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Key Points:
- We evaluated the spatial variability of soil CO_2 and N_2O emissions and their relation to topography in a tropical montane forest
- Soils at midslope position emitted less N_2O than at ridgetop and valley bottom, while no effect of topography on soil CO_2 fluxes was found
- Soil N_2O and CO_2 fluxes show no spatial pattern at plot level, with "hot spots" strongly contributing to the total emissions

Supporting Information:
- Supporting Information S1

Correspondence to:
C. Arias-Navarro,
cristina.arias-navarro@kit.edu

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Spatial variability of soil N_2O and CO_2 fluxes in different topographic positions in a tropical montane forest in Kenya

C. Arias-Navarro[1,2,3], E. Díaz-Pinés[2], S. Klatt[2], P. Brandt[1,4], M. C. Rufino[1,5], K. Butterbach-Bahl[2,3], and L. V. Verchot[6]

[1]Center for International Forestry Research, Nairobi, Kenya, [2]Institute of Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany, [3]Mazingira Centre, Environmental Research and Educational Facility, International Livestock Research Institute, Nairobi, Kenya, [4]Laboratory of Geo-Information Science and Remote Sensing, Wageningen University, Wageningen, Netherlands, [5]Lancaster Environment Centre, Lancaster University, Lancaster, UK, [6]International Center for Tropical Agriculture, Cali, Colombia

Abstract Quantifying and understanding the small-scale variability of nitrous oxide (N_2O) and carbon dioxide (CO_2) emission are essential for reporting accurate ecosystem greenhouse gas budgets. The objective of this study was to evaluate the spatial pattern of soil CO_2 and N_2O emissions and their relation to topography in a tropical montane forest. We measured fluxes of N_2O and CO_2 from 810 sampling locations across valley bottom, midslope, and ridgetop positions under controlled laboratory conditions. We further calculated the minimum number of samples necessary to provide best estimates of soil N_2O and CO_2 fluxes at the plot level. Topography exhibited a major influence on N_2O emissions, with soils at midslope position emitting significantly less than at ridgetops and valley bottoms, but no consistent effect of topography on soil CO_2 emissions was found. The high spatial variation of N_2O and CO_2 fluxes was further increased by changes in vegetation and soil properties resulting from human disturbance associated with charcoal production. Soil N_2O and CO_2 fluxes showed no spatial pattern at the plot level, with "hot spots" strongly contributing to the total emissions (10% of the soil cores represented 73 and 50% of the total N_2O and CO_2 emissions, respectively). Thus, a large number of samples are needed to obtain robust estimates of N_2O and CO_2 fluxes. Our results highlight the complex biogeochemical cycling in tropical montane forests, and the need to carefully address it in research experiments to robustly estimate soil CO_2 and N_2O fluxes at the ecosystem scale.

1. Introduction

Soils are dominant sources of atmospheric carbon dioxide (CO_2) and nitrous oxide (N_2O), important greenhouse gases (GHG) contributing to global warming [*Intergovernmental Panel on Climate Change (IPCC)*, 2014]. Globally, soil respiration releases about 100 Pg C yr^{-1} to the atmosphere [*Bond-Lamberty and Thomson*, 2010] and typically accounts for between 30 and 80% of total ecosystem respiration [*Davidson et al.*, 2006]. Tropical forests contain about 40% of the total terrestrial biomass C stock [*Field et al.*, 1998; *Phillips et al.*, 1998] and contribute approximately two thirds of the global annual total soil C flux [*Bond-Lamberty and Thomson*, 2010]. Therefore, small variations in the soil CO_2 efflux can have a strong influence on the ecosystem C balance. Tropical forests also play a key role in the global atmospheric balance of N_2O [*Werner et al.*, 2007; *van Lent et al.*, 2015], contributing an annual release of 4.4 Tg N (14 to 23% of the total N_2O source strength) [*IPCC*, 2007]. This estimate is associated with a high uncertainty due to both high temporal [*Meixner et al.*, 1997; *Werner et al.*, 2007; *Lin et al.*, 2010] and spatial variability [*Breuer et al.*, 2000; *Allen et al.*, 2010] of soil N_2O fluxes at different scales. In addition, the scarcity of reliable estimates in the peer-reviewed literature hampers drawing general conclusions and upscaling at larger spatial scales, especially in African ecosystems, which remain highly underrepresented [*van Lent et al.*, 2015].

Understanding the factors that affect spatial and temporal variabilities of GHG emissions is an important area of ongoing research. While both soil temperature and water content have been shown to be key factors responsible for the variation in soil CO_2 efflux at scales ranging from global to the plot [*Davidson et al.*, 2000; *Bond-Lamberty and Thomson*, 2010], a different picture is emerging for tropical soils. Because

soil temperature does not vary greatly in many tropical forests, soil water content is often found to be a more significant factor affecting temporal and spatial variations of soil respiration [*Davidson et al.*, 2000].

Soil production of CO_2 is the result of root respiration and heterotrophic decomposition of soil organic matter, which returns to the atmosphere some of the C fixed in the first step through photosynthesis. The microbial processes of nitrification and denitrification are the dominant sources of N_2O from the soil [*Butterbach-Bahl et al.*, 2013]. Soil physical, chemical, and biological factors and their interactions control these processes, which vary in both space and time. As a result, N_2O and CO_2 fluxes emitted from soils usually show a high degree of spatial and temporal variabilities [*Folorunso and Rolston*, 1984; *Parkin*, 1993]. In turn, the parameters controlling the soil GHG fluxes are affected by topography, either directly through dynamics of surface and subsurface water, nutrients, and dissolved organic matter [*Fang et al.*, 2009], or indirectly, via soil texture and vegetation [*Luizão et al.*, 2004].

An analysis of the combined effect of small-scale spatial variability and topography on soil N_2O and CO_2 emissions has been thoroughly investigated in temperate ecosystems [e.g., *Corre et al.*, 1996; *Ambus*, 1998; *Jungkunst et al.*, 2008; *Yu et al.*, 2008]. However, in the tropics this issue has been scarcely studied [*Reiners et al.*, 1998; *Breuer et al.*, 2000; *Fang et al.*, 2009], despite the fact that this information is essential to scale up processes measured at small scales (plots) to larger scales (ecosystem), which is of high relevance in ecological research [*Butterbach-Bahl et al.*, 2013].

To obtain robust estimations at the ecosystem level, large sample sizes are needed, but labor and time constraints limit the number of measurements in soil GHG fluxes studies [*Adachi et al.*, 2005]. Yet laboratory incubations usually allow for measuring trace gas emissions from a larger number of samples than is often possible in field studies, which can be a better approach to addressing spatial variability of soil GHG fluxes more effectively.

