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CARBON FLUX DYNAMICS IN HIGH ALTITUDE PEATLANDS IN THE ECUADORIAN ANDES

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CARBON FLUX DYNAMICS IN HIGH ALTITUDE PEATLANDS IN THE
ECUADORIAN ANDES

By
María Elisa Sánchez

A THESIS
Submitted in partial fulfillment of the requirements for the degree of
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In Applied Ecology

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This thesis has been approved in partial fulfillment of the requirements for the Degree of
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PREFACE

The journal article which is included as the main body of this manuscript was written by María Elisa Sánchez. Data collection and processing were done by Sánchez, as well as figures and tables.

Rod Chimner provided help with the experimental design, gas flux measurements training, and editing advice and assistance.

John Hribljan provided a great part of the gas sampling training, constructed the gas measurement chambers and was essential in troubleshooting while measuring in the mountains.

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ABSTRACT

Although knowledge of peatland CH₄ and CO₂ exchange in temperate mountain ecosystems is available, information about carbon (C) exchange in peatlands of the Andean mountains is limited and these ecosystems may behave differently given the particular characteristics of the Andean tropics. These ecosystems are highly productive and under pressure by grazing. Our first objective was to measure baseline carbon dioxide (CO₂) and methane (CH₄) flux in an undisturbed peatland in Cayambe-Coca National Park. Our second objective was to quantify CO₂ and CH₄ fluxes in an intensively cattle grazed peatland near Antisana Ecological Reserve. CO₂ and CH₄ effluxes were measured using a static chamber method. The mean NEE values for the undisturbed and disturbed site were -0.69 ± 0.08 and -1.25 ± 0.13 g CO₂ m⁻² hr⁻¹ respectively. A significant correlation between microtopography and CO₂ and CH₄ flux was found in the undisturbed site, with higher NEE, GPP, ER and CH₄ values in hummocks than in lawns. Microtopography doesn't seem to be a controller of CO₂ efflux in the grazed site, although the NEE and GPP rates are higher than those found in the undisturbed site, and show a linear relationship with vegetation cover. CH₄ emissions in the undisturbed site were low (8.1 ± 1.17 mgCH₄ m⁻² d⁻¹). However, CH₄ emissions at the grazed site were very high (132.25 ± 34.22 mg CH₄ m⁻² d⁻¹), which might be attributed to the high physical impact and inputs from cattle. In summary, it appears that cattle grazing may be capable of large changes to C exchange and greenhouse gas fluxes in Andean peatlands.

CHAPTER ONE¹

INTRODUCTION

Carbon (C) exchange in peatlands is being studied around the globe due to the importance that methane (CH₄) and carbon dioxide (CO₂) have in the global cycle and climate change (Frolking *et al.* 2006, Lahteenoja *et al.* 2009, Turetsky *et al.* 2014). Peatlands accumulate thick layers of partially decayed plant material (peat), which develops from the slow decomposition of the organic matter under saturated conditions (Gorham, 1991, Rydin & Jeglum, 2006). The C accumulation is due to an imbalance that favors C uptake over the loss of C (Strack *et al.* 2016). This accumulation in undisturbed peatlands occurs by the conversion of atmospheric CO₂ to peat while emitting CH₄ (Huth *et al.* 2012). Both are significant greenhouse gases, but methane has a higher global warming potential and radiative forcing (Solomon *et al.* 2007). As they may behave as sinks or sources of these gases, peatlands have important implications in the global greenhouse gas cycle (Gorham, 1991, Frolking *et al.* 2006).

Peatlands cover approximately only 3% of Earth's land surface but represent 30-40% of the global soil C (Gorham, 1991, Page *et al.* 2011). Although peatlands are most extensive in the boreal and temperate zones, they are also numerous in many tropical regions (Joosten, 2010). Total C stocks of tropical peatlands are estimated to be ~18 % of the global peat stock, with tropical South American peatlands roughly estimated to contain ~24 % of the total tropical peatland area (Page *et al.* 2011). However, recent

¹ The material contained in this chapter is in preparation for submission to the journal *Mires and Peat*.

mapping of peatlands in the South American lowlands shows that there is a considerable amount of C that hasn't been accounted for in regional and global C budgets (Draper *et al.* 2014). Although most attention has been focused on lowland peatlands, tropical peatlands are also very common in mountains, including the Andes (Bosman *et al.* 1993, Samaniego *et al.* 1998, Izurieta, 2005, Chimner & Karberg 2008, Cooper *et al.* 2010, Hribljan *et al.* 2016).

