



Soil greenhouse gas fluxes following conventional selective and reduced-impact logging in a Congo Basin rainforest

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Abstract Selective logging is among the main causes of tropical forest degradation, but little is known about its effects on greenhouse gas (GHG) fluxes from highly weathered Ferralsol soils in Africa. We measured soil CO₂, N₂O, and CH₄ fluxes, and their soil controlling factors at two forests that had undergone conventional selective logging and reduced-impact logging in Cameroon. Each logging system had four replicate plots, each included the disturbed strata (road, logging deck, skidding trail, and felling gap) and an undisturbed reference area. Measurements were conducted monthly from September 2016 to October 2017. Annual GHG fluxes ranged from 4.9 to 18.6 Mg CO₂-C, from 1.5 to 79 kg N₂O-N, and from

– 4.3 to 71.1 kg CH₄-C ha⁻¹ year⁻¹. Compared to undisturbed areas, soil CO₂ emissions were reduced and soil CH₄ emissions increased in skidding trails, logging decks and roads ($P < 0.01$) whereas soil N₂O emissions increased in skidding trails ($P = 0.03–0.05$). The combined disturbed strata had 28% decrease in soil CO₂ emissions, 83% increase in soil N₂O emissions, and seven times higher soil CH₄ emissions compared to undisturbed area ($P \leq 0.01$). However, the disturbed strata represented only 4–5% of the area impacted in both logging systems, which reduced considerably the changes in soil GHG fluxes at the landscape level. Across all strata, soil GHG fluxes were regulated by soil bulk density and water-filled pore space, indicating the influence of soil aeration and gas diffusion, and by soil organic carbon and nitrogen, suggesting the control of substrate availability on microbial processes of these GHG.

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Introduction

Selective logging is the most common management practice used for timber harvesting in the tropics. In Cameroon, conventional selective logging and

reduced-impact logging are commonly used. Conventional logging (CL) is generally carried without a requirement for prior planning of the field operations. In contrast, reduced-impact logging (RIL) has a management plan with a set of measures (e.g., pre-logging forest inventory, mapping of merchantable trees, planning of logging infrastructures, directional tree-felling techniques, and post-harvest closure of roads and skidding trails) to minimize the negative impacts of logging (Putz et al. 2008). Both selective logging systems, however, can result in significant soil organic carbon (SOC) loss and decrease in soil fertility (Tchiofo Lontsi et al. 2019), which may lead to forest degradation. Carbon emissions associated with tropical forest degradation are estimated to be 2 Gt CO₂eq year⁻¹, with selective logging being one of the largest contributor (Hosonuma et al. 2012; Pearson et al. 2017). This estimate took into account only the carbon removed with the harvested timber and the harvest residues left on the forest floor to decompose. However, heavy equipment used to harvest timber also negatively impacts forest soils (e.g., soil compaction and removal of the organic matter-rich topsoil), which can influence soil nutrient levels, aeration, and water infiltration and drainage (Olander et al. 2005; Schnurr-Pütz et al. 2006; Hartmann et al. 2014; Tchiofo Lontsi et al. 2019). These can, in turn, affect soil microbial communities and their function on greenhouse gas (GHG) regulation (Schnurr-Pütz et al. 2006; Hartmann et al. 2014).

The impact of selective logging in tropical forests describes a gradient of disturbance from canopy opening and pulse litter input on felling gaps, soil compaction in skidding trails, logging decks, and roads, to vegetation and topsoil removal in logging decks and roads (Keller et al. 2005; Olander et al. 2005; Tchiofo Lontsi et al. 2019). Changes in soil physical and biochemical properties follow this gradient, with greater changes in roads and logging decks and intermediate in skidding trails and felling gaps as compared to the undisturbed reference area (Olander et al. 2005; Tchiofo Lontsi et al. 2019). The proportion of forest area disturbed by selective logging is related to the tree harvest intensity (Pereira et al. 2002; Tchiofo Lontsi et al. 2019). Where only few trees are harvested per hectare (e.g., in Africa), a large proportion of the logged forest can remain undisturbed (Putz et al. 2019; Tchiofo Lontsi et al. 2019). This undisturbed forest area may remain functionally intact as far

as biogeochemical processes are concerned. For example, a study carried out in a Brazilian rainforest found no significant difference in soil GHG fluxes between the undisturbed areas within the selectively logged forest and the nearby unlogged forest (Keller et al. 2005).

Soil physical and biochemical properties, together with climatic factors and forest management practices, are among the key spatial and temporal drivers of soil GHG emissions from natural tropical forest ecosystems (Koehler et al. 2009a, b; Kim et al. 2016; Matson et al. 2017). Soil CO₂ emissions from some African tropical ecosystems showed positive relationships with both soil moisture and temperature (Werner et al. 2007; Kim et al. 2016; MacCarthy et al. 2018; Wanyama et al. 2019). Additionally, soil characteristics like bulk density (Goutal et al. 2012; Liu et al. 2014; Wanyama et al. 2019), SOC, total N, and extractable P (Schwendenmann et al. 2003; Werner et al. 2007; Liu et al. 2014; Hassler et al. 2015) explain spatial variations in soil CO₂ emissions. Hence, forest logging disturbances from harvest machinery that reduces roots and litter inputs, and decreases SOC and aeration (e.g., due to compaction or increase in soil bulk density) can reduce soil CO₂ emissions (Zerva and Mencuccini 2005; Han et al. 2015; Mori et al. 2017).

Moreover, soil N₂O emissions from tropical forest soils increase with increases in soil N availability and moisture contents (Davidson et al. 2000a, 2004; Keller et al. 2005; Werner et al. 2007; Koehler et al. 2009a; Corre et al. 2014; Hassler et al. 2017; Matson et al. 2017). Forest logging activities that alter soil N availability, microclimate, and aeration can change soil N₂O fluxes (Keller et al. 2005; Yashiro et al. 2008). For example, more compacted soils of logging deck and skidding trail emitted higher N₂O than undisturbed forest (Keller et al. 2005). Another study, although it did not consider the logging-damaged area in its experimental design, also found larger soil N₂O emissions from a selectively logged forest compared to an unlogged forest due to increased soil mineral N content and soil compaction (Yashiro et al. 2008).

CH₄ flux from the soil surface is a net result of concurrently occurring microbial processes of methanogenesis and methanotrophy in soils (Veldkamp et al. 2013; Hassler et al. 2015; Matson et al. 2017). Across an orthogonal gradient of precipitation and soil fertility, highly weathered Ferralsol soils with

intermediate annual rainfall (2360–2690 mm year⁻¹) but high soil N availability have larger CH₄ uptake, followed by Ferralsols with high rainfall (3400 mm year⁻¹), than less weathered Cambisol soils with low annual rainfall (1700–2030 mm year⁻¹) and low N availability (Matson et al. 2017). This suggests that soil CH₄ flux is largely controlled by soil N availability that influences methanotrophic activity (Bodelier and Laanbroek 2004) as well as by precipitation or soil moisture, through its influence on gas diffusivity (for methanotrophs) and anaerobicity (for methanogens) (Verchot et al. 2000; Davidson et al. 2004; Werner et al. 2007; Veldkamp et al. 2013; Matson et al. 2017). Thus, forest disturbance like logging, which changes soil fertility and increases soil bulk density (Olander et al. 2005; Tchifo Lontsi et al. 2019), can change soil CH₄ fluxes. For example, conversion of tropical lowland forests to unfertilized agricultural systems decreases soil N availability which, in turn, decreases CH₄ uptake in the soil (Hassler et al. 2015; Gütlein et al. 2018). Moreover, soil compaction, resulting from intensive agriculture and silvicultural practices, decreases CH₄ uptake (Wanyama et al. 2019). Also, logged forest soils tend to emit CH₄ especially from disturbed areas with strong soil compaction whereas undisturbed well-drained forest soils consume CH₄ (Keller et al. 2005; Zerva and Mencuccini 2005; Yashiro et al. 2008).

