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Title
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Spatial Variation of Soil CO_2, CH_4 and N_2O Fluxes Across Topographical Positions in Tropical Forests of the Guiana Shield

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Abstract

The spatial variation of soil greenhouse gas fluxes (GHG; carbon dioxide—CO_2, methane—CH_4 and nitrous oxide—N_2O) remains 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 nutrient-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.

Key words: tropical forest; GHG soil fluxes; Guiana Shield; soil characteristics; spatial variation; French Guiana

Elodie A. Courtois and Clément Stahl have contributed equally to the manuscript.

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). Although CO_2 effluxes from soils are always emissions,

N$_2$O 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 2000), with generally decreasing fluxes under drier conditions (Davidson and others 2000; 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 2000). Although several studies have highlighted significantly higher CO$_2$ effluxes in lower topographical 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 topographical 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^+–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 in 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 $(NO-2)(NO2-)$. This pathway, called nitrifier denitrification, is now known to proceed from $NO-2NO2-$ via nitric oxide (NO) and N_2O–N_2 (Schmidt and others 2004). Spatial variation and temporal variation in N_2O fluxes from the soil are notoriously high and require more understanding of the underlying soil characteristics that may drive N_2O production.

Soil temperature and moisture directly control production, consumption and transport of N_2O through effects caused by the metabolic activity of microorganisms, soil aeration and diffusivity (Luo and others 2013). Moreover, other environmental parameters have an effect on N_2O fluxes, such as oxygen availability, nutrient availability and pH of the soil (Weslien and others 2009; Rowlings and others 2012; Yang and

others 2017). A recent meta-analysis (van Lent and others 2015) indicates that tropical N_2O and NO fluxes can be expressed as a combination of nitrogen availability and water-filled pore space, even though the predictive power for simulating overall N_2O emissions was low ($R^2 \sim 0.4$). Emissions of N_2O from tropical soils are typically extremely variable in both space and time (Arias-Navarro and others 2017), with transient peaks associated with rain events (Nobre and others 2001; Petitjean and others 2015). N_2O fluxes from tropical forests are generally greater during rainy seasons than during dry seasons, a result observed in Amazon (Davidson and others 2004), Central Africa (Rees and others 2006) and in south Chinese forests (Werner and others 2006). Studies reported thus far generally agree that topographical position does have an effect on N_2O emissions with greater N_2O emissions in the valley bottom positions than top hill or midslope positions (Pennock and others 1992; Corre and others 1996; Silver and others 1999; Arias-Navarro and others 2017), yet the soil properties driving these patterns are not clear.

French Guiana is located in the Guiana Shield, a part of the Amazonian rainforest that remains one of the largest undisturbed tropical forests in the world (Hansen and others 2013). This tropical region lays on a Precambrian geological substrate that is particularly low in P content compared to the generally younger, nutrient-rich soils of western Amazonia (Hammond 2005; Grau and others 2017). Although 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 year^{-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 long dry period from August to November (dry season, Supplementary Figure 1). Precipitation during the dry period is typically less than 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).
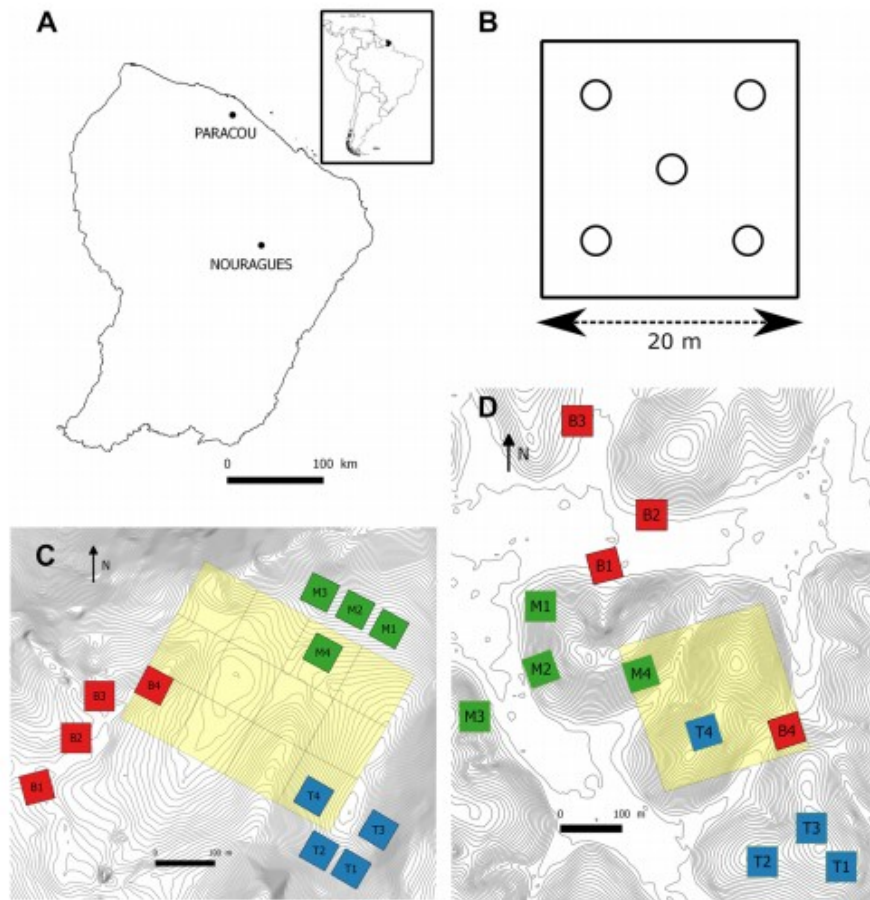
Figure 1. Site locations and experimental design. **A** Location of the two study sites (Paracou and Nouragues) in French Guiana. The insert shows the location of French Guiana in South America. **B** Experimental setup of the five sampling points (collars) in each 20 × 20 m plot (gray). Location of 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) (Color figure online).