The tropical alpine zone of Venezuela, Colombia, Ecuador and Northern Perú (called páramo) is characterized by cold and wet conditions and high solar radiation; it occurs roughly between 3000 to 5000 meters above sea level (masl) (Balslev & Luteyn, 1992, Hofstede, 2003). Due to its tropical location, the páramo has low climate variability throughout the year (Mena & Hofstede, 2006), thus supporting both year-long plant production and saturation of peat soils. The interaction between climate, geographic location and topographic convergence in the Andes, contributes to the formation of very unique peatlands (Buytaert *et al.* 2005).

Andean peatlands, “turberas” or “bofedales”, are common throughout the South American tropics (Chimner & Karberg 2008, Cooper *et al.* 2010, Maldonado Fonkén, 2014). In the Ecuadorian páramo, these environments tend to be dominated by several species of cushion plants (e.g. *Plantago* spp., *Azorella* spp., *Distichia* spp.), grasses (e. g. *Calamagrostis* spp., *Cortaderia* spp.), sedges (e.g. *Carex* spp.), and a variety of mosses that form a heterogeneous ground layer vegetation matrix (Bosman *et al.* 1993, Hribljan *et al.* unpublished data). Peatlands in the Andes are not as extensive as those in the lowlands, hence Ecuadorian páramo peatlands are small but numerous (Hribljan *et al.* unpublished data). The peatlands in this ecozone range in age from 1000 to 8000 years,

but most initiated between 3000–5000 years ago (Samaniego *et al.* 1998, Earle *et al.* 2003, Chimner & Karberg 2008, Hribljan *et al.* 2014, 2016). Although relatively young, Andean peatlands have peat deposits that average ~5–6 m thick with long-term mean C accumulation rates (LARCA) ranging from 12 to 53 gC m⁻² yr⁻¹ (Chimner & Karberg 2008, Hribljan *et al.* 2014, 2016). These C accumulation rates are greater than northern peatlands, which have a mean LARCA of ~18 g m⁻² yr⁻¹ (Yu *et al.* 2010), and are comparable to Amazonian peat swamp forests with LARCA values that range between 39–85 g m⁻² yr⁻¹ (Lahteenoja *et al.* 2009).

Despite the large C deposits in Andean peatlands, data is sparse on their C cycling dynamics and environmental factors that control them. Studies of CO₂ efflux of mountain peatlands in the temperate regions show distinct seasonal patterns, with a broad photosynthesis range of values during the snow-free periods and a significant positive correlation of CO₂ emissions with soil temperature as well as a significant negative correlation of CO₂ emissions with water table (Wickland *et al.* 2001, Chimner & Cooper, 2003, Otieno *et al.* 2009). As CO₂ efflux data is lacking in the tropical Andean region we are uncertain of the values and the factors influencing them.

Studies of CH₄ efflux in peatlands provide contrasting results. A study of a fen dominated by aerenchymatous cushion plants in Patagonia found near zero emissions of CH₄ (Fritz *et al.* 2011), which contradicts prevailing studies that vascular plants with aerenchyma tissues typically have higher CH₄ emissions (Turetsky *et al.* 2014). Fritz *et al.* (2011) attributed this to high levels of soil oxygenation in the rooting zone by aerenchymal cushion plants. In support of this, they measured much greater CH₄ emissions from clipped cushion plant patches, concluding that the environment was

indeed suitable for CH₄ production. In contrast, Teh *et al.* (2014) found that upper montane grasslands in Perú were net CH₄ sources. Since CH₄ emissions in high altitude ecosystems have been rarely measured, it is difficult to generalize these patterns to all Andean peatlands.

Microtopography (e.g. hummocks, lawns and pools) is important in peatlands as these surfaces provide heterogeneity in microclimate and anerobic conditions, which can modify C cycling and species composition (Rydin & Jeglum, 2006). For instance, in temperate peatlands dominated by mosses, hummocks are often associated with higher aerobic CO₂ respiration, whereas lawns are more saturated and may have higher rates of CH₄ efflux (Bubier *et al.* 1992, Johnson *et al.* 2013). Microtopography effects over C exchange in Andean peatlands may be different as many are dominated by vascular cushion plants 15-30 cm above the watertable (Bosman *et al.* 1993).