Studies on soil GHG fluxes in Africa were mostly done in agricultural lands (e.g., Rosenstock et al. 2016; Pelster et al. 2017; MacCarthy et al. 2018; van Straaten et al. 2019; Wanyama et al. 2019). Only a handful of studies have investigated in-situ soil GHG fluxes from tropical rainforests in Africa (Werner et al. 2007; Castaldi et al. 2013; Gütlein et al. 2018). A few studies have estimated C emissions from selective logging in African tropical forests, but these focused mainly on vegetation biomass-C losses and did not include C emissions from the soil (e.g., Pearson et al. 2017; Umunay et al. 2019). Recognizing this knowledge gap, we conducted this study in order to find out the spatial changes in soil GHG fluxes following selective logging in an African forest on highly weathered Ferralsol soil that developed on pre-Cambrian basement rocks. We conducted year-round monthly measurements of soil GHG fluxes and their controlling factors in two lowland rainforests that had undergone conventional selective logging and reduced-impact

logging. Our objectives were to (1) assess the changes in soil CO₂, N₂O and CH₄ fluxes resulting from these selective logging systems, and (2) determine the spatial and temporal controlling factors of the changes in soil GHG fluxes in these selectively logged forests. We included in the experimental design the spatial pattern of logging disturbances (felling gaps, skidding trails, logging decks, and roads) and compared them to undisturbed area within the forests. We hypothesized that (1) soil CO₂ emissions and CH₄ uptake will be higher whereas soil N₂O emissions will be lower in the undisturbed reference area compared to the highly disturbed logging decks and roads. (2) Along the gradient of soil disturbance from felling gaps to roads, decreases in SOC and N availability (due to vegetation and topsoil removal and decomposition of left-over litter) and increases in soil compaction (which influences soil water content or aeration and gas diffusion) will determine the spatial and temporal patterns of these soil GHG fluxes.

Material and methods

Study sites and experimental design

Soil GHG fluxes were measured in a lowland rainforest (30–100 m above sea level) located in the Technical Operational Unit (TOU) Campo-Ma'an in southern Cameroon (2°10'–2°52'N, 9°50'–10°54'E). The geological structure of the area is pre-Cambrian basement rocks that consist of metamorphic micaschists and gneiss (Gwanfogbe et al. 1983). The soils are heavily weathered, sandy loam Ferralsols with acidic pH, low effective cation exchange capacity (ECEC) and base saturation, and high aluminum saturation (Table S1; Tchifo Lontsi et al. 2019). The climate is equatorial with a bi-modal rainfall pattern defining two dry seasons, usually from December to February and July to August, when monthly rainfall is less than 150 mm. The mean annual rainfall is 2693 mm with a mean annual air temperature of 25.4 °C (Climate-Data.org 2018). During our study period (from September 2016 to October 2017), the soil temperature ranged from 23.9 to 30.7 °C. The vegetation in our study sites is dominated by *Sacoglottis gabonensis* and the most common harvested timber species were *Lophira alata*,

Erythroleum ivorense, *Guibourtia ehie*, and *Pterocarpus soyauxii* (Tchiofo Lontsi et al. 2019).

We selected two sites with a relatively flat topography and comparable initial vegetation characteristics (Tchiofo Lontsi et al. 2019), located approximately 40 km apart that were selectively logged 6 to 7 months prior to the start of our study. The first site was located in the multipurpose area of the TOU Campo-Ma'an in Mintom village, which is approximately 4 km east of Campo city. This 750-ha forest site was logged under a local agreement between the village elders and a private operator, so as no management plan was required. Using a so-called conventional selective logging (CL) practices, the logger located the desired trees that were harvested with minimal planning and little consideration to the remaining forest stand. The logging intensity in this CL site was 2.75 m³ timber ha⁻¹, which resulted in an area disturbed from logging (the sum of felling gap, skidding trail, logging deck, and road) of 5.2% of the total forest area (Tchiofo Lontsi et al. 2019). The second site (2350 ha) was located in a logging concession owned by a commercial enterprise that holds a Forest Stewardship Council (FSC) certification for sustainable forest management. Prior to logging, a forest management plan with a 30-year logging cycle was required and logging operations fulfilled the FSC certification requirements. One of the requirements is that the logging company must use reduced-impact selective logging (RIL) protocols, which consist of pre-harvest tree inventory, location planning of skidding trail, road and logging deck, controlled tree felling, and employment of trained and qualified field crews. The logging intensity in the RIL site was 2.78 m³ timber ha⁻¹ and the coverage of the disturbed area from logging was 4% of the total forest area (Tchiofo Lontsi et al. 2019).

At the CL and RIL sites, we established four replicate plots centered around four randomly selected logging decks, and within each plot, we conducted our measurements in four disturbed strata, i.e., felling gap, skidding trail, logging deck, and road, and in an undisturbed reference area (Fig. S1). The reference area was selected at least 50 m away from any disturbed areas. The distance between replicate plots at each site was at least 500 m. Roads and logging decks are the most affected by logging operations, where ECEC, SOC, total N, and Bray-extractable P decrease whereas soil pH and ¹⁵N natural abundance

increase compared to the undisturbed reference area (Table S1; Tchiofo Lontsi et al. 2019).

Soil greenhouse gas fluxes

Soil CO₂, N₂O, and CH₄ fluxes were measured monthly from September 2016 to October 2017, using vented static chambers (e.g., Koehler et al. 2009b; Hassler et al. 2015; Matson et al. 2017; van Straaten et al. 2019). We randomly installed four chamber bases (0.04 m² area, 0.25 m total height, inserted into the soil at approx. 0.02-m depth, and 11 L total volume with cover) within each stratum (i.e., felling gap, skidding trail, logging deck, road, and undisturbed area) at each replicate plot (Fig. S1). The chambers were randomly re-installed on each sampling day in order to prevent them from getting damaged or lost, especially on the roads and logging decks. As there was no vegetation on these strata, measurements started after about two hours following the chamber installation. The chamber bases were closed with polyethylene covers, equipped with Luer-lock sampling ports on the center top. From each chamber, four gas samples (25 mL each) were taken using syringes over a 30-min sampling period (at 2, 12, 22, and 32 min following chamber closure). Gas samples were stored with overpressure into pre-evacuated 12 mL glass vials (Labco Exetainers, Labco Limited, Lampeter, UK) with rubber septa. Our monthly sampling may seem infrequent given the high temporal variability of some soil GHG fluxes (e.g., N₂O; Barton et al. 2015), and the use of four chambers per stratum within each replicate plot may be limited. However, under logistically challenging conditions of our study area, we were able to conduct year-round measurements, which add invaluable information for this understudied region. Previous studies in the Congo Basin rainforest had only campaigned measurement for 3 months (e.g., Serca et al. 1994). In our study, on each measurement month, a total of 640 gas samples (4 time intervals × 4 chambers × 5 strata × 4 replicate plots × 2 logging systems) were taken and transported by air every four months to the University of Goettingen, Germany. These exetainers have been proven in a number of studies conducted by our group to be leak proof (e.g., Hassler et al. 2015; Matson et al. 2017; van Straaten et al. 2019).

The gas samples were analyzed using a gas chromatograph (GC; SRI 8610C, SRI Instruments,

Torrance, CA, USA) equipped with a flame ionization detector to measure CH_4 and CO_2 (with methanizer) concentrations as well as an electron capture detector for N_2O analysis with a make-up gas of 5% CO_2 –95% N_2 . Three calibration gases (Deuste Steininger GmbH, Mühlhausen, Germany) were used to calibrate the GC prior to each analysis with concentrations ranging from 400 to 3000 ppm for CO_2 , 360 to 1600 ppb for N_2O , and 1000 to 5000 ppb for CH_4 . Soil GHG fluxes were calculated from the linear change in concentration with chamber closure time, and adjusted with the field-measured air temperature and atmospheric pressure during sampling (e.g., Koehler et al. 2009a). The quality check of our individual chamber flux measurements was based on the linear increase in CO_2 concentration with time. In few cases (< 3% of the data) where CO_2 concentration curved at a particular point, that problematic data point was excluded, and the fluxes of the three GHG were calculated based on the remaining three sampling intervals that showed a linear increase in CO_2 concentration with the duration of chamber closure ($R^2 > 0.9$). For CH_4 and N_2O , all flux measurements were included in the data analysis, including zero and negative fluxes in order to avoid bias.

Annual soil CO_2 , N_2O , and CH_4 fluxes were estimated based on trapezoidal rule between measured fluxes and sampling day intervals, assuming constant flux rates per day (e.g., Koehler et al. 2009a, b; Veldkamp et al. 2013; Hassler et al. 2015; Matson et al. 2017). For each replicate plot, we calculated the overall annual CO_2 , N_2O or CH_4 fluxes from the four disturbed strata by weighting them with their percentage areal coverage (i.e., respective coverages at the RIL and CL sites are 1.0% and 1.1% for felling gap, 1.7% and 2.4% for skidding trail, 0.1% and 0.2% for logging deck, and 1.2% and 1.4% for road; Tchifo Lontsi et al. 2019). To quantify the effect of logging on soil CO_2 , N_2O or CH_4 fluxes, we subtracted the annual values of the disturbed strata (area-weighted average) from the annual fluxes of the undisturbed reference area at each replicate plot, similar to the calculation method of Keller et al. (2005).

