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Short title: GHG soil fluxes in the Guiana shield

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EAC, CS, JVB, JP and IJ designed the study; EAC, CS, LVL an UI did the field work; LVL, AR and UI performed the chemical analysis, EAC and CS analyzed the data and all co-authors wrote the paper.

ABSTRACT

The spatial variation of soil greenhouse gas fluxes (GHG; carbon dioxide - CO_2, methane - CH_4 and nitrous oxide - N_2O) remain poorly understood in highly complex ecosystems such as tropical forests. We used 240 individual flux measurements of these three GHGs from different soil types, at three topographical positions and in two extreme hydric conditions in the tropical forests of the Guiana shield (French Guiana, South America) to (1) test the effect of topographical positions on GHG fluxes and (2) identify the soil characteristics driving flux variation in these nutrients-poor tropical soils. Surprisingly, none of the three GHG flux rates differed with topographical position. CO_2 effluxes covaried with soil pH, soil water content (SWC), available nitrogen and total phosphorus. The CH_4 fluxes were best explained by variation in SWC, with soils acting as a sink under drier conditions and as a source under wetter conditions. Unexpectedly, our study areas were generally sinks for N_2O and N_2O fluxes were partly explained by total phosphorus and available nitrogen concentrations. This first study describing the spatial variation of soil fluxes of the three main GHGs measured simultaneously in forests of the Guiana Shield lays the foundation for specific studies of the processes underlying the observed patterns.

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

soil surface, cannot differentiate the simultaneously occurring production and consumption within the soil but gives the result of these co-occurring processes.

Soil CO_2 efflux is the result of two main sources of CO_2 production in the soil: CO_2 respired by living roots and the rhizosphere, and CO_2 respired by heterotrophic microorganism activities during decomposition of fresh litter and soil organic matter (Hanson and others 2000; Janssens and others 2001). Soil temperature exerts a dominant control over the seasonal variation of CO_2 effluxes in temperate forests but is less important in tropical soils where temperatures are particularly high and stable year-round (Smith and others 2003). In contrast, in tropical soils, soil moisture and more generally the variation in precipitation are factors responsible for most of the seasonal variation in soil CO_2 effluxes (Davidson and others 2000b), with generally decreasing fluxes under drier conditions (Davidson and others 2000b; Bonal and others 2008; Rowland and others 2014; Meir and others 2015). Although microbial activity is often limited in dry conditions, very wet conditions can also inhibit CO_2 production in soils by limiting O_2 availability for decomposition processes and gas diffusivity (Davidson and others 2000b). While several studies have highlighted significantly higher CO_2 effluxes in lower topographic positions as compared to higher positions (Epron and others 2006; Brito and others 2009; Martin and Bolstad 2009; Riveros-Iregui and McGlynn 2009), such patterns are not always consistent (Arias-Navarro and others 2017). This could be due to high spatial heterogeneity in CO_2 effluxes, soil characteristics and nutrient availability in tropical forests.

CH_4 production is the result of the obligate relationships between fermentative bacteria and methanogenic archaea. This production primarily takes place in wetland soils (Bartlett and Harriss 1993) but can also occur in upland soils in anaerobic microsites (Silver and others 1999; Teh and others 2005; Liptzin and others 2011). In many parts of tropical forests, especially in lowlands, the soils can remain anoxic, for sometimes long periods, simulating wetland environments and enhancing methane production (Liptzin and others 2011). In well-aerated

soils, CH_4 can be oxidized by methanotrophic microorganisms and CH_4 oxidation normally exceeds production, which results in a net CH_4 uptake (Von Fischer and Hedin 2002, 2007). At an annual scale, the soils of tropical forests are generally a net sink for CH_4 (Dutaur and Verchot 2007). At fine temporal and spatial scales, the emission or consumption of CH_4 can vary depending on nutrient availability (Veldkamp and others 2013), soil oxygen availability (Silver and others 1999; Teh and others 2005; Liptzin and others 2011), bacterial community composition (Teh and others 2008), soil structure (Teh and Silver 2006) or soil water content (Davidson and others 2008). Similar to CO_2, contrasting evidence suggests either an effect (CH_4 uptake in ridges and slopes and emissions in valleys) (Silver and others 1999) or lack of an effect (Reiners and others 1998; Wolf and others 2012) of topographic position on CH_4 fluxes.

The microbial processes of nitrification and denitrification are the dominant sources of N_2O from the soil (Butterbach-Bahl and others 2013). This occurs during the conversion of NH_4^+ to NO_3^- when ammonia is oxidized in nitrate in the presence of oxygen, and during the conversion of NO_3^- to N_2O or N_2 when nitrate is used as an electron acceptor instead of oxygen (Davidson and Verchot 2000; Hall and others 2004). The relative importance of nitrification as a source of N_2O may depend on the microbial populations involved in ammonia oxidation which in turn can vary with soil pH (Hink and others 2017, Prosser and Nicol 2008). N_2O is emitted during these processes particularly when N availability is high. Production of N_2O, controlled by N availability and soil moisture is commonly found in tropical soils (Davidson and Verchot 2000; van Lent and others 2015). It is generally assumed that denitrification, the electron-transport-linked reduction of nitrogen oxides during respiration of heterotrophic bacteria, is responsible for N_2O consumption (Bremner, 1997). This also occurs in all biomes ranging from the tropics to the poles (Chapuis-Lardy and others 2007; Schlesinger 2013). In addition, nitrifiers also play a role in the consumption of N_2O as they are able to produce N_2 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^2~0.4). 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