Besides their ecological relevance, Andean peatlands are socio-economically important to local communities and cities, which benefit from their ecosystem services (Suárez, 2001, Izurieta, 2005). Páramo peatlands play an important role in watershed hydrology and are sources of water for large cities downslope (Buytaert *et al.* 2005). The use of these lands by local communities for agriculture and grazing is also very common (Izurieta, 2005, Young, 2009). However, since the introduction of hoofed grazing animals to the Andean páramo around 200 years ago and the growth of agricultural practices, the vegetation has suffered a significant decrease in coverage (Millones, 1982, Molinillo & Monasterio, 2002). Of the total land area of Ecuador, approximately 5% is páramo ecosystem (from 3500 to 5000 masl), 40% of these páramo ecosystems in Ecuador are protected in a national park or an ecological reserve and the remaining 60% has been

altered by human intervention or is currently being degraded (Beltrán *et al.* 2009). Grazing is a widespread practice in the Andes (Balslev & Luteyn, 1992, Hofstede, 1995), and one of the main reasons for degradation of peatlands in this region (Salvador *et al.* 2014). The constant presence of cattle as well as the increasing intensity could lead to a significant change in the characteristics of these ecosystems.

Cattle can affect peatlands by both grazing and trampling (Sjögersten *et al.* 2011). Trampling reduces the peat's bulk density causing peat subsidence (Rydin & Jeglum, 2006), and oxygenates the upper peat layer, leading to increased CO₂ emissions (Strack, 2008). Grazing and the addition of nutrients with faecal matter could cause a change of the vegetation cover towards a graminoid dominance (Falk *et al.* 2015), or the removal of photosynthetically active biomass (Falk *et al.* 2014). These changes in above ground biomass affect the system's net C exchange, in some cases potentially shifting it to a net source of CO₂ (Sjögersten *et al.* 2011, Falk *et al.* 2014), or lead to an increase in photosynthesis and net ecosystem uptake (Falk *et al.* 2015). The input of nutrient from faeces in peatlands in the Colombian Andes has also been linked to increased above ground biomass as well as higher decomposition rates (Urbina & Benavides, 2015). CH₄ emissions in peatlands that have been affected by grazing have contrasting results, with some studies relating them to higher emissions (e. g. Aerts & de Caluwe, 1999, Fritz *et al.* 2011, Boon *et al.* 2014), and others to lowered or no impact in emissions (e. g. Falk *et al.* 2015, Sjögersten *et al.* 2011).

Because of the lack of information on carbon cycling in tropical Andean peatlands, our first objective was to measure baseline fluxes in an undisturbed peatland. Since grazing is widespread in the tropical Andes, our second objective was to quantify

CO₂ and CH₄ fluxes in an intensively grazed site. We hypothesized that: 1. Microtopography affects the C efflux, and we expect i. a higher C uptake on hummocks than in lawns; and ii. a higher CH₄ emissions in lawns. 2. We believe that disturbance by intensive grazing will affect both the CO₂ and CH₄ flux, specifically we expect i. a reduction of the net ecosystem exchange and gross primary production with increasing disturbance; and ii. an increase in CH₄ efflux with higher disturbance.

METHODS

Study sites

The study was conducted in two peatlands in the Ecuadorian Andes (Figure 1, and Table 1). Our first site, Cayambe-Coca (CC), is located in the Cayambe-Coca National Park and our second site, Antisana (AN), is located in the Pullurima cattle farm that borders the Antisana Ecological Reserve to the west. The temperature in these sites varies greatly during the day (Table 1); as the Ecuadorian Andes are located in the tropical zones, there is minimal seasonality and precipitation is present almost every day of the year (Suárez, 2001).

CC is well-protected from human disturbance, including grazing. The basin-shaped peatland is adjacent to a small pond (Figure 2). Precipitation in this site is high due to an orographic effect, which helps in the formation of peatlands (Buytaert *et al.* 2006, Mitsch and Gosselink, 2015). This peatland is located in the Guamaní mountain range that divides the northeastern Ecuadorian highlands from the eastern cloud forest. Specifically, the site is located in the Potrerillos lava flow that is part of the Chacana Caldera (Hall and Mothes, 2008). Vegetation communities in CC are dominated by the cushion plant *Plantago rigida* (Plantaginaceae), and brown mosses interspersed with a

few dwarf shrubs, mostly *Disterigma empetrifolium* (Ericaceae). Although CC is well protected it is not considered as a control for the disturbed site because of many variables, the most notable being differences in geomorphology, altitude and local climatic conditions, that differ from the AN site.

The AN site has a higher degree of disturbance due to long history of cattle grazing (Whymper, 1880). Currently cattle are allowed free range throughout the greater AN region, and the peatland is particularly affected by trampling, peat compaction and fertilization with manure and urine. The sloping AN peatland is located adjacent to a stream in the foothills of the Antisana volcano (Figure 2), and the most denuded areas are those near the access to the watercourse. Vegetation at AN site is dominated by *Plantago rigida* and *Eleocharis albibracteata* (Cyperaceae). Plant cover at the sub-meter scale varies greatly within the site due to trampling by cattle, ranging from 0 to 100 %.

