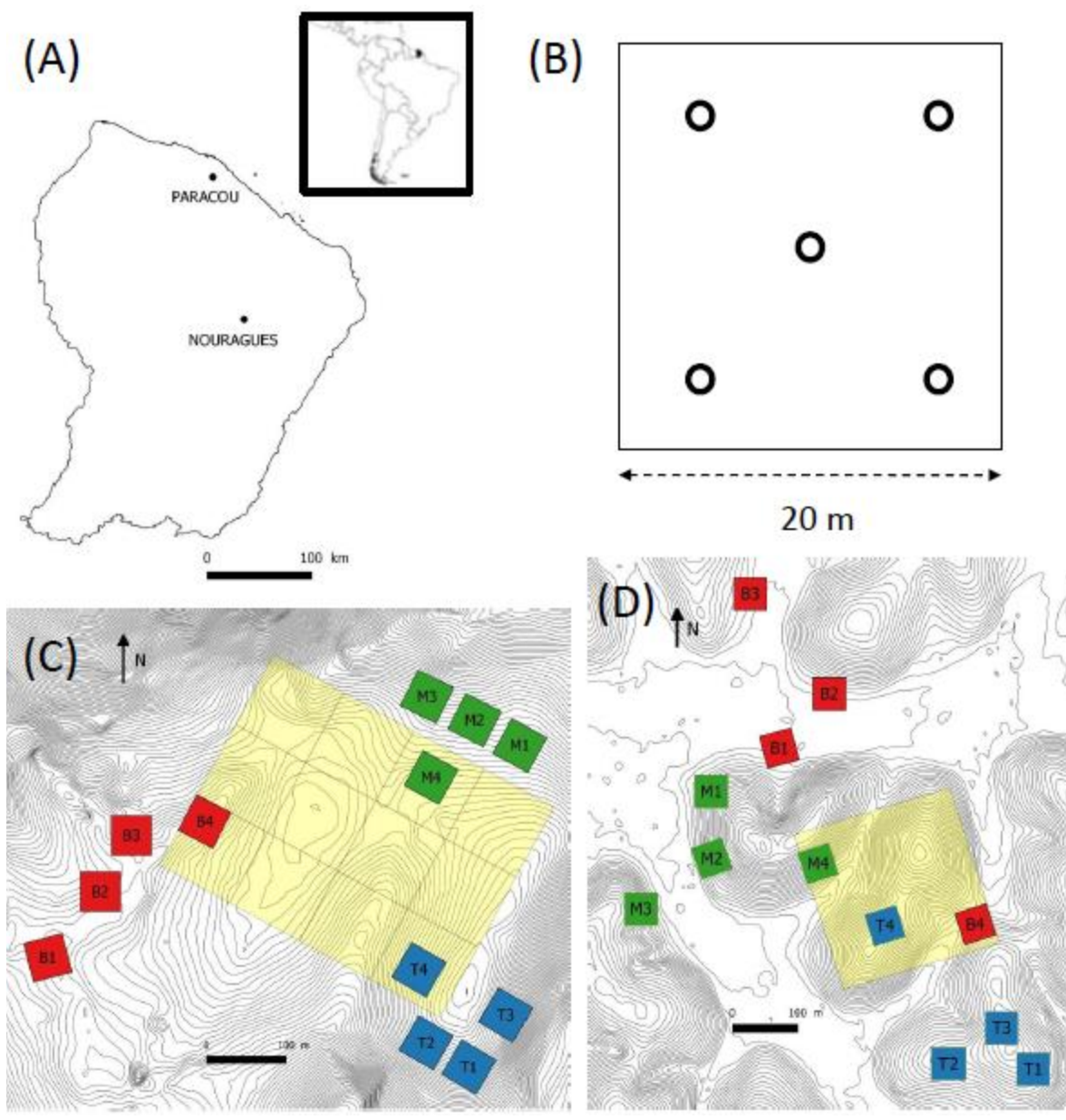
493

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) CO₂, (B) CH₄ and (C) N₂O. This value is computed as the total reduction

