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Land-use change and Biogeochemical controls of soil CO_2, N_2O and CH_4 fluxes in Cameroonian forest landscapes

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ABSTRACT

Deforestation and land-use change are accelerating in the Congo Basin and elsewhere in the tropics affecting the soil-atmosphere exchange of greenhouse gases (GHG). There is a lack of data from Central Africa. We quantified fluxes of CO_2, CH_4, and N_2O at the soil-atmosphere interface in a secondary forest, a cocoa agroforest, and an unfertilized cropland. Soil respiration was highest in the secondary forest (15.37 ± 3.42 Mg C ha^{-1} y^{-1}), intermediate in the cacao agroforest (12.26 ± 2.91 Mg C ha^{-1} y^{-1}) and the lowest in the unfertilized cropland (8.74 ± 2.62 Mg C ha^{-1} y^{-1}). Likewise, N_2O fluxes were highest in the secondary forest (2.17 ± 0.20 kg N ha^{-1} y^{-1}), intermediate in the cacao agroforest (1.40 ± 0.08 kg N ha^{-1} y^{-1}) and lowest in the unfertilized cropland (1.04 ± 0.15 kg N ha^{-1} y^{-1}). Soils were a sink for atmospheric CH_4 and sink strength was high in the secondary forest (-3.60 ± 1.83 kg CH_4 ha^{-1} y^{-1}) and cacao agroforest (-3.61 ± 2.09 kg CH_4 ha^{-1} y^{-1}) and low in the unfertilized cropland (-1.9 ± 1.59 kg CH_4 ha^{-1} y^{-1}). Variation in soil water content rather than temperature was the dominant driver of seasonal variations of the fluxes at all study sites and N availability affected both N_2O and CH_4 fluxes. Our results suggest that tropical land-use change is decreasing soil respiration, decreasing the strength of the soil CH_4 sink and decreasing N_2O emissions, in landscapes that do not practice agriculture with chemical fertilization.

1. Introduction

While carbon dioxide (CO_2) is the predominant greenhouse gas (GHG) emitted by land-use change, fluxes of non-CO_2 GHGs between the biosphere and the atmosphere are also greatly affected (Davidson and Kanter 2014; Saunois et al. 2016; Le Quéré et al. 2018). In

particular, fluxes of nitrous oxide (N_2O) and methane (CH_4) are significantly altered by deforestation and conversion of forests to agricultural systems (Verchot et al. 1999, 2000). Although tropical regions are known to be key sources for atmospheric N_2O (e.g. Werner et al. 2007), global budgets of these gases are poorly constrained. Improving our understanding of soil N_2O, CH_4 and CO_2 fluxes, particularly in the tropics, is needed to reduce uncertainties, improve global models, and inform policy decisions in the UN Climate Change Convention (Grassi et al. 2018).

Dynamic global vegetation models indicate that in the absence of land-use change, both heterotrophic and autotrophic respiration in soils are increasing with climate change (Sitch et al. 2015). Conversion of forest to agriculture results in loss of soil carbon (Solomon et al. 2007; Don et al. 2011; van Straaten et al. 2015) and changes to soil respiration (Davidson et al. 2000; Nagy et al. 2018; Wanyama et al. 2019). The interactions of climate and land-use change on soil carbon storage are complex because of differential impacts of both factors on inputs and outputs from the soil carbon pool. For example, warmer temperatures are expected to increase organic matter decomposition, but water and substrate quality limitations may limit the temperature effects (Davidson and Janssens 2006; Eglin et al. 2010). Thus, the magnitude and distribution of changes to the soil organic carbon pool are highly uncertain; reducing this uncertainty requires a better understanding of the biogeochemical processes that control soil organic matter turnover.

Deforestation and other forms of land-use change alter soil N_2O emissions, typically resulting in transient increased emissions following the conversion of native forests to grazing lands or croplands (van Lent et al. 2015; Meurer et al. 2016; McDaniel et al. 2019). The transient increase lasts from a few years to a decade or more. Over time, with the depletion of the soil N pool, N_2O emissions decrease and ultimately stabilize at levels that are lower than those that had been occurring under native vegetation, in the absence of fertilization. Fertilized systems typically show increasing N_2O emissions over time, with the rate of emission often being a function of nitrogen fertilization rates. Agriculture is responsible for approximately 80% of anthropogenic N_2O emissions (Janssens-Maenhout et al. 2019). Restoration of natural vegetation over a period of one to two decades does not lead to the recovery of N_2O emissions to the levels of the original vegetation (McDaniel et al. 2019).

Non-wetland soils are the largest biotic sink of atmospheric CH_4, but soils both produce and consume the gas. This sink is a small part of the global CH_4 budget, but its magnitude is similar to that of the rate of accumulation of the gas in the atmosphere (Kirschke et al. 2013). Thus, changes to the sink could affect accumulation rates of the gas in the atmosphere. The major factor that controls the spatial and temporal variability of the sink is the rate of gas diffusion into the soil (Striegl 1993; Verchot et al. 2000). Thus, soil texture and land cover have an important effect on CH_4 uptake in soils (Dutaur and Verchot 2007; Yu et al. 2017). Coarse textured soils take up more CH_4 than medium and fine-textured soils, and forests take up more than other ecosystems. Soil water content also affects diffusivity, so dry soils take up more CH_4 than wet soils. Nitrogen fertilization and atmospheric deposition affect the soil microbial community and stimulate soil CH_4 uptake in nitrogen-limited soils at low levels of N input, while higher fertilization rates decrease uptake via enzymatic competition (Serrano-Silva et al. 2014). Cumulative and repeated fertilization events have progressively greater enzymatic suppression effects (Tate 2015). While

modelling studies (Curry 2009; Xu et al. 2016; Yu et al. 2017) have shown that the global soil sink has increased since the second half of the 20th century, observations suggest that the sink is decreasing (Ni and Groffman 2018).

Most conversion of forests to agriculture occurs in the tropics, and while datasets from this region have increased over the past several decades, there are still large data gaps and especially gaps in our understanding that limit our ability to constrain non-CO_2 GHG budgets. There have been a number of studies that have quantified the effects of land-use change on gas fluxes from Asia and Latin America (Keller et al. 1993; Verchot et al. 1999, 2000, 2008; Erickson et al. 2001; Veldkamp et al. 2008, 2013; Aini et al. 2015; van Lent et al. 2019), but only a few studies have been conducted in Africa (Arias-Navarro et al. 2017; Wanyama et al. 2018, 2019). In this study, we report new data on GHG emissions from various typical land-uses from a Congolean rainforest landscape in Cameroon, where swidden agriculture is being replaced by cacao agroforestry.

In addition to quantifying the effects of land-use on the fluxes of CO_2, N_2O and CH_4 between the atmosphere and the soil, we tested several mechanistic hypotheses about biogeochemical controls on the spatial and temporal variability of these fluxes. For soil respiration, our hypothesis is that, in the Central African context where soil temperature does not vary widely over the year, soil water content is the primary driver of within and between land-use spatial and temporal variability (Davidson et al. 2000; Davidson and Janssens 2006). For N_2O, our hypothesis is informed by the hole-in-the-pipe model (Firestone and Davidson 1989; Davidson and Verchot 2000) that spatial and temporal variability of the flux is driven by nitrogen availability and soil water content. For CH_4, our hypothesis is that gas-phase transport across the soil-atmosphere boundary is the determinant of CH_4 uptake in well-drained soils so the flux will vary with soil water content (Striegl 1993). We also examined the importance of nitrogen (N), where N availability can stimulate CH_4 uptake in N limited soils or inhibit uptake through enzymatic competition (Aronson and Helliker 2010; Zhuang et al. 2013).