Given the few studies investigating N_2O and CO_2 fluxes from African tropical montane forest soils and the limited knowledge on both their spatial variability and controlling factors, we collected intact topsoil cores (0–5 cm) from 810 spatially explicit locations at three topographic positions (valley bottom, midslope, and ridgetop) in the Southwest Mau Forest Complex in Kenya and estimated potential soil N_2O and CO_2 fluxes through laboratory incubations under standardized conditions.

This study was designed to provide estimates of potential soil-atmosphere N_2O and CO_2 exchange rates from a tropical montane forest in Kenya, assess and quantify the spatial variability of soil N_2O and CO_2 emission potential and soil properties at varying topographic positions, and determine the minimum number of samples necessary to provide best estimates of soil N_2O and CO_2 fluxes at plot level.

We hypothesized that (i) topographic position (valley bottom, midslope, and ridgetop) would influence the soil emission rates of N_2O and CO_2 and (ii) that soil physico-chemical properties would be useful parameters for explaining spatial variability of soil N_2O and CO_2 fluxes at the plot level.

2. Study Site

The Mau Forest Complex in Kenya is the largest closed canopy forest in the country as well as indigenous Afromontane forest in East Africa covering an area of about 417,000 ha. The study site lies in the Southwest Mau part, east of Kericho town (−0°22′3°S, 35°16′59°E) (Figure 1) at approximately 2500 m above sea level. The climate is a cool, humid-tropical with a mean annual precipitation between 1800 and 1950 mm (1979–2009) [*Omumbo et al.*, 2011]. The area has a bimodal rainfall pattern, with the "long rains" falling between April and August and "short rains" between October and December, respectively, while January and February are generally the driest months. The mean annual temperature ranges from 15.7 to 17.5°C (1979–2009) [*Omumbo et al.*, 2011] with slight variations over the year. The geology is dominated by Tertiary lavas from the mid-Miocene epoch [*Blackie and Edwards*, 1981]. The soils are well drained, very deep, dark reddish-brown, clayey, and with an acidic humic topsoil [*Krhoda*, 1988; *Jaetzold et al.*, 2010] and classified as Andic Humic Nitisols [*International Union of Soil Sciences Working Group World Reference Base*, 2015].

The Mau Forest has undergone large-scale deforestation and degradation since the mid-1990s due to forest excisions and illegal logging, encroachments, and charcoal burning [*United Nations Environment Programme*,

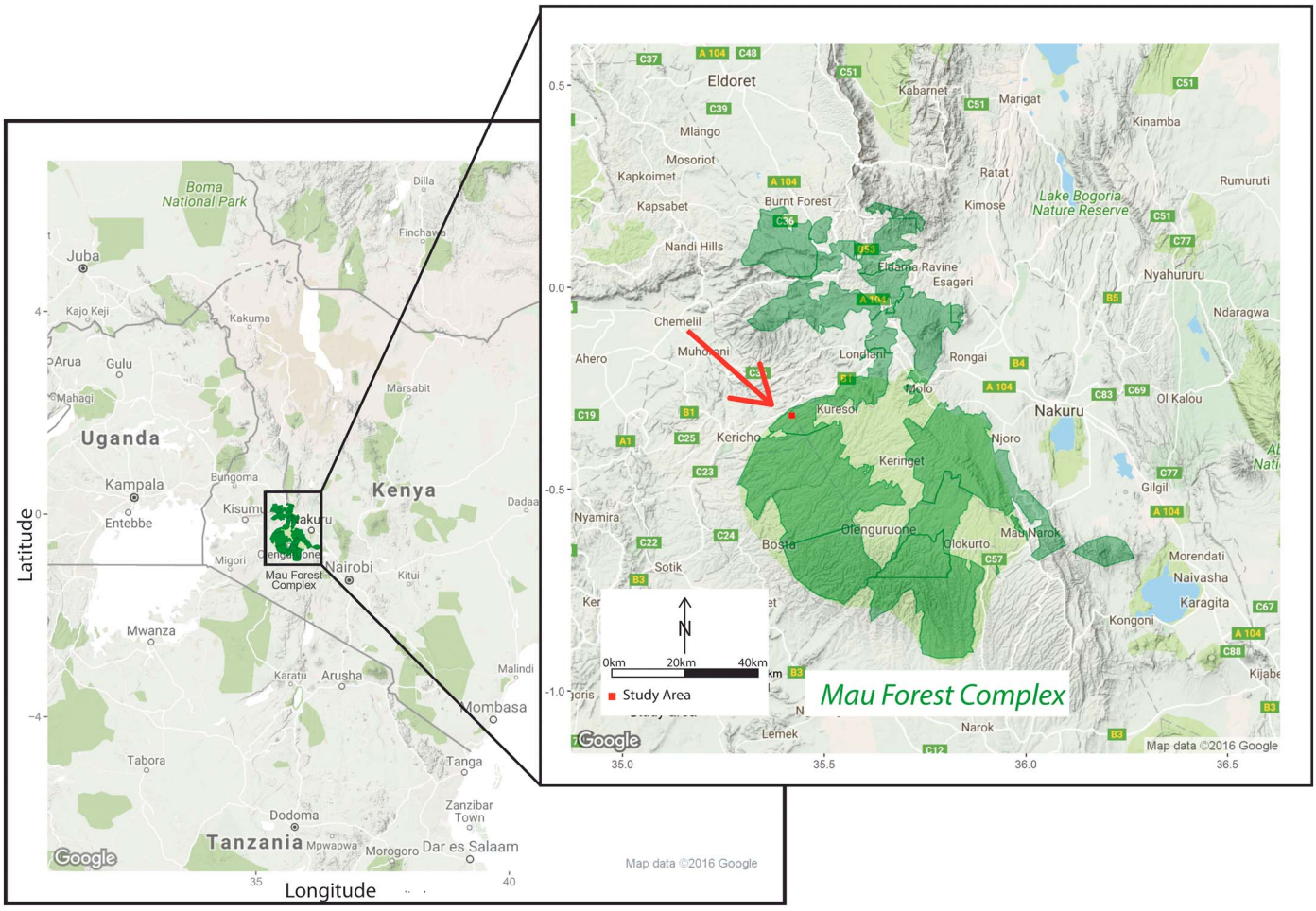

Figure 1. Localization of the study area.

2009; *Were et al.*, 2013]. Especially in the southwest part of the Mau, due to the proximity to smallholder farms, the use of temporary charcoal kilns for production of charcoal on-site in the forest is still common.