the Guiana shield (Janssens and others 1998; Epron and others 2006; Bonal and others 2008; Bréchet and others 2011), only one study recently measured N_2O fluxes (Petitjean and others 2015) and none, to our knowledge, focused on CH_4. Soil water content and nutrient availabilities vary with topographical position in French Guianese tropical forests (Epron and others 2006; Ferry and others 2010; Stahl and others 2011; Allié and others 2015). This local spatial variation (less than 200 m) creates specific habitats that differ in terms of soil characteristics, aboveground vegetation (Sabatier and others 1997), forest structure (Baraloto and others 2007; Allié and others 2015) and forest dynamics (Ferry and others 2010). Here, we simultaneously measured the three soil GHG fluxes together with soil chemistry and characteristics in two hydrologically contrasting periods (dry and wet conditions) along three topographical positions (top hill, middle slope and bottom slope). Our main objectives were (1) to test whether topographical position has an impact on GHG fluxes and (2) to identify the main environmental drivers of the three GHG fluxes in these nutrient-poor soils.

METHODS

Description of the sites

This study was conducted in French Guiana, which is part of the Guiana Shield, one of three South American cratons (Gibbs and Barron 1993). More specifically, we sampled two sites: the Nouragues research station (Bongers 2001) (04°05′N, 52°40′W) and the Paracou research station (Gourlet-Fleury and others 2004) (04°15′N, 52°55′W) (Figure 1A). Both sites are covered by pristine tropical forest, receive similar mean annual quantities of rainfall (2990 and 3041 mm y^{-1} at Nouragues and Paracou, respectively) and have a mean annual air temperature near 25.7 °C (Bongers 2001; Gourlet-Fleury and others 2004). The tropical wet climate of French Guiana is highly seasonal due to the north/south movement of the Inter-Tropical 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 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 20×20 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 (± 0.5 cm) in the 20×20 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-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***

Two single-survey sampling campaigns were conducted at each site, one during the dry period (October 2015) and one during the wet period (May 2016) corresponding to the two extreme conditions in soil water content (Supplementary Figure 1) in order to capture the full range of local environment difference. We measured the soil fluxes of CO_2, CH_4 and N_2O during each campaign using opaque (no light allowed) static soil PVC chambers (volume, 0.0026 m^3; area, 0.029 m^2, designed in Antwerp laboratory) between 10 am and 2 pm in order to avoid diurnal variability (Teh et al 2014, Yan et al. 2014, Brechet et al. 2011). In total, 240 flux estimations were made during the two sampling campaign (60 sampling points in each forest in the two periods and the two sites). Each sampling point was therefore only measured once in each period. After the chambers were sealed onto the soil collars, four headspace gas samples were collected, one immediately after closure and then at subsequent 10-min intervals. Air samples were taken with a 12-mL syringe whose needle was inserted through a septum in the chamber and then injected into pre-evacuated 12-mL vials (Labco Limited, Ceredigion, UK). To mix the air in the chamber headspace prior to sampling, air was flushed five times with the syringe volume prior to the second, third and fourth air samples in each chamber. The CO_2, CH_4 and N_2O mole fractions in the gas samples were determined by gas chromatography (Trace GC Ultra, Thermo Fisher Scientific, Vienna, Austria) equipped with a vacuum dosing system (S+H Analytics, Germany). Gas samples were filled into a 1 ml sample loop at a pressure of 600 mbar. We used a flame ionization detector (FID) with a methanizer for CO_2 and CH_4 detection and a pulsed-discharge detector for N_2O detection.

The limits of detection (LoD) of CH_4 and N_2O were calculated from Least-Square Regression data according to the ICH (International Council for Harmonization). We used the "residual standard deviation of the regression line" method between the peak area and concentration of certified standards that were in the range of the detection limit (0.29, 0.54 and 0.91 ppm N_2O and 1.01, 2.16 and 4.17 ppm CH_4). We also checked our data for

homoscedasticity (i.e., independence of the peak area dispersion from the concentration of the standards). The LoD of the samples was then calculated as 3 times the standard deviation of the residuals divided by the slope of the linear regression of the calibration. For comparison, we also used the "standard deviation of the intercept" method, which yielded LoD values in the same range than the residual method. By using the "residual standard deviation of the regression line" method, we determined the LoD to be 0.116 ppm for N_2O and 0.202 ppm for CH_4 over all standards (n=54). Between different sample batches, the LoD varied only slightly between 0.115 and 0.130 ppm for N_2O and between 0.166 and 0.247 ppm for CH_4, respectively.