2. Methods

2.1 Southern Cameroon and the Congo Basin

The study was carried out in Ayos District, located in Nyong and Mfoumou Division in the Centre Region of Cameroon (Figure 1). The study site has a subequatorial climate with a bimodal rainfall regime and total annual rainfall is approximately 1700 mm. Dry seasons occur between December and March and between July and August; the first rainy season starts in September and ends in November and the second extends from April to June. The altitude of the study sites is about 720 m and the mean annual temperature is 27°C.

The natural vegetation of the region is dense, semi-deciduous forest (Letouzey 1985), characterized by dominant tree species such as *Ceiba pentandra, Terminalia superba, Triplochyton scleroxylon* and *Musanga cercropiodes* (Olivry 1986). The soils are Ferralitic red soils (Oxisols) (Soil Survey Staff 1999) formed on schist and quartzite (Olivry 1986), and classified as Acric Ferralsols according to World Reference Base classification. Agriculture in Ayos District includes cacao (*Theobroma cacao*), coffee (*Coffea arabica*), cassava (*Manihot esculenta*), arrowleaf or macabo (*Xanthosoma sagittifolium*), plantain (*Musa x paradisiaca*), maize (*Zea mays*), groundnuts (*Arachis hypogaea*), and vegetables. Only
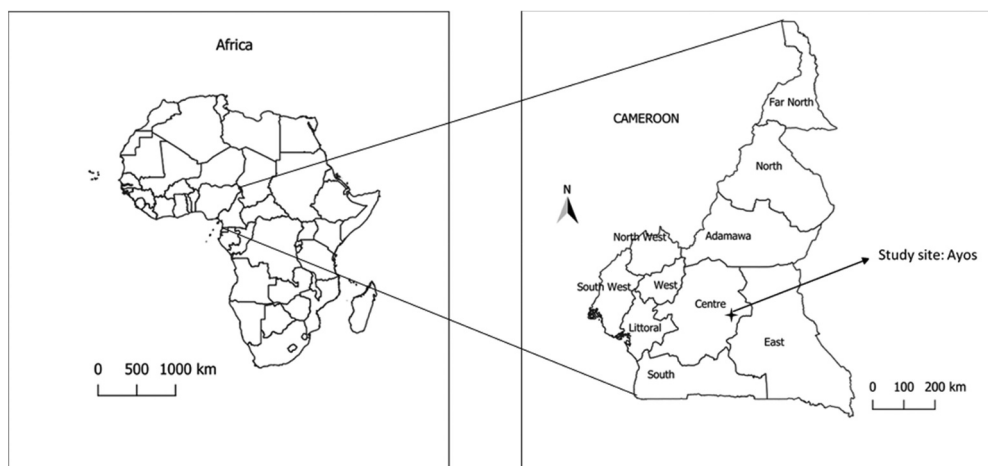
Figure 1. Location of study site in Ayos, Centre Region of Cameroon.

vegetable crops receive mineral fertilizer applications. Annual crops are produced in swidden systems with short cultivation periods and fallow periods up to 20 years.

To assess the effects of land-use, we measured gas fluxes over a 17-month period (August 2014 to December 2015) in a secondary forest site (03°97′25.3″N; 012°42′15.4″E), a cacao agroforest (03°97′47.1″N; 012°41′75.8″E) and an unfertilized cropland (03°97′32.2″N, 012°44′29.6″E). The unfertilized cropland was created by cutting a 20-year-old fallow in January 2014, followed by the cultivation of cassava in March of the same year. The owner gradually introduced other crops including maize, arrowleaf, groundnut, and plantain. At each site, we established four plots, each with an area of approximately 100 m^2.

2.2 Physicochemical soil parameters

Site-level soil characterization of texture and pH was done with composite disturbed soil samples taken at depths 0–20 cm with a calibrated hand trowel in the area around the gas measurement frames. In the laboratory, the samples were air-dried and ground to pass through a 2 mm sieve. Soil pH in water and 1 *N* KCl were determined with a combination electrode in a 1:2.5 (w/v) soil: water suspension (Thomas 1996). Soil texture was determined by the hydrometer method (Gee and Or 2002).

For bulk density, porosity, total C and N, and cation exchange capacity, replicate samples were taken as intact samples with a ring sampler from one soil pit per plot; we report results at 2 depths, 0–10 cm and 10–30 cm. Bulk density was determined gravimetrically by drying the soil at 105°C until the samples reached a constant weight. Cation exchange capacity (CEC) was determined using the ammonium acetate method at pH 7 (Sumner and Miller 1996). For C and N analysis, soils were finely ground to pass through a 0.5 mm sieve. Soil organic C (SOC) was determined by chromic acid digestion and spectrophotometric analysis (Heanes 1984). Total N was determined in a two-step digestion with hydrogen peroxide and boiling sulphuric acid (Buondonno et al. 1995). For quality control, we included five internal reference samples and four external reference

samples from international soil exchange program in every batch. All results are expressed on a dry mass basis.

2.3 Soil mineral nitrogen concentrations

We collected soil samples during each sampling campaign between October 2014 and March 2015 and then monthly from April 2015 to December 2015 for determination of soil mineral nitrogen concentrations. Three soil samples (0–5 cm depth) were collected in the immediate vicinity of each point selected for gas sampling with a calibrated trowel and pooled into a single composite sample for each plot. Thus, we collected four composite samples per site at each sampling time. Samples were transferred to the laboratory in Yaoundé for immediate extraction. For this purpose, 5 g of fresh soil was extracted using 1 M KCl at a soil: solution ratio of 1:4 (Dannenmann et al. 2006). Spectrometric methods were used for the determinations of NH_4^+ and NO_3^-, with the sodium salicylate reaction (Kempers and Zweers 1986) and the Griess-Illosvay reaction (Bundy and Meisinger 1994), respectively. A subsample of soil was used for determination of gravimetric water content by drying at 105°C until constant weight. We used gravimetric water content to express results on a dry mass basis.

2.4 Soil-atmosphere exchange of GHGs

For gas sampling, we used a manual static chamber method with 16 soil frames and chambers at each treatment. The 16 chambers were distributed across the four plots (4 chambers per plot) and were sampled at weekly intervals. To quantify GHG flux rates, we collected five gas samples from the chambers through a septum 0, 5, 10, 15 and 25 minutes after fixing the chambers to the frames using the sample pooling technique within each plot (Arias-Navarro et al., 2013). Consequently, one gas flux rate pooled from four chambers was obtained for each gas at each plot. The chambers had a size of 26.7 × 37.3 x 11.5 cm and were equipped with a battery-driven fan to avoid the formation of concentration gradients, and were fitted with a 1/8 inch vent that allowed for pressure equilibration during gas sampling. Gas samples were taken with 60 mL syringes and immediately transferred to 10 mL crimp cap vials. The vial was first flushed with 40 mL of the headspace gas and then the remaining 20 mL were injected in the vial with over-pressure (Arias-Navarro el al, 2013). During gas sampling, we measured soil temperature and moisture at 5 cm depth around each chamber with a ProCheck hand-held reader coupled to a GS3 soil moisture and temperature probe (Decagon Devices Inc., USA). We measured air temperature inside each chamber at the beginning and end of each flux measurement with a thermometer, and we used the average value to calculate the flux.

Gas samples were immediately transferred to the gas chromatography facilities of the Centre for International Forestry Research (CIFOR) located in the International Institute of Tropical Agriculture (IITA) laboratory in Yaoundé and analysed for concentrations of N_2O, CH_4 and CO_2 within 1 week with a SRI GHG gas chromatograph 8610 C (SRI Inc., USA). N_2O was detected using a [63]Ni electron capture detector; a flame ionization detector in conjunction with a methanizer was used for the detection of both CO_2 and CH_4. GHG flux rates were calculated from linear changes in chamber headspace concentrations over the five time points and converted to moles using the ideal gas law (Rehschuh et al. 2019).