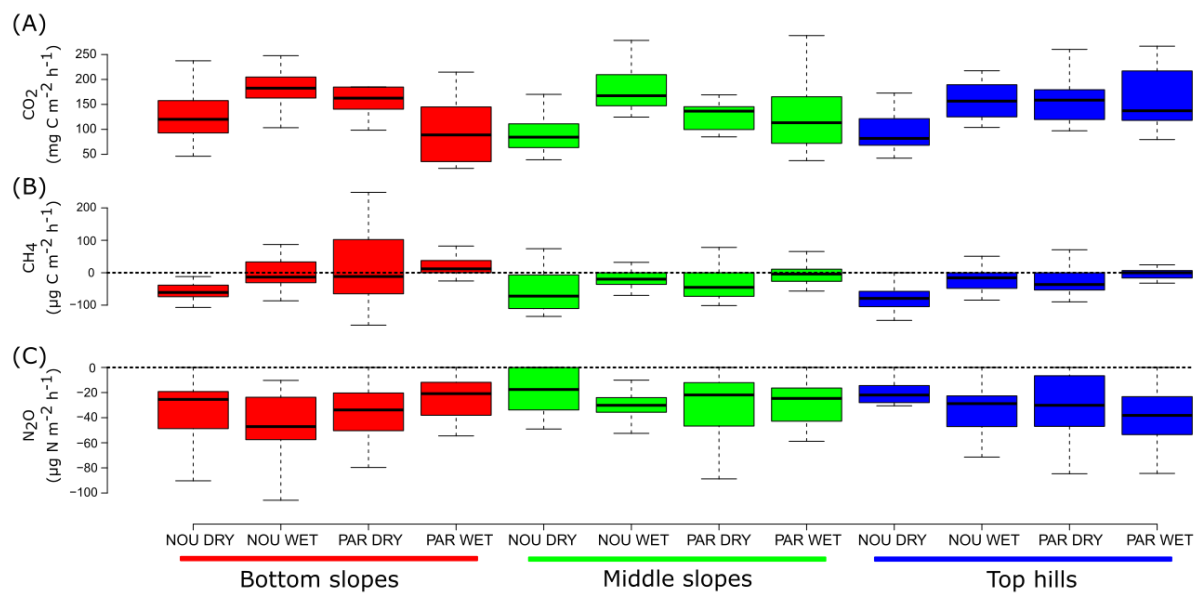
497 in the validation statistic (generalized cross-validation estimate of error) when each predictor's
498 feature is added to the model. Significant variables in GAMs are indicated by an asterisk.