For 17 fluxes measurements (10 in wet period and 7 in dry period), data points were missing either due to problems in the field (i.e. leaks) or during laboratory analyses and these estimations were removed for the three gases. All other fluxes were computed using the HMR package (Pedersen 2010) for the three gases using Linear Regression (LR), or revised Hutchinson/Mosier (HMR) methods following recommendations from Pedersen and others (2010) (70% HMR and 30% LR for CO_2; 55% HMR and 45% LR for CH_4; 65% HMR and 35% LR for N_2O). Gas mixing ratios (ppm) were converted by using the Ideal Gas Law to solve for the quantity of gas in the headspace (on a mole or mass basis), normalized by the surface area of each static flux chamber.

Calculation of minimum detectable flux (MDF) of N_2O was made with the methodology developed by Parkin and others (2012). The mean concentration (i.e., ambient concentration) of 0.300 ppm of N_2O and the coefficient of variation of 0.05 was defined from values of N_2O at sampling time 0. Minimum detectable flux was ± 8.3 μg N m^{-2} h^{-1}, 27 fluxes (11%) were below the minimum detection limit (MDL) and included in the analysis as null fluxes.

Statistical analyses

In order to test the effect of topographical position on GHG fluxes, we performed a linear mixed-effects model (LMM) using topographical position (top hill, middle slope or bottom slope) as fixed explanatory variables and period (dry or wet season conditions) and site (Paracou or Nouragues) as random factor. Variables were transformed as follows: log (flux) for CO_2 and log (flux – min (flux) +1) for CH_4 and N_2O for this analysis. Significance was tested by comparing the null model to a model including topographical positions as fixed factor with a chi-square test.

The variations of soil characteristics were assessed with a principal component analysis (PCA) using eight soil variables (Total P, C:N ratio, SWC, air soil surface temperature - Temperature, soil density, soil pH, available P and available N). The spatial segregations of the measurements across period (dry or wet period), site (Paracou or Nouragues) and topographical position (top hill, middle slope or bottom slope) along the two main PCA axes were tested using permutational MANOVA (multivariate analysis of variance).

We used generalized additive model (GAM) for each gas to identify the best set of variables explaining the variation in the gas fluxes (candidates variables: Total P, C:N ratio, SWC, air soil surface temperature - Temperature, soil density, soil pH, available P and available N). GAMs are semi-parametric extensions of generalized linear models allowing non-linear and non-monotonic relationships between a response and a set of explanatory variables. The form of the predictor function is the principal originality of this method (Fewster and others 2000). The best model (i.e. explaining most of the variation) is selected using Akaikes's information criterion. Once the model best fitting the data is selected, a second step using recursive feature elimination allows for the ranking of variables using their importance in the model. For this, variables were backward selected using recursive feature elimination. Variable importance was then defined as the total reduction in the validation statistic (generalized cross-validation estimate of error) when each predictor's feature is added to the model.

All data were processed with R statistical software (R Development Core Team, 2010) using the package HMR (Pedersen and others 2010) for flux computation, the packages ade4 (Dray and Dufour 2007) and Momocs (Bonhomme and others 2014) for PCA analysis and permutational MANOVA respectively, the package lme4 (Bates and others 2014) for LMM, the packages mgcv (Wood and Wood 2007) for GAM, , and the package caret (Kuhn 2008) for recursive feature elimination of variables. .

RESULTS

Variation in GHG fluxes

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 mg C m^{-2} h^{-1} in the wet period (Figure 2, Supplementary table 1). Soils tended to be sinks of CH_4 in the dry campaign and sources of CH_4 in the wet campaign (mean fluxes of -27.7 ± 129.8 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, Supplementary table 1). Fifty percent of the CH_4 fluxes in the wet period were net emissions, and only 17% were net emissions in the dry period. Mean N_2O fluxes were negative in both campaigns (mean fluxes of -30.7 ± 30.3 µg Nm^{-2} h^{-1} in the dry season and -33.4 ± 47.4 µg N m^{-2} h^{-1} in the wet season, Figure 2, Supplementary table 1). Overall, 98% of the sampling points in the dry season and 95% in the wet season were sinks of N_2O.

Topographic positions and soil characteristics

Topographic position (top hill, middle slope, bottom slope) had no effect on any of the three gas fluxes (LMM; CO_2 χ^2=1.19 p=0.55; CH_4 χ^2=3.48 p=0.18; N_2O χ^2=0.16 p=0.92). The PCA classified the environmental variables over all sites into two principal components (PCs), which accounted for 51.4% of variation in the soil characteristics. PC1 (Figure 3A) explained 28.5% of the variance and was correlated positively with soil bulk density and temperature and

negatively with available N and total P and. PC2 (Figure 2A) explained 22.9% of the variance and was correlated positively with SWC and negatively with C:N. Soil characteristics in the dry and wet periods are differentiated using these two axes (MANOVA, $F=121.54$, $p<0.001$), mostly along the second axis (Figure 3B). Sites are also differentiated using these two axes (MANOVA, $F=33.14$, $p<0.001$), mostly along the first axis (Figure 3C). Despite the large overlapping areas in PCA (Figure 3D), MANOVA also indicated that Topographic position can be distinguished using this set of variables (MANOVA, $F=34.08$, $p<0.001$).