Experimental setup

Polyvinyl chloride (PVC) collars (diameter 40.6 cm, height 10 cm, and thickness of wall 0.5 cm) were placed in pairs in adjacent hummock and lawn areas. Collars were carefully inserted into the peat to a depth of 5 cm to create a solid seal between the peat and the collar, and left in place for the entire length of the study. In CC, a total of 8 collars (4 pairs) were laid along a transect that bisected the peatland (Figure 2a). In AN, a total of 16 collars (8 pairs) were laid along a grazing disturbance gradient: half of the collars were intentionally placed in areas that showed less disturbance and had 100 % vegetation cover. The other half were placed in more disturbed areas with vegetation cover varying from 0 to 95 % (Figure 2b).

A set of boardwalks were constructed at both sites to prevent disturbance on the peatland while sampling. Four PVC pipes of 10.2 cm diameter by 50 cm long were inserted in the peat for each pair of collars, and left throughout the length of the study as supports for the boardwalks.

Carbon dioxide flux measurements

CO₂ flux was measured with an EGM-4 Infrared Gas Analyzer (IRGA; PP Systems, Amesbury, USA) connected to a custom made clear acrylic chamber (diameter 40.6 cm, height 59 cm, volume 76,533 cm³; Hustchinson & Mosier, 1981). The IRGA has a closed path system with a constant flow rate of 200-400 cm³/min. The acrylic chamber was equipped with a detachable top, mixing fan, vent valve, and a photosynthetically active radiation (PAR) sensor. The IRGA was zeroed and calibrated *in situ* for every visit with a 400 ppm calibration CO₂ mixture (Mesa, California, USA). Due to the high altitude and low pressure, calibration of the IRGA was problematic, because on each visit the calibration with the 400 ppm standard occurred at different values. Our sites occur above 3900 masl and below 650 mbar, which is outside the bench tested range of the PP-Systems IRGA (850–1150 mbar, or around 1400–1200 masl; PP-Systems, personal communication, October 20th, 2014). To check IRGA stability at the higher altitudes, a curve of concentration vs altitude was created (Figure 3). Tests of the IRGA along an altitudinal gradient with a 400 ppm calibration standard from 3500-4100 masl, reported a CO₂ concentration that is offset from the standard gas and linearly increases as pressure decreases with altitude. Therefore, a range of CO₂ standards (300, 400, 500, and 600 ppm) were measured at the field sites, to prepare a curve for posterior slope correction. Standards were prepared using both 400 and 10000 ppm CO₂ calibration mixtures by

Mesa, a gas tight syringe (Super Syringe S-500, Hamilton, Reno, USA), and Tedlar bags (500 and 1000 ml Tedlar air sample bag, SKC, Pennsylvania, USA). Calibration curves were linear (mean R^2 of 0.96) and were not significantly different between dates, which showed a linear relation between CO₂ flux measurements and the actual values. From the mean slope of the curves (0.70 ± 0.08) a correction factor of 1.43 was created to be used for adjusting the CO₂ flux values.

To perform a CO₂ measurement, the acrylic chamber was placed on the collar and sealed with a wide rubber gasket placed over the chamber/collar seam. After letting the chamber equilibrate briefly, the lid was closed and sealed with a rubber gasket. The CO₂ flux measurements were taken over a 124 sec period (Ballantyne et al. 2014). Clear chamber measurements for net ecosystem exchange (NEE) were taken first, capturing photosynthesis and both plant and microbial respiration. At the end of the measurement, the chamber lid was opened briefly to re-equilibrate, closed and sealed again, then covered with a white opaque cloth to block sunlight and prevent photosynthesis, and ecosystem respiration (ER) was measured. Gross primary production (GPP) was determined by the difference between NEE and ER. In this study, positive values indicate a release of CO₂ from the ecosystem to the atmosphere, negative values represent an uptake of CO₂ by the ecosystem from the atmosphere. All measurements were randomized across collars and taken between 9:00 and 16:00. Data collection was performed in 11 campaigns for CC and 9 for AN, from July 2014 to February 2016 at intervals of approximately 1–2 months.

