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

Paula Alejandra Lamprea Pineda[1], Marijn Bauters[2, 3], Hans Verbeeck[3], Selene Baez[4], Matti Barthel[5] and Pascal Boeckx[2]

[1]Environmental Organic Chemistry and Technology - ENVOC, Department of Green Chemistry and Technology, Ghent University, Gent, 9000 Belgium
[2]Isotope Bioscience Laboratory – ISOFYS, Department of Green Chemistry and Technology, Ghent University, Gent, 9000 Belgium
[3]Computational and Applied Vegetation Ecology – CAVElab, Department of Environment, Ghent University, Gent, 9000 Belgium
[4]Departamento de Biología, Escuela Politécnica Nacional del Ecuador, Ladrón de Guevera E11-253 y Andalucía, Quito, Ecuador
[5]Department of Environmental Systems Science, ETH Zurich, Zurich, 8092, Switzerland

Correspondence to: Paula Lamprea (paulaalejandra.lampreapineda@ugent.be)

Co-authors: marijn.bauters@UGent.be, hans.verbeeck@UGent.be, selene.baez@epn.edu.ec, matti.barthel@usys.ethz.ch, pascal.boeckx@UGent.be

Keywords: Tropical Forests - Soil CO_2, CH_4 and N_2O fluxes - Altitudinal Gradients - N_2O Stable Isotopes.

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, with bulk isotope ^{15}N-N_2O data indicating net N_2O reduction at high altitude. 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, with additional samples for bulk ^{15}N of N_2O ($\delta^{15}N^{Bulk}$). 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 1) to determine the magnitude of the soil-atmosphere exchange of CO_2, CH_4 and N_2O during the dry season, and 2) to support and couple the N_2O fluxes with their isotopic signatures. 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 µg CH_4-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 soil water content, temperature, and N availability observed at these sites (Fig. S2, S3 and Table 2). 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). 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. Rising temperatures lead to a positive feedback in microbial metabolism; 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).

Besides the soil isotope signatures, the bulk N_2O isotope signatures (Fig 2) support the net N_2O consumption at higher altitudes, and net N_2O emission at lower altitudes, and rule out that our net consumption rates are due to sampling artifacts. Previous studies have indicated that during the reduction of N_2O to N_2, N_2O-reductase fractionates against ^{15}N (Barford et al., 1999; Butterbach-Bahl et al., 2013; Menyailo and Hungate, 2006; Pérez et al., 2000). Consequently, complete denitrification i.e. consumption of N_2O, leads to a ^{15}N enrichment of the residual N_2O, and thus to higher $\delta^{15}N_s^{Bulk}$ values (Denk et al., 2017; Park et al., 2011) relative to the atmospheric bulk N_2O composition (6.3‰ (Harris et al., 2017)). This in fact is reflected in the relatively enriched $\delta^{15}N_s^{Bulk}$ values measured during N_2O consumption, while a relative depletion was observed during N_2O production (two samples taken in September at S_400) (Fig. 2; Table S3). This is also in line with Park et al. (2011) and Pérez et al. (2000) who have attributed $\delta^{15}N_s^{Bulk}$ values between -22 and 2‰ in natural tropical forest soils to denitrification.

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.

5 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. This net N_2O uptake was in fact confirmed independently by soil and N_2O ^{15}N isotope signatures. 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 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.

Table S2. $\delta^{15}N_S^{Bulk}$ values and N_2O fluxes.

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 performed the bulk isotope ^{15}N-N_2O analysis. All authors contributed to the ideas presented and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgments

This research has been supported by Ghent University, the VLIR-UOS South Initiative COFOREC (EC2018SIN223A103) and COFOREC II (EC2020SIN279A103). We also thank Mindo Cloud Forest Foundation, El Cedral Ecolodge and the Escuela

Politécnica Nacional del Ecuador, for the logistic support in Ecuador. M. Barthel was supported through ETH Zurich core funding provided to Johan Six, and M. Bauters is funded as a postdoctoral fellow of the research Foundation – Flanders (FWO).