Study Plots

For this study, we picked three topographical 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 topographical position were established (distances between plots of 10–200 m) in the vicinity of long-term undisturbed plots that have been monitored at both sites for 30 years (Figure 1). The sand content was higher, and the clay content 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 chloride (PVC) collars 20 cm in diameter were inserted into the soil 6 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).

Table 1. Environmental Characteristics of Each Topographical Position (Top Hill, Middle Slope and Bottom Slope) at Two Tropical Forest Sites (Nouragues and Paracou)

	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 (m^2 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

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.

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 (that is collars) was analyzed. Soil water content (SWC) at a depth of 10 cm and air surface temperature (average of three measurements) were recorded around each collar and on each sampling occasion using a time-domain reflectometer (IMKO-HD2 portable meter fitted with a PICO64 probe, Ettlingen, Germany). Soil bulk density to a depth of 5 cm was measured with 100-cm^3 cylinders. All other soil characteristics were measured on 0–15 cm top soil at each sampling point (once in the dry period and once in the wet period). Soil pH (KCl) was measured by mixing 10 g of moist soil with 1 M KCl in a 1:2.5 ratio. The resulting slurry was stirred for 1 h and then allowed to sit for another hour before pH was measured using a pH probe. The amount of total phosphorus (P in ppm) was determined through microwave digestion (CEM, MARS-5) of pulverized soils, previously dried for 48 h at 70°C, in trace-metal-free acid (mixture of concentrated HNO_3, HCl and HF). P concentrations in digests were measured on ICP-MS (Optima 4300 DV, Perkin-Elmer, Waltham, USA). The amount of available P (in ppm) was measured by Bray-P acid fluoride extraction (Bray and Kurtz 1945) of soil dried at 60°C for 48 h, and the resulting solution was analyzed on an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific). The amount of available nitrogen (N in ppm) was measured by extracting moist soil with 1 M KCl, after which the concentrations of NH_4^+ and NO_3^- were determined colorimetrically on a

SAN++ continuous flow analyzer (Skalar Inc, Breda, the Netherlands). The concentrations of NH_4^+ and NO_3^- were summed and treated as a single value during analyses and are reported hereafter as available N. Soil C and N concentrations (in percent) were determined by combustion (Elemental Analyzer, CE Instruments/Thermo Electron, Milan, Italy) coupled with gas chromatography/mass spectrometry (Delta V Advantage, Thermo Fisher Scientific, Cambridge, USA). Soil C:N ratios were obtained by dividing C concentrations (percent) by N concentrations (percent).

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) 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 a.m. and 2 p.m. to avoid diurnal variability (Teh and others 2014; Yan and others 2014; Brechet and others 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 (that is, 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 (that is, leaks) or during laboratory analyses and these estimations were removed for the three gases. All other fluxes were computed using the HMR package (Pedersen and others 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 (that is, 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} and 27 fluxes (11%) were below the minimum detection limit (MDL) and included in the analysis as null fluxes.