Spatial variation of soil GHG fluxes

The spatial variation in CO_2 efflux was significantly explained by four variables (GAM, SWC > soil pH > available N> Total P, Table 2, Figure 4). These four variables in combination explained 20.7% of the variation. The variation in the CH_4 flux was explained by only one variable (GAM, SWC, Table 2, Figure 4), which explained 4.5% of the variation. The CH_4 fluxes were higher in wetter soils (Figure 4). The variation in N_2O flux was explained by two variables (GAM, CN> Total P, Table 2, Figure 4), which explained 9.2% of the variation.

DISCUSSION

CO_2 effluxes did not differ among topographical positions but were partly explained by soil physical and chemical characteristics

The soil CO_2 effluxes measured in this study were within the ranges of previous studies in French Guianese forests (Janssens and others 1998; Epron and others 2006; Bonal and others 2008; Bréchet and others 2011; Rowland and others 2014). Contrary to previous studies in tropical forest (Brito and others 2009; Martin and Bolstad 2009; Riveros-Iregui and McGlynn 2009), even one conducted in French Guiana (Epron and others 2006), soil CO_2 fluxes were not related to topographic position. However, soil characteristics represented by the PCA analysis

also did not differ as much at the different topographic positions defined in this study as in other studies, which might explain this contrast. Moreover, in Epron and others (2006), all measurements were made in September, during the dry season only, which might explain the discrepancy between our study and their results. A recent study conducted in tropical areas (Arias-Navarro and others 2017) also did not detect any effect of topographic position on CO_2 effluxes despite a very good spatial coverage of the study site. This result is explained by the very large diversity of tree species in tropical forests (as in our two tropical pristine forest, Table 1), leading to heterogeneity in the chemical, structural, and functional traits of roots and leaves affecting biogeochemical processes (Hättenschwiler and others 2008; Townsend and others 2008) and resulting in a high spatial heterogeneity in soil respiration.

SWC and soil pH were the main drivers of soil CO_2 effluxes across topographical positions even if only 20.7% of the variation was explained by the model. In agreement with previous studies conducted in French Guiana (Bonal and others 2008; Rowland and others 2014), we found a positive relationship between SWC and CO_2 effluxes. Soil pH was negatively correlated with soil CO_2 effluxes as found in a previous study (Epron and others 2006) while in temperate areas several studies have highlighted the opposite pattern (Reth and others 2005; Chen and others 2015). This could be due to the relatively low pH (3.9 ± 0.2) of these French Guianese soils. The effect of pH alone is unknown on soil CO_2 effluxes but some studies suggest a combined effect of pH with some others components like clay content and soil organic matter (Epron and others 2006) or via decreased root respiration (Chen and others 2015). Nutrients availability also appears to have an influence on CO_2 effluxes as CO_2 effluxes were positively correlated with available Nitrogen and negatively with total Phosphorus.

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

As previously shown for other tropical sites (Reiners and others 1998; Wolf and others 2012), we found no impact of topographic positions on CH_4 fluxes. Soil CH_4 fluxes were correlated with SWC with only 4.5% of the variation explained by this variable. CH_4 fluxes shifted from uptake under dryer conditions to moderate emissions under wet conditions, similar to other tropical forest sites (Keller and Reiners 1994; Keller and others 2005; Davidson and others 2008; Teh and others 2014). Increased precipitation is likely to decrease rates of O_2 diffusion into the soil (Silver and others 1999; Teh and others 2005; Liptzin and others 2011), decreasing CH_4 oxidation, and increasing CH_4 emissions. Since no other studies are currently available in the surrounding area and as the temporal coverage of this study is not sufficient to estimate annual budgets from forests of the Guiana Shield, further investigations on soil CH_4 fluxes need to be conducted.

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

Surprisingly, most of the N_2O fluxes measured in this study were negative across the topographic positions and between hydric conditions (98% of the total samples). This was unexpected in light of the N-rich, wet conditions of these forests and based on previous results from French Guiana (Petitjean and others 2015) and other tropical soils (Teh and others 2013, 2014; van Lent and others 2015; Arias-Navarro and others 2017). The spatial resolution in our study is in line with an extensive survey of N_2O fluxes in Africa (Arias-Navarro and others 2017) which suggest that measurements at 78 ± 5 locations per hectare are needed to obtain an estimate of N_2O fluxes within 10% of the true mean (in our study, 5 sampling locations per 400 m^2 corresponds to 125 locations per hectare).We did not detect effects of topographic position on the magnitude of the uptake. The mean flux of -32 µg N m^{-2} h^{-1} measured in our study falls 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 the review by Chapuis-Lardy et al. (2007). More data at a broader spatial and temporal scale

are urgently needed to confirm the generality of this pattern and estimate the annual sink capacity of French Guianan soils.

The flux of N_2O measured with soil chambers at the soil/atmosphere interface is the result of dynamic production and consumption processes in the soil. This capacity of the soil to act as an N_2O sink is linked to the abundance and phylogenetic diversity of a group of N_2O-reducing microbes (Jones and others 2014). The community composition of these -micro-organisms is influenced by soil properties and in particular by soil stoichiometry (total P and C:N ratio) (Butterbach-Bahl and others 2013). While N_2O fluxes were significantly correlated with soil nutrients, most of the variation in N_2O fluxes remained unexplained in our study (only 9.2% of the variation explained by the model).