2.5 Statistical analyses

Q-Q plots and the Shapiro–Wilk tests were used to assess the normality of the data prior to analysis. Logarithmic transformations of some of the data were necessary to achieve a normal distribution. We used parametric analyses, ANOVA, and repeated measures ANOVA on data that met normality and heterogeneity of variance criteria. When data did not meet the criterion of normal distribution, we used Kruskal–Wallis non-parametric methods and Friedman repeated measures ANOVA on ranks for time series analyses. Relationships between variables were analysed through least squares regression and multiple linear regression approaches. Inorganic-N data were not normally distributed, so we used non-parametric statistics to test for differences between land-uses during the dry and wet seasons. We used multiple linear regression to test biogeochemical and land-use hypotheses and we integrated land use into the regression with the use of dummy variables. To make decisions about parameters to be included in the models we used a P-value cut-off of 0.15. Statistical analyses were performed using SAS Studio version 3.8 (SAS Institute, Cary, NC) and SigmaPlot version 13 (Systat software Inc., San Diego, CA).

3. Results

3.1 Site characterization

Soils were similar across the sites with a clay texture in the upper horizons of each site (Table 1). Because we analysed only one composite sample per site for soil particle size, we cannot determine significant differences in these parameters between land-uses. The analysis of the replicated samples from the soil pits showed that the soils were acidic, with similar pH in the secondary forest and cacao agroforestry land-uses and higher pH in the unfertilized cropland. Cation exchange capacity was similar across sites. Soil organic C and N concentrations were lower in the cropland compared to the secondary forest. Because we analysed only one composite sample for these chemical properties, we cannot determine significant differences in these parameters between land-uses.

Soil water content followed the annual rainfall pattern and was higher in the wet seasons than in the dry seasons (Figure 2). On average, soil water content was similar in the cropland and in the forest, and higher in the cacao plantation (P < 0.001). We

Table 1. Soil characteristics for the different land-uses for the upper layers of the soil profile.

|	Secondary forest		Cacao plantations		Mixed crop fields	
Depth (cm)	0–10	10–30	0–10	10–30	0–10	10–30
Bulk density (g cm^{-3})	1.11	1.28	1.15	1.33	1.13	1.18
Porosity (%)	58	52	57	50	57	55
CEC (cmol$^{(+)}$ kg^{-1})	6.84	5.62	6.06	5.19	5.71	4.81
SOC (g kg^{-1})	23.9	14.6	20.1	12.4	19.8	11.8
TN (g kg^{-1})	1.6	0.8	1.3	0.7	1.4	0.7
C/N	15.2	17.8	14.9	17.7	16.4	15.7
Depth (cm)	0–20		0–20		0–20	
Sand (%)	40.8		39.8		44.5	
Silt (%)	5.6		5.8		5.3	
Clay (%)	53.6		55.0		49.7	
pH (water)	3.8 (0.1)[b]		3.7 (0.0)[b]		4.3 (0.1)[a]	
pH (KCl)	3.5 (0.1)[b]		3.5(0.0)[b]		3.8 (0.1)[a]	
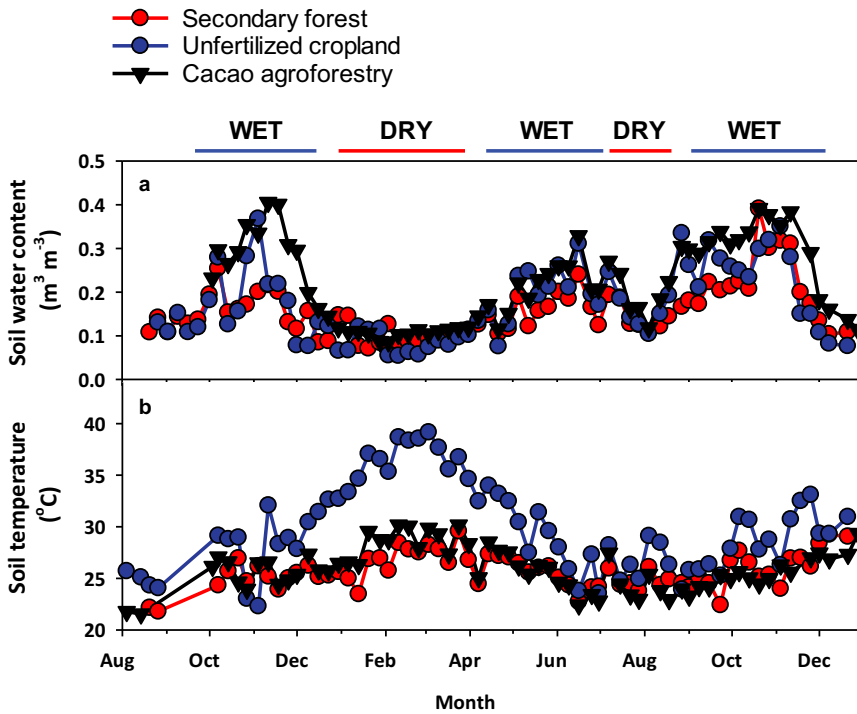
Figure 2. Soil water content (A) and soil temperature (B) over the course of the measurement period.

observed the greatest differences in soil water content between the cacao plantation and the other fields during the wet seasons (Table 2). Soil temperature was significantly higher in the cropland relative to the forest and cacao plantation (P < 0.001), with the greatest difference during the dry seasons.

Because the beginnings and ends of wet and dry seasons are variable, we estimated the changes between the wet and dry seasons from changes in soil water content. Average soil water content in each land-use was significantly different between the wet and dry seasons (P < 0.001), and we found no difference in average temperatures (Table 2).

3.2 Nitrogen availability

The measurements of soil inorganic N concentrations were more frequent during the first part of the experiment. Concentrations of NH_4^+-N and NO_3^--N did not closely follow

Table 2. Soil water contents and temperatures for the land-uses by season. Values are mean ± standard error (SE). The statistical test is for differences between seasons; values for each parameter that are followed by the same letter are not significantly different from each other (P < 0.05).

	Volumetric soil water content (m³ m⁻³)		Soil temperature (°C)	
	Dry	Wet	Dry	Wet
Secondary forest	0.12 ± 0.01[b]	0.19 ± 0.01[a]	26.1 ± 0.4[a]	25.4 ± 0.2[a]
Unfertilized cropland	0.12 ± 0.01[b]	0.22 ± 0.01[a]	31.3 ± 0.9[a]	28.6 ± 0.5[b]
Cacao agroforestry	0.15 ± 0.01[b]	0.28 ± 0.01[a]	26.6 ± 0.4[a]	25.3 ± 0.2[b]

a seasonal pattern (Figures 3A and 3B). NH_4^+-N concentrations were mostly similar across land-uses, particularly early in the measurement period. NO_3^--N showed significant differences between land-uses during most months, with significantly elevated levels in the forest ($P < 0.05$) and similar levels in the cacao and unfertilized cropland sites, particularly early in the measurement period. We report the relative proportion of NO_3^--N in the soil inorganic-N pool as an indicator of N availability (Davidson and Verchot 2000). NO_3^--N was the predominant inorganic-N form in the secondary forest and cacao agroforestry land-uses, with N availability ratios >0.5 for most of the measurement period. The predominance of NH_4^+-N or NO_3^--N in the cropland was more variable, with around half of the observations of the nitrate proportion <0.50 (Figure 3C).

