Ideas and perspectives: patterns of soil CO_2, CH_4 and N_2O fluxes along an altitudinal gradient - a pilot study from an Ecuadorian Neotropical montane forest

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Abstract

Tropical forest soils are an important source and sink of greenhouse gases (GHG) with tropical montane forests, in particular, poorly studied. The understanding of this ecosystem function is of vital importance for future global change and climate research. In this study, we explored soil fluxes of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) of four tropical forest sites located on the western flanks of the Andes in northern Ecuador. The measurements were carried out during the dry season from August to September 2018, and along an altitudinal gradient from 400 to 3010 m a.s.l. During this short-term campaign, our measurements showed 1) an unusual but marked increase of CO_2 emissions at high altitude, possibly linked to changes in soil pH and/or root biomass; 2) a consistent atmospheric CH_4 sink over all altitudes with high temporal and spatial variability; and 3) a transition from net N_2O source to sink along the altitudinal gradient. Our results provide arguments and insights for future and more detailed studies on tropical montane forests. Furthermore, they stress the relevance of using altitudinal transects as a biogeochemical open-air laboratory, with a steep *in-situ* environmental gradient over a limited spatial distance. Although short-term studies of temporal variations can improve our understanding of the mechanisms behind the production and consumption of soil GHGs, the inclusion of more rigorous sampling for forest management events, forest rotation cycles, soil type, hydrological conditions and drainage status, ground vegetation composition and cover, soil

microclimate, and temporal (seasonality) and spatial (topographic positions) variability are needed, this in order to obtain more reliable estimates of the CO_2, CH_4 and N_2O source/sink strength of tropical montane forests.

1 The importance of tropical forests for GHG budgets

Soils play a vital role in the global GHG budget. Tropical forest soils, in particular, represent a net sink of carbon (C) (Pan et al. 2011), but at the same time, they are the largest natural source of N_2O, with an estimated contribution of 14-23% to the annual, global N_2O budget (Werner et al., 2007). In general, soil CO_2 is produced mainly by root respiration, microbial respiration, litter decomposition, and oxidation of soil organic matter (Dalal and Allen, 2008). CH_4 is consumed by methanotrophic bacteria (Jang et al., 2006), however, forest soils prone to inundation emit CH_4 by methanogenic microorganisms (*Archaea* domain). N_2O is emitted through denitrification or a number of alternative pathways (e.g. nitrification, nitrifier-denitrification, chemodenitrification, etc. (Butterbach-Bahl et al., 2013; van Cleemput, 1998; Clough et al., 2017)), but can also be consumed during complete denitrification (Butterbach-Bahl et al., 2013). Overall, tropical forests soils emit on average 12.1 t CO_2-C $ha^{-1}y^{-1}$ (heterotrophic and autotrophic respiration), slightly less than the net primary productivity (NPP) (12.5 t CO_2-C $ha^{-1}y^{-1}$), i.e. the net C sink (below and aboveground) of tropical forests is ~ 0.4 t CO_2-C $ha^{-1}y^{-1}$ (Dalal and Allen, 2008; Grace et al., 2006). Under aerobic conditions, CH_4 fluxes vary from -0.7 to -30.0 kg CH_4-C $ha^{-1}y^{-1}$, with an average consumption of -3.0 kg CH_4-C $ha^{-1}y^{-1}$, while the mean rate of N_2O emissions from tropical forest soils is 3.03 ± 0.52 kg N_2O-N $ha^{-1}y^{-1}$ (Dalal and Allen, 2008), i.e. 2-3 times higher than the mean N_2O emissions from temperate forest soils (1.0 ± 0.36 kg N_2O-N $ha^{-1}y^{-1}$; Chapui-Lardy et al., 2007; Van Groenigen et al., 2015).