In contrast to other studies in tropical forest soils (Butterbach-Bahl and others 2004; Tang and others 2006; Luo and others 2013), SWC was not linked with N_2O fluxes. This could be mostly due to the fact that we almost only measured N_2O consumption in our study (98% of all sampling points) while other studies report mostly N_2O emission. Moreover, soils with a low water-retention capacity (which is the case for most of the French Guianan soils with high sand content) have limited anaerobic conditions. In addition, competition for NO_3^- between different nitrate-reducing processes under varying moisture conditions (e.g. dissimilatory nitrate reduction to ammonium versus denitrification) may obscure the relationship between soil moisture content and N_2O flux (Morley and Baggs, 2010, Morley et al., 2008). N_2O emissions from tropical soils can be sporadic and transient, e.g. after heavy rains (Breuer and others 2000; Nobre and others 2001), and are characterized by short pulses of emissions associated with higher nitrogen inputs (Bai and others 2014) or high precipitation events (Breuer and others 2000; Nobre and others 2001; Geng and others 2017). Nevertheless, we detected only one high N_2O emission event which could not be linked to a heavy rain, but this study was not designed to capture such a fine level of temporal variation. These transient strong

peaks of N_2O emission are likely responsible for the net emission budget of tropical soils highlighted in another study (Nobre and others 2001); a high frequency of N_2O flux measurements is urgently needed to confirm this relationship.

Conclusion and Perspectives

Our study has shed new light on the drivers of the three main GHG fluxes in tropical soils of the Guiana Shield. The fluxes of the three gases did not differ among topographical positions. Nevertheless, we highlighted the significant role of soil physical (SWC) and chemical (pH, Available N, C:N ratio and total P) properties as drivers of soil GHG fluxes even if most of the variation in the three GHG fluxes remains unexplained highlighting again their high spatial variability. Proximate controls on soil fluxes are complex and difficult to elucidate from field measurements alone and more experimental studies are also needed in order to disentangle the effect of different soil characteristics and microbial processes, which result in a modification of soil GHG fluxes. Nitrogen deposition is expected to increase in tropical areas (Penuelas and others 2013) which can induce soil acidification (Tian and Niu 2015) and changes in soil stoichiometry and could impact GHG emissions in the future. Tropical forest soils contribute an estimated 28% to the global CH_4 uptake (Dutaur and Verchot 2007), which is large enough to alter the accumulation of CH_4 in the atmosphere if large changes occur in this sink due to climate change such as increased drought (Brumme and others 1999).

Specific studies should be conducted to assess the influence of climatic changes (especially changes in precipitation and an increased occurrence or severity of drought) combined with modifications to soil stoichiometry (mainly by N deposition) on the magnitude of soil GHG fluxes in these poor-nutrient tropical soils over a long period in order to determine (1) the relative frequencies of consumption and emission and (2) the net GHG balance at annual scales.

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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

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**

TABLE LEGENDS

Table 1: Environmental characteristics of each topographical position (top hill, middle slope and bottom slope) at two tropical forest site sites (Nouragues and Paracou). Values are means ± standard errors (N=4). Percentages of sand and clay contents were determined for a composite sample from each topographical position at each site, so only one value is available for each topographical position.

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

FIGURE CAPTIONS

Figure 1: Site locations and experimental design. (A) Location of the two study sites (Paracou and Nouragues) in French Guiana. The insert shows the location of French Guiana in South America. (B) Experimental set-up of the five sampling points (collars) in each 20×20 m plot (gray). Location of the 12 plots by topographical position (top hill, blue; middle slope, green and bottom slope, red) at the Nouragues site (C) and the Paracou site (D) near the long-term undisturbed monitoring plots (yellow).