Both NH_4^+-N and NO_3^--N concentrations were higher during the dry seasons than during the wet seasons (Kruskal-Wallis, $P < 0.001$, Table 3). NO_3^--N was the predominant inorganic-N form in all land-uses during both seasons, except for the unfertilized cropland

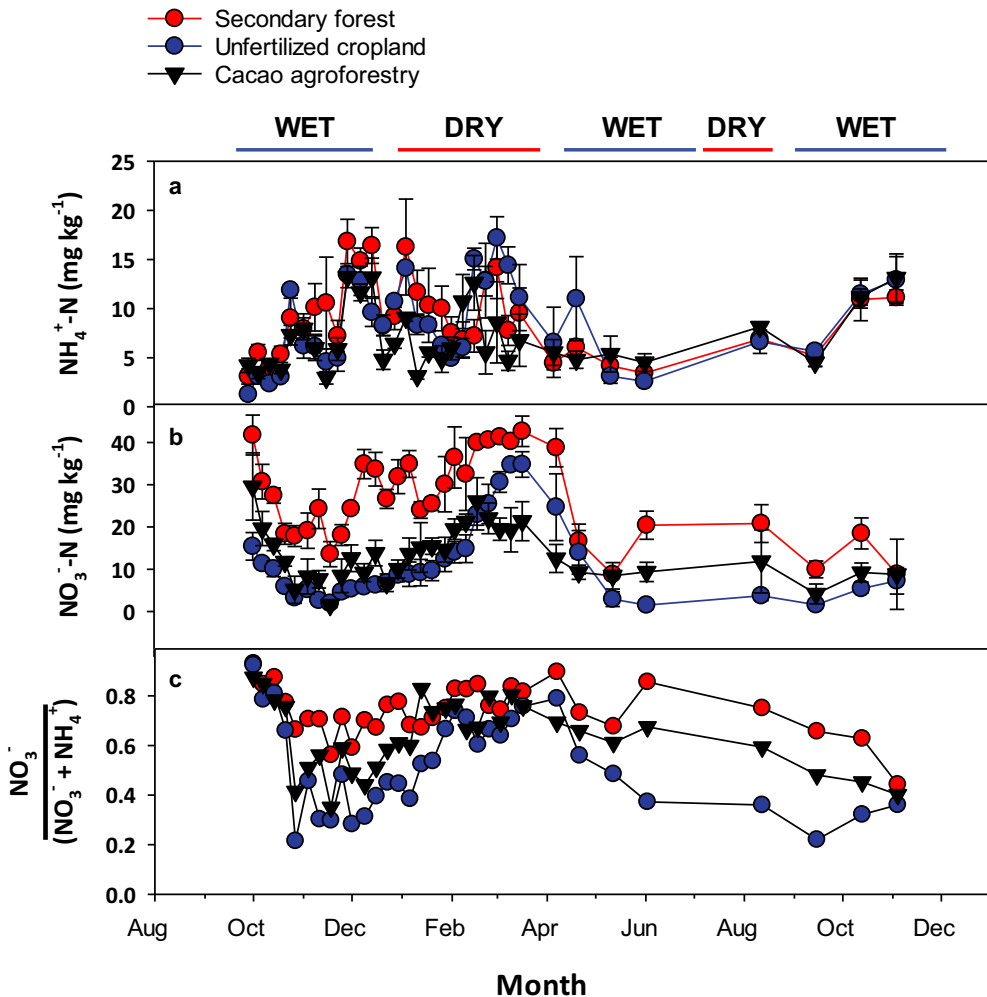**Figure 3.** Inorganic N pools of NH_4^+-N (A), NO_3^--N (B) and the NO_3^--N proportion of the inorganic-N pool (C) over the course of the measurement period. Error bars show ± 1 standard error (SE).

Table 3. Soil inorganic-N concentrations by season. Values are mean ± standard error (SE). Separation statistics were calculated to test for differences between land use; for each inorganic-N form and within each season, numbers followed by the same letter are not significantly different from each other. In the absence of a statistical difference, no superscripts are used.

	NH_4^+-N (mg kg^{-1} soil)		NO_3^--N (mg kg^{-1} soil)	
Land-use	Dry	Wet	Dry	Wet
Secondary forest	10.98 ± 0.87[a]	6.76 ± 0.70	32.96 ± 1.66[a]	20.81 ± 2.43[a]
Unfertilized cropland	10.60 ± 0.88[a]	6.05 ± 0.59	14.96 ± 2.57[b]	7.37 ± 1.59[b]
Cacao agroforestry	7.94 ± 0.80[b]	5.93 ± 0.27	16.00 ± 1.27[b]	10.61 ± 1.66[b]

during the wet season. The secondary forest had significantly higher NO_3^--N than the other land-uses (P < 0.001). During the wet season, there was no difference in NH_4^+-N concentrations between land-uses.

3.3 GHG fluxes

Soil respiration followed a seasonal pattern, with high rates of CO_2 fluxes from soils during the wet seasons and lower levels during the dry season in all land-uses (Figure 4A). On a monthly basis, CO_2 fluxes from the unfertilized cropland were mostly significantly lower than the forest or cacao plantations. During the September to November rainy seasons, the CO_2 fluxes in the forest were significantly higher than in the other land-uses. Over the course of the measurement period, each land-use was significantly different from the others (log transformation, repeated measures ANOVA, P < 0.001) and followed the order secondary forest > cacao agroforestry > unfertilized cropland.

Fluxes of N_2O were high and variable at the beginning of the measurement period and decreased as the measurement period progressed (Figure 4B). After the initial and highly variable period, week-to-week variability decreased. With the exception of the unfertilized cropland, fluxes followed seasonal patterns with higher emissions during the wet seasons and lower fluxes during the dry seasons. Over the course of the measurement period, all land-uses were significantly different from each other and followed the order secondary forest > cacao agroforestry > unfertilized cropland (Friedman repeated measures on ranks ANOVA, P < 0.001).

Methane fluxes showed predominantly net uptake in all land-uses and throughout the measurement period. Methane fluxes followed a seasonal pattern with stronger uptake during the dry seasons (Figure 4C) and reduced uptake during the wet seasons. Brief periods of CH_4 emission were observed during the wet seasons, primarily in the cropland and in the cacao land-uses. Over the course of the measurement period, all sites showed net CH_4 uptake, but uptake was weaker in the unfertilized cropland than in the secondary forest and cacao agroforestry land-uses (repeated measures ANOVA, P < 0.001).