References

Barford, C. C., Montoya, J. P., Altabet, M. A. and Mitchell, R.: Steady-state nitrogen isotope effects of N2 and N2O production in Paracoccus denitrificans, Appl. Environ. Microbiol., 65, 989–994, doi:10.1128/aem.65.3.989-994.1999, 1999.

Barrena, I., Menéndez, S., Duñabeitia, M., Merino, P., Florian Stange, C., Spott, O., González-Murua, C. and Estavillo, J. M.: Greenhouse gas fluxes (CO2, N2O and CH4) from forest soils in the Basque Country: Comparison of different tree species and growth stages, For. Ecol. Manage., 310, 600–611, doi:10.1016/j.foreco.2013.08.065, 2013.

Bauters, M., Verbeeck, H., Demol, M., Bruneel, S., Taveirne, C., Van Der Heyden, D., Cizungu, L. and Boeckx, P.: Parallel functional and stoichiometric trait shifts in South American and African forest communities with elevation, Biogeosciences, 14, 5313–5321, doi:10.5194/bg-14-5313-2017, 2017.

Bonan, G. B.: Forests and climate change: forcings, feedbacks, and the climate benefits of forests, Science (80-.)., 320, 1444–1449, doi:10.1126/science.1155121, 2008.

Bubb, P., May, I., Miles, L. and Sayer, J.: Cloud Forest Agenda, in United Nations Environment Programme-World Conservation Monitoring Centre, p. 33, Cambridge, UK. [online] Available from: http://www.unep-wcmc.org/index.html?http://www.unep-wcmc.org/resources/publications/UNEP_WCMC_bio_series/20.htm~main, 2004.

Butterbach-Bahl, K., Kock, M., Willibald, G., Hewett, B., Buhagiar, S., Papen, H. and Kiese, R.: Temporal variations of fluxes of NO, NO2, N2O, CO2, and CH4 in a tropical rain forest ecosystem, Global Biogeochem. Cycles, 18, 1–11, doi:10.1029/2004GB002243, 2004.

Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R. and Zechmeister-boltenstern, S.: Nitrous oxide emissions from soils: how well do we understand the processes and their controls?, Phil Trans R Soc B, 368, 1–20, doi:20130122, 2013.

Castaldi, S., Bertolini, T., Valente, a., Chiti, T. and Valentini, R.: Nitrous oxide emissions from soil of an African rain forest in Ghana, Biogeosciences, 10(6), 4179–4187, doi:10.5194/bg-10-4179-2013, 2013.

Chapui-Lardy, L., Wrage, N., Metay, A., Chotte, J.-L. and Bernoux, M.: Soils, a sink for N2O? A review, Glob. Chang. Biol., 13, 1–17, doi:10.1111/j.1365-2486.2006.01280.x, 2007.

van Cleemput, O.: Subsoils: chemo-and biological denitrification, N2O and N2 emissions, Nutr. Cycl. Agroecosystems, 52, 187–194, doi:10.1023/a:1009728125678, 1998.

Clough, T. J., Lanigan, G. J., de Klein, C. A. M., Sainur Samar, M., Morales, S. E., Rex, D., Bakken, L. R., Johns, C., Condron, L. M., Grant, J. and Richards, K. G.: Influence of soil moisture on codenitrification fluxes from a urea-affected pasture soil, Sci. Rep., 7, 1–12, doi:10.1038/s41598-017-02278-y, 2017.

Courtois, E. A., Stahl, C., Van den Berge, J., Bréchet, L., Van Langenhove, L., Richter, A., Urbina, I., Soong, J. L., Peñuelas, J. and Janssens, I. A.: Spatial variation of soil CO2, CH4 and N2O fluxes across topographical positions in tropical forests of the Guiana Shield, Ecosystems, 21, 1445–1458, doi:10.1007/s10021-018-0232-6, 2018.

Dalal, R. C. and Allen, D. E.: TURNER REVIEW No. 18 Greenhouse gas fluxes from natural ecosystems, Aust. J. Bot., 56, 369–407, doi:10.1071/BT07128, 2008.

Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V. and Veldkamp, E.: Testing a conceptual model of soil emissions of nitrous and nitric oxides, Bioscience, 50, 667–680, doi:10.1641/0006-3568(2000)050[0667:tacmos]2.0.co;2, 2006.