3. Materials and Methods

3.1. Experimental Design

We used a stratified sampling approach to select sampling plots based on topographic information. Gridded elevation data were obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER, v. 2) in a 30 m × 30 m grid cell resolution. We calculated the standardized topographic position index (TPI) for each grid cell segmenting the study area (4 km × 3 km; Figure 2a) into three topographic classes that represent ridgetop, midslope, and valley bottom positions [*Wilson and Gallant*, 2000] by using ArcGis 10.1 and the Land Facet Corridor Designer (v. 1.2.884). We further restricted the three TPI classes to level and gentle slopes (<7%) for ridgetop and valley bottom positions, and steep slopes (>= 7%) for midslope positions, to avoid potential mispositioning of sampling plots due to vertical errors inherent to ASTER data [*Advanced Spaceborne Space Borne Thermal Emission and Reflection Radiometer Global Digital Elevation Model Validation Team*, 2011]. Three transects across the forest served as spatial replicates. One 1 ha plot for each topographic position was selected along these transects, resulting in nine sampling plots (Figure 2a). Within each sampling plot, 90 sampling locations were randomly placed on the nodes of a grid of 5 m × 5 m (Figure 2b), yielding a total of 810 sampling locations.

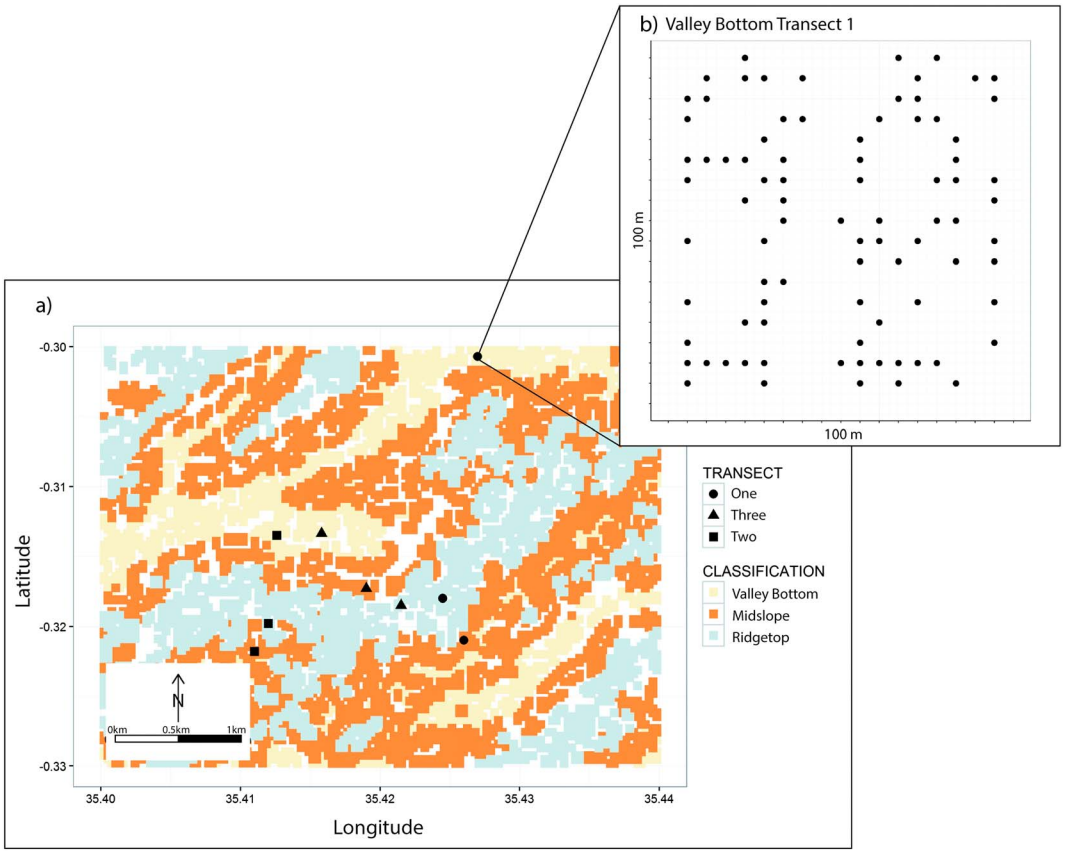

Figure 2. (a) Topographic classification of the study area and localization of the sampling plots. (b) Diagram of the sampling scheme in the valley bottom transect 1 showing the 90 random sampling locations on a grid of 5 m × 5 m.

3.2. Soil Sample Collection

Soil core sampling was conducted in February and March 2014, under stable meteorological conditions without rainfall. To minimize disturbance we used intact soil cores in our study [*Reichstein et al.*, 2005]. Prior to the core collection, the forest floor was removed. At each sampling location seven soil cores ($n = 5670$) were collected from the uppermost 5 cm of the mineral soil profile by using sharpened-edge PVC cylinders (5 cm inner diameter, 5 cm height). The cylinders were gently hammered into the soil with the help of a wooden block to keep soil compaction to a minimum. The cylinders were carefully taken out of the soil, sealed with Parafilm® (Bemis NA, Neenah WI, USA), and transported to the laboratory at Mazingira Centre, International Livestock Research Institute (Nairobi, Kenya), for analysis. The intact soil cores were air-dried and stored at ambient temperature until analyses were conducted, on an average of 4 weeks after sampling. Four intact soil cores were used for GHG sampling and the other three for soil analysis.

There were indications of anthropogenic disturbance on most of the plots, such as charcoal burning and illegal logging. To capture these disturbance effects, we recorded at each sampling location (i) the percentage of canopy cover using a Crown Mirror-Densiometer (Grube KG Forstgerätestelle, Bispingen, Germany) and (ii) the shortest distance to a charcoal kiln. Further, we recorded the number of charcoal kilns within each 1 ha plot.

3.3. Soil Laboratory Incubations

3.3.1. Potential N_2O and CO_2 Flux Measurements: Experiment 1

We measured potential N_2O and CO_2 emissions from air-dried and rewetted soil samples equivalent to a rainfall of 10 mm. The soil was allowed to equilibrate for 24 h to the new moisture condition before starting measurements for N_2O and CO_2 production. The water content in this study was roughly 50% water-filled pore space (WFPS), which is sufficient to induce a peak for microbial activity [*Liebig et al.*, 1996; *Appel*, 1998; *Haney and Haney*, 2010], and it was close to the moisture content of the soil during sample collection.