We present seasonal average and annual total values for the fluxes for each gas in Table 4. Annual total values were calculated based on seasonal averages and using 183 days y^{-1} for the dry seasons and 182 days y^{-1} for the wet seasons. With the exception of N_2O during the dry seasons, there were significant differences between land-uses for each gas within each season (P < 0.001). Generally, forest fluxes of these gases were significantly higher or similar to other land uses; fluxes were significantly weakest (lower emissions in the case of CO_2 and N_2O, and lower uptake in the case of CH_4) in the
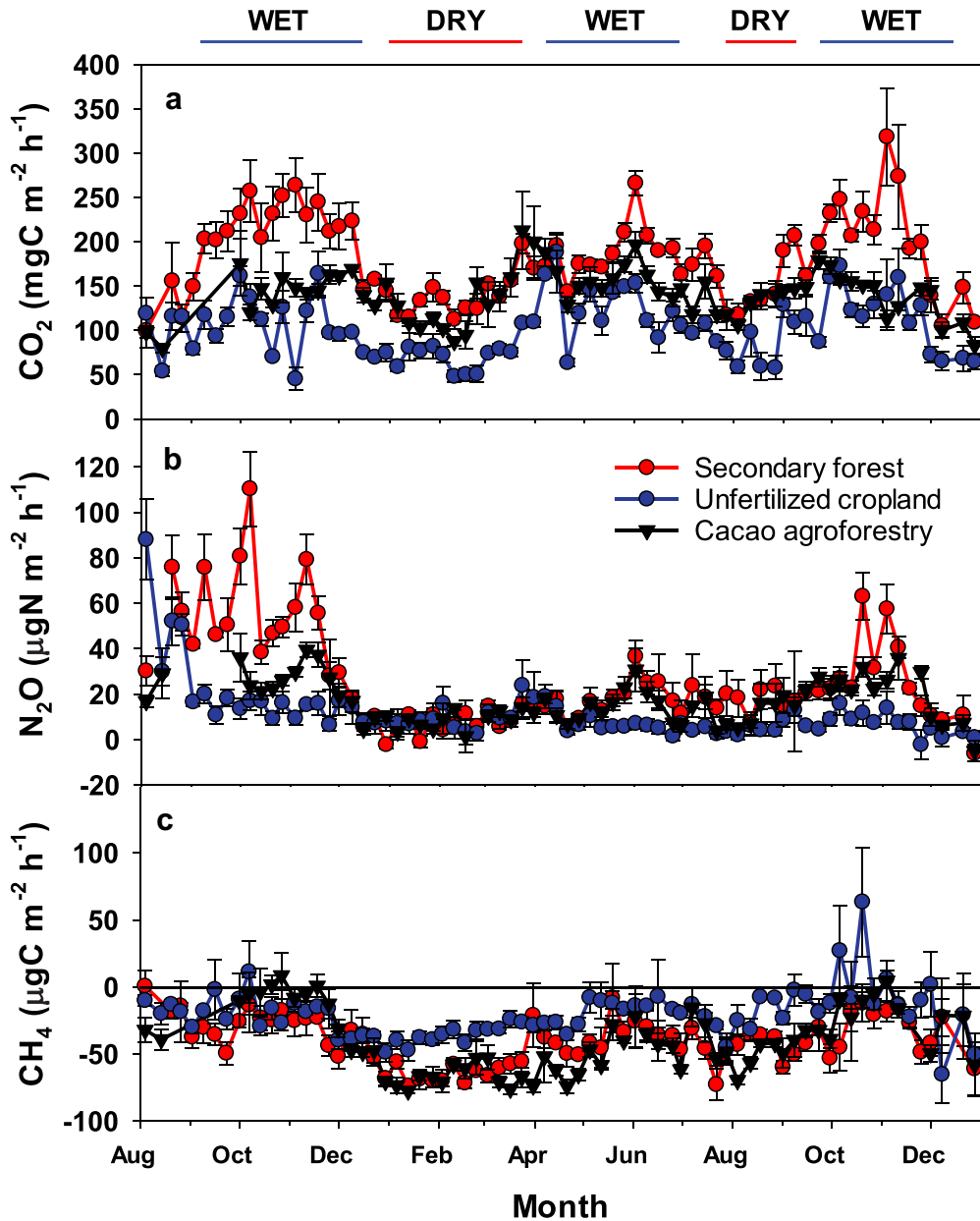
Figure 4. Flux data for CO_2 (A), N_2O (B), and CH_4 (C) from measurement campaigns in 2014 and 2015. Error bars show ± 1 standard error (SE).

unfertilized cropland. We infer differences in annual fluxes between land-uses from the intervals provided with the SE values and note that for both CO_2 and N_2O, the flux strength follows the order secondary forest > cacao agroforest > unfertilized cropland. For CH_4, the sink strength follows the order secondary forest = cacao agroforest > unfertilized cropland.

Table 4. Average seasonal fluxes for each land-use and annual total flux. Values are mean ± SE. Separation statistics were calculated to test for differences between land uses; for each gas and within a season and for the annual total, numbers followed by the same letter are not significantly different from each other.

Gas	Land-use	Dry season	Wet season	Annual Total
CO_2		– – – – – mgC m^{-2} h^{-1} – – – – –		– Mg C ha^{-1} y^{-1} –
	Secondary forest	141.7 ± 5.4[a]	209.4 ± 5.7[a]	15.4 ± 3.4[a]
	Unfertilized cropland	78.0 ± 3.6[b]	121.8 ± 4.8[c]	8.7 ± 2.6[c]
	Cacao agroforest	128.5 ± 5.9[a]	151.5 ± 3.1[b]	12.3 ± 2.9a[b]
N_2O		– – – – – µgN m^{-2} h^{-1} – – – – –		– kg N ha^{-1} y^{-1} –
	Secondary forest	15.13 ± 2.9	34.41 ± 3.63[a]	2.17 ± 0.20[a]
	Unfertilized cropland	13.76 ± 3.25	9.91 ± 0.82[b]	1.04 ± 0.15 [c]
	Cacao agroforest	9.89 ± 1.21	22.02 ± 1.44[a]	1.40 ± 0.08[b]
CH_4		– – – – – µgC m^{-2} h^{-1} – – – – –		– kg C ha^{-1} y^{-1} –
	Secondary forest	−48.69 ± 3.63[a]	−33.39 ± 2.05[a]	−3.60 ± 1.83[a]
	Unfertilized cropland	−30.93 ± 2.51[b]	−12.40 ± 2.61[b]	−1.90 ± 1.59[b]
	Cacao agroforest	−54.96 ± 2.89[a]	−27.46 ± 3.81[a]	−3.61 ± 2.09[a]

4. Biogeochemical mechanisms

We set out several hypotheses regarding the mechanisms that control the spatial and temporal variability of these gases. Soil respiration is typically modelled as a function of temperature, but there is growing evidence that in tropical conditions, where soil temperature does not vary greatly over the course of time, that soil water content better explains the variability of this flux. In Figure 5, we used daily average site data and we show that indeed, the relationship between respiration and soil temperature is nonexistent or weak, but significant (P = 0.512, 0.009, and 0.009 for forest, unfertilized cropland, and cacao agroforestry, respectively). The relationships varied between land uses, but were best characterized by a second-order curve and as temperature increased beyond a maximum CO_2 flux decreases. We can also see statistically significant relationships between soil respiration and soil water content in the secondary forest and the cacao agroforest land-uses (P < 0.001), and only a weak, but significant relationship in the unfertilized cropland (P = 0.004). Soil water content explains a larger proportion of the spatial and temporal variability than soil temperature in the forest and unfertilized cropland. Inorganic-N availability showed no significant relationships within any of the land uses.

For N_2O, we found a weak relationship with soil temperature for secondary forest (P = 0.003) and cacao agroforest (P = 0.006), also using daily average site values (Figure 6A). Although
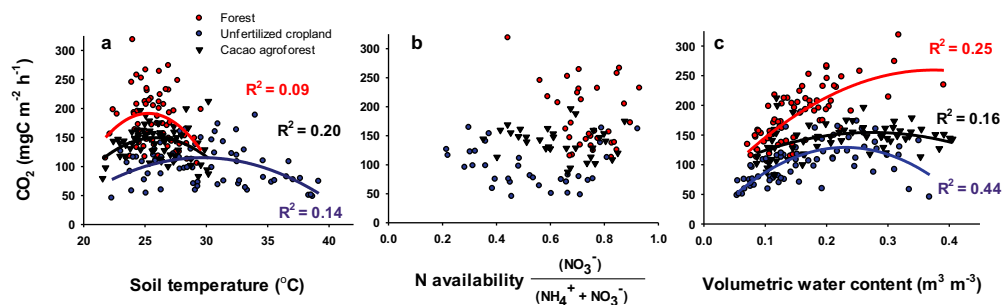