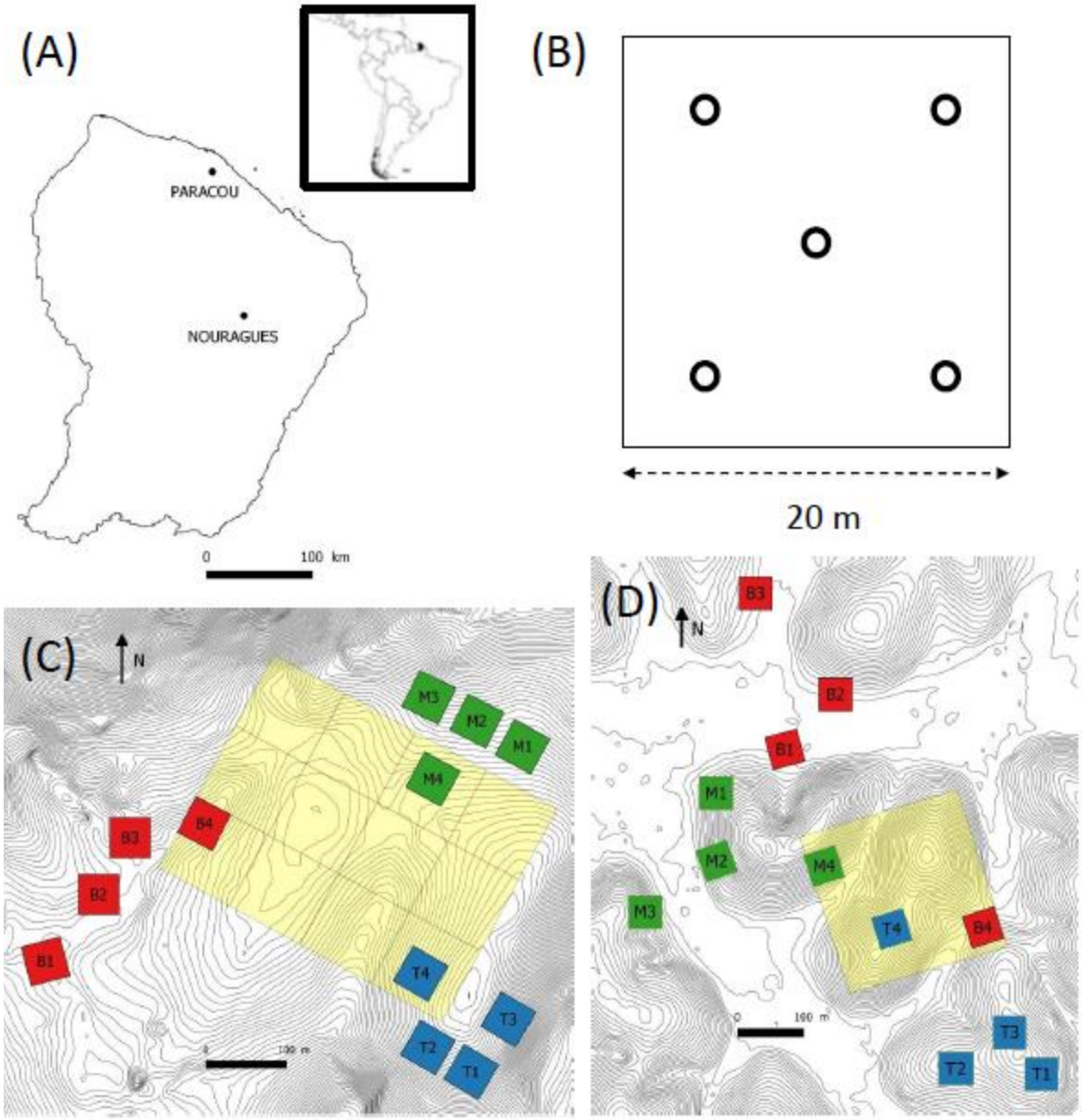
Figure 2: Variation of GHGs fluxes among topographical positions. Boxplot of (A) CO_2, (B) CH_4 and (C) N_2O by topographical position (T - top hill in blue; M - middle slope in green and B - bottom slope in red) for each site (Paracou – PAR; Nouragues – NOU) and each campaign (DRY – Dry period; WET – Wet period).

Figure 3: Principal component analysis of the soil variables. (A) Circular correlation plots of PC1 and PC2. (B) Projections of the water condition classes (dry period, orange; wet period, brown) on PC1 and PC2. (C) Projections of the site classes (Nouragues, light gray; Paracou, dark gray) on PC1 and PC2. (D) Projections of the topographical position (T, top hill, blue; M, middle slope, green and B, bottom slope, red) on PC1 and PC2 These two axes explain 51.4% of the variation in soil characteristics (28.5% for PC1, 22.9% for PC2 and 15.71% for PC3).

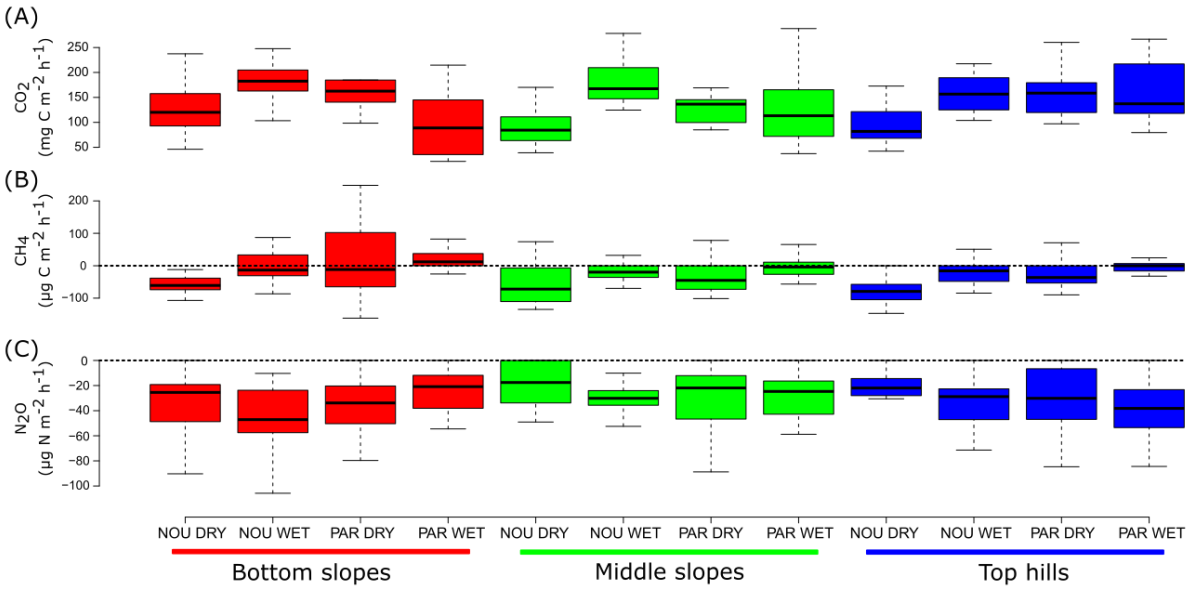
Figure 4: Variable importance. Importance of the variables (P - Total P, C:N, SWC, Temp - Temperature, Dens - density, pH, Av. P - Available P and Av. N - Available N) to the variation in the fluxes of (A) CO_2, (B) CH_4 and (C) N_2O. This value is computed as the total reduction