Air temperature during the incubation was kept constant at 17°C as this represents the annual mean temperature. Soil cores were incubated by using adapted gas-tight Kilner jars (volume 640 cm^3) fitted with rubber septum in the lid for headspace gas sampling by a syringe. We homogenized the jar headspace by pumping with an extra empty syringe before sampling. No ambient air was injected to correct for the change in pressure associated with the removal of air sample. We used four soil core replicates and pooled the samples as per *Arias-Navarro et al.* [2013] for each flux calculation; i.e., a 10 mL gas sample was taken from each individual jar headspace at 15 min intervals (0, 15, 30, and 45 min after chamber closure) with the same syringe at each time interval resulting in a 40 mL composite sample. The first 20 mL of the sample was used to flush a 10 mL glass vial, which was filled with the remaining 20 mL creating overpressure to minimize the risk of contamination by ambient air. The concentrations of CO_2 and N_2O in the gas samples were analyzed within 2–3 days by gas chromatography (8610C; SRI Instruments, Torrance, CA, USA) with a ^{63}Ni-electron capture detector for N_2O and flame ionization detector equipped with a methanizer for CO_2. Further details on the analytical procedure can be found in *Rosenstock et al.* [2015]. We calculated the CO_2 and N_2O fluxes from the linear change of the gas concentrations over time, considering the headspace volume, and referred the fluxes to the soil surface of the core. No saturation effect in the headspace was observed over the entire incubation period.

3.3.2. Effect of Soil Moisture: Experiment 2

A second incubation study was conducted to examine the effect of soil water content on soil N_2O and CO_2 fluxes at the different topographic positions. We used a subset of samples from transect 3. Potential N_2O emissions (from experiment 1) were sorted from smallest to largest and then divided in groups by terciles ($<$33%: low-emission potential group, 34–66%: medium-emission potential group, and $>$ 67%: high-emission potential group). We randomly selected 20 sampling locations from each group to represent each tercile. Maximum water-holding capacity (WHC) was determined on one spare soil core by placing the soil wrapped in absorbent filter paper into a glass jar and saturating it with water. The soil core was weighed after 4 h, dried at 105°C to constant weight, and weighed again. The water-holding capacity was calculated as gram water per gram dry weight of soil based on the difference. During the incubation, gas pooling was applied [*Arias-Navarro et al.*, 2013], yielding five replicates of four sampling locations each. The air-dried soil cores were measured at each incubation to record the baseline emission. Afterward, the soil cores were adjusted to soil moisture contents of 20, 40, 70, and 90% WHC each, by adding water before the flux measurements started. Soil cores were incubated and measured 4, 24, 48, and 72 h after the initial rewetting. Determination of GHG concentrations and calculation of GHG fluxes were performed similarly to experiment 1. Cumulative N_2O and CO_2 emissions were calculated from the integrated individual fluxes, assuming a constant flux rate between gas sampling times.

3.4. Soil Properties

We measured total soil organic carbon (SOC), total nitrogen (TN), pH, and bulk density (BD) for each of the 810 sampling locations, using three spare soil cores. Total SOC and TN were analyzed with an elemental combustion analyzer (ECS 4010, Costech Analytical Technologies, Inc., Milan, Italy). Soil pH was measured in deionized water suspension (water:soil weight ratio 2.5:1), using a glass electrode. Bulk density (BD) was calculated as the mass of the oven-dry soil (105°C) divided by the core volume. Stones or coarse fragments were absent so no correction was needed.

3.5. Sample Size Required for Accurate Estimates

In order to estimate the minimum number of samples needed to reliably represent the heterogeneity observed by measuring at 90 points we compared the mean soil CO_2 and N_2O fluxes and soil properties of various smaller sample sizes with those considering the 90 samples (true mean). That is, we calculated the distance between the true mean and the mean values with sample sizes K ($K = 1, 2\ldots, 89$), hereafter M_K . The M_K values are computed by using a large number of sample subsets of size K from the set of 90 points to obtain ranges of means. Because of the enormous number of possible subsets for most K, we randomly drew 100,000 distinct sample subsets without replacements for each M_K [*Jackson and Somers*, 1989]. To produce all combinations with equal probabilities, we used a uniform random generation algorithm. For each K we analyzed the range of the means and identified the minimum K being within 10% to 30% of the true mean of various confidence levels (80%–95%).

3.6. Statistical Analysis

Pearson's correlation coefficient was used to identify significant correlations between measured variables. One-way analysis of variance (ANOVA)—with transects as blocking factor—was used to test differences in

Table 1. Summary (Mean ± Standard Deviation) of Soil Properties and Disturbance Variables of Each Topographic Position and Results of the Analysis of Variance ANOVA of Log-Normally Transformed Soil N_2O and CO_2 Fluxes, Soil Properties, and Canopy Cover for Each Topographic Position[a]

	F value	Pr > F	Valley Bottom	Midslope	Ridgetop
Log N_2O	7.5	0.000568 ***	4.2 ± 1.3^{a}	3.8 ± 1.4^{b}	4.2 ± 1.4^{a}
Log CO_2	12.1	6.34e − 06 ***	3.6 ± 0.6^{b}	3.7 ± 0.6^{b}	3.8 ± 0.4^{a}
Total carbon (g kg^{-1})	6.3	0.00194 **	152.5 ± 49.3^{b}	166.5 ± 25.9^{a}	154.9 ± 20.4^{b}
Total nitrogen (g kg^{-1})	3.7	0.025 *	13.6 ± 3.9^{ab}	14.2 ± 4.0^{a}	13.3 ± 3.6^{b}
pH	33.2	1.43e − 14 ***	6.2 ± 0.4^{a}	6.0 ± 0.6^{b}	5.8 ± 0.5^{c}
Bulk density (g cm^{-3})	0.5	0.584	0.5 ± 0.2^{a}	0.5 ± 0.2^{a}	0.5 ± 0.2^{a}
Canopy cover (%)	2.5	0.0854 .	53.4 ± 35.6^{a}	49.7 ± 36.1^{a}	46.8 ± 35^{a}
No. charcoal kilns per hectare			1.3 ± 1.2	4 ± 2.1	2.6 ± 1.2

[a]Values within the same row followed by the same letter indicate no statistical difference among topographic positions ($p > 0.05$). Significance codes: 0 "***," 0.001 "**," 0.01 "*," 0.05 "." and 0.1 " " 1.

soil N_2O and CO_2 fluxes, canopy cover, and soil properties across topographic positions. Two-way ANOVA was used to test differences between measured N_2O and CO_2 fluxes at the various % WHC and topographic positions. The data were tested for normality and homogeneity of variances, and a log transformation was used for both N_2O and CO_2 fluxes. If the ANOVA results showed significant difference, a post-hoc Student-Newman-Keuls test method was used to identify the difference. The contribution of soil parameters and disturbance variables to the N_2O and CO_2 gas fluxes was calculated by using stepwise multiple regression analysis. The final models were chosen based on the lowest Akaike information criterion. All statistical analyses and plotting were carried out by using R 3.3.2 [*R Core Team*, 2016]. Downloading and formatting Google Maps images were done with the ggmap package [*Kahle and Wickham*, 2013]. We have used the functions aov {stats} to fit ANOVA models and lm {stats} to carry out regressions. Statistical models were interpreted by using effect displays for a particular term in the model (R Package effects [*Fox et al.*, 2003]). Spatial analyses were carried out by using the R package for geostatistical analysis gstat [*Pebesma*, 2004] based on variography and interpolation techniques. We computed *z* scores (differences between each value and the mean divided by standard deviation) by using the R package outliers [*Komsta*, 2011] and defined "hot spots" as observations that exceeded the 90th percentile based on a given score. Statistical significance is given at the 95% confidence level ($p \leq 0.05$). Significance of statistical tests is noted as follows: *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$; n.s. = $p > 0.05$.