The understanding of the mechanisms and processes underlying GHG flux variability has greatly improved during the last decades (Butterbach-Bahl et al., 2013; Heil et al., 2016; Müller et al., 2015; Sousa Neto et al., 2011; Su et al., 2019; Teh et al., 2014). However, there is still 1) considerable uncertainty about the overall balances of many ecosystems (Castaldi et al., 2013; Heil et al., 2014; Kim et al., 2016b; Pan et al., 2011; Purbopuspito et al., 2006), 2) a strong imbalance in field observations, skewed towards the Northern hemisphere (Jones et al., 2016; Montzka et al., 2011), and 3) a bias towards the quantification of emissions in lowland forests within the tropics (Müller et al., 2015; Purbopuspito et al., 2006; Wolf et al., 2011). For instance, based on a compilation made of CO_2, CH_4 and N_2O fluxes in South America (Table S1) from 1983 to 2019, there are only six studies carried out on tropical montane forests (i.e. > 2000 m. a.s.l.), while they represent more than 11% of the world's tropical forests (Müller et al., 2015; Teh et al., 2014). In fact, Teh et al. (2014) and Spahni et al. (2011) have argued that tropical upland soils are one potentially important source of CH_4 and N_2O, overlooked in both, bottom-up and top-down emissions inventories; their sink/source strength might be comparable or greater than their lowland counterparts, and therefore, quantitatively important in regional and global GHG budgets.

2 Altitudinal gradients as a biogeochemical open-air laboratory

To further improve our understanding of the role of tropical forest ecosystems in the global GHG balance, environmental gradients (altitudinal, latitudinal, etc.) can offer great opportunities to study the influence of abiotic factors on biogeochemical processes under field conditions (Bauters et al., 2017; Jobbágy and Jackson, 2000; Kahmen et al., 2011; Laughlin and Abella, 2007); which complements the knowledge on short term responses from experimental approaches. In the case of altitudinal gradients, these responses are driven by abiotic variables that co-vary with elevation, which, amongst others, creates a distinctly strong climate gradient over a short spatial distance (Bubb et al., 2004; Killeen et al., 2007; Körner, 2007; Myers et al., 2000). Moreover, since altitudinal gradients reflect long-term adaptations based on a broad range of factors, they provide valuable insights into the influence that climate change may have on ecosystem processes (Malhi et al., 2010). There is indeed a growing concern regarding the sensitivity of tropical forests to climate change, mainly because species in the tropics have evolved with narrow thermal tolerances compared to their temperate counterparts; which makes them particularly vulnerable to changes in global climate (Fadrique et al., 2018; Perez et al., 2016). Therefore, the effects of global warming are expected to be severe in the tropics, and the understanding and integration of the magnitude of their feedbacks in the Earth system is important to come up with appropriate forest management options to mitigate climate change (Bonan, 2008; Li et al., 2020).

To address these knowledge gaps, we present a pilot study of the soil-atmosphere exchange of CO_2, CH_4 and N_2O along an altitudinal gradient in a Neotropical montane forest located on the western flanks of the Andes in northern Ecuador. The sampling campaign took place from August 6th to September 28th, 2018. Four study sites (Fig. S1) were selected: Río Silanche at 400 m a.s.l (hereinafter: S_400), Milpe at 1100 m a.s.l. (hereinafter: M_1100), El Cedral at 2200 m a.s.l. (hereinafter: C_2200) and Peribuela at 3010 m a.s.l. (hereinafter: P_3010). Gas samples were taken using a static flux chamber method once per day during two weeks per stratum. Samples of soil were collected once during the whole field campaign for analysis of bulk density (ρ_b), pH, nitrate (NO_3^-) and ammonium (NH_4^+) content, C and nitrogen (N) concentrations, stable N isotope signatures ($\delta^{15}N$) and soil texture. Additionally, soil moisture (expressed as water-filled pore space (WFPS)) and soil temperature were measured daily. Specifically, we aimed to determine the magnitude of the soil-atmosphere exchange of CO_2, CH_4 and N_2O during the dry season. By working along this altitudinal gradient, we wanted to explore the potential effect of altitude on the GHG fluxes of the forest soils. Findings from this research could provide insights for future and more detailed studies on tropical montane forests.

3 What did we see in Ecuador?

Across our study sites, P_3010 (the highest stratum) exhibited the highest soil CO_2 emissions (Fig. 1a and Table 1), probably due to a dominant role of soil pH and shifts in C allocation patterns. The highest soil pH_{water} was observed in this site (Table 2), and under acid conditions, Sitaula et al. (1995) and Persson & Wiren (1989) have reported a decrease in CO_2 emissions with decreasing pH_{water}. On the other hand, although not measured nor estimated in this study, an increase in fine root biomass is expected in tropical mountain forests compared to lowland forests, due to imbalances or limitations in resource (water and/or nutrients) availability at higher altitudes (Bauters et al., 2017; Leuschner et al., 2007). Therefore, the observed increase in CO_2 emissions at P_3010 might be further driven by an increase in root biomass, as the latter has been shown to be positively correlated with soil respiration (Han et al., 2007; Luo and Zhou, 2006a; Reth et al., 2005; Silver et al., 2005).