Methane flux measurements

CH₄ emissions were quantified by a static chamber technique (diameter 40.6 cm, height 31 cm, volume 40,212 cm³; Hustchinson & Mosier, 1981). A portable flame ionization detector (FID; INFICON-Photovac MicroFID II, USA) was used to determine CH₄ concentrations. Given that a minimum of 17 % oxygen is required to start the hydrogen flame (INFICON, 2012) and the percent oxygen in both study sites is around 13 %, samples were taken *in situ* and analyzed on the FID in the laboratory at a lower elevation. A gas syringe was used to extract 500 ml gas samples through a septum on the side of the chamber, and injected into Tedlar bags that were pre-flushed with nitrogen zero grade 99 % by Mesa. For each collar, a sample of ambient air was taken over the vegetation. The chamber (equipped with a vent tube) was then placed over the collar, tightly sealed with a wide rubber gasket placed over the chamber/collar seam, and a gas sample was taken from the chamber at 0, 15, 30 and 45 min for a total of five samples, including ambient, per collar. In the laboratory (~2400 masl) the FID was calibrated using a two span calibration (100 ppm CH₄ standard mixture from Mesa and a 10 ppm dilution). For CH₄ concentration measurement, gas bags were connected to the FID and a period of ~8 seconds was necessary for stabilization and reading. CH₄ flux was calculated using the PP-Systems CO₂ efflux equation adapted for CH₄ equation (1) (PP-Systems, personal communication, November, 2014). A headspace correction was calculated to account for chamber gas dilution when a gas sample was taken from the chamber. The difference between the CH₄ flux calculated with and without the headspace correction was less than 2.7%. Data collection was performed in 8 campaigns for CC and 6 for AN from November 2014 to February 2016 in intervals of approximately 1–2 months.

$$F_{CH_4} = \frac{\Delta C}{\Delta t} \times \frac{P}{1013} \times \frac{273}{273 + T} \times \frac{16.043 \text{ kg}}{22.414 \text{ m}^3} \times \frac{V_c}{A_c} \times \frac{\text{mol}}{10^6 \mu\text{mol}} \times \frac{86400 \text{ s}}{d} \times \frac{10^6 \text{ mg}}{\text{kg}} \quad (1)$$

where: F_{CH_4} is the CH_4 efflux ($\text{mg m}^{-2} \text{ d}^{-1}$), $\Delta C/\Delta t$ is the change in CH_4 with time ($\mu\text{mol mol}^{-1} \text{ s}^{-1}$), P is the barometric pressure (atm), T is the air temperature at soil surface ($^{\circ}\text{C}$), 16.043 g is the molecular weight of CH_4 , and a mol of gas occupies 22.414 L at standard temperature and pressure (STP) (values are transformed to kg and m^3 respectively), V_c is the chamber and collar volume (m^3) and A_c is the area of chamber (m^2). The CH_4 emissions are scaled to 24 hours of the day for ease of comparison with other studies.

Environmental parameters and vegetation cover

Ambient temperature, peat temperature (at 5 cm depth), and barometric pressure were recorded during each gas efflux measurement. An iButton (1-Wire Digital Thermometer DS18B20, Dallas Semiconductor, Maxim) was placed on each collar for continuous peat temperature logging every 4 hours. Peat temperature data are available from June 2014 to March 2015 for CC and from October 2014 to May 2015 for AN. The percent vegetation cover was determined for each collar by visually assessing the cover area of each species or genus.

Hydrology

Water table levels were measured at each site in a 1 m long x 6.3 cm diameter fine-mesh-covered PVC slotted pipe inserted into a pre-cored hole and flushed several times to clear well of sediment from installation. A PVC cap was installed on the wells to exclude infiltration from rain. A water level datalogger (Levellogger Model 3001, Solinst, Canada)

was placed inside each well. Additionally, a barometric pressure datalogger (Barologger Model 3001, Solinst, Canada) was placed in a smaller PVC pipe on a drier section of the peatland. Atmospheric pressure correction was made to the Levelogger values and a daily measurement of water table levels was obtained for each site. Manual well measurements were conducted through the sampling season to confirm Levelogger accuracy. A single pH measurement was made for each site in March 2015.

Statistical analyses

For the CO₂ analyses, a total of 84 measurements were included for CC and 124 for AN, taken on 11 and 9 dates, respectively (Appendix A1). For the CH₄ analyses, a total of 64 measurements were used for CC and 49 for AN, taken on 8 and 6 dates, respectively (Appendix A1). In AN the CH₄ measurements were only made consistently in lawns due to logistical issues. Some data were omitted from both sites due to missing values of either flux or environmental variables. The relation between peat temperature (measured with iButtons) and microtopography was analyzed with a paired t-test. At AN, the effects of the explanatory variables: vegetation cover and microtopography were analyzed on CO₂ flux; and the effects of vegetation cover on CH₄ flux. In CC the effects microtopography were analyzed on CH₄ and CO₂ flux. The Proc Mixed (SAS version 9.4) procedure was used to perform a repeated measures analysis with mixed effects. The analyses used the collar as a subject and the collar pairs as a block effect, and microtopography was used as a group effect. The normality of the dependent variables was tested before performing the analysis. Residuals were checked for homogeneity of variances. In the results, data are presented as mean \pm SE, and significance was determined at an alpha value of 0.05.