4. Results

4.1. Soil Properties

Soil properties for each topographic position are shown in Table 1. Soil organic carbon was very high (118.6–171.9 g kg^{-1}) in all plots and showed significantly higher values in the midslope position compared to the ridgetop and valley bottom. Total nitrogen (TN) ranged from 12.5 to 15.3 g kg^{-1}.Soils at midslope position showed as well the highest TN content although not significantly different from valley bottom position. The lowest soil pH values were found at the ridgetop positions and increased along the topographic gradient. No significant differences among topographic positions were found for BD and canopy cover. The presence of charcoal kilns in our study were higher in midslope plots.

4.2. Experiment 1

4.2.1. Potential N_2O and CO_2 Fluxes

The water addition increased water content in the soil cores to approximately 50% WHC. Soil N_2O and CO_2 fluxes showed a large variability among sampling locations within each plot (results from valley bottom transect 1 are provided in Figure 3 as an example; the rest of the plots are included in the supporting information). Potential soil N_2O emission rates ranged from 1.3 to 980.0 $\mu g\,N\,m^{-2}\,h^{-1}$ for valley bottom, 0.05 to 1184.6 $\mu g\,N\,m^{-2}\,h^{-1}$ for midslope, and 0.2 to 1356.3 $\mu g\,N\,m^{-2}\,h^{-1}$ for ridgetop plots. Coefficients of variation were between 115 and 143% for each plot. Our analyses show that topographic position significantly influenced N_2O flux emission potentials (Table 1). Mean N_2O fluxes from midslope plots (105.0 ± 9.4 $\mu g\,N\,m^{-2}\,h^{-1}$) were significantly lower than the fluxes from ridgetop (135.2 ± 9.9 $\mu g\,N\,m^{-2}\,h^{-1}$) and valley bottom plots (156.3 ± 12.0 $\mu g\,N\,m^{-2}\,h^{-1}$).

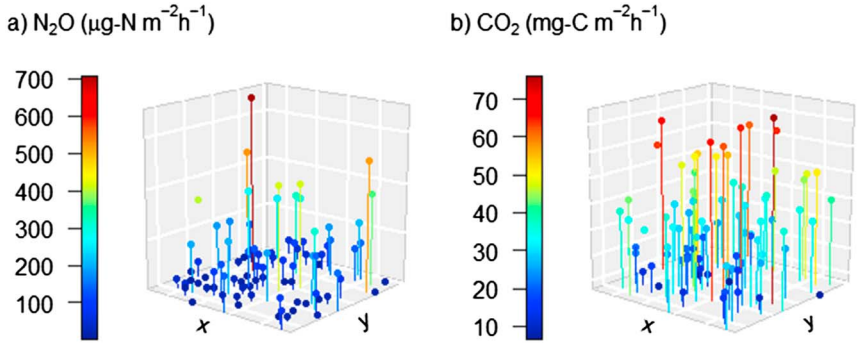

Figure 3. Potential soil (a) N_2O and (b) CO_2 fluxes 24 h after a 10 mm rainfall simulation (experiment 1) in the valley bottom transect 1. Symbols denote individual fluxes. The *x* axis is the coordinate *x*, and the *y* axis is the coordinate *y* of the sampling points.

Potential soil CO_2 flux rates ranged from 3.0 to 104.0 mg C m^{-2} h^{-1} for the valley bottom, from 4.4 to 145.0 mg C m^{-2} h^{-1} for the midslope, and from 1.7 to 98.6 mg C m^{-2} h^{-1} for the ridgetop plots. Coefficients of variation were between 20 and 50%. Soil CO_2 mean fluxes decreased along the topographic gradient with ridgetop (50.4 ± 1.0 mg C m^{-2} h^{-1}) having significantly higher fluxes than the valley bottom (44.8 ± 1.3 mg C m^{-2} h^{-1}) and the midslope (46.3 ± 1.3 mg C m^{-2} h^{-1}).

4.2.2. Spatial Variability

The multiple linear regression models for N_2O and CO_2 fluxes using measured soil properties and canopy cover had very low explanatory power, with an adjusted R^2 of 0.04 and 0.20, respectively. Soil N_2O and CO_2 fluxes were weakly but significantly correlated ($R = 0.19$, $p \leq 0.001$). Soil N_2O fluxes were positively correlated with TN ($R = 0.19$, $p \leq 0.001$) and SOC ($R = 0.15$, $p \leq 0.001$) and negatively correlated with BD ($R = -0.15$, $p \leq 0.001$). No correlation was found between the soil C:N ratio and flux data. The soil CO_2 flux showed a negative correlation with pH ($R = -0.24$, $p \leq 0.001$), BD ($R = -0.12$, $p \leq 0.001$), SOC ($R = -0.10$, $p \leq 0.05$), and soil C:N ratio ($R = -0.13$, $p \leq 0.001$). Bulk density was negatively correlated with TN and SOC ($R = -0.57$ and -0.59, respectively, $p \leq 0.001$). The presence of charcoal kilns affected soil N_2O and CO_2 fluxes and soil properties. Inside the zone of influence of a charcoal kiln (i.e., within 5 m) the soils emitted less N_2O ($p \leq 0.05$). The distance to charcoal kiln was negatively correlated with CO_2 ($R = -0.26$, $p \leq 0.001$). Higher numbers of charcoal kilns in a plot were associated with higher CO_2 fluxes ($R = 0.12$, $p \leq 0.001$) and BD values ($R = 0.17$, $p \leq 0.001$). Canopy cover showed positive correlations ($R = 0.18$, $p \leq 0.001$) with the soil C:N ratio, pH ($R = 0.11$, $p \leq 0.001$), and distance to charcoal kiln ($R = 0.24$, $p \leq 0.001$).