In contrast to P_3010, the low CO_2 emissions observed at C_2200 could be attributed to 1) the lower WFPS (Fig. S3), 2) the lower contents of C and N (Table 2), and 3) the higher bulk density (Table 2). The lowest soil water content was observed at this site in August at 5 cm depth, and exactly in this month, the lowest emissions of CO_2 were obtained. The low contents of C and N exhibited in C_2200 (indeed, the lowest from all the sites), could also have hampered the CO_2 emissions (Dalal and Allen, 2008; Luo and Zhou, 2006a; Oertel et al., 2016). Additionally, this site had the highest soil bulk density (i.e. lowest porosity), which could have led to a decrease in soil respiration either by a physical impediment for root growth or by a decrease in soil aeration for microbial activities (Dilustro et al., 2005; Luo and Zhou, 2006b, 2006a).

All sites acted as net sinks for CH_4 (Fig. 1b and Table 1) (i.e. uptake of atmospheric CH_4 by soils). During the entire field campaign (10 days), only one chamber at one site (S_400) and a specific date (08/09/2018) showed a net source of CH_4 (43.2 $\mu g\ CH_4\text{-}C\ m^{-2}\ h^{-1}$). However, there were no statistical differences between months, and all sites exhibited indeed a high temporal and spatial variability.

Only S_400 and M_1100 (both months) (i.e. plots located at the lower locations) acted as net sources of N_2O (Fig. 1c and Table 1). Whereas the plots located at the highest stratum (P_3010 & C_2200) showed a general net N_2O consumption during August and September.

The N_2O emissions obtained at the lowest strata corroborate with literature data on lowland tropical forests (Butterbach-Bahl et al., 2004, 2013; Koehler et al., 2009), and could be mainly attributed to the soil water content, temperature, and N availability observed at these sites (Fig. S2, S3 and Table 2). Firstly, N_2O emissions in tropical forest soils are predominantly governed by WFPS, which influences microbial activity, soil aeration, and thus diffusion of N_2O out of the soil (Davidson et al., 2006; Werner et al., 2007). Secondly, an increase in temperature leads to an increase in soil respiration and thus to a depletion of oxygen concentrations, which is indeed a major driver in N_2O emissions. In fact, rising temperatures lead to a positive feedback in microbial metabolism, where the stimulation of mineralization and nitrification processes induces an increase in the availability of substrates for denitrification, and thus to an increase in N_2O emissions (Butterbach-Bahl et al., 2013; Sousa Neto et al., 2011). Finally, the dependency of N_2O emissions on WFPS and temperature is affected by substrate availability (NO_3^-). High contents of NO_3^- give an indication of an open or “leaky” N cycle with higher rates of mineralization, nitrification, and thus N_2O emissions (Davidson et al., 2006). Moreover, NO_3^- is normally preferred as an electron acceptor over N_2O and it can also inhibit the rate of N_2O consumption to N_2 (Dalal and Allen, 2008).

In contrast to the low elevation sites where net N_2O emissions were observed, P_3010 and C_2200 (Fig. 1c and Table 1) presented net consumption (negative values, i.e. fluxes from the atmosphere to the soil). From 35 valid measurements only one resulted in net emission at P_3010 (range: -9.3 to 0.95 µg N_2O-N m^{-2} h^{-1}), whereas from 36 valid measurements, 19 resulted in net emissions at C_2200 (range: -104.9 to 9.3 µg N_2O-N m^{-2} h^{-1}). Net N_2O consumption is often related to N-limited ecosystems and it is presumably the cause in our case. At low NO_3^- concentrations, atmospheric and/or soil gaseous N_2O may be the only electron acceptor left for denitrification (Chapui-Lardy et al., 2007; Goossens et al., 2001). P_3010 had the lowest content of NO_3^-, along with the lowest soil $\delta^{15}N$ (Table 2), which clearly reflects the shift towards a more closed N cycle at higher elevations (Bauters et al., 2017; Gerschlauer et al., 2019). In fact, studies performed by Teh et al. (2014) and Müller et al. (2015) in the Southern Peruvian and Ecuadorian Andes, respectively, related the decrease in N_2O emissions and thus the potential for N_2 production in soils at high elevations to differences in NO_3^- availability. Moreover, Wolf et al. (2011) and Martinson et al. (2013) have indicated that N availability was 1) a dominant control on N_2O fluxes and 2) inversely proportional to altitude. In addition, the low N_2O fluxes could also be supported by the high content of clay (Table 2) and CO_2 emissions (Fig. 1a) (i.e. development of microsites for N_2O reduction), along with the low soil water content (% of WFPS) (Fig. S3) (i.e. better diffusion of atmospheric N_2O into the soil) and higher soil pH-value (Table 2) (i.e. less severe inhibition of the nitrous oxide reductase) observed at P_3010 (Chapui-Lardy et al., 2007).