499

500



503 **FIGURE 2**

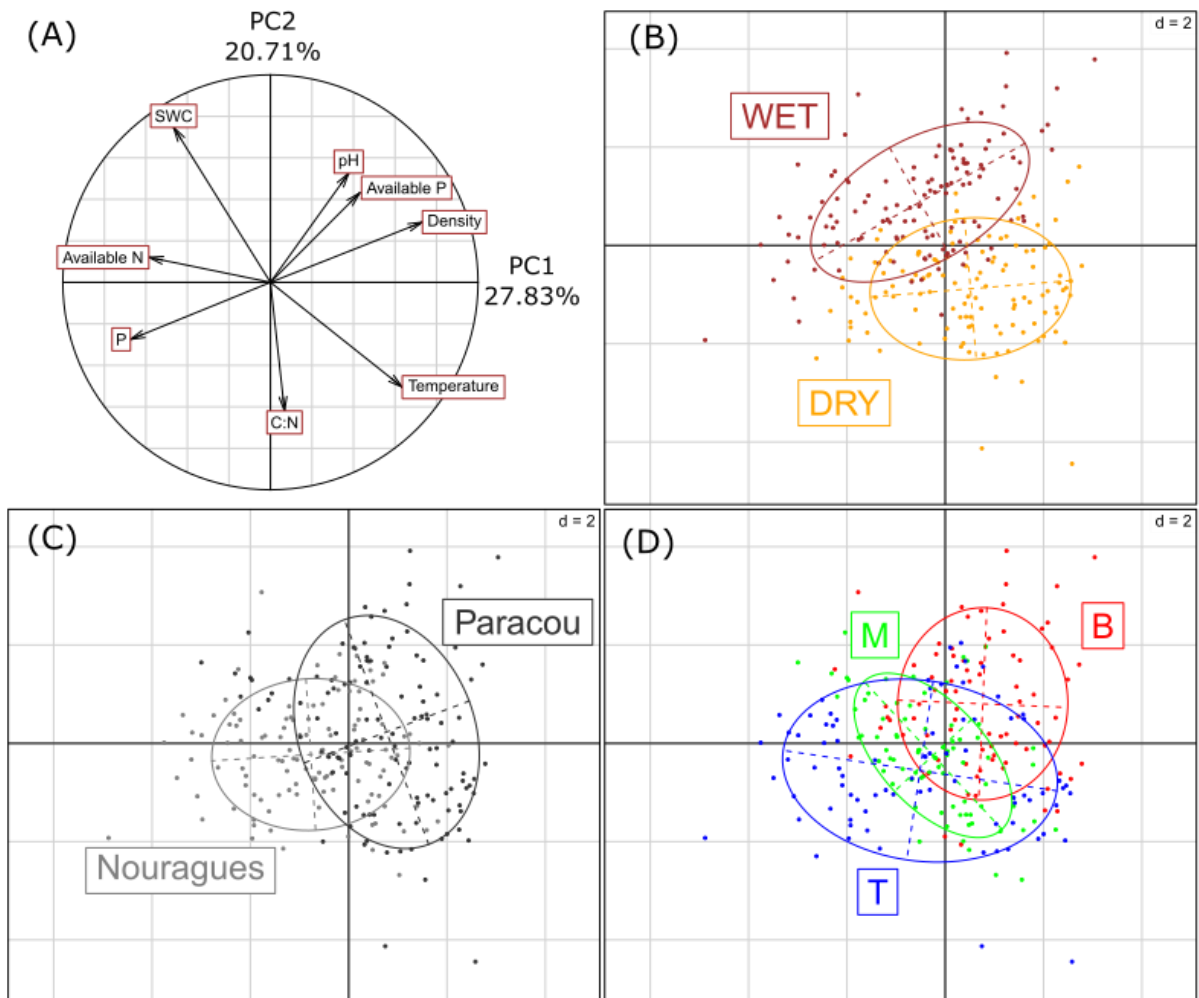


504

505

506

507 **FIGURE 3**

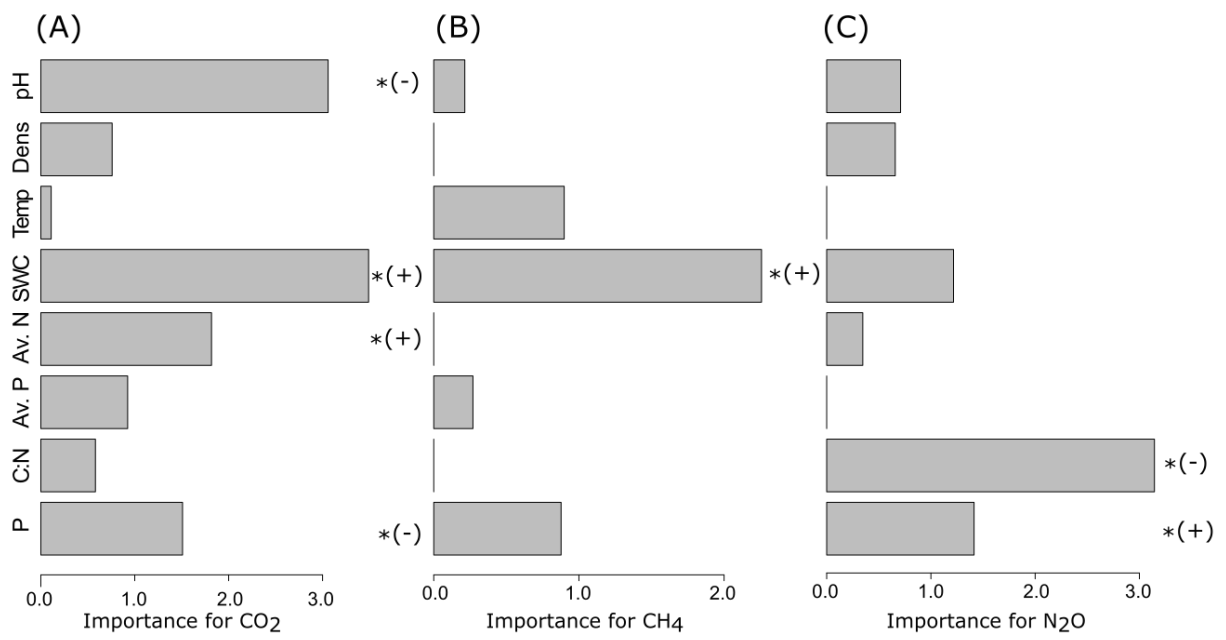


508

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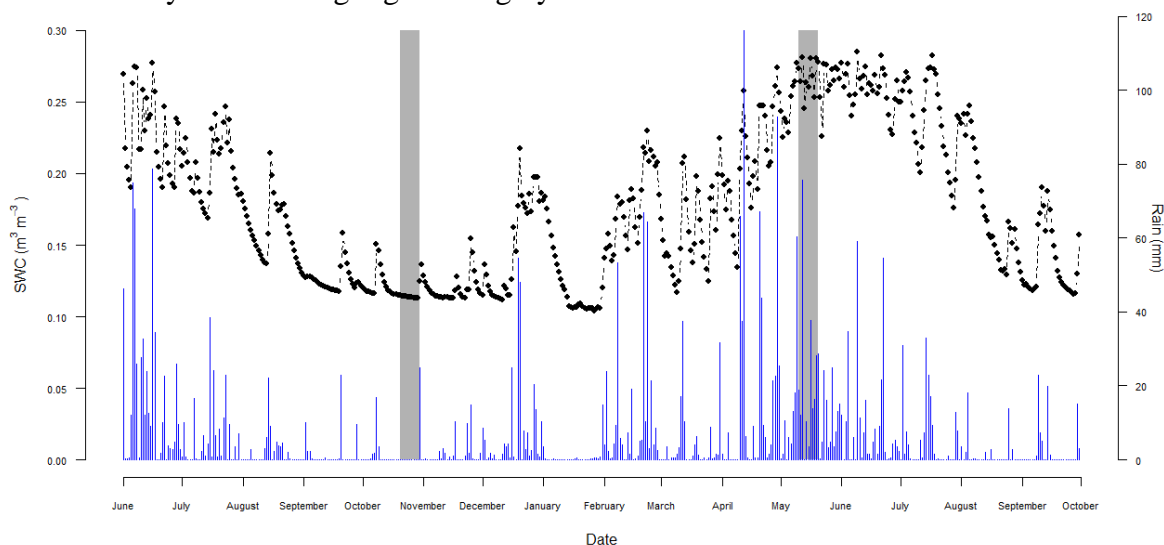
510 **FIGURE 4**

511



512

513 **Supplementary Figure 1:** Soil water content (in m^3m^{-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 \pm 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	CO ₂ (mg C m ⁻² h ⁻¹)	92.6 \pm 34.4	89.9 \pm 37.8.9	131.0 \pm 64.2.4	104.7 \pm 50.5	165.2 \pm 50.2	131.7 \pm 34.3	189.6 \pm 96.8	161.7 \pm 68.0	131.9 \pm 65.8
	CH ₄ ($\mu\text{g C m}^{-2} \text{h}^{-1}$)	-64.0 \pm 69.7	6.6 \pm 237.9	-49.9 \pm 50.1	-35.8 \pm 146.8	-44.0 \pm 139.7	-19.9 \pm 79.5	6.6 \pm 103.7	-19.1 \pm 109.3	-27.7 \pm 129.8