Denk, T. R. A., Mohn, J., Decock, C., Lewicka-Szczebak, D., Harris, E., Butterbach-Bahl, K., Kiese, R. and Wolf, B.: The nitrogen cycle: A review of isotope effects and isotope modeling approaches, Soil Biol. Biochem., 105, 121–137, doi:10.1016/j.soilbio.2016.11.015, 2017.

Dilustro, J. J., Collins, B., Duncan, L. and Crawford, C.: Moisture and soil texture effects on soil CO2 efflux components in southeastern mixed pine forests, For. Ecol. Manage., 204, 85–95, doi:10.1016/j.foreco.2004.09.001, 2005.

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia, L., Silman, M., Farfán-Ríos, W., Malhi, Y., Young, K. R., Cuesta C, F., Homeier, J., Peralvo, M., Pinto, E., Jadan, O., Aguirre, N., Aguirre, Z. and Feeley, K. J.: Widespread but heterogeneous responses of Andean forests to climate change, Nature, 564, 207–212, doi:10.1038/s41586-018-0715-9, 2018.

Gerschlauer, F., Saiz, G., Schellenberger Costa, D., Kleyer, M., Dannenmann, M. and Kiese, R.: Stable carbon and nitrogen isotopic composition of leaves, litter, and soils of various ecosystems along an elevational and land-use gradient at Mount Kilimanjaro, Tanzania, Biogeosciences, 16, 409–424, doi:10.5194/bg-16-409-2019, 2019.

Goossens, A., Visscher, A. De, Boeckx, P. and Cleemput, O. Van: Two-year field study on the emission of N2O from coarse and middle-textured Belgian soils with different land use, Nutr. Cycl. Agroecosystems, 60, 23–34, doi:10.1023/A:1012695731469, 2001.

Grace, J., José, J. S., Meir, P., Miranda, H. S. and Montes, R. A.: Productivity and carbon fluxes of tropical savannas, J. Biogeogr., 33, 387–400, doi:10.1111/j.1365-2699.2005.01448.x, 2006.

GRAMP: Forest-DNDC, About For. [online] Available from: http://gramp.ags.io/models/1 (Accessed 18 July 2020), 2013.

Van Groenigen, J. W., Huygens, D., Boeckx, P., Kuyper, T. W., Lubbers, I. M., Rütting, T. and Groffman, P. M.: The soil n cycle: New insights and key challenges, Soil, 1(1), 235–256, doi:10.5194/soil-1-235-2015, 2015.

Hall, S. J. and Matson, P. A.: Nitrogen oxide emissions after nitrogen additions in tropical forests, Lett. to Nat., 400, 152–155, doi:10.1038/22094, 1999.

Han, G., Zhou, G., Xu, Z., Yang, Y., Liu, J. and Shi, K.: Biotic and abiotic factors controlling the spatial and temporal variation of soil respiration in an agricultural ecosystem, Soil Biol. Biochem., 39, 418–425, doi:10.1016/j.soilbio.2006.08.009, 2007.

Harris, E., Henne, S., Hüglin, C., Zellweger, C., Tuzson, B., Ibraim, E., Emmenegger, L. and Mohn, J.: Tracking nitrous oxide emission processes at a suburban site with semicontinuous, in situmeasurements of isotopic composition, J. Geophys. Res., 122(3), 1850–1870, doi:10.1002/2016JD025906, 2017.

Heil, J., Wolf, B., Brüggemann, N., Emmenegger, L., Tuzson, B., Vereecken, H. and Mohn, J.: Site-specific 15N isotopic signatures of abiotically produced N2O, Geochim. Cosmochim. Acta, 139, 72–82, doi:10.1016/j.gca.2014.04.037, 2014.

Heil, J., Vereecken, H. and Brüggemann, N.: A review of chemical reactions of nitrification intermediates and their role in

nitrogen cycling and nitrogen trace gas formation in soil, Eur. J. Soil Sci., 67, 23–39, doi:10.1111/ejss.12306, 2016.