It is important to mention that the region where these measurements were taken is characterized by a marked seasonality in rainfall. We measured at the end of the dry season; thus, it is expected to have fluctuations on net fluxes (sources vs sinks) depending on the season. Moreover, although our limited dataset did not allow us to corroborate the main drivers that controlled these fluxes, daily measurements as those carried out here, reflect the importance of evaluating short-term variations. As such, the net N_2O consumption with increasing altitude might be overlooked in an annual analysis, but equally important to 1) understand the mechanisms behind the production and consumption of N_2O, and 2) have reliable estimates of the N_2O source/sink strength of tropical forests for regional and even global GHG budgets. Moreover, in order to corroborate the net consumption observed at high altitudes and improve the understanding of N_2O dynamics in terrestrial ecosystems, disentangling gross N_2O production and consumption at field scale is needed. Although the most common used method to measure N_2O fluxes via static chambers only allows the quantification of net fluxes, stable isotope techniques would greatly contribute to our mechanistic understanding of gross fluxes. For instance, enrichment and natural abundance approaches (^{18}O, ^{15}N) can be used to identify and estimate the contribution of different microbial processes to N_2O production/consumption (Butterbach-Bahl et al., 2013; Yu et al., 2020). Nevertheless, 1) the coupling of isotope techniques with molecular analyses of functional genes is paramount to fully understand the complexity of the microbial processes present, and 2) the improvement of measuring techniques for N_2O reduction is needed to close N ecosystem balances (Butterbach-Bahl et al., 2013; Chapui-Lardy et al., 2007). In fact, microbial composition and diversity, as well as the presence or absence of important genes (e.g. N_2O reductase *nosZ I* and *nosZ II* (Van Groenigen et al., 2015b)) can help to detect N_2O consumption. Similarly, analytical techniques such as Raman gas spectroscopy could be used to detect and quantify N_2 fluxes from denitrification (Frosch et al., 2016), which is indeed a novel and simple approach compared to previously widely used techniques that may have led to underestimations (Fang et al., 2015).

4 Conclusions and future directions

GHG fluxes from tropical montane forests in South America are particularly scarce, with limited spatial coverage and seasonal fluctuation in rainfall, but important to be considered in future field measurements and modeling research. Overall, we found an unusual but marked increase of CO_2 emissions at the highest altitude; probably explained by soil pH and root biomass, even though the latter was not measured nor estimated. Our CH_4 uptake fluxes exhibited a high temporal and spatial variability but reiterate the role of humid tropical forest soils as CH_4 sinks. Contrary to the net N_2O emissions observed in the lowest strata, the net consumption at higher elevations seems to be quite unique, and it might reflect the shift towards a more closed N cycle at higher altitudes reported previously in tropical regions. Our results highlight the importance of short-term variations in N_2O fluxes, but it calls for more and broader studies especially in tropical montane forests, including the impact of spatial and temporal variability, forest management events and forest rotation cycles, ground vegetation composition and cover, soil microclimate and hydrological conditions, as well as the implementation of isotope techniques, the coupling of microbial analysis with N_2O fluxes, and the response of tropical forests to current and future changes in N content.