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

FIGURE 1


(A)
PARACOU
NOURAGUES
0
100 km
(B)
20 m
(C)
N
M3
M2
M1
M4
B3
B4
B2
B1
T4
T3
T2
T1
(D)
N
B3
B2
B1
M1
M2
M4
M3
T4
B4
T3
T2
T1

503 **FIGURE 2**



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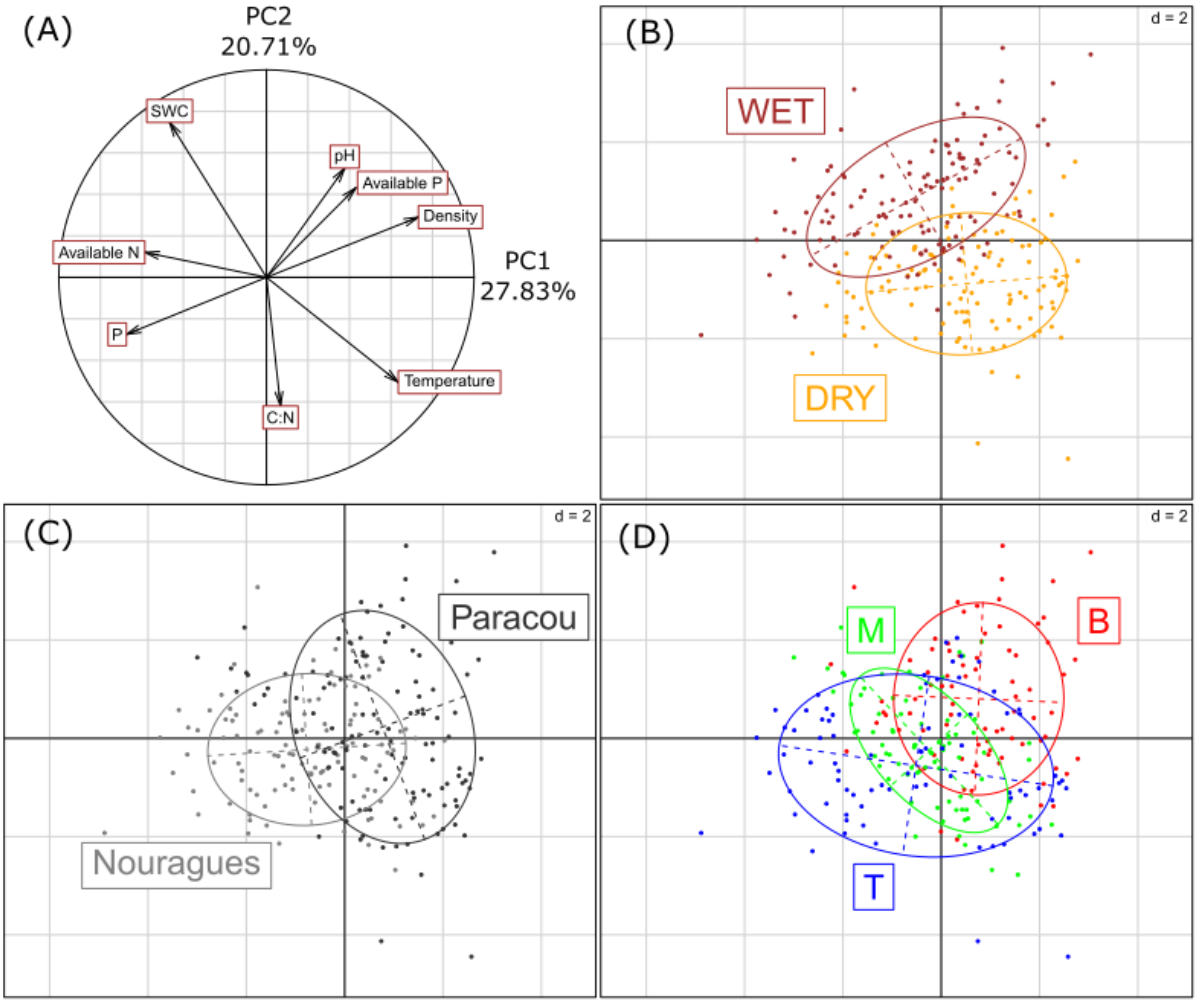
507 **FIGURE 3**