Jang, I., Lee, S., Hong, J. H. and Kang, H.: Methane oxidation rates in forest soils and their controlling variables: A review and a case study in Korea, Ecol. Res., 21, 849–854, doi:10.1007/s11284-006-0041-9, 2006.

Jauhiainen, J., Alm, J., Bjarnadottir, B., Callesen, I., Christiansen, J. R., Clarke, N., Dalsgaard, L., He, H., Jordan, S., Kazanavičiūtė, V., Klemedtsson, L., Lauren, A., Lazdins, A., Lehtonen, A., Lohila, A., Lupikis, A., Mander, Ü., Minkkinen, K., Kasimir, Å., Olsson, M., Ojanen, P., Óskarsson, H., Sigurdsson, B. D., Søgaard, G., Soosaar, K., Vesterdal, L. and Laiho, R.: Reviews and syntheses: Greenhouse gas exchange data from drained organic forest soils - a review of current approaches and recommendations for future research, Biogeosciences Discuss., 4687–4703, doi:10.5194/bg-2019-261, 2019.

Jobbágy, E. G. and Jackson, R. B.: The vertical distribution of soil organic carbon and its relation to climate and vegetation, Ecol. Appl., 10, 423, doi:10.2307/2641104, 2000.

Jones, S. P., Diem, T., Huaraca Quispe, L. P., Cahuana, A. J., Reay, D. S., Meir, P. and Teh, Y. A.: Drivers of atmospheric methane uptake by montane forest soils in the southern Peruvian Andes, Biogeosciences, 13, 4151–4165, doi:10.5194/bg-13-4151-2016, 2016.

Kahmen, A., Sachse, D., Arndt, S. K., Tu, K. P., Farrington, H., Vitousek, P. M. and Dawsona, T. E.: Cellulose δ18O is an index of leaf-to-air vapor pressure difference (VPD) in tropical plants, PNAS, 108, 1981–1986, doi:10.1073/pnas.1018906108, 2011.

Killeen, T. J., Douglas, M., Consiglio, T., Jørgensen, P. M. and Mejia, J.: Dry spots and wet spots in the Andean hotspot, J. Biogeogr., 34, 1357–1373, doi:10.1111/j.1365-2699.2006.01682.x, 2007.

Kim, D.-G., Thomas, A. D., Pelster, D., Rosenstock, T. S. and Sanz-Cobena, A.: Greenhouse gas emissions from natural ecosystems and agricultural lands in sub-Saharan Africa: Synthesis of available data and suggestions for further research, Biogeosciences, 13, 4789–4809, doi:10.5194/bg-13-4789-2016, 2016a.

Kim, D. G., Thomas, A. D., Pelster, D., Rosenstock, T. S. and Sanz-Cobena, A.: Greenhouse gas emissions from natural ecosystems and agricultural lands in sub-Saharan Africa: Synthesis of available data and suggestions for further research, Biogeosciences, 13(16), 4789–4809, doi:10.5194/bg-13-4789-2016, 2016b.

Koehler, B., Corre, M. d., Veldkamp, E., Wullaert, H. and Wright, S. J.: Immediate and long-term nitrogen oxide emissions from tropical forest soils exposed to elevated nitrogen input, Glob. Chang. Biol., 15, 2049–2066, doi:10.1111/j.1365-2486.2008.01826.x, 2009.

Koehler, B., Corre, M. D., Steger, K., Well, R., Zehe, E., Sueta, J. P. and Veldkamp, E.: An in-depth look into a tropical lowland forest soil: Nitrogen-addition effects on the contents of N2O, CO2 and CH4 and N2O isotopic signatures down to 2-m depth, Biogeochemistry, 111, 695–713, doi:10.1007/s10533-012-9780-6, 2012.

Körner, C.: The use of “altitude” in ecological research, Trends Ecol. Evol., 22, 569–574, doi:10.1016/j.tree.2007.09.006, 2007.

Laughlin, D. C. and Abella, S. R.: Abiotic and biotic factors explain independent gradients of plant community composition in ponderosa pine forests, Ecol. Modell., 205, 231–240, doi:10.1016/j.ecolmodel.2007.02.018, 2007.