In terms of spatial variation, GHG fluxes may vary between lower slope, mid-slope and/or ridge (see Table S1) (Courtois et al., 2018; Teh et al., 2014; Wolf et al., 2011, 2012). Fluctuations of net fluxes can be observed depending on the season and the transition between them (see Table S1) (Butterbach-Bahl et al., 2013; Kim et al., 2016a). Management events (e.g. thinning, clear cutting, fertilization, draining improvements) and/or forest composition and growth stage (e.g. young vs mature forest) may influence e.g. forest vegetation, soil characteristics, hydrology, and nutrient management among others, and ultimately lead to changes on soil GHG fluxes (Barrena et al., 2013; Jauhiainen et al., 2019; Kim et al., 2016a). Moreover, soil hydrology (runoff, evapotranspiration, soil moisture, etc.) may affect biogeochemical cycles (Kim et al., 2016a). Microbial composition and diversity could be a key to understand the variability of N_2O fluxes (Butterbach-Bahl et al., 2013). Changes in N content -due to e.g. urban development and increasing use of agricultural land- could cause shifts on soil N cycling and thus CO_2, CH_4 and N_2O fluxes (Koehler et al., 2012). Besides this, the effects of climate change in tropical regions (e.g. increases in temperature and CO_2 concentrations, as well as changes in rainfall patterns and drought events) may also affect soil GHG fluxes. Therefore, a strategic plan must be implemented. Long-term data with at least one or two hydrological years is needed, with sampling intervals covering seasonal fluctuations and appropriate to the type of land (i.e. spatial variability across different topographical positions). The effect of N content and climate change on tropical forests could be evaluated using laboratory (e.g. incubations under controlled conditions) and/or field experiments (e.g. see Koehler et al., (2009, 2012), Hall and Matson (1999), and Martinson et al., (2013)); with the use of altitudinal gradients as biogeochemical open-air laboratories. Finally, although sampling conditions in tropical montane regions can be challenging, 1) establishing networks and collaborations with local communities (i.e. citizen science) could contribute not only in terms of data acquisition, but also in the development of local knowledge (e.g. how climate and land use change might affect ecosystems and people), and 2) modeling approaches for C and N biogeochemistry in forest ecosystems (e.g. Forest-DNDC (GRAMP, 2013)) could help to up-scale fluxes from site to regional level. Nevertheless, the cooperation and contribution between field researchers and scientific organizations e.g. in South America and across the world, as well as the capacity building in the respective countries, are crucial to improve our understanding of soil GHG fluxes from tropical regions, and paramount to get tangible datasets of remote regions such as montane forests.

Supplementary information

1 Materials and methods

2 Results

Fig. S1. Overview map with the location of the study areas.

Fig. S2. Monthly average soil temperature (°C)±standard deviations (SD).

Fig. S3. Monthly average water-filled pore space (WFPS)±standard deviations (SD).

Table S1. Measured and estimated CO_2, CH_4 and N_2O fluxes from tropical forest soils of South America.

Table S2. Characteristics of the study areas.

Author contributions

M.Bauters, H.V., SB. and P.B. developed the project; P.L. and M. Bauters carried out the fieldwork and analyzed the data; and M. Barthel and S.B provided technical and analytical support analyzing the gas and soil samples. All authors contributed to the ideas presented and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Average measurements±standard deviations (SD) of soil CO_2, CH_4 and N_2O fluxes at Río Silanche (400 m a.s.l.; S_400), Milpe (1100 m a.s.l.; M_1100), El Cedral (2200 m a.s.l.; C_2200) and Peribuela (3010 m a.s.l.; P_3010) per month.

Month	Plot	Average CO_2 flux (mg C m^{-2} h^{-1})	Average CH_4 flux (µg C m^{-2} h^{-1})	Average N_2O flux (µg N m^{-2} h^{-1})
August	S_400	64.5±17.2	-59.6±21.6	11.3±18.4
	M_1100	60.5±7.4	-48.7±19.6	0.8±6.9
	C_2200	46.4±18.3	-47.6±14.5	-2.3±6.8
	P_3010	98.6±23.5	-39.8±12.6	-4.4±2.4
September	S_400	89.9±18.8	-59.8±29.9	3.8±5.7
	M_1100	65.5±21.6	-48.9±14.6	12.9±27.8
	C_2200	53.4±19.3	-57.9±19.4	-4.7±27.0
	P_3010	87.7±18.9	-33.7±10.6	-3.7±1.4

Note: flux values represent the mean of 5 chambers per site and measurement week, using four-point time series and considering the constraint set to evaluate linearity in each measurement cycle ($R^2 > 0.65$).