Soil controlling factors

On each measurement day of soil GHG fluxes, we also measured soil temperature, moisture, and mineral N concentration in the top 5 cm mineral soil. We were

only able to measure soil mineral N during the last six months of the fieldwork, as the needed chemicals shipped from Germany arrived late due to administrative issues in Cameroon, involving custom clearance of shipped supplies. Soil temperature was measured near each chamber base using a portable thermometer (Greisinger GMH 3210, Greisinger Messtechnik GmbH, Regenstauf, Germany).

Soil in the top 5-cm depth was sampled at about 1-m away from each of the four chamber bases per stratum for mineral N extraction and soil moisture determination. The four soil sub-samples were then thoroughly mixed to have one composite sample for each specific stratum in each replicate plot. One part of these soil samples was used for soil mineral N extraction, which was done in-situ to avoid changes in mineral N concentrations due to storage of disturbed soil samples (Arnold et al. 2008). In the field, freshly sampled soils were added into prepared extraction bottles (250 mL plastic bottles containing 150 mL of 0.5 M K_2SO_4 solution) and shaken thoroughly. Upon arrival at the local field station, the bottles were shaken again for one hour and filtered. The filtered extracts were stored in 20 mL scintillation vials and immediately frozen for transport to the University of Goettingen, Germany. At the laboratory of Goettingen University, soil extracts were analyzed for total extractable N, NH_4^+ , and NO_3^- using continuous flow injection colorimetry (SEAL Analytical AA3). Total extractable N was determined by ultraviolet-persulfate digestion followed by hydrazine sulfate reduction (Autoanalyzer Method G-157-96), NH_4^+ by salicylate and dicloro isocyanuric acid reaction (Autoanalyzer Method G-102-93), and NO_3^- by cadmium reduction method with NH_4Cl buffer (Autoanalyzer Method G-254-02). Soil moisture content was determined from the remaining soil samples, upon arrival at the field station in Cameroon. Gravimetric moisture content was measured by oven-drying soils at 105 °C for 24 h and was expressed as water-filled pore space (WFPS) using the measured bulk density (Table S1) and the particle density of mineral soil (2.65 g cm^{-3}). The gravimetric moisture content was also used to calculate the dry mass of soil extracted for mineral N.

Soil physical and biochemical characteristics in the top 50-cm depth were reported in our previous study (Tchifo Lontsi et al. 2019); and those in the top

10-cm depth are reported in Table S1. Soil sampling and analysis are described in detail in the supplementary material (Text S1).

Statistics

Statistical tests of the repeatedly measured soil GHG fluxes and soil parameters (WFPS, soil temperature, and mineral N concentrations) were conducted using linear mixed-effects (LME) models followed by Fisher's least significant difference (LSD) test at $P \leq 0.05$. These tests were carried out on the average of the four chambers (as subsamples) on a given sampling day, representing each stratum within each replicate plot, and conducted on data across all sampling days. Each parameter was first checked for normality (Shapiro–Wilk test) and in cases of non-normal distribution, we used a logarithmic (e.g., CH₄, soil temperature, mineral N) or a square root (e.g., CO₂, NO₃⁻) transformation. For LME tests, either strata (when comparing among road, logging deck, skidding trail, felling gap and reference area within each logging system) or logging systems (when comparing between CL and RIL) were considered as the fixed factor whereas replicate plots and sampling days were taken as random factors. If the relative goodness of the model (based on the Akaike information criterion) was improved, we included in the model heteroscedasticity of the fixed-factor variances (using varIdent function) and/or the decreasing autocorrelation of sampling days with increasing time interval (using corAR1 function). The LME model was also used to assess seasonal difference in soil GHG fluxes and soil parameters for each stratum (first, separately for each logging system, and then combined when there were no difference between logging systems) with season as the fixed factor and the random factors as above.

The relationships between soil GHG fluxes and temporal and spatial soil controlling factors were assessed by linear and non-linear regressions, represented by the best-fit regression between soil GHG and controlling variables. We conducted the regression analyses across logging systems, as almost all soil controlling factors did not differ between CL and RIL. To assess how monthly measured soil factors (WFPS, soil temperature, and mineral N) influenced the temporal variations of soil GHG fluxes, we used the

means of the four replicate plots for each stratum on each sampling day and conducted the regression across the 12 monthly measurements. The regression analyses were carried out across all strata ($n = 120$ (2 logging systems \times 5 strata \times 12 months), except for mineral N with six monthly measurements, for which $n = 60$) as well as separately for the undisturbed reference area ($n = 24$ (2 logging systems \times 12 months), except for mineral N for which $n = 12$). To assess the influence of one-time measured soil physical and biochemical characteristics (Table S1) on the spatial variations of soil GHG fluxes, we used the annual GHG flux for each replicate plot, and carried out the regression analyses across all strata ($n = 40$ (2 logging systems \times 4 plots \times 5 strata)) as well as for the undisturbed reference area ($n = 8$ (2 logging systems \times 4 plots)). Regression coefficients were considered significant at $P \leq 0.05$. All statistical analyses were performed using the open-source statistical software R version 3.5.1 (R Core Team 2018).

Results

Soil GHG fluxes and controlling factors in the undisturbed reference areas

The undisturbed reference areas of CL and RIL consistently emitted N₂O and consumed CH₄ throughout the measurement period (Fig. 1c–f). Across the 12-month measurement period, soil CO₂, N₂O, and CH₄ fluxes from the undisturbed reference areas did not differ between CL and RIL ($P = 0.15$ – 0.41 ; Fig. 1a–f; Table 1). We also did not find any difference in these soil GHG fluxes between dry and wet seasons in each or both logging systems ($P = 0.13$ – 0.20 ; Table 2).

Soil temperature, NH₄⁺, and NO₃⁻ contents did not differ between CL and RIL undisturbed areas as well as between the dry and wet seasons ($P = 0.17$ – 0.94 ; Fig. 2c, d; Table 2). However, WFPS was higher in the wet season than the dry season ($P < 0.01$; Fig. 2a, b; Table 2). Monthly WFPS explained 29%, 28%, and 54% of the temporal variability in soil CO₂, N₂O, and CH₄ fluxes, respectively (Fig. 3a, c, e). Additionally, we found a negative relationship between soil CH₄ fluxes and NO₃⁻ ($R^2 = 0.49$, $P = 0.01$, $n = 12$).