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M. and Hertel, D.: Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador, Basic Appl. Ecol., 8, 219–230, doi:10.1016/j.baae.2006.02.004, 2007.

Li, L., Zheng, Z., Wang, W., Biederman, J. A., Xu, X., Ran, Q., Qian, R., Xu, C., Zhang, B., Wang, F., Zhou, S., Cui, L., Che, R., Hao, Y., Cui, X., Xu, Z. and Wang, Y.: Terrestrial N2O emissions and related functional genes under climate change: A global meta-analysis, Glob. Chang. Biol., 26, 931–943, doi:10.1111/gcb.14847, 2020.

Luo, Y. and Zhou, X.: Controlling Factors, in Soil Respiration and the Environment, pp. 79–105, Elsevier Inc., San Diego, U.S.A., 2006a.

Luo, Y. and Zhou, X.: Responses to disturbances, in Soil Respiration and the Environment, pp. 133–158, Elsevier Inc., San Diego, U.S.A., 2006b.

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S.: Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research, Glob. Chang. Biol., 16, 3171–3175, doi:10.1111/j.1365-2486.2010.02323.x, 2010.

Martinson, G. O., Corre, M. D. and Veldkamp, E.: Responses of nitrous oxide fluxes and soil nitrogen cycling to nutrient additions in montane forests along an elevation gradient in southern Ecuador, Biogeochemistry, 112, 625–636, doi:10.1007/s10533-012-9753-9, 2013.

Menyailo, O. V. and Hungate, B. A.: Stable isotope discrimination during soil denitrification: Production and consumption of nitrous oxide, Global Biogeochem. Cycles, 20, 1–10, doi:10.1029/2005GB002527, 2006.

Montzka, S. A., Dlugokencky, E. J. and Butler, J. H.: Non-CO2 greenhouse gases and climate change, Nature, 476, 43–50, doi:10.1038/nature10322, 2011.

Müller, A. K., Matson, A. L., Corre, M. D. and Veldkamp, E.: Soil N2O fluxes along an elevation gradient of tropical montane forests under experimental nitrogen and phosphorus addition, Front. Earth Sci., 3, 1–12, doi:10.3389/feart.2015.00066, 2015.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J.: Biodiversity hotspots for conservation priorities, Nature, 043, 853–858, doi:10.1080/21564574.1998.9650003, 2000.

Myhre, G., Shindell, D., Bréon, F.-M., Collins, W., Fuglestvedt, J., Huang, J., Koch, D., Lamarque, J.-F., Lee, D., Mendoza, B., Nakajima, T., Robock, A., Stephens, G., Takemura, T. and Zhang, H.: Anthropogenic and natural radiative forcing. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergorvernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., 2013.

Oertel, C., Matschullat, J., Zurba, K., Zimmermann, F. and Erasmi, S.: Greenhouse Gas Emissions From Soil - A review, Chemie der Erde, 76, 327–352, doi:10.1016/j.chemer.2016.04.002, 2016.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Philips, O. L., Shvidenko, A., Lwis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, D. A., Piao, S., Rautiainen, A., Sitch, S. and Hayes, D.: A large and persistent carbon sink in the world's forests, Science (80-.)., 333, 988–992, doi:10.1126/science.1201609, 2011.

Park, S., Pérez, T., Boering, K. A., Trumbore, S. E., Gil, J., Marquina, S. and Tyler, S. C.: Can N2O stable isotopes and

isotopomers be useful tools to characterize sources and microbial pathways of N2O production and consumption in tropical soils?, Global Biogeochem. Cycles, 25, 1–16, doi:10.1029/2009GB003615, 2011.

Pérez, T., Trumbore, S. E., Tyler, S. C., Davidson, E. A., Keller, M. and de Carmargo, P. B.: Isotopic variability of N2O emissions from tropical forest soils, Global Biogeochem. Cycles, 14, 525–535, doi:10.1029/1999GB001181, 2000.

Perez, T. M., Stroud, J. T. and Feeley, K. J.: Thermal trouble in the tropics, Science (80-.)., 351, 1392–1393, doi:10.1126/science.aaf3343, 2016.