Table 2. Physicochemical soil properties of the study areas Río Silanche (400 m a.s.l.; S_400), Milpe (1100 m a.s.l.; M_1100), El Cedral (2200 m a.s.l.; C_2200) and Peribuela (3010 m a.s.l.; P_3010) at 5 and 20 cm depth, including mean values±standard deviation (SD) of bulk density (ρb), porosity, pH in water (pH_{water}) and KCl suspension (pH_{KCl}), nitrate (NO_3^-) and ammonium (NH_4^+) concentration, bulk nitrogen (N) and carbon (C) content, carbon-to-nitrogen ratio (C/N) and δ^{15}N signatures from samples of soil taken in August. Similar lowercase letters in superscript and next to some values within one row and per depth (5 and 20 cm) indicate no significant difference at $P < 0.05$ between sites (S_400, M_1100, C_2200 and P_3010).

	S_400		**M_1100**		**C_2200**		**P_3010**	
	5 cm	**20 cm**	**5 cm**	**20 cm**	**5 cm**	**20 cm**	**5 cm**	**20 cm**
Soil class	Andosol[1]		Andosol[1]		Andosol[1]		Andosol[1]	
Soil texture	Loam	Loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Loam	Loam
Sand (%)	41.0	40.0	70.8	67.0	63.7	60.5	41.9	45.0
Silt%)	43.4	47.0	21.7	27.9	29.7	34.4	32.5	34.9
Clay (%)	15.6	13.1	7.6	5.0	6.6	5.2	25.6	20.1
ρb (g cm^{-3})	0.43±0.15^{b}	0.58±0.07^{b}	0.62±0.09^{a,b}	0.86±0.12^{a}	0.70±0.11^{a}	0.92±0.05^{a}	0.62±0.09^{a,b}	0.81±0.06^{a}
Porosity (%)	83.8±5.5^{a}	78.0±2.5^{a}	76.5±3.3$^{a.b}$	67.7±4.7^{b}	73.7±4.1^{b}	65.4±2.0^{b}	76.7±3.4^{a,b}	69.6±2.1^{b}
pH_{water}	4.6±0.7^{a,b}	5.2±0.5	4.6±0.8^{b}	5.5±0.4	4.8±0.4^{a,b}	4.8±0.6	5.7±0.5^{a}	5.6±0.5
pH_{KCl}	4.4±0.2^{b}	4.9±0.3^{a,b}	4.5±0.2^{b}	5.0±0.0^{a}	4.5±0.1^{b}	4.6±0.0^{b}	5.1±0.2^{a}	4.9±0.2^{a,b}
NO_3-N (μg g^{-1})[2]	71.9±39.5^{a}	35.7±29.5^{a}	23.1±15.9^{b}	6.7±7.7^{a,b}	30.6±19.4^{a,b}	7.3±4.3^{a,b}	0.8±0.3^{b}	3.6±7.1^{b}
NH_4-N (μg g^{-1})[2]	34.3±14.8	27.9±16.1^{a,b}	22.6±4.0	11.9±2.4^{b}	26.5±16.0	18.8±4.9^{b}	22.9±11.3	40.4±13.5^{a}
N (%)	0.8±0.2	0.5±0.1^{a}	0.6±0.2	0.2±0.1^{b}	0.6±0.2	0.3±0.0^{a,b}	0.6±0.0	0.4±0.2^{a,b}
C (%)	8.9±2.4	4.0±1.0^{a,b}	7.1±1.8	2.4±0.7^{b}	6.6±1.7	3.3±0.4^{a,b}	8.6±0.5	4.8±1.5^{a}
C/N[3]	10.6±0.4^{c}	8.9±0.4^{c}	11.9±0.6^{b}	10.6±0.7^{b}	11.8±0.8^{b}	10.4±0.5^{b}	14.6±0.5^{a}	12.8±1.3^{a}
δ^{15}N (‰)[4]	6.2±0.5^{a}	8.6±0.9^{a}	6.0±0.8^{a}	6.7±0.8^{b}	4.0±1.2^{b}	4.8±0.5^{c}	3.7±0.6^{b}	4.2±0.4^{c}

Notes: mean values±SD were calculated from soil samples taken adjacent to each soil chamber (n = 5), except for soil texture, where composites for each site at 5 and 20 cm depth were made from the soil samples taken from each chamber.

[1] Commonly known as *Andisol* in the USDA Soil Taxonomy; [2] expressed per gram of dry soil; [3] calculated by dividing C (%) by N (%) in each soil sample; and [4] expressed relative to the international standard AIR.