Figure 5. Mechanistic relationships between soil respiration and temperature (A), N availability (B), and soil water content (C). Values are site averages for each sampling day.
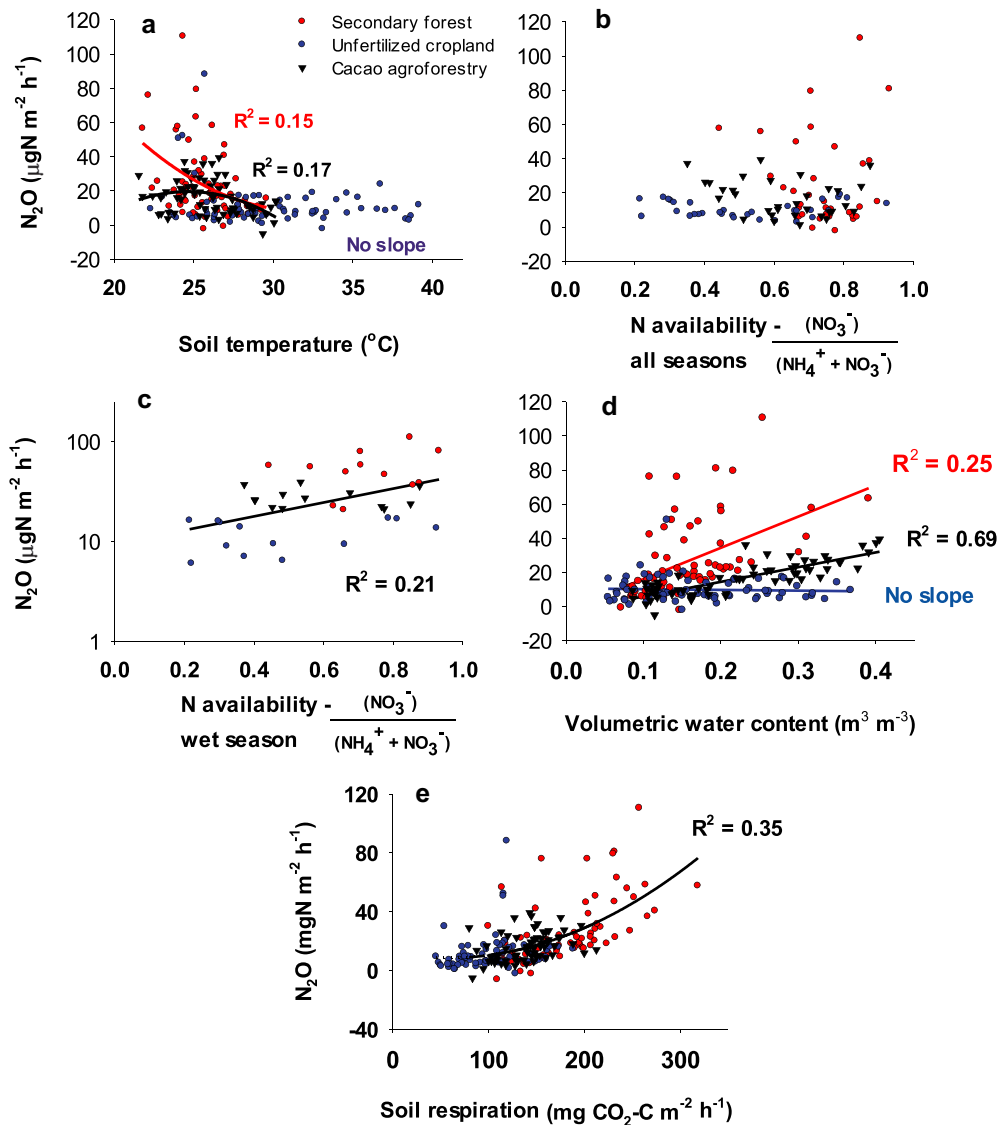
Figure 6. Mechanistic relationships based on the hole-in-the-pipe model between N_2O fluxes and soil temperature (A) nitrogen availability for all seasons (B), nitrogen availability for the wet seasons only (C) volumetric soil water content (D), and soil respiration (E). Note that the relationship in panels C and E are for all of the data in the site, while those shown on panel A and D are for individual land-uses. Values are site averages for each sampling day.

emissions appeared less variable at high temperatures, we note that these observations were primarily associated with the cropland, where higher temperatures corresponded with the dry seasons. Thus, attributing causality is difficult. We tested the hole-in-the-pipe mechanisms that relate the flux to N availability and soil water content. In these sites, we saw no significant relationship between N availability and N_2O fluxes across sites and seasons, but we note that variability of the flux increases with increasing NO_3^--N proportion of the inorganic-N pool (Figure 6B). This phenomenon is unique to the forest land-use. There was a significant

relationship with N availability across land uses during the wet seasons (P = 0.003), when N_2O fluxes were highest. We did find a significant and strong relationship between soil water content and N_2O emissions in the cacao agroforestry land-use and a significant, but weak relationship in the forest (P < 0.001 for both). We found no relationship in the unfertilized cropland, where emissions were particularly low. The high emissions in the forest when soil water content was low were unexpected because soil conditions were aerobic, but this observation is consistent with the high NO_3^--N levels observed during this period, suggesting that

N_2O production was from nitrification rather than denitrification. We note the possibility that O_2 consumption as a result of high respiration may also have created anaerobic microsites in the aerated soil, which could also explain high N_2O fluxes (Figure 6E).

We found no relationship between soil temperature and net CH_4 exchange at the soil–atmosphere interface (Figure 7A; P = 0.998). The hypotheses for CH_4 relate to the impact of inorganic-N on the sink strength and the impact of soil water content on gas-phase transport across the atmosphere-soil boundary. We did find evidence that decreasing N availability with land-use change explains part of the reduced sink strength of agricultural soils with a significant (P < 0.001), but weak relationship in Figure 7B (note that the line in the plot is for all data across treatments). The strongest relationship among the different N availability indices was with the total inorganic-N pool. We also found evidence that high soil water content limits diffusion of CH_4 into the soil as this factor showed the highest explanatory power for CH_4 fluxes (Figure 7C). The relationships differ across the land-uses.

Finally, we combined the explanatory variables into multiple linear regression models to examine their combined power to account for spatial and temporal variability of gas fluxes. For each gas, we produced a model with land-use effects and one with only the measured biogeochemical parameters. We used dummy variables to account for land use in the regression models: for the variable IsFor, we assigned a value of 1 for forest observations and 0 for non-forest; for the variable IsCrop we assigned a value of 1 for cropland and 0 for non-cropland. Log transformations improved the distribution of residuals for both CO_2 and N_2O, but there was still some bias in the residuals for N_2O. We added 10 to all N_2O values prior to transformation to accommodate negative values. No transformation was necessary for CH_4.

For CO_2, we found that the regression based solely on soil water content, soil temperature and N availability explained just over 60% of the temporal and spatial variability and the
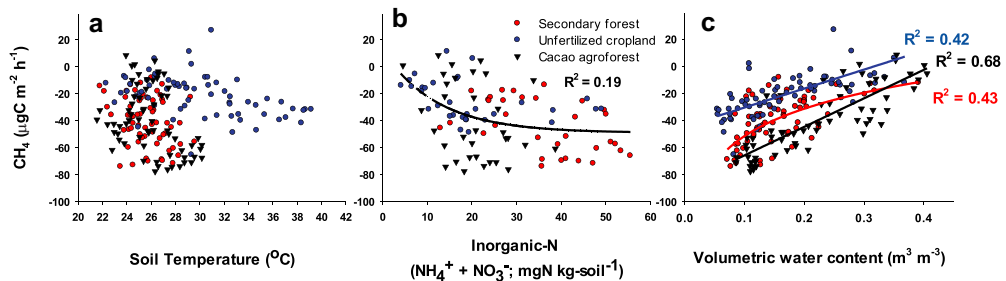

Figure 7. Mechanistic relationships between CH_4 fluxes and soil temperature (A), nitrogen availability (B), and soil water content (C). Values are site averages for each sampling day.

model that included land use explained over 70% of the temporal and spatial variability (Table 5). In this last model, coefficients for N availability and soil temperature were not significant and were therefore excluded. Models for N_2O with and without land use explained less than 40% of the variation across space and time. The best-fit biogeochemical parameter model included the main drivers of the hole in the pipe model. For the land-use model, only the distinction between forest and non-forest was significant. The model for CH_4 based solely on the biogeochemical parameters included only soil temperature and soil water content; N availability did not have a significant coefficient and was excluded from the model. The CH_4 model that integrated land use with the biogeochemical parameters explained over 75% of the flux variation over time and across land uses.