Persson, T. and Wiren, A.: Microbial activity in forest soils in relation to acid/base and carbon/nitrogen status, in Air Pollution as Stress Factor in Nordic Forests, pp. 83–95, Norwegian Institute for Forest Research, Aas., 1989.

Purbopuspito, J., Veldkamp, E., Brumme, R. and Murdiyarso, D.: Trace gas fluxes and nitrogen cycling along an elevation sequence of tropical montane forests in Central Sulawesi, Indonesia, Global Biogeochem. Cycles, 20, 11, doi:10.1029/2005GB002516, 2006.

Reth, S., Reichstein, M. and Falge, E.: The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO2 efflux - a modified model, Plant Soil, 268, 21–33, doi:10.1007/s11104-005-0175-5, 2005.

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., Crill, P. M. and Keller, M.: Fine root dynamics and trace gas fluxes in two lowland tropical forest soils, Glob. Chang. Biol., 11, 290–306, doi:10.1111/j.1365-2486.2005.00903.x, 2005.

Sitaula, B. K., Bakken, L. R. and Abrahamsen, G.: N-fertilization and soil acidification effects on N2O and CO2 emission from temperate pine forest soil, Soil Biol. Biochem., 27, 1401–1408, doi:10.1016/0038-0717(95)00078-S, 1995.

Sousa Neto, E., Carmo, J. B., Keller, M., Martins, S. C., Alves, L. F., Vieira, S. A., Piccolo, M. C., Camargo, P., Couto, H. T. Z., Joly, C. A. and Martinelli, L. A.: Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest, Biogeosciences, 8, 733–742, doi:10.5194/bg-8-733-2011, 2011.

Spahni, R., Wania, R., Neef, L., Van Weele, M., Pison, I., Bousquet, P., Frankenberg, C., Foster, P. N., Joos, F., Prentice, I. C. and Van Velthoven, P.: Constraining global methane emissions and uptake by ecosystems, Biogeosciences, 8, 1643–1665, doi:10.5194/bg-8-1643-2011, 2011.

Su, Q., Domingo-Félez, C., Jensen, M. M. and Smets, B. F.: Abiotic nitrous oxide (N2O) production is strongly pH dependent, but contributes little to overall N2O emissions in biological nitrogen removal systems, Environ. Sci. Technol., 53, 3508–3516, doi:10.1021/acs.est.8b06193, 2019.

Teh, Y. A., Diem, T., Jones, S., Huaraca Quispe, L. P., Baggs, E., Morley, N., Richards, M., Smith, P. and Meir, P.: Methane and nitrous oxide fluxes across an elevation gradient in the tropical Peruvian Andes, Biogeosciences, 11, 2325–2339, doi:10.5194/bg-11-2325-2014, 2014.

Werner, C., Kiese, R. and Butterbach-Bahl, K.: Soil-atmosphere exchange of N 2 O, CH 4 , and CO 2 and controlling environmental factors for tropical rain forest sites in western Kenya, J. Geophys. Res., 112(D3), D03308, doi:10.1029/2006JD007388, 2007.

Wolf, K., Veldkamp, E., Homeier, J. and Martinson, G. O.: Nitrogen availability links forest productivity, soil nitrous oxide

and nitric oxide fluxes of a tropical montane forest in southern Ecuador, Global Biogeochem. Cycles, 25, 1–12, doi:10.1029/2010GB003876, 2011.

Wolf, K., Flessa, H. and Veldkamp, E.: Atmospheric methane uptake by tropical montane forest soils and the contribution of organic layers, Biogeochemistry, 111, 469–483, doi:10.1007/s10533-011-9681-0, 2012.