Occasional locations with particularly high rates (i.e., hot spots) contributed substantially to the mean N_2O and CO_2 fluxes, as it is visualized in the empirical cumulative density functions (Figure 4). The contribution of the samples above the 90th percentile to the total N_2O and CO_2 fluxes was 73% and 50%, respectively. For N_2O, 84 sampling locations were identified as hot spots (mean value: 545.1 µg N m^{-2} h^{-1}) and 73 for CO_2 (mean value: 54.66 mg C m^{-2} h^{-1}). When the "hot spot" data are excluded, the overall N_2O mean emission rate decreased from 132.3 µg N m^{-2} h^{-1} to 83.7 µg N m^{-2} h^{-1}, while the average soil respiration rate decreased from 47.2 mg C m^{-2} h^{-1} to 46.4 mg C m^{-2} h^{-1}.

The geostatistical analyses indicated that N_2O and CO_2 fluxes and soil properties had no spatial autocorrelation, at least for the range of distances investigated here (5–90 m). Semivariograms for CO_2 and N_2O fluxes and soil properties for the nine sampling plots are presented in the supporting information. Due to the lack of an identifiable semivariance structure, kriging interpolation for the plot level is not appropriate. This result enabled us to consider our measurement locations as independent samples for inferential statistics.

4.2.3. Minimum Sample Size for Accurate Estimates

Our results indicate that measurements at 37 ± 5 locations at each plot are needed to obtain an estimate within 30% of the true mean of N_2O at a confidence level of 95%. For 20% and 10% precision, 55 ± 5 and 78 ± 5 locations are needed, respectively. Measurements at 6 ± 2, 11 ± 5, and 30 ± 11 locations are needed to obtain an estimate within 30%, 20%, and 10% of the true mean for CO_2. These numbers are average values for all nine sampling plots. Variability among plots was small as can be noted in the small standard deviation

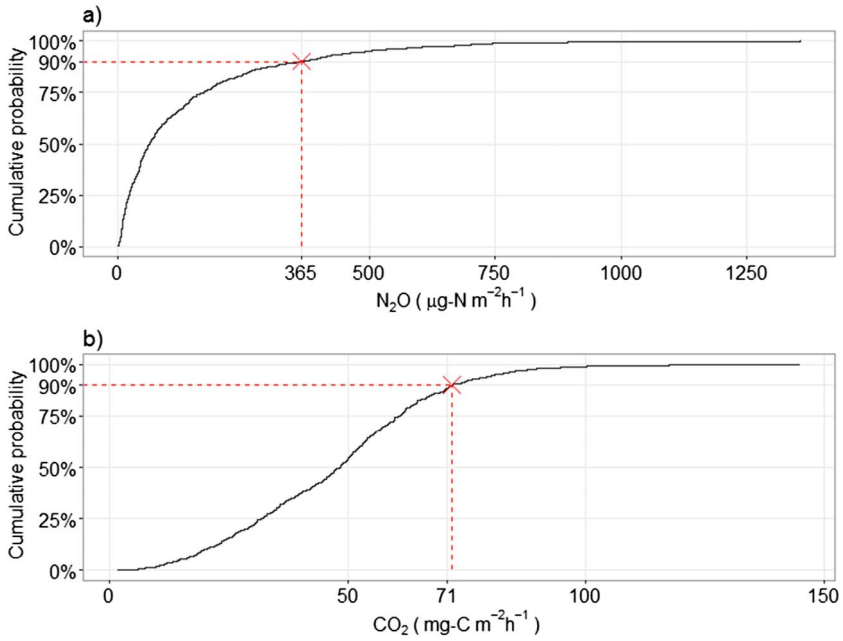

Figure 4. Empirical cumulative density function for (a) N_2O and (b) CO_2 fluxes. The red crosses represent the 90th percentile.

in the number of samples needed to reach a desired precision. Three samples are needed for estimating soil properties within 20% of variation with respect to the true mean, except for BD, where nine samples are necessary (Table 2).

4.3. Effect of Soil Moisture: Experiment 2

Detectable N_2O emissions were observed 4 h after watering the cores. At 30 and 50% WHC, soils reached maximum emission rates immediately after water application; in the case of 70 and 90% WHC treatments, N_2O production steadily increased until 48 h after the initial wetting, when the highest emission rates were observed. The N_2O pulse emissions correlated positively with % WHC at all topographic positions (20% WHC: 11.1 $\mu g\,N\,m^{-2}\,h^{-1}$, 50% WHC: 122.0 $\mu g\,N\,m^{-2}\,h^{-1}$, 70% WHC: 452.9 $\mu g\,N\,m^{-2}\,h^{-1}$, and 90% WHC: 899.6 $\mu g\,N\,m^{-2}\,h^{-1}$). Cores from the midslope position tended to emit less N_2O compared with ridgetop or valley bottom positions although there was no significant difference between topographic positions at 20% and 50% WHC. At 70% and 90% WHC, the midslope N_2O flux was significantly lower than the valley bottom but not the ridgetop (Figure 5a).

Increased CO_2 emissions were detected 4 h after watering the cores with CO_2 fluxes of 19.0, 24.7, 27.4, and 52.4 $mg\,C\,m^{-2}\,h^{-1}$ for soils at 20, 50, 70, and 90% WHC, respectively. Emissions decreased the following day for 20, 50, and 90% WHC, while soils at 70% WHC showed a second pulse (40.3 $mg\,C\,m^{-2}\,h^{-1}$) after 2 days. Soil CO_2 flux rates leveled off after 3 days for all topographic positions and water contents. Soil CO_2 fluxes from the three topographic positions increased at 70 and 90% WHC compared with low moisture contents (20 and 50% WHC treatments). No significant differences among topographic positions were observed at any WHC level (Figure 5b).

Table 2. Number of Samples Required for Various Levels of Precision (±10%, ± 20%, and ± 30% of the True Mean) for a Confidence Level of 95% Based on a Population of 90 Measurements (1 ha)[a]

	No. of samples		
	±10%	±20%	±30%
N_2O	78 (±3)	55 (±4)	37 (±6)
CO_2	30 (±11)	11 (±5)	6 (±2)
Total organic carbon	3 (±0)	3 (±0)	3 (±0)
Total nitrogen	3 (±0)	3 (±0)	3 (±0)
pH	3 (±0)	3 (±0)	3 (±0)
Bulk density	25 (±8)	9 (±3)	5 (±1)

[a]Values are mean (standard deviation) of the nine plots.