Statistical Analyses

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$_2$O 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 semiparametric extensions of generalized linear models allowing nonlinear 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 (that is, 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.
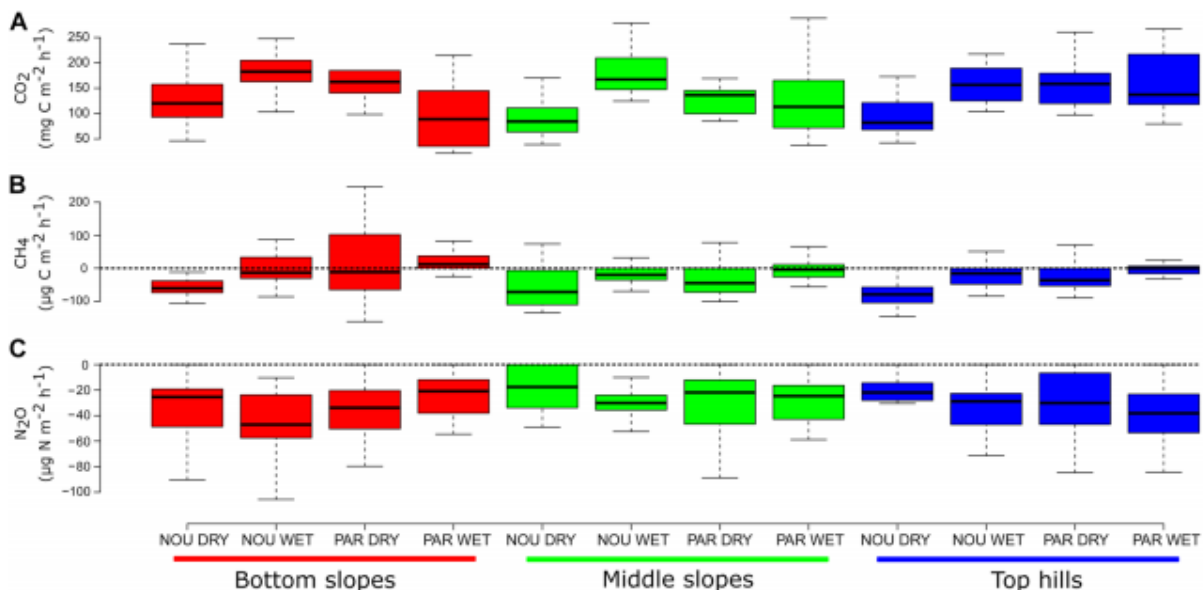

Figure 2. Variation of GHGs fluxes among topographical positions. Boxplot of **A** CO_2, **B** CH_4 and **C** N_2O by topographical position (*T*, top hill in blue; *M*, middle slope in green; and *B*, bottom slope in red) for each site (Paracou—PAR; Nouragues—NOU) and each campaign (DRY—dry period; WET—wet period) (Color figure online).

Topographical Positions and Soil Characteristics

Topographical position (top hill, middle slope, bottom slope) had no effect on any of the three 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 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 topographical position can be distinguished using this set of variables (MANOVA, $F = 34.08$, $p < 0.001$).
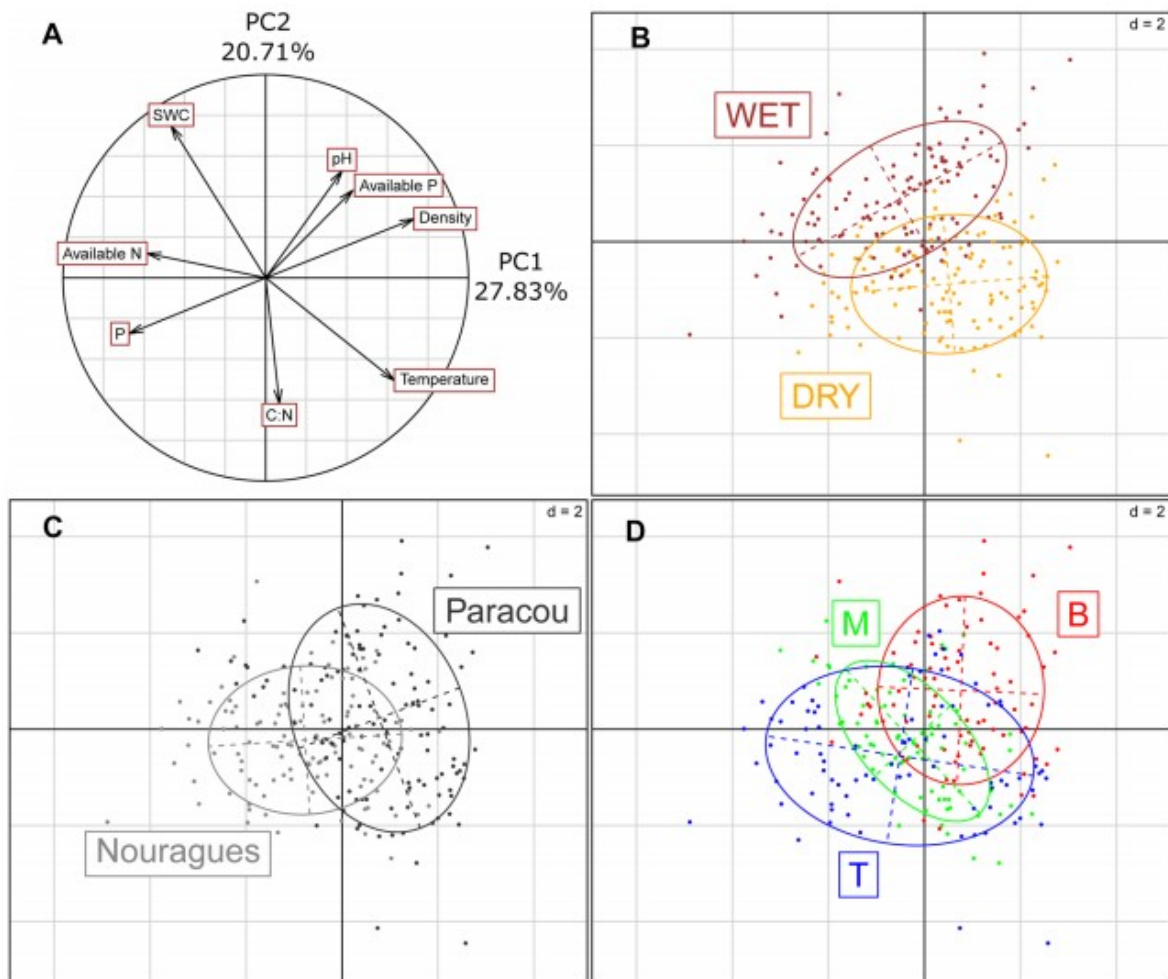