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 the 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 $\delta^{15}N$ 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}	$0.62\pm0.09^{a,b}$	0.86 ± 0.12^{a}	0.70 ± 0.11^{a}	0.92 ± 0.05^{a}	$0.62\pm0.09^{a,b}$	0.81 ± 0.06^{a}
Porosity (%)	83.8 ± 5.5^{a}	78.0 ± 2.5^{a}	$76.5\pm3.3^{a,b}$	67.7 ± 4.7^{b}	73.7 ± 4.1^{b}	65.4 ± 2.0^{b}	$76.7\pm3.4^{a,b}$	69.6 ± 2.1^{b}
pH_{water}	$4.6\pm0.7^{a,b}$	5.2 ± 0.5	4.6 ± 0.8^{b}	5.5 ± 0.4	$4.8\pm0.4^{a,b}$	4.8 ± 0.6	5.7 ± 0.5^{a}	5.6 ± 0.5
pH_{KCl}	4.4 ± 0.2^{b}	$4.9\pm0.3^{a,b}$	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}	$4.9\pm0.2^{a,b}$
NO_3-N (μg g^{-1})[2]	71.9 ± 39.5^{a}	35.7 ± 29.5^{a}	23.1 ± 15.9^{b}	$6.7\pm7.7^{a,b}$	$30.6\pm19.4^{a,b}$	$7.3\pm4.3^{a,b}$	0.8 ± 0.3^{b}	3.6 ± 7.1^{b}
NH_4-N (μg g^{-1})[2]	34.3 ± 14.8	$27.9\pm16.1^{a,b}$	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	$0.3\pm0.0^{a,b}$	0.6 ± 0.0	$0.4\pm0.2^{a,b}$
C (%)	8.9 ± 2.4	$4.0\pm1.0^{a,b}$	7.1 ± 1.8	2.4 ± 0.7^{b}	6.6 ± 1.7	$3.3\pm0.4^{a,b}$	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}
$\delta^{15}N$ (‰)[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.