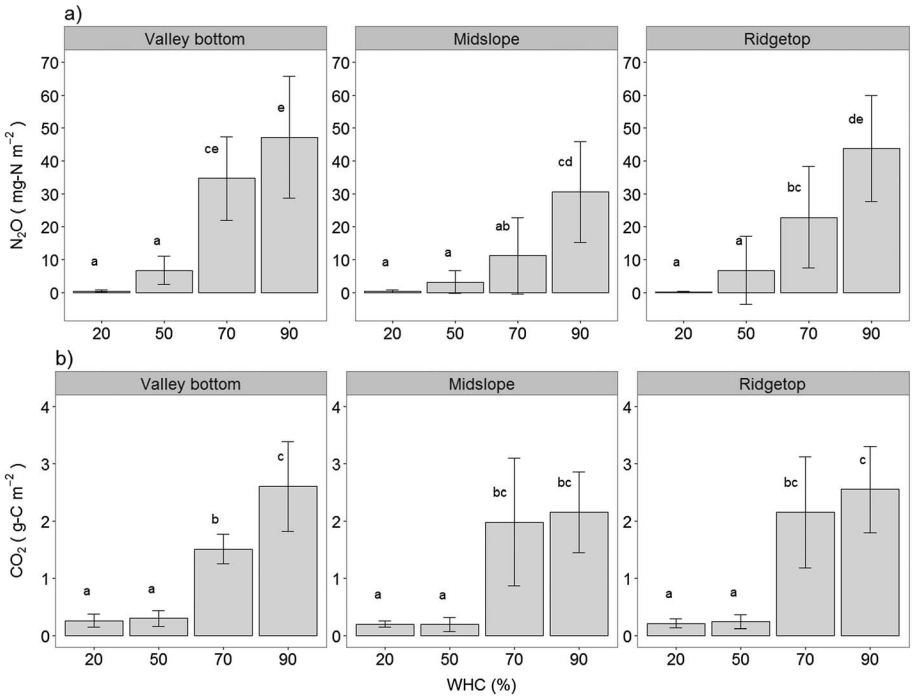

Figure 5. Time-weighted average cumulative soil (a) N_2O and (b) CO_2 emission rates during a 3 day incubation for different positions and levels of water-holding capacity (WHC). The vertical bars denote standard deviation. Columns with the same letters indicate no significant differences ($p>0.05$) between positions and WHC levels in soil N_2O or CO_2 fluxes.

5. Discussion

Soil properties showed no or weak correlations with N_2O fluxes, as observed in other studies examining the factors governing spatial variability of N_2O emission at different levels [e.g., *van den Heuvel et al.*, 2009]. Positive correlation of N_2O emissions with TN is in agreement to observations from *Booth et al.* [2005] from a wide range of ecosystems. Surprisingly, soil CO_2 fluxes were negatively correlated with SOC, possibly because areas with high SOC were associated with higher levels of black C, i.e., a highly stable C form, due to charcoal making. Soils in our study had low BD, were very porous, and had high organic matter content and high water storage capacity. Bulk density was strongly related to SOC as has been found in numerous other studies [*Tamminen and Starr*, 1994]. The low BD values found here are in good agreement to other studies in tropical montane forest and have been associated to the high organic matter content in the topsoil [*Hafkenscheid*, 2000; *Jeyanny et al.*, 2014].

The importance of landscape position on N_2O emissions has been documented by other studies [*Pennock et al.*, 1992; *Corre et al.*, 1996], which found greater N_2O emissions in the valley bottom than in the ridgetop or midslope positions. Differences in moisture content along the slope usually explain the N_2O flux variability [*Vilain et al.*, 2010, 2011; *Negassa et al.*, 2015], with higher fluxes in the lower positions closely correlated with the higher WFPS. However, our approach involved standardized soil moisture levels across the treatments, and we still observed position-driven variations of N_2O emission with lower N_2O emitted at the steeply sloping plots when compared with flat plots (ridgetop and valley bottom plots). Experiment 2 corroborated the results from experiment 1, with a lower N_2O emissions in cores taken from the midslope position for all moisture contents. This result indicates that topography is an important factor influencing N_2O emissions, in line with our first hypothesis. Significant effects of topographic position on multiple aspects of the N cycle have been shown by *Weintraub et al.* [2014], indicating lower N availability and a less open N cycle in steep parts of the landscape compared to a relatively flat terrain, supporting our findings.

Soil water content (expressed as % WHC) in our study was a determinant parameter for the N_2O flux rates in all topographic positions. Microbial denitrification, which yields N_2O, is mainly driven by redox potential,

substrate availability, and oxygen diffusion, which strongly depend on the water availability and the water-free pore space in soil [*Dobbie and Smith*, 2003; *Bateman and Baggs*, 2005]. Higher N_2O fluxes at high soil water contents have been reported from laboratory [*Hergoualc'h et al.*, 2007; *Schaufler et al.*, 2010; *Werner et al.*, 2014] and field studies [*Pennock et al.*, 1992; *van Kessel et al.*, 1993; *Corre et al.*, 1996; *Pennock and Corre*, 2001] and have been associated to increasing denitrifying activity due to reduced O_2 diffusion into the soil [*Ruser et al.*, 2006; *Yanai et al.*, 2007].

Soil moisture also played a major role in the soil CO_2 fluxes, which is consistent with other studies where, at constant temperature, wetter soils emitted more CO_2 due to better conditions for microbial respiration [*Zhou et al.*, 2013]. This observation is only true until the point of water saturation when CO_2 fluxes tend to decrease, as those conditions favor the development of anaerobiosis, slowing down the decomposition of organic matter and reducing CO_2 diffusion to the atmosphere [*Smith*, 1990; *Knowles et al.*, 2015], but our soils were predominantly aerobic even at 90% WHC due to the low BD of the topsoils (<1 g cm^{-3}). Contrary to previous studies [*de Figueiredo Brito et al.*, 2009; *Martin and Bolstad*, 2009; *Riveros-Iregui and McGlynn*, 2009] soil CO_2 fluxes were not related to topographic position. The decreased susceptibility to microbial SOC degradation caused by the presence of allophane minerals in our plots [*McBride*, 1994; *Parfitt*, 2009] and the high tree diversity may have influenced to some extent the spatial pattern of the soil CO_2 efflux [*Katayama et al.*, 2009; *Matvienko et al.*, 2014]. Large diversity of tree species in tropical forests lead to heterogeneity in chemical, structural, and functional traits that affect biogeochemical processes [*Hättenschwiler et al.*, 2008; *Townsend et al.*, 2008] contributing to the spatial heterogeneity of soil respiration.