Figure 3. Principal component analysis of the soil variables. **A** Circular correlation plots of PC1 and PC2. **B** Projections of the water condition classes (dry period, orange; wet period, brown) on PC1 and PC2. **C** Projections of the site classes (Nouragues, light gray; Paracou, dark gray) on 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) (Color figure online).

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.

Table 2. Results from GAM Analysis

	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**

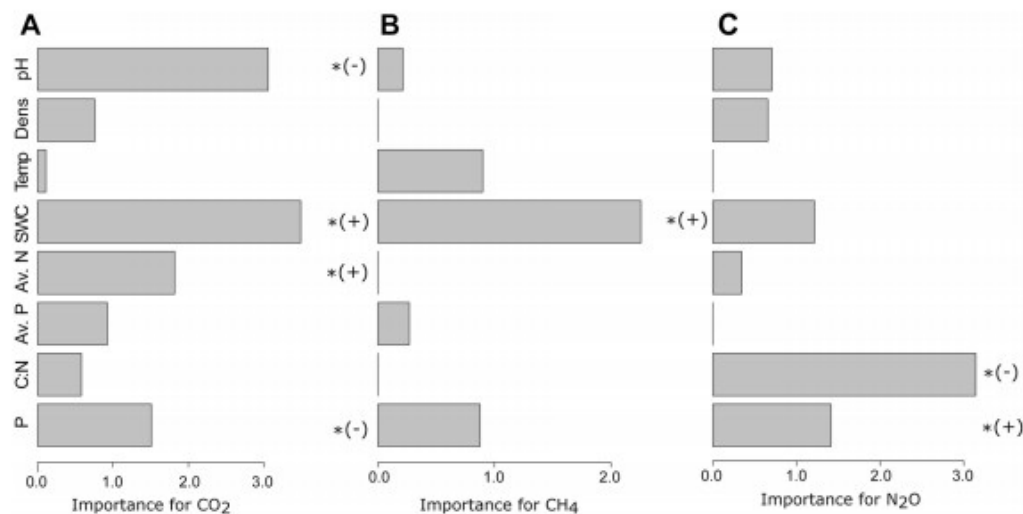*Significant p values are highlighted in bold.*

Figure 4. Variable importance. Importance of the variables (P, total P, C:N, SWC; Temp, temperature; Dens, density, pH; Av. P, available P; 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 in the validation statistic (generalized cross-validation estimate of error) when each predictor's feature is added to the model. Significant variables in GAMs are indicated by an asterisk.