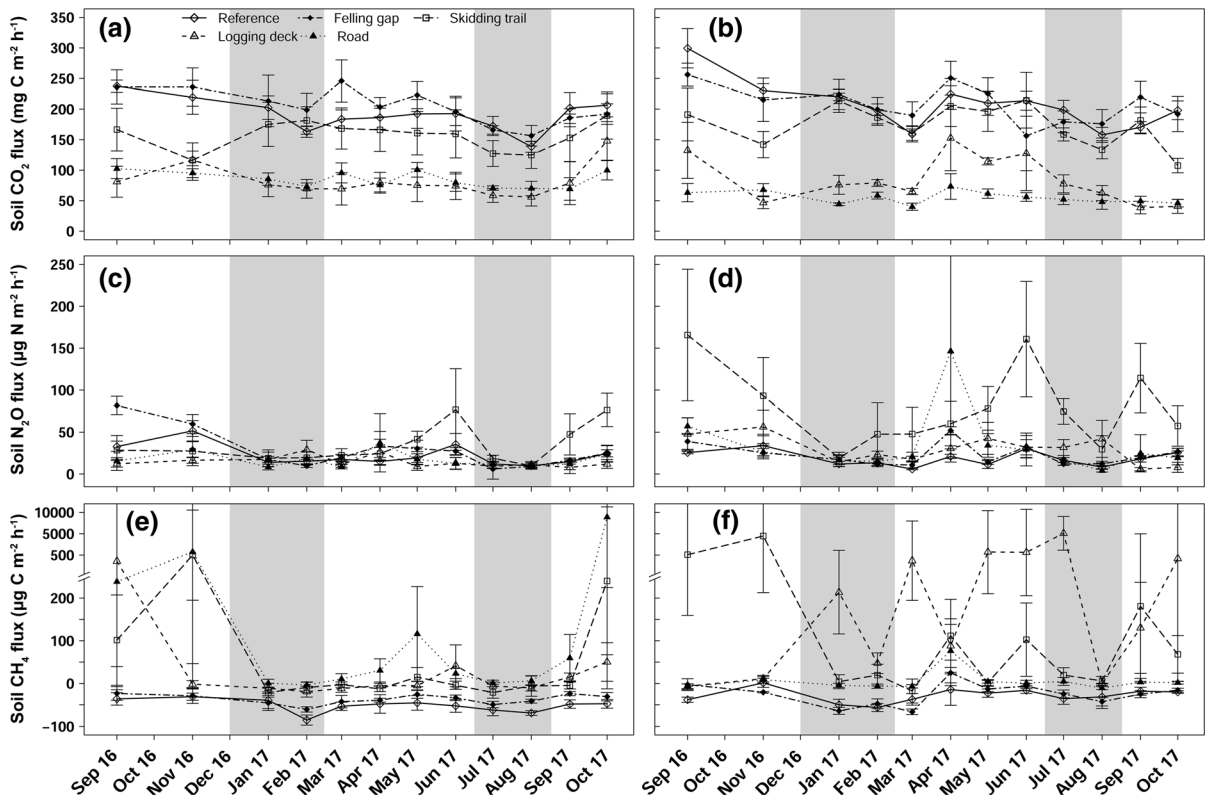


Fig. 1 Soil CO₂, N₂O and CH₄ fluxes (mean ± SE, *n* = 4 plots) from the undisturbed reference area (◇), felling gap (◆), skidding trail (□), logging deck (Δ), and road (▲) in

conventional selective (a, c, and e) and reduced-impact logging (b, d and f) in a Congo Basin rainforest of Cameroon. Grey shadings mark the dry season

Effects of selective logging on soil GHG fluxes and controlling factors

All three soil GHG showed similar patterns of changes in the disturbed strata as compared to the reference areas in both CL and RIL ($P < 0.01–0.05$; Fig. 1a–f; Table 1). Soil GHG fluxes were largely altered in roads, logging decks, and skidding trails, whereas felling gaps showed comparable fluxes with the undisturbed reference area. For roads, there were larger soil CO₂ emissions from the CL than RIL ($P < 0.01$; Table 1). Nonetheless, the overall changes in soil GHG fluxes from the disturbed strata (weighted by their respective areal coverages) relative to the undisturbed reference area did not differ between CL and RIL ($P = 0.06–0.92$).

Soil CO₂ emissions decreased in skidding trails, logging decks, and roads as compared to the undisturbed reference area in CL and RIL ($P < 0.01$; Fig. 1a, b; Table 1), and were comparable between the

dry and wet seasons ($P = 0.08–0.64$; Table 2). In comparison to the undisturbed reference area, area-weighted annual soil CO₂ emissions from the combined disturbed strata decreased by 26% and 30% in CL and RIL, respectively ($P < 0.01–0.03$; Table 1).

Soil N₂O emissions from the skidding trails were higher than the other disturbed strata ($P = 0.03–0.05$; Fig. 1c–d; Table 1). Seasonal pattern also showed larger soil N₂O emissions in the wet season than in the dry season for skidding trails ($P < 0.01–0.05$; Table 2). Annual soil N₂O emissions from the disturbed strata as a whole increased by 9% and 175% relative to the undisturbed reference area in CL and RIL, respectively ($P = 0.58$ and 0.03 ; Table 1), with an average change of 83% in both logging systems.

Soil CH₄ fluxes were larger in skidding trails, logging decks, and roads compared to the undisturbed reference area ($P < 0.01$; Fig. 1e, f; Table 1). Soils in skidding trails and roads displayed net CH₄ uptake

Table 1 Soil CO₂, N₂O and CH₄ fluxes from undisturbed reference area and disturbed strata following conventional selective and reduced-impact logging in a Congo Basin rainforest of Cameroon

Logging system/ Strata	CO ₂ emission (mg C m ⁻² h ⁻¹)	Annual CO ₂ emission (Mg C ha ⁻¹ year ⁻¹)	N ₂ O emission (μg N m ⁻² h ⁻¹)	Annual N ₂ O emission (kg N ha ⁻¹ year ⁻¹)	CH ₄ fluxes (μg C m ⁻² h ⁻¹)	Annual CH ₄ fluxes (kg C ha ⁻¹ year ⁻¹)
Conventional logging (CL)						
Reference	191 ± 6 ^a	17.0 ± 1.0	22 ± 3 ^{ab}	2.1 ± 0.4	-52 ± 4 ^c	-4.3 ± 0.8
Felling gap	204 ± 8 ^a	18.2 ± 1.2	28 ± 4 ^{ab}	2.7 ± 0.3	-37 ± 3 ^c	-3.2 ± 0.8
Skidding trail	157 ± 9 ^b	13.5 ± 2.2	34 ± 6 ^a	2.7 ± 0.3	72 ± 39 ^{ab}	8.3 ± 4.1
Logging deck	82 ± 7 ^c	7.2 ± 1.4	15 ± 2 ^b	1.3 ± 0.3	42 ± 40 ^b	3.3 ± 3.5
Road	85 ± 4 ^{c,A}	7.5 ± 0.7	17 ± 3 ^b	1.5 ± 0.5	873 ± 721 ^a	46.2 ± 44.1
Area-weighted average of the disturbed strata		12.5 ± 1.6		2.3 ± 0.3		16.3 ± 14.6
Reduced-impact logging (RIL)						
Reference	206 ± 7 ^a	18.3 ± 1.1	18 ± 2 ^b	1.6 ± 0.3	-29 ± 5 ^c	-2.5 ± 0.8
Felling gap	207 ± 8 ^a	18.6 ± 0.7	23 ± 2 ^b	2.0 ± 0.2	-26 ± 5 ^c	-2.4 ± 0.4
Skidding trail	174 ± 8 ^b	15.4 ± 1.0	79 ± 12 ^a	6.7 ± 2.3	469 ± 359 ^{ab}	71.1 ± 59.3
Logging deck	84 ± 9 ^c	7.2 ± 0.9	29 ± 4 ^b	2.8 ± 0.8	726 ± 339 ^a	51.1 ± 31.2
Road	55 ± 3 ^{d,B}	4.9 ± 0.4	34 ± 10 ^b	2.9 ± 1.1	5 ± 6 ^b	0.5 ± 0.5
Area-weighted average of the disturbed strata		12.9 ± 0.7		4.4 ± 1.4		32.0 ± 26.9

Measurements were conducted monthly from September 2016 to October 2017. Means (± SE, $n = 4$ plots) followed by different lowercase letters indicate significant differences among strata within a logging system and different uppercase letters indicate significant differences between logging systems within a stratum (linear mixed-effect models with Fisher's LSD test at $P \leq 0.05$). Annual soil CO₂, N₂O and CH₄ fluxes were not statistically tested for differences between strata or logging systems since these annual values are trapezoidal interpolations. Area-weighted average of the disturbed strata uses the respective areal coverages at CL and RIL sites of 1.1% and 1.0% for felling gap, 2.4% and 1.7% for skidding trail, 0.2% and 0.1% for logging deck, and 1.4% and 1.2% for road

during the dry season but net CH₄ emission during the wet season (Table 2). On the other hand, soils in logging decks emitted CH₄ year-round (Fig. 1e, f; Table 2). Area-weighted annual soil CH₄ emissions from the entire disturbed strata were four and 13 times (CL and RIL, respectively) higher than the annual soil CH₄ consumption in the undisturbed reference areas ($P < 0.01$ – 0.04 ; Table 1).

The disturbed strata generally showed comparable WFPS between CL and RIL ($P = 0.15$ – 0.41 ; Fig. 2a, b). Among strata, WFPS was higher in skidding trails, roads, and logging decks compared to the undisturbed reference area, while felling gaps were comparable with the reference area ($P \leq 0.01$; Fig. 2a, b; Table 2). Seasonally, WFPS was higher in the wet than in the dry season ($P < 0.01$ – 0.03 ; Table 2), except for the roads that showed no seasonal differences ($P = 0.09$;

Table 2). Soil temperature was higher in logging decks and roads compared to skidding trails, felling gaps, and the reference areas ($P < 0.01$; Fig. 2c, d; Table 2) and did not differ between seasons ($P = 0.47$ – 0.85 ; Table 2). Total extractable mineral N (NH₄⁺ + NO₃⁻) was lower ($P < 0.01$) in roads and logging decks compared to felling gaps and the reference areas, whereas skidding trails showed intermediate values (Table 2). Extractable mineral N did not show a seasonal variation ($P = 0.43$ – 0.92) and its dominant form was NH₄⁺ in all the strata (Table 2).