5. Discussion

Tropical landscapes are important sources and sinks of GHGs to the atmosphere and some of the most poorly studied components of global GHG budgets. A recent estimate suggests that the tropics are a sink for atmospheric CO_2 and changes in the region represent around 65% of the increase in the land sink over the past 2 decades (Sitch et al. 2015). These authors report that dynamic global vegetation models (DGVMs) estimate tropical soil heterotrophic respiration to be about 25 Pg C y^{-1} and the flux is increasing due primarily to CO_2 fertilization. The tropics are also important natural sources of N_2O to the atmosphere and anthropogenic emissions from the region are increasing due to growing fertilizer use and the expansion of livestock production (Davidson 2009; Dangal et al. 2019). Global natural N_2O emissions are around 11 Tg N y^{-1} and emissions from the tropics have decreased by around 1 Tg N due to tropical deforestation (Davidson and Kanter 2014). Emissions of N_2O from agricultural lands in the tropics and subtropics make up around half of anthropogenic agricultural emissions (Stehfest and Bouwman 2006). Tropical soils are also important in the global CH_4 cycle and represent about 35% of the global soil CH_4 sink (Dutaur and Verchot 2007). While the global soil CH_4 sink is likely to grow as climate warms, most of the growth will be outside the tropics (Curry 2009). Most global inventories of CH_4 treat land use as static and do not account for changes due to deforestation and conversion to agriculture, which typically weakens sink strength and in many instances creates a source in place of the natural sink (Verchot et al. 2000; Fernandes et al. 2002; McDaniel et al. 2019). In general, modelling and inventory papers all cite data limitations and limits in our understanding of processes as a key constraint to improving global predictions of GHG accumulation in the atmosphere. The first objective

Table 5. Summary of multiple regression models for the three gases based on mechanistic relationships. For all models, the parameters included were significant at P < 0.01.

Model	R^2
$Log(CO_2) = 2.399 - 0.024 \cdot Temp\_soil + 2.846 \cdot Vol\_water - 6.138 \cdot Vol\_water^2 + 0.219 \cdot N\_avail$	0.608
$Log(CO_2) = 1.743 + 0.128 \cdot IsFor - 0.151 \cdot IsCrop + 3.854 \cdot Vol\_water - 7.563 \cdot Vol\_water^2$	0.738
$Log(N_2O + 10) = 0.786 + 2.959 \cdot Vol\_water - 3.615 \cdot Vol\_water^2 + 0.363 \cdot N\_avail$	0.335
$Log(N_2O + 10) = 0.931 + 0.131 \cdot IsFor + 1.505 \cdot Vol\_water + 0.242 \cdot N\_avail$	0.385
$CH_4 = -161.593 + 2.664 \cdot Soil\_Temp - 365.506 \cdot Vol\_water - 304.627 \cdot Vol\_water^2$	0. 671
$CH_4 = -142.121 + 10.913 \cdot IsFor + 22.651 \cdot IsCrop + 1.356 \cdot Soil\_Temp + 250.576 \cdot Vol\_water$	0.763

[a]Variables are: Soil_temp = soil temperature ($^{\circ}C$), Vol_water = volumetric water content (cm cm^{-3}), N_avail = (NO_3^-)/ $(NH_4^+ + NO_3^-)$ (µg $µg^{-1}$); IsFor = 1 if land use is forest; IsCrop = 1 if land use is unfertilized cropland.

of this paper was to assess the impact of land-use change on soil gas fluxes of CO_2, N_2O and CH_4. The second was to test hypotheses about the biogeochemical mechanisms that explain temporal and spatial variation of the fluxes of these gases.

5.1 Land-use change

The effects of land-use on soil CO_2 fluxes vary between studies and land-use change can both increase and decrease soil respiration; however, globally land-use change is estimated to reduce this flux (Raich and Schlesinger 1992; Raich and Potter 1995). Most studies reporting higher soil respiration are associated with the conversion of forest to pasture, but not all studies comparing forest to nearby pasture show increased soil respiration (Davidson et al. 2000; Salimon et al. 2004; Wanyama et al. 2019). We found the secondary forest soil respiration to be 15.4 Mg C ha^{-1} y^{-1}, which is lower than the soil respiration in secondary forests on similar soils in Acre, Brazil, which ranged from 17 to 19 Mg C ha^{-1} y^{-1} (Salimon et al. 2004). Soil CO_2 efflux is a good indicator of ecosystem productivity and below-ground carbon allocation (Raich and Nadelhoffer 1989; Salimon et al. 2004), so we expected that the unfertilized cropland would have lower respiration rates than a secondary forest. The cropland indeed showed a 43% lower soil respiration than the secondary forest, while the annual total in the cacao agroforestry land-use, which had a significant tree cover with several tree strata (Sonwa et al. 2017) was 24% lower. Average wet season fluxes were around 50% higher than the average dry season fluxes in the secondary forest and cacao agroforestry land-uses, but seasonality was attenuated in the unfertilized cropland, where the average seasonal flux was only 17% higher in the wet season compared to the dry season. This different inter-seasonal dynamics may be due to higher litter inputs during the dry seasons in the land-uses with trees.

Lowland tropical forests typically have annual N_2O fluxes around 1.2 kg N ha^{-1} y^{-1} and land-use change results in lower N_2O fluxes (Werner et al. 2007), although there is often a flush of increased N_2O emissions associated with increased organic matter mineralization following deforestation. Higher emissions can persist for several years before emission rates fall below the initial forest levels (Verchot et al. 1999; van Lent et al. 2015). We observed higher emissions in the recently cleared (8 months at the beginning of the measurement period) unfertilized cropland only during the first month of the time series, and it is impossible to determine whether this was part of a post-conversion pulse. The lack of a persistent pulse may be due to the fact that the forest that was cleared for the field was a secondary forest, and inorganic-N availability may be below what has been observed in studies where the conversion was from primary forest. N_2O fluxes are related to N availability and it is not surprising that we saw absolute higher NO_3^--N levels and a larger portion of the inorganic-N pool being made up on NO_3^--N in the secondary forest (average 74%) where N_2O emissions were high, compared to the other land-uses (cacao agroforestry: 63% NO_3^--N; unfertilized cropland: 52% NO_3^--N). Relative to the secondary forest we observed lower N_2O emissions by 61% and 38% in unfertilized cropland and cacao agroforestry sites, respectively. Variation in N availability and N_2O fluxes had strong seasonal signals. Inorganic-N concentrations were higher during the dry season, but the relative proportion of NO_3^--N to NH_4^+-N was consistent across seasons. We saw no difference between the N_2O fluxes in the different land-uses

during the dry season, while the differentiation was pronounced during the wet season. Observations vary in this regard and differing results may be due to the intensity of the differences between seasons, or other underlying factors. A similar pattern was observed in southern Amazonia (Neill et al. 2005), while a study in the western Amazon found significant differences in both seasons (Verchot et al. 1999) and a study in Sumatra was unable to detect land-use differences in either wet or dry seasons (Aini et al. 2015).