	N ₂ O ($\mu\text{g N m}^{-2} \text{h}^{-1}$)	-20.4 \pm 15.0	-20.1 \pm 17.4	-32.5 \pm 21.6	-25.0 \pm 19.1	-31.2 \pm 27.5	-41.4 \pm 54.5	-35.7 \pm 21.8	-36.1 \pm 37.2	-30.7 \pm 30.3
WET	CO ₂ (mg C m ⁻² h ⁻¹)	159.6 \pm 36.5	191.7 \pm 66.5	188.8 \pm 50.2	180.1 \pm 54.0	161.6 \pm 62.9	138.3 \pm 88.7	94.8 \pm 57.4	131.0 \pm 75.1	156.4 \pm 69.3
	CH ₄ ($\mu\text{g C m}^{-2} \text{h}^{-1}$)	-19.9 \pm 70.3	43.2 \pm 274.0	9.4 \pm 64.9	15.0 \pm 171.1	3.7 \pm 40.1	-1.9 \pm 41.2	23.9 \pm 34.6	8.9 \pm 39.5	12.0 \pm 125.2
	N ₂ O ($\mu\text{g N m}^{-2} \text{h}^{-1}$)	-30.7 \pm 30.9	-31.9 \pm 15.5	-55.4 \pm 47.6	-39.1 \pm 35.0	-49.7 \pm 49.8	-19.3 \pm 45.1	-18.0 \pm 70.9	-19.8 \pm 26.0	-33.4 \pm 47.4

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