Temporal and spatial controls of soil GHG fluxes

As opposed to the undisturbed area, where soil CO₂ emissions showed positive relationship with WFPS (Fig. 3a), there was a weak negative relationship of

Table 2 Dry- and wet-season soil greenhouse gas fluxes and soil controlling factors (measured in the top 5 cm) for the undisturbed reference area and disturbed strata in both logging systems in a Congo Basin rainforest of Cameroon

Strata	CO ₂ fluxes (mg C m ⁻² h ⁻¹)	N ₂ O fluxes (μg N m ⁻² h ⁻¹)	CH ₄ fluxes (μg C m ⁻² h ⁻¹)	WFPS (%)	Temperature (°C)	NH ₄ ⁺ (mg N kg ⁻¹)	NO ₃ ⁻ (mg N kg ⁻¹)
Wet season							
Reference	208 ± 6 ^a	24 ± 2 ^{bc}	- 34 ± 4 ^b	49.5 ± 1.7 ^{c,A}	25.1 ± 0.1 ^c	3.2 ± 0.3 ^a	0.6 ± 0.1 ^a
Felling gap	214 ± 7 ^a	32 ± 3 ^{b,A}	- 23 ± 4 ^{b,A}	50.6 ± 2.0 ^{c,A}	25.7 ± 0.1 ^c	3.9 ± 0.4 ^a	0.9 ± 0.2 ^a
Skidding trail	167 ± 8 ^b	70 ± 10 ^{a,A}	406 ± 270 ^{a,A}	70.2 ± 1.9 ^{a,A}	25.5 ± 0.1 ^c	2.8 ± 0.2 ^{ab}	0.5 ± 0.1 ^{ab}
Logging deck	90 ± 8 ^c	22 ± 3 ^c	243 ± 90 ^a	58.4 ± 2.1 ^{b,A}	28.4 ± 0.4 ^a	2.7 ± 0.7 ^{bc}	0.1 ± 0.0 ^b
Road	74 ± 4 ^c	32 ± 8 ^{bc}	660 ± 541 ^{a,A}	63.6 ± 2.0 ^a	27.4 ± 0.3 ^b	1.8 ± 0.2 ^c	0.1 ± 0.1 ^b
Dry season							
Reference	181 ± 8 ^a	13 ± 1 ^b	- 54 ± 6 ^c	36.1 ± 1.5 ^{b,B}	25.3 ± 0.2 ^c	3.1 ± 0.4 ^a	3.2 ± 1.2 ^a
Felling gap	189 ± 8 ^a	12 ± 2 ^{b,B}	- 47 ± 4 ^{c,B}	36.4 ± 2.2 ^{b,B}	25.8 ± 0.2 ^c	2.9 ± 0.4 ^a	2.2 ± 0.7 ^a
Skidding trail	162 ± 9 ^b	30 ± 6 ^{a,B}	- 1 ± 6 ^{b,B}	55.1 ± 3.0 ^{a,B}	25.5 ± 0.2 ^c	2.5 ± 0.3 ^{ab}	1.0 ± 0.4 ^{ab}
Logging deck	69 ± 5 ^c	22 ± 4 ^{ab}	666 ± 490 ^a	41.4 ± 4.6 ^{b,B}	28.9 ± 0.6 ^a	2.4 ± 0.5 ^{ab}	0.3 ± 0.1 ^b
Road	63 ± 4 ^c	13 ± 2 ^b	- 2 ± 2 ^{b,B}	48.7 ± 3.6 ^{ab}	27.2 ± 0.4 ^b	1.7 ± 0.2 ^b	0.2 ± 0.1 ^b

Means (± SE, $n = 8$ plots) followed by different lowercase letters indicate significant differences among strata within each season, and different uppercase letters indicate significant differences between seasons within each stratum (linear mixed-effect models with Fisher's LSD test at $P \leq 0.05$)

monthly soil CO₂ emissions with WFPS across all strata during the wet season ($R^2 = 0.06$, $P = 0.03$, $n = 80$) when WFPS was high (Fig. 2a, b; Table 2). When we excluded the strata with highly compacted soil and reduced organic matter (i.e., logging decks and roads with increased soil bulk density and reduced SOC and total N; Table S1), monthly soil CO₂ emissions showed a positive relationship with WFPS ranging from 25 to 45% and a negative relationship with WFPS ranging from 46 to 90% (Fig. 3b). We detected a negative relationship of monthly soil CO₂ emissions with soil temperature ($R^2 = 0.29$, $P < 0.01$, $n = 120$). However, this was not a temporal control of soil temperature but rather a spatial pattern brought about by the reduced soil CO₂ emissions from logging decks and roads (Table 1), where soil temperatures had increased (Table 2) but SOC stocks had decreased (Table S1). For example, when considering only the undisturbed area, felling gaps, and skidding trails, monthly soil CO₂ emissions showed a positive relationship with soil temperature across the measurement period ($R^2 = 0.07$, $P = 0.02$, $n = 72$), whereas there was no correlation across the year when only

considering logging decks and roads ($R^2 = 0.04$, $P = 0.14$, $n = 48$). Monthly soil CO₂ emissions increased with increase in total mineral N (NH₄⁺ + NO₃⁻) ($R^2 = 0.21$, $P < 0.01$, $n = 60$); as with soil temperature, this correlation with mineral N depicted more the parallel spatial patterns with soil CO₂ emissions across strata rather than their temporal patterns since mineral N did not show seasonal difference (Tables 1 and 2). Furthermore, monthly soil N₂O emissions were positively correlated with WFPS across strata during the whole-year measurements (Fig. 3d). There was also a positive relationship between monthly soil N₂O emissions and total mineral N when considering only the logging decks and roads ($R^2 = 0.21$, $P = 0.02$, $n = 24$). Monthly soil CH₄ fluxes were positively correlated with WFPS across strata during the measurement period (Fig. 3f).

Across strata and logging systems, annual soil CO₂ emissions were positively correlated with SOC, total N, Bray-extractable P, and ECEC (Fig. 4a–c) and negatively with soil bulk density (Fig. 4d). Annual soil CH₄ fluxes were positively correlated with soil C:N ratio ($R^2 = 0.10$, $P = 0.05$, $n = 40$). Annual soil N₂O

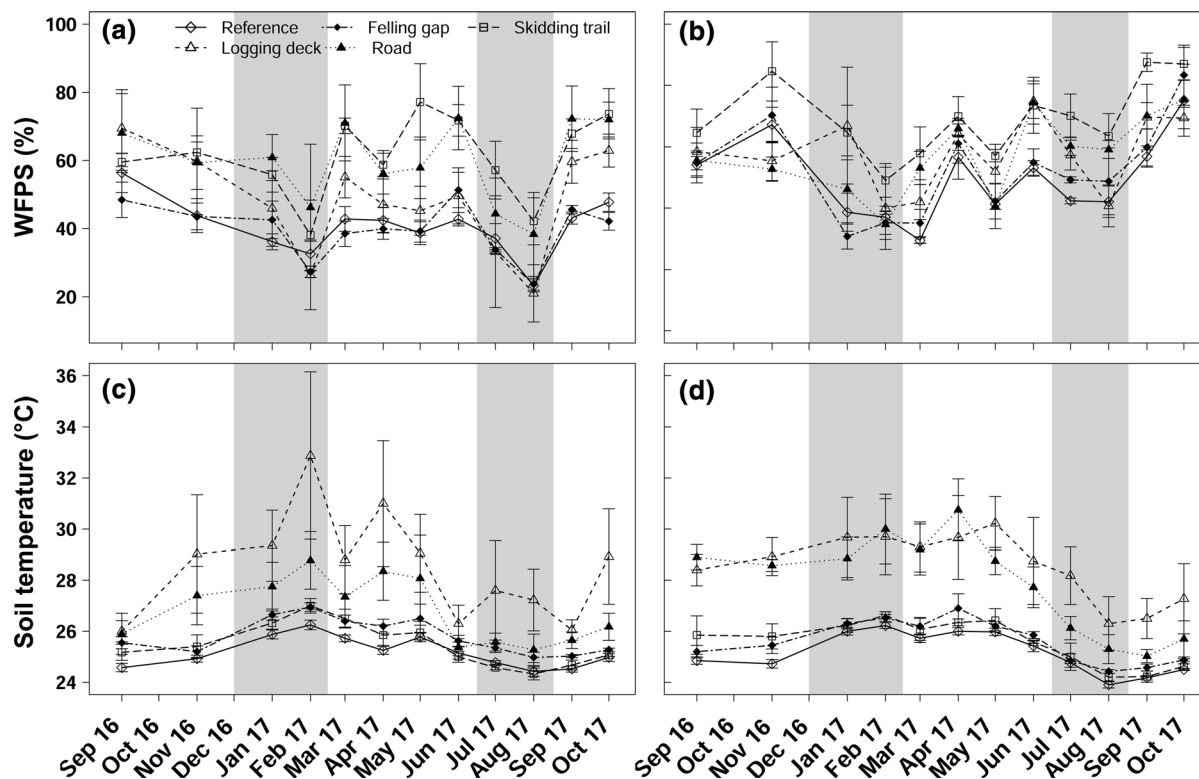


Fig. 2 Soil water-filled pore space (WFPS) and soil temperature (mean \pm SE, $n = 4$ plots) in the top 5 cm from the undisturbed reference area (\diamond), felling gap (\blacklozenge), skidding trail