Tropical forests are a sink of atmospheric CH_4, and typically absorb between 1 and 7 kg C $ha^{-1} y^{-1}$, with a mean uptake rate of around 3 kgC $ha^{-1} y^{-1}$ (Verchot et al. 2000; Dutaur and Verchot 2007). We found similar uptake in the forest and cacao agroforest land-uses and magnitude of the uptake was similar to the global average. The unfertilized cropland was a weaker sink, with fluxes that were 53% below those of the secondary forest and the strongest decrease in the sink strength relative to the other ecosystems was during the wet season. Average soil water content in the cropland was intermediate relative to the other land-uses during the wet seasons, which suggests that there may be other factors that we did not measure, like the effects of tillage on soil aggregate stability that explains the differences in land-use effects. Because gas-phase transport across the atmosphere-soil boundary limits the uptake of CH_4 by soils, we expected to see the seasonal pattern that we observed, with stronger uptake during the dry season when soil pores are not filled with water and where diffusion is not impeded.

5.2 Biogeochemical mechanisms

Improving our understanding of mechanisms is essential for anticipating the impacts of climate change and feedbacks in the carbon and nitrogen cycles in terrestrial ecosystems. The importance of the relationship between respiration and temperature has received attention recently, because it will affect how the biosphere continues to react to increasing global temperatures and CO_2 levels (Singh et al. 2010; Crowther et al. 2016; Wieder et al. 2018). At the moment, the terrestrial biosphere is a net sink of atmospheric CO_2 (Houghton and Nassikas 2017; Le Quéré et al. 2018) and the magnitude of the sink has more than doubled since the 1960s. Many earth system models project that the magnitude of this sink will decrease over this century (Friedlingstein et al. 2014). The discussions of the current state and future of the land sink are influenced by the perception that temperature is the dominant factor limiting respiration and that respiration responds to environmental drivers in a uniform fashion regardless of location of the ecosystem. Models typically use exponential functions with temperature sensitivity defined by global Q_{10} values (Friedlingstein et al. 2006; Mahecha et al. 2010). However, temperature effects on organic matter decomposition and respiration are constrained by other factors in ecosystems, including water availability, organic substrate quality, pH, and N availability (Davidson and Janssens 2006).

In this study, we observe a stronger relationship of soil respiration to soil water content than to soil temperature, but we note that these factors were correlated in the cacao agroforestry (R = −0.56) and cropland (R = −0.673) sites. Seasonal temperature variation in the secondary forest and cacao agroforestry land-uses was small because the soil was shaded, ranging between 22°C and 28°C, and in the unfertilized cropland the variation was more important, ranging between 24°C and 39°C. We did not find evidence for the

typical exponential Q_{10} function (Mahecha et al. 2010) at the ecosystem or landscape scale in this study, but rather that the temperature response was constrained by soil water availability. N availability also showed an important relationship with respiration that significantly strengthened the explanatory power of the biogeochemical multiple regression model, suggesting that nutrient limitation constraints are also important in explaining soil respiration variation. What we did observe was strong and individualized relationships between soil respiration and volumetric soil water content in the secondary forest and the unfertilized cropland, and no apparent relationship in the cacao agroforest. Soil water affects both heterotrophic respiration by regulating microbial activity and autotrophic respiration by limiting O_2 availability. The relationships were parabolic, which is consistent with our understanding, but we note that the water content where maximum respiration was observed differed between the cropland and the secondary forest. Biological activity increases as water becomes more available at low water content levels and then declines as pore space saturates and reduces O_2 diffusion into the soil profile. We did not partition heterotrophic and autotrophic respiration in this measurement, but one explanation could be that a larger portion of the CO_2 flux in the recently cleared field was from the decomposition of the root systems of the cleared fallow vegetation. There may also be effects of the timing of litter inputs in the secondary forest and cacao agroforestry land-uses. The fact that we observed distinct relationships between the land-uses may indicate the effects of organic substrate supply or quality (Davidson and Janssens 2006).

The hole-in-the-pipe model states that the flux of N-oxides from a soil is proportional to the rate of N cycling and that the relative proportion of each gas is a function of soil water content, which regulates the redox status of the soil (Firestone and Davidson 1989). According to this model, N availability is related to the total N-oxide flux and water content regulates the relative proportion of the two oxides: the reduced N_2O, and the oxidized NO. Thus, we see a significant relationship during the wet season, when the predominant gas emitted is N_2O, but the lack of a strong relationship when soils are dry masks the relationship in the annual dataset because we did not measure NO. During the dry season, we expect NO emissions to predominate over N_2O emissions (Davidson et al. 2000). The relationship between N_2O and soil water content was not consistent across land-uses; we found a strong relationship in the cacao agroforestry land-use where soils tended to be wetter (Figure 6), a weak relationship in the secondary forest and no relationship in the unfertilized cropland. Temperature has a strong effect on denitrification (Butterbach-Bahl et al. 2013) and should, in turn, affect N_2O fluxes; however, with the narrow temperature ranges observed here and the fact that high temperatures were associated with the dry seasons, temperature effects did not explain an important part of the spatial and temporal variability of the soil emissions.

Diffusion limits the rates of CH_4 uptake by soils globally (Potter et al. 1996; Curry 2007). We found strong evidence for a weaker sink at high soil water contents and even short periods of emissions in the unfertilized cropland. We did not find a consistent relationship across the land-uses, which was surprising given the consistent bulk density and porosity of the soils. This may be due to cultivation, weeding and other soil disturbances in the mixed cropland, which may be limiting CH_4 uptake. We also found a positive relationship between inorganic N and CH_4 uptake. A meta-analysis by Aronson and Helliker (2010) showed that low levels of N addition to non-wetland soils stimulate CH_4 uptake due to the

relaxation of the N demand of methanotrophs. While we typically think of lowland tropical soils to be P limited, (Hall and Matson 1999), our results suggest that N may also be a limiting element in this environment because we see a relationship with inorganic-N levels. Predictions about the future of the soil CH_4 sink (Curry 2009; Xu et al. 2016; Yu et al. 2017) do not take into account changes in land-use and the resulting changes to the biogeochemical processes that affect sink strength. Results from this and other studies suggest that land-use change will at least partially offset the expected increase in this CH_4 sink (Ni and Groffman 2018).

6. Conclusion

Research on the effects of land-use change on soil trace gas fluxes in the tropics has increased during the past two decades; however, Africa remains strongly underrepresented. Most studies focus on the conversion of forest to croplands and pastures, and interest in plantation tree crops is only recent, and primarily focused on pulpwood, rubber, and oil palm production systems. This study adds to the growing literature on the effects of land-use change on biosphere–atmosphere interactions and it fills a gap with primary data from the African lowland forest frontier. It also fills a gap with respect to understanding the impact of the expansion of tree crops in the tropics on these exchanges.

The approach used here shows that our understanding of the complexity of the underlying biogeochemical mechanisms of the microbial mediated exchange of these gases with the atmosphere and the interactions of the biological and physical processes is limited. Nevertheless, the picture that emerges from this and other studies is that land-use change is having a large impact at regional and global scales. Models generally predict increased biosphere-atmosphere exchanges of GHGs, but these conclusions often exclude the effects of land-use change. Our results suggest that tropical land-use change is decreasing soil respiration, decreasing the soil CH_4 sink and decreasing N_2O emissions, in landscapes that do not practice agriculture with chemical fertilization.

Disclosure statement

No potential conflict of interest was reported by the authors.

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