RESULTS

Environmental parameters and hydrology

Both sites were very wet, with frequent, almost daily, precipitation during the study period (Figure 4). Frequent precipitation led to stable water table levels at both sites until reduced precipitation associated with an El Niño event that started in October 2015 lowered water tables in January-February 2016. Prior to the El Niño event, water table levels in CC typically ranged from ~3 cm above to ~5 cm below the soil surface; while water table levels at AN were slightly lower, ranging from ~0 cm to ~20 cm below the soil surface (Figure 4 and Table 2).

Peat temperature (measured automatically with iButtons) at 10 cm depth ranged from 0.5 °C and 17.5 °C for CC and -3.5 °C and 41.5 °C for AN over the length of the study. The minimum and maximum peat temperatures typically occurred at ~02:00 and ~14:00, respectively, in both sites (Table 2). A paired t-test showed a significant difference between the daily mean peat temperatures of hummocks and lawns for CC, $t(278) = 27.83$, $p < 0.001$, and AN, $t(221) = 43.87$, $p < 0.001$, with higher temperatures on lawns.

Carbon dioxide and methane fluxes

In CC, CO₂ fluxes were significantly different between hummocks and lawns (Table 3, Figure 5). GPP was roughly five times greater on hummocks (-2.28 ± 0.13 g CO₂ m⁻² hr⁻¹) compared to lawns (-0.43 ± 0.06 g CO₂ m⁻² hr⁻¹), $F = 146.79$, $p < 0.0001$. ER was four times greater in hummocks (1.08 ± 0.07 g CO₂ m⁻² hr⁻¹) than lawns (0.24 ± 0.03 g CO₂ m⁻² hr⁻¹), $F = 314.87$, $p < 0.0001$. NEE was eight times higher on hummocks (-1.19 ± 0.12 g CO₂ m⁻² hr⁻¹) compared to lawns (-0.19 ± 0.04 g CO₂ m⁻² hr⁻¹), $F = 50.35$, p

< 0.0001 . CH_4 efflux was not significantly different between hummocks ($10.15 \pm 2.06 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) and lawns ($6.07 \pm 1.01 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$).

In contrast, at the disturbed site (AN) there was no significant effect of microtopography on any of the fluxes. There was, however, a significant effect of percent vegetation cover on NEE ($F = 15.37$, $p = 0.0005$), GPP ($F = 10.70$, $p = 0.0037$) and CH_4 ($F = 9.91$, $p = 0.01$). A linear relation for NEE, GPP and CH_4 flux vs. percent vegetation cover was found (Figure 6). When analyzed by cover classes rather than percent cover (100% vegetation cover vs. <100% vegetation cover). Average NEE and GPP values decreased by roughly 50% in the less vegetated areas, while there was a 50% increase in CH_4 emissions in the less vegetated areas (Figure 7), although these relations are not statistically significant in our model.

GPP was also influenced by PAR, but the effects of microtopography on PAR differed. In CC light response curves showed a high saturation point at around $2500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ with a marked difference between hummocks and lawns (Figure 8 and Table 4). Lawns in CC show a much lower initial slope and GPP at the saturation point than hummocks. In AN the light response curves (generated only using 100% vegetation cover) show no clear differences between hummocks and lawns, but the saturation point was similar to AN.

DISCUSSION

CO_2 fluxes

Despite the extremely high elevation of the páramo ($>4000 \text{ masl}$) and the cold and cloudy conditions, plant production appears to be high in these peatlands. Mean GPP for the undisturbed site, CC, was $-1.35 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$, and for the grazed site, AN, -2.87 g CO_2

$\text{m}^{-2} \text{ hr}^{-1}$. These GPP values are greater than those reported for temperate low altitude *Sphagnum* dominated peatlands of -0.71 and $-1.03 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (Carroll & Crill, 1997, Johnson *et al.* 2013, Ballantyne *et al.* 2014), but in the range of values reported for sedge dominated mountain ecosystems in temperate regions with GPP values ranging between -0.01 and $-6.32 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (Wickland *et al.* 2001, Otieno *et al.* 2009, Millar *et al.* 2016). The vegetation in these peatlands seems to be suited to the extreme high altitude conditions, allowing them to stay active throughout the year (Beck, 1994), thus showing high photosynthetic values.