(\square), logging deck (Δ), and road (\blacktriangle) in conventional selective (a and c) and reduced-impact logging (b and d) in a Congo Basin rainforest of Cameroon. Grey shadings mark the dry season

emissions did not correlate with any of the measured soil characteristics in Table S1.

Discussion

Soil CO₂ emissions

Soil CO₂ emissions from the undisturbed reference area (Table 1) were within the range reported for tropical rainforests on Ferralsol soils in Central and South America (92.7–228.3 mg C m⁻² h⁻¹; Davidson et al. 2000b, 2004; Schwendenmann et al. 2003; Chambers et al. 2004; Keller et al. 2005; Sotta et al. 2006; Matson et al. 2017). The few studies in Africa conducted in forests and savannah with drier conditions (900–2050-mm annual rainfall) have lower soil CO₂ emissions (71.8–175.3 mg C m⁻² h⁻¹; Werner et al. 2007; MacCarthy et al. 2018; Wanyama et al. 2019) compared to our measurements (Table 1). The positive interaction between soil CO₂ emissions and

WFPS in the undisturbed reference area (Fig. 3a) showed that under low WFPS soil moisture limits root and microbial activities, and this is alleviated with increasing WFPS and thus increasing soil respiration (e.g., Schwendenmann et al. 2003; Koehler et al. 2009b; van Straaten et al. 2011).

The seasonal pattern of soil CO₂ emissions, as driven by soil moisture content, was confounded by the increases in soil bulk densities of the disturbed strata that influenced WFPS. For example, increased WFPS in skidding trails, logging decks, and roads particularly during the wet season (Table 2) can be explained by the increase in soil bulk density (Table S1), which may have hampered water drainage. Thus, the high WFPS with low soil CO₂ emissions from these disturbed strata showed a negative correlation during the wet season. High WFPS might have restricted oxygen diffusion into the soil, which, in turn, might have limited microbial activity; similarly, high WFPS could have hampered CO₂ transport within and from the soil surface (e.g., Davidson et al. 2000b; Sotta

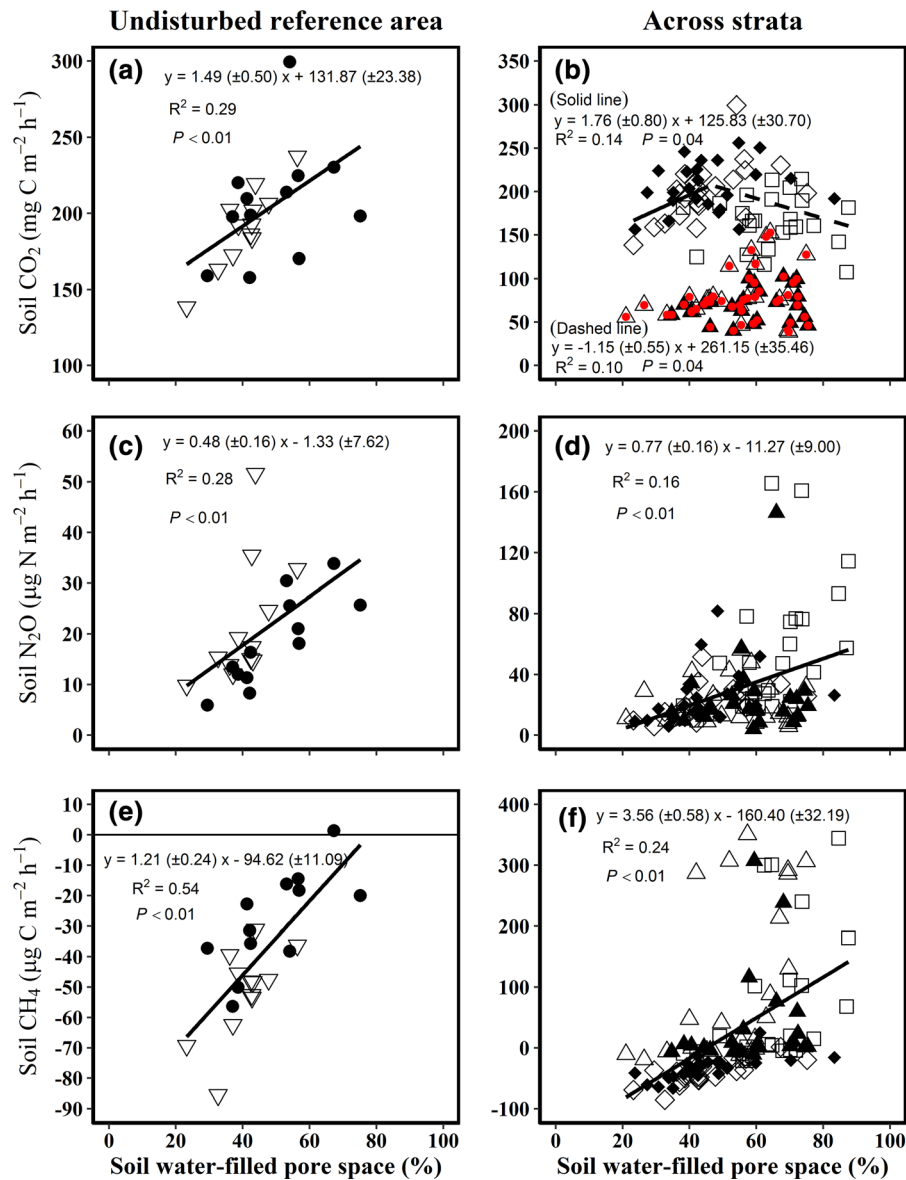


Fig. 3 Relationships between soil CO₂ emissions (a, b), soil N₂O fluxes (c, d), soil CH₄ fluxes (e, f) and water-filled pore space (WFPS) in the top 5 cm in a Congo Basin rainforest of Cameroon. For the undisturbed reference area (a, c, e; $n = 24$): conventional logging (∇) and reduced-impact logging (\bullet). For regressions across logging systems and strata (b, d, f; $n = 120$): undisturbed reference area (\diamond), felling gap (\blacklozenge), skidding trail

(\square), logging deck (Δ), and road (\blacktriangle). For (b), significant relationship was observed only when excluding logging decks and roads (red dots), and with separate linear regressions for below and above 45% WFPS. Regression analysis was conducted using the monthly means (from September 2016 to October 2017) of four replicate plots per stratum

et al. 2006; Koehler et al. 2009b). Moreover, the influence of soil moisture on the seasonal pattern of soil CO₂ emissions was also confounded by the reduced SOC and total N stocks (i.e., roads; Table S1) and the absence of root respiration from vegetation removal in highly disturbed strata (i.e.,

logging decks and roads). The generally recognized parabolic relationship between soil CO₂ emissions and WFPS in natural tropical forests (Schwendenmann et al. 2003; Sotta et al. 2006; van Straaten et al. 2011; Matson et al. 2017) was observed in our present study only when excluding logging decks and roads