Furthermore, the disturbance caused by charcoal making also affected soil CO_2 fluxes. Charcoal production implies felling of trees or parts of them and wood carbonization in traditional kilns, affecting the soil at two different levels. First, soil is disturbed at the kiln site due to the extreme heat generated during the carbonization process and the digging to make a pit or to use the soil to cover the wood pile. Second, charcoal production impacts the area surrounding the kiln where the wood is harvested [*Chidumayo and Gumbo*, 2013]. We suggest that the increase in soil CO_2 emissions in the vicinity of the charcoal kilns could have been driven by a priming effect triggered by increased production of extracellular enzymes due to the added substrate which "cometabolize" soil organic matter [*Zimmerman et al.*, 2011], but indirect mechanisms are also possible, such as the stimulation of microbial activity through nitrogen or other nutrient additions [*Kuzyakov et al.*, 2009; *Smith et al.*, 2010; *Wang et al.*, 2012], similar to the effects of biochar addition to soil on CO_2 evolution reported in many types of laboratory and field studies [*Kuzyakov et al.*, 2014]. A review by *Glaser et al.* [2002] on the effects of charcoal in tropical soils confirmed that carbonization results in higher nutrient retention and availability on the kiln sites, supporting our findings. In our study, the highest SOC content was found in the midslope plot with highest number of charcoal kilns (six), suggesting that charcoal production in the area affects SOC dynamics. In addition, charcoal, as well as biochar, may increase the N_2O-reducing activity of denitrifying communities, which might cause a decrease in N_2O emissions [*Cavigelli and Robertson*, 2001] in agreement with the reduction of N_2O observed inside the zone of influence of a charcoal kiln.

Forest regeneration on kiln sites following charcoal production is different from that of surrounding areas [*Chidumayo and Gumbo*, 2013], with forest recovery being delayed due to the intense impact at the kiln site [*Boutette and Karch*, 1984]. Therefore, the secondary vegetation on kiln sites is usually dominated by herbaceous plants for several decades, in agreement with the observed positive correlation between distance to the charcoal kiln and canopy cover. Canopy openness favors the establishment of pioneer and light-demanding species in the forest [*Schnitzer and Carson*, 2001]; therefore, shifts in tree species composition might cause a difference of soil CO_2 fluxes [*Katayama et al.*, 2009; *Díaz-Pinés et al.*, 2014]. Furthermore, vegetation structure and species composition affect C allocation patterns [*Wang et al.*, 2006] and modify microclimate and substrate availability [*Raich and Tufekcioglu*, 2000; *Butler et al.*, 2012], all of which may have affected soil N_2O and CO_2 fluxes as well as their respective spatial patterns. However, the interaction between N_2O and CO_2 emissions and the presence of charcoal kilns need further investigation, which should address both the short- and long-term effects on CO_2 and N_2O fluxes during vegetation succession.

We are confident that the large number of sampling locations per plot yielded a low uncertainty in the mean estimate of soil N_2O and CO_2 fluxes and soil properties, capturing spatial heterogeneity adequately

[*Savage and Davidson*, 2003]. Spatial variability in our study, especially of soil N_2O fluxes, was high, as expected in tropical forest soils [*Vitousek et al.*, 1989; *Verchot et al.*, 1999, 2006; *Breuer et al.*, 2000]. Because of the presence of hot spots in soil, trace gas production and emission can vary substantially on a scale of less than 1 m [*Folorunso and Rolston*, 1984; *Parkin*, 1993; *Ambus and Christensen*, 1994]. Since we chose 5 m as the shortest distance between measurement points, we cannot exclude the existence of a small-scale (distances smaller than 5 m) spatial pattern of soil N_2O and CO_2 emission rates in our plots. The lack of spatial dependence of N_2O and CO_2 emissions, as it was observed in our study, has been reported by other studies [e.g., *Nishina et al.*, 2009].

Production of N_2O was localized in hot spots to a greater extent than CO_2, and therefore, a larger number of samples are required to achieve the same level of precision. For example, 78 ± 3 and 30 ± 11 samples are needed for N_2O and CO_2, respectively, to obtain an estimate within 10% of the true mean at 95% confidence level. Our results for CO_2 are comparable with *Yim et al.* [2003], who calculated that between 27 to 33 samples were needed for estimating the soil respiration rates in a larch plantation for the same error and probability level. *Davidson et al.* [2002] reported 41 for a temperate mixed hardwood forest, and *Adachi et al.* [2005] reported 50 for a tropical forest. For N_2O emissions rates, *Turner et al.* [2008] estimated 181 as the number of measurements required for the sample mean to be within 10% of the true mean for a $90\ m \times 90\ m$ pasture field using the mean and standard deviation from a large sampling size [*Folorunso and Rolston*, 1984]. While we assumed that our 90 sample points represent the true population mean of our plots, they used a more conservative approach.

The inherent spatial variability of the N_2O and CO_2 emissions and their controlling factors makes it difficult to reduce uncertainty in emission estimates by taking a manageable number of flux measurements with chamber investigations. The compositing procedure that we developed previously and that we used here should help overcome this problem [*Arias-Navarro et al.*, 2013]. It should, however, be noted that we used soil cores covering few square centimeters so that the observed variability is likely larger compared to chamber measurements, as the latter would overcome centimeter-scale variability.

Although the cause for the substantial spatial variability could not be linked to the parameters measured, we attribute this observation to the presence of small-scale denitrification hot spots in the soil (e.g., due to the scattered availability of organic material in anaerobic microsites), and to the presence of charcoal kilns (which affects SOC dynamics).

In our case, omitting hot spots could have led to an underestimation of the site-specific mean emission rates of roughly 2% for CO_2 and 37% for N_2O, indicating that having too few sampling locations or discarding the observations of high fluxes could lead to a systematic bias in CO_2 and N_2O budgets from tropical forests, strongly underlining the importance of carefully addressing spatial heterogeneity when designing field sampling.

6. Conclusions

This study provides evidence of the complexity of the mechanisms controlling the spatial variability of soil N_2O and CO_2 fluxes in tropical montane forest ecosystems. The intrinsically high spatial variation of soil N_2O and CO_2 fluxes at our study sites was probably further increased by changes in vegetation and soil properties resulting from charcoal production and associated disturbances. Because of the large spatial dispersion of soil N_2O and CO_2 emissions, it remains a challenge for future measurements and modeling to adequately reproduce the spatial variability both between and within sites.

Although the soil physical properties were not significant predictors of either the N_2O or CO_2 flux, topography was shown to affect the N_2O flux—but not the CO_2 flux. Plots with lower N_2O emissions coincided with steeper slopes, regardless of soil moisture levels. There was no spatial correlations of the soil N_2O and CO_2 fluxes with measured soil parameters, for distances equal or larger than 5 m. We conclude that N_2O and CO_2 fluxes from tropical montane forest soils must be estimated from an ensemble that is (a) sufficient in size and (b) representative for the topography of the site. Further investigations at both the plot and landscape level are strongly needed to evaluate the seasonal and annual fluctuations of emission rates to reliably estimate CO_2 and N_2O budgets from African tropical forest soils.

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