The high GPP values are coupled with high daytime NEE. The mean NEE reported in this study for both sites (CC: -0.69 , AN: $-1.25 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$) are greater than those reported for *Sphagnum* dominated temperate peatlands which range between -0.005 and $-0.5 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (Carroll & Crill, 1997, Riutta *et al.* 2007, Johnson *et al.* 2013, Ballantyne *et al.* 2014). However, the NEE values reported in this study are in the range (-0.79 to $-1.58 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$) of those reported for mountain peatlands in Southern Germany.

Microtopography had a large influence on CO_2 fluxes at the undisturbed site (CC), with higher NEE, GPP and ER values on hummocks than lawns. This pattern has been observed in other studies in the northern regions (e.g., Strack *et al.* 2006, Sullivan *et al.* 2008). The increased value of NEE, GPP and ER in hummocks gives CC a heterogeneous CO_2 exchange pattern. When fully vegetated, NEE, GPP and ER mean values in AN showed no significant differences between hummocks and lawns, which could suggest that the influence of grazing might reduce the heterogeneity of CO_2 flux patterns in peatlands dominated by cushion plants.

The mean GPP and NEE values measured for fully vegetated collars are roughly two and a half times greater in our grazed site, AN, than in the undisturbed site, CC. The higher GPP and NEE could be due to higher PAR, lower elevation, and higher temperatures, but it might also be due to an increased abundance of vascular plants that occurs after grazing (Falk *et al.* 2015, Stark & Ylanne, 2015). Additionally, the higher plant productivity could be explained by fertilization by cow manure and urine. This observation is supported by a study conducted in cushion plant dominated peatlands in the Andes of Colombia, that found greater above ground biomass as well as greater decomposition rates in plots disturbed by trampling and manure addition (Urbina & Benavides, 2015). The constant fertilization could be adding nutrients that promote growth of the above ground biomass, which could be increasing GPP and ER (Boon *et al.* 2014). On the other hand, in the less vegetated areas of the grazed site the constant grazing and trampling is exposing the peat and reducing the photosynthetically active biomass. Other studies have shown a relation between NEE and plant biomass, reporting a decrease in NEE with grazing in arctic mires (Sjögersten *et al.* 2011, Falk *et al.* 2014). Our NEE values indicate that areas with less than 90% vegetation cover are likely a source of CO₂ once night-time respiration is accounted for.

CH₄ fluxes

Our measured CH₄ emissions in the undisturbed site (CC) were detectable but low, averaging 8.1 mg CH₄ m⁻² d⁻¹. In contrast, the CH₄ emissions in the grazed site, AN, were much greater, averaging 132.3 mg CH₄ m⁻² d⁻¹. In a global review, Turetsky *et al.* 2014 found that average CH₄ emissions ranged from ~50-200 mg CH₄ m⁻² d⁻¹ for pristine boreal and temperate peatlands and developed equations for calculating CH₄ emissions

based on mean annual temperature. Using the mean annual air temperature of both sites (5 °C) this equation estimated a mean flux of $\sim 45 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, which is several times greater than the values we measured for CC, the undisturbed site. However, these growing season rates differ from annual flux rates due to the seasonality differences between the tropics and temperate-boreal zones (Chimner, 2004). Most peatlands in temperate-boreal regions have significantly lower CH_4 emissions during winter (due to the inhibited microbial activity), and much higher growing season rates (Dise, 1992, Alm *et al.* 1999 and Huth *et al.* 2012). These findings would suggest that the annual CH_4 efflux throughout the year of the peatlands assessed in this study could be closer to the mean reported for the temperate and boreal zones. Although the annual CH_4 emissions reported for northern peatlands are highly variable, literature reports a mean between $\sim 4\text{--}15 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ (e.g., Alm *et al.* 1999, Roulet, 2007, Abdalla *et al.* 2016, Pypker *et al.* 2013). This puts the mean annual values measured in the undisturbed site, $3 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$, close to the low end of reported values for bogs and fens in the temperate and boreal zones.