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 though one conducted in French Guiana (Epron and others 2006), soil CO_2 fluxes were not related to topographical position. However, soil characteristics represented by the PCA analysis also did not differ as much at the different topographical positions defined in this study as in other studies, which might explain this contrast. Moreover, in Epron and others (2006), all measurements were taken 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 topographical 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 forests, 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), whereas 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 topographical 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. Because 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 topographical 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 correspond to 125 locations per hectare). We did not detect effects of topographical 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 and others (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 microorganisms is influenced by soil properties and in particular by soil stoichiometry (total P and C:N ratio)

(Butterbach-Bahl and others 2013). Although 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), whereas 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 (for example, dissimilatory nitrate reduction to ammonium versus denitrification) may obscure the relationship between soil moisture content and N_2O flux (Morley and Baggs 2010; Morley and others 2008). N_2O emissions from tropical soils can be sporadic and transient, for example, 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 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 to determine (1) the relative frequencies of consumption and emission and (2) the net GHG balance at annual scales.

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References

Allié E, Pélissier R, Engel J, Petronelli P, Freycon V, Deblauwe V, Soucémarianadin L, Weigel J, Baraloto C. 2015. Pervasive local-scale tree-soil habitat association in a tropical forest community. PLoS ONE 10:e0141488.

Arias-Navarro C, Díaz-Pinés E, Klatt S, Brandt P, Rufino MC, Butterbach-Bahl K, Verchot L. 2017. Spatial variability of soil N_2O and CO_2 fluxes

in different topographic positions in a tropical montane forest in Kenya. J Geophys Res Biogeosci 122:514–27.

Bai Z, Yang G, Chen H, Zhu Q, Chen D, Li Y, Wang X, Wu Z, Zhou G, Peng C. 2014. Nitrous oxide fluxes from three forest types of the tropical mountain rainforests on Hainan Island, China. Atmos Environ 92:469–77.

Baraloto C, Morneau F, Bonal D, Blanc L, Ferry B. 2007. Seasonal water stress tolerance and habitat associations within four neotropical tree genera. Ecology 88:478–89.

Bartlett KB, Harriss RC. 1993. Review and assessment of methane emissions from wetlands. Chemosphere 26:261–320.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: linear mixed-effects models using Eigen and S4. R Package Version 1(7):1–23.

Bonal D, Bosc A, Ponton S, Goret J, Burban B, Gross P, Bonnefond J, Elbers J, Longdoz B, Epron D. 2008. Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. Glob Change Biol 14:1917–33.

Bongers F. 2001. Nouragues: dynamics and plant-animal interactions in a Neotropical rainforest. Berlin: Springer.

Bonhomme V, Picq S, Gaucherel C, Claude J. 2014. Momocs: outline analysis using R. J Stat Softw 56(13):1–24.

Bray RH, Kurtz LT. 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59:39–46.

Bréchet L, Ponton S, Alméras T, Bonal D, Epron D. 2011. Does spatial distribution of tree size account for spatial variation in soil respiration in a tropical forest? Plant Soil 347:293–303.

Bremner JM. 1997. Sources of nitrous oxide in soils. Nutrient Cycl Agroecosyst 49:7–16.

Breuer L, Papen H, Butterbach-Bahl K. 2000. N_2O emission from tropical forest soils of Australia. J Geophys Res Atmos 105:26353–67.

Brito LDF, Marques Júnior J, Pereira GT, Souza ZM, La Scala Júnior N. 2009. Soil CO_2 emission of sugarcane fields as affected by topography. Sci Agric 66:77–83.

Brumme R, Borken W, Finke S. 1999. Hierarchical control on nitrous oxide emission in forest ecosystems. Glob Biogeochem Cycles 13:1137–48.

Butterbach-Bahl K, Kock M, Willibald G, Hewett B, Buhagiar S, Papen H, Kiese R. 2004. Temporal variations of fluxes of NO, NO_2, N_2O, CO_2, and CH_4 in a tropical rain forest ecosystem. Glob Biogeochem Cycles 18(3):GB3012.

Butterbach-Bahl K, Baggs E, Dannenmann M, Kiese R, Zechmeister-Boltenstern S. 2013. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Philos Trans R Soc Lond Ser B 368(1621):20130122.

Chapuis-Lardy L, Wrage N, Metay A, Chotte J, Bernoux M. 2007. Soils, a sink for N_2O? A review. Glob Change Biol 13:1–17.

Chen D, Li J, Lan Z, Hu S, Bai Y. 2015. Soil acidification exerts a greater control on soil respiration than soil nitrogen availability in grasslands subjected to long-term nitrogen enrichment. Funct Ecol 30(4):658–69.

Corre M, Van Kessel C, Pennock D. 1996. Landscape and seasonal patterns of nitrous oxide emissions in a semiarid region. Soil Sci Soc Am J 60:1806–15.

Davidson EA, Verchot LV. 2000. Testing the hole-in-the-pipe model of nitric and nitrous oxide emissions from soils using the TRAGNET database. Glob Biogeochem Cycles 14:1035–43.

Davidson EA, Verchot LV, Cattanio JH, Ackerman IL, Carvalho J. 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48:53–69.