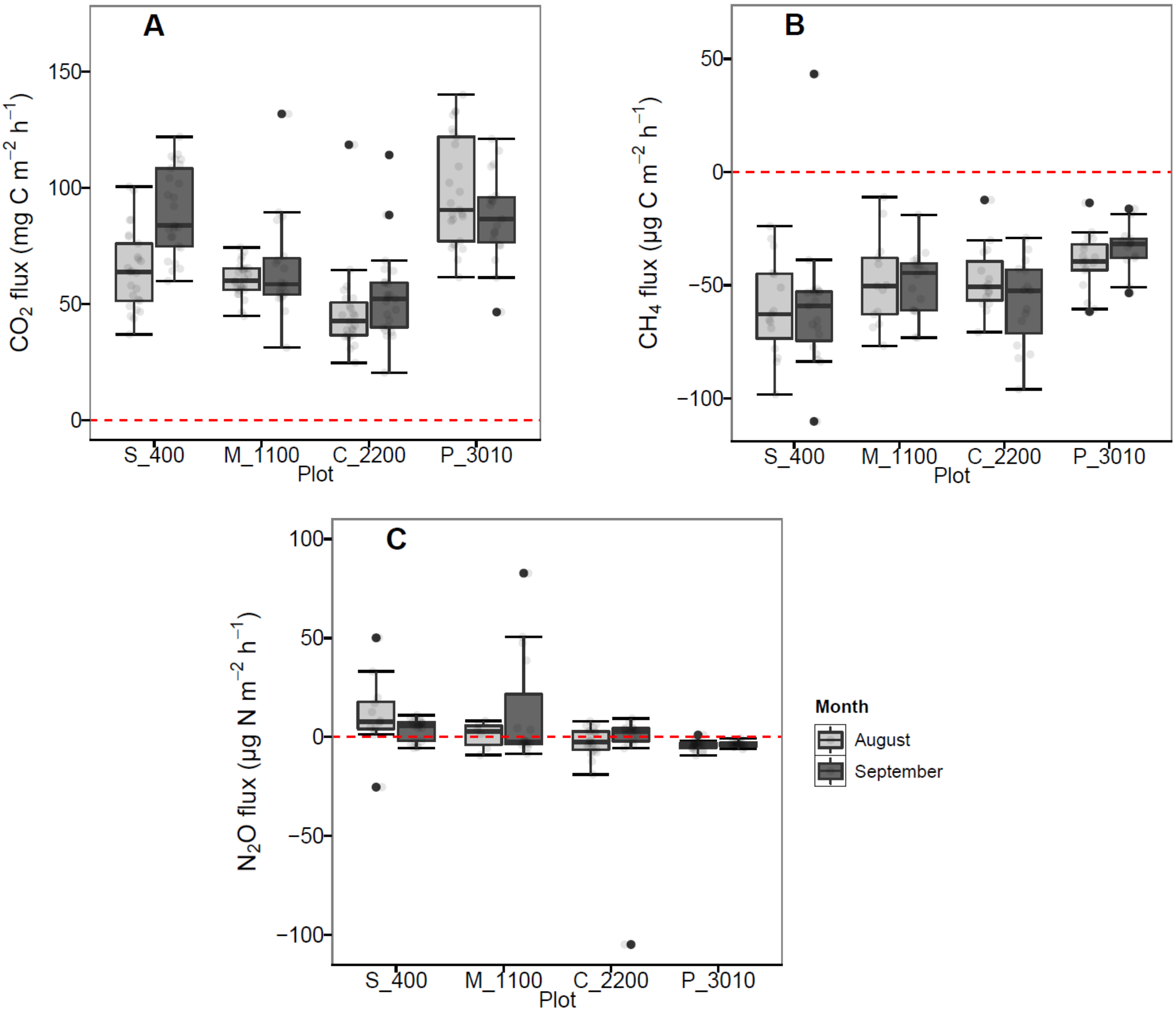

Fig. 1. A) Soil CO_2 (mg C m^{-2} h^{-1}), B) CH_4 (µg C m^{-2} h^{-1}) and C) N_2O (µg N m^{-2} h^{-1}) fluxes per month at Río Silanche (400 m a.s.l.; S_400), Milpe (1100 m a.s.l.; M_1100), El Cedral (2200 m a.s.l.; C_2200) and Peribuela (3010 m a.s.l.; P_3010). Light gray boxplots indicate the fluxes in August 2018, whereas dark gray boxplots, the fluxes in September 2018. Light gray dots in each boxplot represent the measurements taken each day; and black dots, outliers of the respective site. The red dotted line across the boxes indicates zero net flux.