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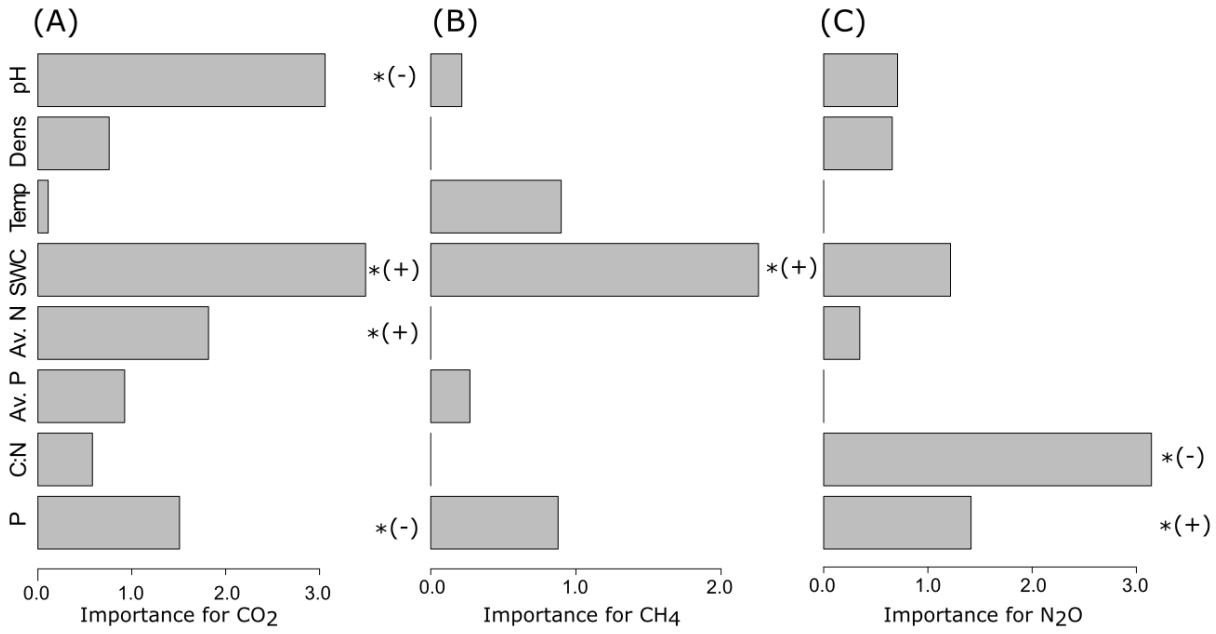
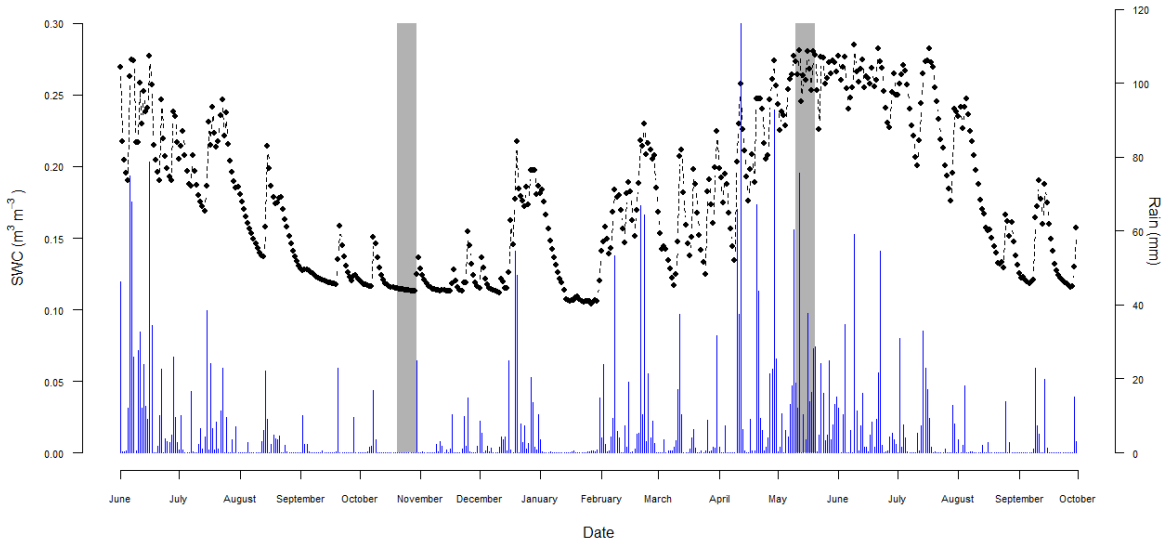
510 **FIGURE 4**

511



512

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



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

		Nouragues				Paracou				Total
		T	M	B	All	T	M	B	All	
DRY	CO_2 (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
	CH_4 (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**
	N_2O (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	CO_2 (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
	CH_4 (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
	N_2O (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**

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