Davidson EA, Ishida FY, Nepstad DC. 2004. Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. Glob Change Biol 10:718–30.

Davidson EA, Nepstad DC, Ishida FY, Brando PM. 2008. Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. Glob Change Biol 14:2582–90.

Dray S, Dufour AB. 2007. The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20.

Dutaur L, Verchot LV. 2007. A global inventory of the soil CH_4 sink. Glob Biogeochem Cycles 21:GB4013. https://doi.org/10.1029/2006GB002734.

Epron D, Bosc A, Bonal D, Freycon V. 2006. Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana. J Trop Ecol 22:565–74.

Fang Y, Gundersen P, Zhang W, Zhou G, Christiansen JR, Mo J, Dong S, Zhang T. 2009. Soil–atmosphere exchange of N_2O, CO_2 and CH_4 along a slope of an evergreen broad-leaved forest in southern China. Plant Soil 319:37–48.

Ferry B, Morneau F, Bontemps J, Blanc L, Freycon V. 2010. Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. J Ecol 98:106–16.

Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD. 2000. Analysis of population trends for farmland birds using generalized additive models. Ecology 81:1970–84.

Geng S, Chen Z, Han S, Wang F, Zhang J. 2017. Rainfall reduction amplifies the stimulatory effect of nitrogen addition on N_2O emissions from a temperate forest soil. Sci Rep 7:43329.

Gibbs AK, Barron CN. 1993. The geology of the Guiana Shield. Oxford: Oxford University Press.

Gourlet-Fleury S, Guehl J-M, Laroussinie O. 2004. Ecology and management of a neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana: Elsevier.

Grau O, Peñuelas J, Ferry B, Freycon V, Blanc L, Desprez M, Baraloto C, Chave J, Descroix L, Dourdain A. 2017. Nutrient-cycling mechanisms other than the direct absorption from soil may control forest structure and dynamics in poor Amazonian soils. Sci Rep 7:45017.

Hall SJ, Asner GP, Kitayama K. 2004. Substrate, climate, and land use controls over soil N dynamics and N-oxide emissions in Borneo. Biogeochemistry 70:27–58.

Hammond DS. 2005. Tropical forests of the Guiana shield: ancient forests in a modern world. Wallingford: CABI.

Hanson P, Edwards N, Garten C, Andrews J. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–46.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova S, Tyukavina A, Thau D, Stehman S, Goetz S, Loveland T. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–3.

Hättenschwiler S, Aeschlimann B, Coûteaux M, Roy J, Bonal D. 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytol 179:165–75.

Hink L, Nicol GW, Prosser JI. 2017. Archaea produce lower yields of N_2O than bacteria during aerobic ammonia oxidation in soil. Environ Microbiol 19:4829–37.

Hörtnagl L, Wohlfahrt G. 2014. Methane and nitrous oxide exchange over a managed hay meadow. Biogeosci Online 11:7219.

Janssens IA, Barigah ST, Ceulemans R. 1998. Soil CO_2 efflux rates in different tropical vegetation types in French Guiana. In: EDP sciences, Vol. 55, pp 671–80.

Janssens I, Lankreijer H, Matteucci G, Kowalski A, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grünwald T. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Glob Change Biol 7:269–78.

Jones CM, Spor A, Brennan FP, Breuil M-C, Bru D, Lemanceau P, Griffiths B, Hallin S, Philippot L. 2014. Recently identified microbial guild mediates soil N_2O sink capacity. Nat Clim Change 4:801–5.

Keller M, Reiners WA. 1994. Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. Glob Biogeochem Cycles 8:399–409.

Keller M, Varner R, Dias JD, Silva H, Crill P, de Oliveira Jr RC, Asner GP. 2005. Soil–atmosphere exchange of nitrous oxide, nitric oxide, methane, and carbon dioxide in logged and undisturbed forest in the Tapajos National Forest, Brazil. Earth Interact 9:1–28.

Kuhn M. 2008. Caret package. J Stat Softw 28:1–26.

Liptzin D, Silver WL, Detto M. 2011. Temporal dynamics in soil oxygen and greenhouse gases in two humid tropical forests. Ecosystems 14:171–82.

Luizao RC, Luizao FJ, Paiva RQ, Monteiro TF, Sousa LS, Kruijt B. 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. Glob Change Biol 10:592–600.

Luo G, Kiese R, Wolf B, Butterbach-Bahl K. 2013. Effects of soil temperature and moisture on methane uptake and nitrous oxide emissions across three different ecosystem types. Biogeosciences 10:3205–19.

Martin JG, Bolstad PV. 2009. Variation of soil respiration at three spatial scales: components within measurements, intra-site variation and patterns on the landscape. Soil Biol Biochem 41:530–43.