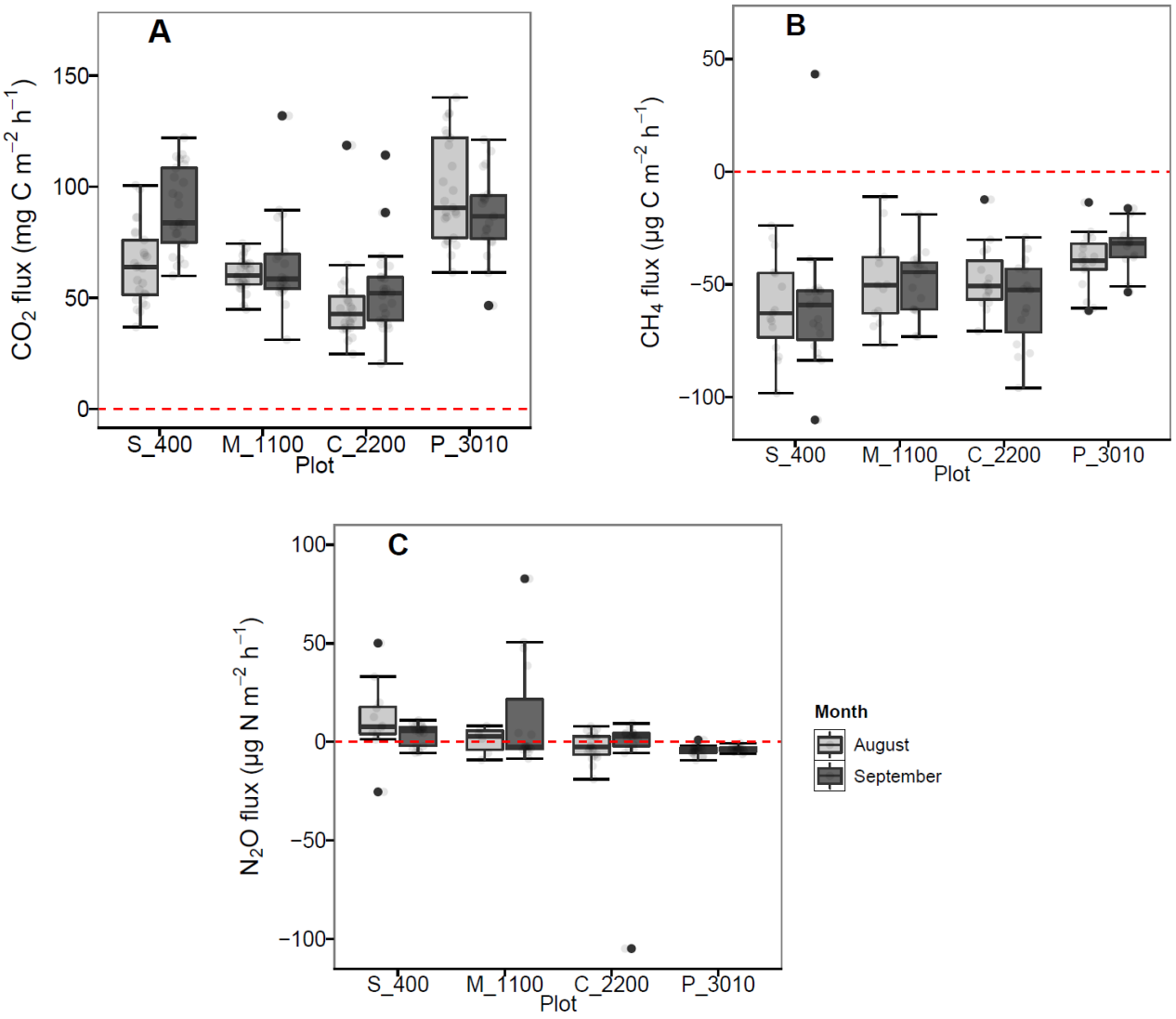

Fig. 1. A) Soil CO_2 (mg C m^{-2} h^{-1}), B) CH_4 (µg C m^{-2} h^{-1}) and C) N_2O (µg N m^{-2} h^{-1}) fluxes per month at Río Silanche (400 m a.s.l.; S_400), Milpe (1100 m a.s.l.; M_1100), El Cedral (2200 m a.s.l.; C_2200) and Peribuela (3010 m a.s.l.; P_3010). Light gray boxplots indicate the fluxes 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.

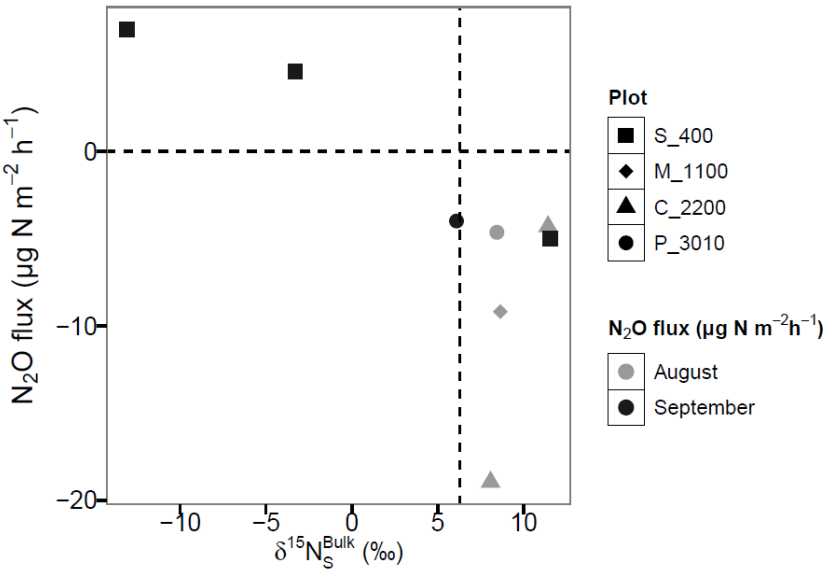

Fig. 2. N_2O fluxes plotted against the bulk isotopic signature of soil N_2O ($\delta^{15}N_S^{Bulk}$) for point samples taken at Río Silanche - squares (400 m a.s.l.; S_400), Milpe - diamonds (1100 m a.s.l.; M_1100), El Cedral - triangles (2200 m a.s.l.; C_2200) and Peribuela - circles (3010 m a.s.l.; P_3010) during August (grey) and September (black). Note: the dotted vertical line at 6.3‰ represents the atmospheric bulk N_2O composition (Harris et al., 2017); and $\delta^{15}N_S^{Bulk}$ values were calculated based on a two-source mixing model, considering a threshold of 20 ppb to exclude low fluxes and thus, avoid larger uncertainties in the source calculation.