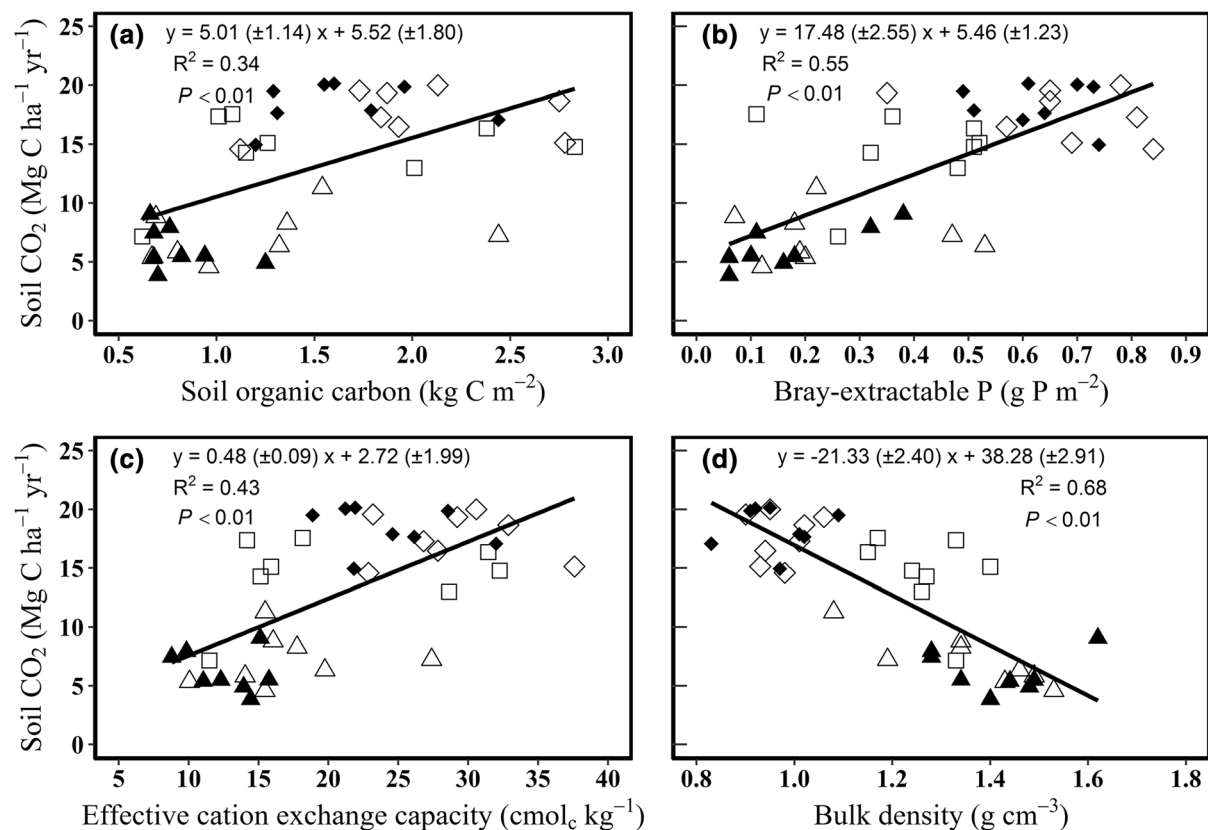


Fig. 4 Relationships between annual soil CO₂ emissions and soil organic carbon (a), bray-extractable phosphorus (b), effective cation exchange capacity (c) and soil bulk density (d) in the top 5 cm in conventional selective and reduced-impact

logging ($n = 40$) in a Congo Basin rainforest of Cameroon: undisturbed reference area (◇), felling gap (◆), skidding trail (□), logging deck (△), and road (▲)

(Fig. 3b). The highly compacted soils with reduced stocks of soil organic matter and absence of root respiration in logging decks and roads had consistently lowered soil CO₂ emissions regardless of the range of WFPS (Tables 1 and 2). Furthermore, a similar underlying mechanism can be attributed to the relationships observed for soil CO₂ emissions with soil temperature (negative correlation) and mineral N (positive correlation). These relationships might not be due to temperature or mineral N per se but instead due to the reduced stocks of soil organic matter in logging decks and roads (Table S1), where soil temperatures had increased and mineral N had decreased (Table 2). Low mineral N content in logging decks and roads might have resulted from reduced mineralization, as a consequence of reduced total N stocks (Table S1) and absence of litter input (Tchiofo Lontsi et al. 2019).

The large decreases in soil CO₂ emissions in skidding trails, logging decks, and roads compared to the undisturbed area (Table 1; Fig. 1a, b) were, firstly, attributed to the decrease in soil organic matter (i.e., decreases in SOC and total N; Table S1) as signified by their positive relationship across all strata (Fig. 4a). Previous studies in (sub)tropical ecosystems have reported a decrease in soil respiration following management practices that led to reduction in soil organic matter (e.g., Sheng et al. 2010; Liu et al. 2014; Hassler et al. 2015). Reduced amount of organic matter from the removal of the vegetation, surface litter and organic matter-rich topsoil in roads and logging decks might have decreased substrate for heterotrophic respiration, as litter respiration accounts 29–35% and soil organic matter respiration contributes 45% of total soil respiration (van Straaten et al. 2011; Liu et al. 2014; Han et al. 2015). Also, removal of vegetation reduces eliminates root

(autotrophic) respiration, which can account for up to 50% of total soil respiration (van Straaten et al. 2011; Schlesinger and Bernhardt 2013; Mori et al. 2017). Secondly, the positive correlations of soil CO₂ emissions with Bray-extractable P and ECEC across strata suggest regulation by nutrient availability, as P and base cations are commonly the limiting nutrient for decomposition activity in highly weathered Ferralsol soils (Kaspari et al. 2008). Extractable P and ECEC also correlated with SOC, which decreases with increasing degree of disturbance across strata (Table S1; Tchifo Lontsi et al. 2019), depicting the decreases in soil CO₂ emissions (Table 1). Thirdly, the negative correlation found between soil CO₂ emissions and bulk density across strata (Fig. 4d) was the result of soil compaction (Table S1). Increased soil bulk density with increased degree of disturbance was the combined effect of heavy logging machinery and reduced organic matter (Table S1; Tchifo Lontsi et al. 2019), resulting in reduced soil CO₂ emissions (Table 1). Indeed, large soil bulk density (or reduced porosity) could have restricted gas diffusion into and from the soil (Yashiro et al. 2008; Goutal et al. 2012), similar to the effect of high WFPS discussed above.

In summary, the observed decreases in soil CO₂ emissions following disturbance from selective logging reflected the absence of root respiration in combination with a reduction in soil organic matter (SOC and N) which, in turn, reduced soil fertility (mineral N, extractable P and ECEC) and increased soil bulk density. The latter increased WFPS that bolstered the decrease in soil respiration in disturbed areas.

Soil N₂O emissions

Soil N₂O emissions from the undisturbed reference area (Table 1) were within the range of values reported for most tropical forests on Ferralsol soils across the humid tropics (3.4–29.7 μg N m⁻² h⁻¹; Verchot et al. 1999; Castaldi et al. 2013; Aini et al. 2015; Matson et al. 2017; Bauters et al. 2019). One study on a Ferralsol soil in Brazil (Keller et al. 2005) reported soil N₂O emissions approximately four times higher than our values, which may be attributed to that study site's clay-textured soil compared to our sandy loam Ferralsol. Moreover, our values were within the range of annual soil N₂O emissions measured from some African rainforests (1.6–2.8 kg N ha⁻¹ year⁻¹;

Werner et al. 2007; Castaldi et al. 2013; Bauters et al. 2019).

The positive relationship found between soil N₂O emissions and WFPS in the undisturbed reference area (Fig. 3c), suggests the favorable anaerobic conditions with increased WFPS for microbial production of N₂O in tropical moist forest soils (e.g., Davidson et al. 2000a; Corre et al. 2014). We did not detect a correlation between soil N₂O emissions and mineral N contents in the undisturbed area possibly because of the low and narrow range of mineral N contents (Table 2).