Meir P, Wood TE, Galbraith DR, Brando PM, Da Costa AC, Rowland L, Ferreira LV. 2015. Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: insights from field experiments. BioScience 65:882–92.

Merbold L, Steinlin C, Hagedorn F. 2013. Winter greenhouse gas fluxes (CO_2, CH_4 and N_2O) from a subalpine grassland. Biogeosciences 10:3185–203.

Merbold L, Wohlfahrt G, Butterbach-Bahl K, Pilegaard K, DelSontro T, Stoy P, Zona D. 2015. Preface: towards a full greenhouse gas balance of the biosphere. Biogeosciences 12:453–6.

Morley N, Baggs EM. 2010. Carbon and oxygen controls on N_2O and N_2 production during nitrate reduction. Soil Biol Biochem 42:1864–71.

Morley N, Baggs EM, Dörsch P, Bakken L. 2008. Production of NO, N_2O and N_2 by extracted soil bacteria, regulation by NO_2 − and O_2 concentrations. FEMS Microbiol Ecol 65:102–12.

Nachtergaele FO, Spaargaren O, Deckers JA, Ahrens B. 2000. New developments in soil classification: world reference base for soil resources. Geoderma 96:345–57.

Nobre A, Keller M, Crill P, Harriss R. 2001. Short-term nitrous oxide profile dynamics and emissions response to water, nitrogen and carbon additions in two tropical soils. Biol Fertil Soils 34:363–73.

Parkin TB, Venterea RT, Hargreaves SK. 2012. Calculating the detection limits of chamber-based soil greenhouse gas flux measurements. J Environ Qual 41:705–15.

Pedersen AR, Petersen SO, Schelde K. 2010. A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers. Eur J Soil Sci 61(6):888–902.

Peichl M, Arain A, Moore T, Brodeur J, Khomik M, Ullah S, Restrepo-Coupé N, McLaren J, Pejam M. 2014. Carbon and greenhouse gas balances in an age sequence of temperate pine plantations. Biogeosciences 11:5399–410.

Pennock D, Van Kessel C, Farrell R, Sutherland R. 1992. Landscape-scale variations in denitrification. Soil Sci Soc Am J 56:770–6.

Penuelas J, Poulter B, Sardans J, Ciais P, van der Velde M, Bopp L, Boucher O, Godderis Y, Hinsinger P, Llusia J. 2013. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nat Commun 4:2934.

Petitjean C, Hénault C, Perrin A-S, Pontet C, Metay A, Bernoux M, Jehanno T, Viard A, Roggy J-C. 2015. Soil N_2O emissions in French Guiana after the conversion of tropical forest to agriculture with the chop-and-mulch method. Agric Ecosyst Environ 208:64–74.

Prosser JI, Nicol GW. 2008. Relative contributions of archaea and bacteria to aerobic ammonia oxidation in the environment. Environ Microbiol 10:2931–41.

Reiners WA, Keller M, Gerow KG. 1998. Estimating rainy season nitrous oxide and methane fluxes across forest and pasture landscapes in Costa Rica. Water Air Soil Pollut 105:117–30.

Rees RM, Wuta M, Furley PA, Li C. 2006. Nitrous oxide fluxes from savanna(miombo) woodlands in Zimbabwe. J Biogeogr 33:424–37.

Reth S, Reichstein M, Falge E. 2005. The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO_2 efflux—a modified model. Plant Soil 268:21–33.

Riveros-Iregui DA, McGlynn BL. 2009. Landscape structure control on soil CO_2 efflux variability in complex terrain: Scaling from point observations to watershed scale fluxes. J Geophys Res Biogeosci 114:G2.

Rowland L, Hill TC, Stahl C, Siebicke L, Burban B, Zaragoza-Castells J, Ponton S, Bonal D, Meir P, Williams M. 2014. Evidence for strong seasonality in the carbon storage and carbon use efficiency of an Amazonian forest. Glob Change Biol 20:979–91.

Rowlings D, Grace P, Kiese R, Weier K. 2012. Environmental factors controlling temporal and spatial variability in the soil-atmosphere exchange of CO_2, CH_4 and N_2O from an Australian subtropical rainforest. Glob Change Biol 18:726–38.

Sabatier D, Grimaldi M, Prévost M-F, Guillaume J, Godron M, Dosso M, Curmi P. 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecol 131:81–108.

Schlesinger WH. 2013. An estimate of the global sink for nitrous oxide in soils. Glob Change Biol 19:2929–31.

Schmidt I, van Spanning RJM, Jetten MSM. 2004. Denitrification and ammonia oxidation by *Nitrosomonas europaea* wild-type, and NirK- and NorB-deficient mutants. Microbiology 150:4107–14.

Silver WL, Lugo A, Keller M. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44:301–28.

Smith K, Ball T, Conen F, Dobbie K, Massheder J, Rey A. 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. Eur J Soil Sci 54:779–91.

Stahl C, Burban B, Goret J-Y, Bonal D. 2011. Seasonal variations in stem CO_2 efflux in the Neotropical rainforest of French Guiana. Ann For Sci 68:771–82.

Tang X, Liu S, Zhou G, Zhang D, Zhou C. 2006. Soil-atmospheric exchange of CO_2, CH_4, and N_2O in three subtropical forest ecosystems in southern China. Glob Change Biol 12:546–60.

Teh YA, Silver WL. 2006. Effects of soil structure destruction on methane production and carbon partitioning between methanogenic pathways in tropical rain forest soils. J Geophys Res Biogeosci 111:G1.

Teh YA, Silver WL, Conrad ME. 2005. Oxygen effects on methane production and oxidation in humid tropical forest soils. Glob Change Biol 11:1283–97.

Teh YA, Dubinsky EA, Silver WL, Carlson CM. 2008. Suppression of methanogenesis by dissimilatory Fe(III)-reducing bacteria in tropical rain forest soils: implications for ecosystem methane flux. Glob Change Biol 14:413–22.

Teh Y, Diem T, Jones S, Huaraca Quispe L, Baggs E, Morley N, Richards M, Smith P, Meir P. 2013. Methane and nitrous oxide fluxes from the tropical Andes. Biogeosci Discuss 10:17397–438.

Teh Y, Diem T, Jones S, Huaraca Quispe LP, Baggs E, Morley N, Richards M, Smith P, Meir P. 2014. Methane and nitrous oxide fluxes across an elevation gradient in the tropical Peruvian Andes. Biogeosciences 11:2325–39.

Tian D, Niu S. 2015. A global analysis of soil acidification caused by nitrogen addition. Environ Res Lett 10:024019.

Townsend AR, Asner GP, Cleveland CC. 2008. The biogeochemical heterogeneity of tropical forests. Trends Ecol Evol 23:424–31.

van der Meer PJ, Bongers F. 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. J Ecol 84(1):19–29.

van Lent J, Hergoualc'h K, Verchot L. 2015. Reviews and syntheses: soil N_2O and NO emissions from land use and land use change in the tropics and subtropics: a meta-analysis. Biogeosciences 12:7299–313.

Veldkamp E, Koehler B, Corre M. 2013. Indications of nitrogen-limited methane uptake in tropical forest soils. Biogeosciences 10:5367–79.

Von Fischer JC, Hedin LO. 2002. Separating methane production and consumption with a field-based isotope pool dilution technique. Glob Biogeochem Cycles 16(3):8-1–8-13. https://doi.org/10.1029/2001GB001448.

Von Fischer JC, Hedin LO. 2007. Controls on soil methane fluxes: tests of biophysical mechanisms using stable isotope tracers. Glob Biogeochem Cycles. https://doi.org/10.1029/2006GB002687.

Werner C, Zheng X, Tang J, Xie B, Liu C, Kiese R, Butterbach-Bahl K. 2006. N_2O, CH_4 and CO_2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. Plant Soil 289:335–53.

Weslien P, Kasimir Klemedtsson Å, Börjesson G, Klemedtsson L. 2009. Strong pH influence on N_2O and CH_4 fluxes from forested organic soils. Eur J Soil Sci 60:311–20.

Wolf K, Flessa H, Veldkamp E. 2012. Atmospheric methane uptake by tropical montane forest soils and the contribution of organic layers. Biogeochemistry 111:469–83.

Wood S, Wood MS. 2007. The mgcv package. www R-Proj Org.

Yan J, Zhang W, Wang K, Qin F, Wang W, Dai H, Li P. 2014. Responses of CO_2, N_2O and CH_4 fluxes between atmosphere and forest soil to changes in multiple environmental conditions. Glob Change Biol 20(1):300–12.

Yang H, Detto M, Liu S, Yuan W, Hsieh C-I, Wang X, Chen R, Chen H, Peng C, Jiang X, Li Y, Xu H, Liu W, Yang Q. 2017. Effects of canopy gaps on N_2O fluxes in a tropical montane rainforest in Hainan of China. Ecol Eng 105:325–34.

Zona D, Janssens IA, Aubinet M, Gioli B, Vicca S, Fichot R, Ceulemans R. 2013. Fluxes of the greenhouse gases (CO_2, CH_4 and N_2O) above a short-rotation poplar plantation after conversion from agricultural land. Agric For Meteorol 169:100–10.