The 83% increase in soil N₂O emissions from the disturbed area relative to the undisturbed reference area corroborated previous studies on logging in tropical forests (e.g., Keller et al. 2005; Yashiro et al. 2008). These increased soil N₂O emissions from the disturbed area were driven by high emissions from skidding trails (Table 1). Although other compacted areas, such as logging decks and roads, showed increased WFPS (Table 2; Fig. 2), these did not result in increases in N₂O emissions due to their decreased mineral N contents (Table 2). Removal of litter layer and topsoil and absence of organic material inputs in roads and logging decks reduce soil fertility (Tchifo Lontsi et al. 2019), including total N stocks (Table S1), as also evident by the reduced mineral N content compared to the undisturbed area, and thus limiting N₂O production even during conditions with high WFPS (Tables 1 and 2). Leaf-litter removal from the forest floor had also been shown to reduce soil N₂O emissions by approximately 42% relative to the control in a wet tropical forest of Costa Rica (Wieder et al. 2011). The positive relationship between soil N₂O emissions and mineral N content in logging decks and roads further illustrated the influence of mineral N, as this correlation suggests that even small variation in mineral N across monthly measurements could intensify N₂O emissions under their favorable high WFPS (Table 2). Moreover, skidding trails had comparable soil mineral N content as the undisturbed reference areas and felling gaps but the former had larger WFPS than the latter (Table 2), resulting in higher soil N₂O emissions from skidding trails than all other strata (Table 1). Altogether, these patterns were consistent with the hole-in-the-pipe model (Davidson et al. 2000a) postulating the two most important controlling factors of soil N₂O emissions, soil N availability and moisture content.

Soil CH₄ fluxes

Undisturbed forest soils in our study area were sinks for atmospheric CH₄, and the uptake rate (Table 1) was within the range reported for African forest soils (-12.5 to $-56.4 \mu\text{g C m}^{-2} \text{h}^{-1}$; Werner et al. 2007; Kim et al. 2016; Gütlein et al. 2018; Wanyama et al. 2019). In comparison with other studies from tropical lowland forests on Ferralsol soils, our values were higher than the soil CH₄ uptake rate measured in Brazil and Panama (-3.1 to $-21.1 \mu\text{g C m}^{-2} \text{h}^{-1}$; Davidson et al. 2004; Keller et al. 2005; Matson et al. 2017). In contrast to these studies' clay-textured Ferralsol soils, the coarse texture at our sites (sandy loam) had possibly facilitated diffusion of atmospheric CH₄ into the soil, which usually limit CH₄ oxidation in soil, as exemplified by the pattern of CH₄ uptake with soil texture across tropical forest soils (Veldkamp et al. 2013). The effect of soil aeration status on soil CH₄ fluxes from the undisturbed area was further illustrated by their positive correlations with WFPS across monthly measurements (Fig. 3e). Increases in WFPS reduce gas diffusivity in the soil, decreasing CH₄ availability for methanotrophs, as well as increase anaerobic conditions in the soil, promoting methanogenic activity (Schlesinger and Bernhardt 2013; Raut et al. 2014), and thus resulting in increases in soil CH₄ fluxes (e.g., Davidson et al. 2004; Keller et al. 2005; Veldkamp et al. 2013). The negative correlation between soil CH₄ fluxes and NO₃⁻ content in the undisturbed area suggests an N limitation on CH₄ uptake in tropical forest soils (Veldkamp et al. 2013; Hassler et al. 2015; Matson et al. 2017). Indeed, increasing N availability may either have enhanced methanotrophic activity or increased their population that leads to high CH₄ consumption in soils (Bodelier and Laanbroek 2004).

Soils in the disturbed strata changed from a sink to a net source of CH₄, except in felling gaps where CH₄ uptake was comparable to the undisturbed area (Table 1). Area-weighted average of CH₄ emissions from the disturbed strata (Table 1) was very large and comparable in magnitude to the diffusive CH₄ flux measured at the surface of an Amazonian floodplain lake ($22.5 \text{ kg C ha}^{-1} \text{ year}^{-1}$; Crill et al. 1988). Our results corroborated some previous studies that reported an increase in soil CH₄ emissions following logging (Keller et al. 2005; Zerva and Mencuccini 2005; Yashiro et al. 2008). On the other hand, no effect

of logging on soil CH₄ fluxes was found in a Malaysian forest 14 years after logging (Mori et al. 2017). We speculate that either the time since logging may have allowed the soil properties (e.g., bulk density and N availability, regulating CH₄ processes) to recover or that its experimental design (one-off sampling and no consideration of the spatial pattern of selective logging disturbances) may have failed to capture the spatial changes in soil CH₄ fluxes. By including the different disturbed strata in our design, we were able to capture the changes in soil CH₄ fluxes and their drivers across a gradient of damage intensity from felling gaps to roads (Tables 1 and 2).

The net CH₄ emissions from the most disturbed strata (i.e., skidding trails, logging decks, and roads) were the result of increased occurrence of anaerobic conditions due to soil compaction (high bulk density; Table S1), which directly influenced WFPS (Fig. 2a, b; Table 2) and thus gas diffusion in the soil. The compacted soils in these highly disturbed strata have limited CH₄ consumption by restricted gas diffusion while CH₄ production was enhanced by increased WFPS (Verchot et al. 2000; Veldkamp et al. 2008; Schlesinger and Bernhardt 2013), resulting in net CH₄ emissions. Furthermore, the net CH₄ uptake during the dry season and net CH₄ emissions during the wet season in the skidding trails and roads suggest that CH₄ consumption dominated over production at lower WFPS despite soil compaction. This highlights the dominance of WFPS as driver of soil CH₄ fluxes (e.g., Veldkamp et al. 2008, 2013; Matson et al. 2017). There was, however, no seasonal difference in net CH₄ emissions from logging decks, where ruts produced by heavy machinery were submerged during the wet season, which might have kept the subsoils moist even during the dry season. Therefore, due to anaerobic conditions in both dry and wet seasons, some areas of the logging decks became hot spots of CH₄ emissions as shown by the high variability among measurement chambers (i.e., large error bar; Fig. 1e, f). Moreover, the positive correlation between annual soil CH₄ fluxes and C:N ratio (as indicator of N availability) across all strata lent additional support to the control of N availability on soil CH₄ uptake, as explained above.

Conclusions

Soil CO₂, N₂O and CH₄ fluxes were all affected by selective logging. Ground disturbance and vegetation removal associated with selective logging lowered soil CO₂ emissions by 28% and increased soil N₂O emissions by 83%. The largest change was for soil CH₄ flux, as emissions from the disturbed area were on average seven times higher than CH₄ consumption in undisturbed area, and thus becoming comparable to CH₄ emissions from tropical wetlands. However, the disturbed strata represented only 4–5.2% of the logged area in both logging systems, which reduced considerably the changes in soil GHG fluxes when reported at the scale of the entire forest (i.e., a decrease of 1% and 36% for soil CO₂ emissions and soil CH₄ uptake, respectively, and an increase of 3% for soil N₂O emissions relative to the undisturbed forest area). Conversely, this implies that an increase in disturbed area (e.g., resulting from unplanned logging operations) can substantially affect local GHG budgets. The magnitude of changes in soil GHG fluxes and soil factors (WFPS, soil temperature, extractable mineral N) varied with the degree of disturbance among logging strata. This supports our first hypothesis and highlights the importance of considering the spatial pattern of disturbance when assessing the soil GHG flux footprint of selective logging. Changes in soil bulk density and WFPS that control gas diffusion and aeration status in the soil as well as changes in soil organic matter quantity and quality (SOC, total N, Bray-extractable P, ECEC, C:N, extractable mineral N) mainly explained the spatial and temporal variations of soil CO₂, N₂O and CH₄ fluxes, supporting our second hypothesis.

In our study, the CL operator used similar logging equipment and employed previously trained crews as those used by RIL company, and thus we observed similar effects of these two selective logging systems on soil GHG fluxes. The difference between these two logging systems may therefore arise from the areal coverage of the disturbed strata, which can change with logging intensity and frequency. In our study site, however, the extent of ground disturbance resulting from CL was unusually small, but there is a high possibility of re-logging the forest after only short periods, as CL generally occurs in unmanaged forests (or no requirement of a management plan). Since our study was conducted six to seven months after a single

logging event, it is unknown how large the cumulative disturbed area will be after consecutive re-logging entries, and how long the logging-induced changes in soil GHG fluxes will last. Looking beyond these limitations, our study shows that stronger disturbance (e.g., high logging intensities, frequent logging or clear-cutting) is likely to cause higher changes in soil GHG fluxes at the landscape level. Our study constitutes a valuable basis for further longitudinal research to improve knowledge on soil GHG-flux changes following low-intensity selective logging in Congo Basin rainforests.

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Author contributions RTL, MDC and EV designed the study. RTL performed data collection and material preparation. NAI assisted in field and material preparation. All authors contributed to the data analysis and manuscript writing, and approved the final manuscript.

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Data availability Data for this study are deposited in the institutional data repository of Goettingen University (<https://data.goettingen-research-online.de/>). They are freely available at <https://doi.org/10.25625/TWSFRU>.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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