Although CH_4 emissions in CC are low compared to northern peatlands in temperate and boreal zones, they are not zero. This is in contrast with findings by Fritz *et al.* (2011) who reported zero CH_4 emissions in a cushion plant dominated peatland in Patagonia, Argentina. This discrepancy could be explained by differences in altitude, latitude (Fritz *et al.* study was held at 40 masl in a temperate zone), and/or associated plant communities (Turetsky *et al.* 2014). To explore the influence of vegetation further, we can look at the effect of microtopography on CH_4 emissions in the undisturbed site. Microtopography seems to be an important control on CH_4 emissions in CC, with higher

CH₄ emissions for hummocks than those in lawns. Literature correlates CH₄ efflux with higher photosynthetic activity that leads to the supply of root exudates for CH₄ production and the subsequent emission through aerenchymatous tissues (Whiting *et al.* 1992, Lai *et al.* 2014). The cushion plants that dominate our study sites are vascular plants that may have aerenchymatous tissues, as described for other species in the genus *Plantago* (Striker *et al.* 2007). Although Fritz *et al.* attribute the absence of CH₄ emissions to oxygenation of the rooting zone of densely growing cushion plants, the plant communities in our study may have different characteristics, as it has been found that porosity values for roots with aerenchyma differ among plant species, even between genotypes (Colmer, 2003). The presence of these cushion plants in our site may be enhancing the CH₄ emissions out of the anaerobic rooting zone by the use of aerenchymatous tissues (Joabsson *et al.* 1999). The influence of vegetation on gas flux is also evidenced by the strong positive association of graminoids with CH₄ emissions (Turetsky *et al.* 2014). In the Andes this is consistent with a study by Teh *et al.* 2014 who reported a value of 15.6 mg CH₄ m⁻² d⁻¹ for montane grasslands in Perú. Those values are roughly double the emissions described for the undisturbed site in this study.

Our measured CH₄ emissions in the grazed site averaged 132 mg CH₄ m⁻² d⁻¹, with an annual emission of 48 g CH₄ m⁻² yr⁻¹. These values are 22 times higher than the undisturbed site, and in the high range of those reported for pristine peatlands in the northern regions (Nykanen *et al.* 1995, Turestky *et al.* 2014). Because most grazed peatlands are drained, studies have often found lower values of CH₄ emissions in grazed peatlands due to the absence of saturated conditions (e.g. Nykanen *et al.* 1995, Turestky *et al.* 2014). However, exclosures of muskox grazing in an undrained high arctic mire in

Greenland found that there was a 44% decrease in CH₄ emissions for excluded areas compared to control (Falk *et al.* 2015). The browsing patterns of muskox and the differences in location might not be comparable with our study. However, the undrained, often saturated conditions of AN make a perfect environment for the production of CH₄ (Rydin & Jeglum, 2006). In addition, the presence of cattle in AN could be increasing CH₄ flux emissions due to the constant input of cattle urine and manure. Nutrient additions increase CH₄ emissions as it has been shown that ammonium (NH₄⁺) may inhibit an enzyme in CH₄ oxidizing bacteria and boost CH₄ production (Dobbie & Smith, 1996, Boon *et al.* 2014, Aerts & de Caluwe, 1999). Furthermore, microbial data collected at the AN site was found to have a high relative abundance of methanogens compared to other sites in the Andean mountains, and higher methanogen to methanotroph ratio, especially in surface horizons (Lilleskov E.A., personal communication, September 19th 2016). These findings confirm the unexpectedly high CH₄ emissions of the site and suggest that the methanogen activity that usually thrives in deeper anaerobic zones has moved to surface layers. Additionally, as with CO₂ flux values, CH₄ values reported in Figures 9 and 10 suggest that reduction of vegetation cover by grazing and trampling may be increasing CH₄ emissions by approximately 50%. This hypothesis is supported by Fritz *et al.*(2011), who found that the emissions from the clipped cushion plants were higher than those reported for the intact cushion.

CONCLUSIONS

These data are the first to report CO₂ and CH₄ emissions in high altitude peatlands in the Ecuadorian Andes, and one of only a handful of studies for the Andean region. This study

provides a baseline knowledge of C fluxes in an understudied ecosystem at the same time that it opens new questions for research.

The two peatlands differ in CO₂ and CH₄ exchange patterns, and even though this difference might be due to the variation of altitude and consequent change in climatic conditions, the presence of cattle could also be a leading contributor. Microtopography and vegetation cover are two factors that influence CO₂ and CH₄ emissions in these peatlands. The presence of hummocks and lawns gives the peatlands a heterogeneous C exchange. The effects of anthropogenic disturbance in these peatlands might be causing a change in their unique exchange patterns. The intensity of cattle activity and its effect on vegetation cover influences the NEE, GPP and CH₄ values. CH₄ fluxes in the grazed site are much higher than those reported at the undisturbed site; the presence of cattle and the constant anaerobic conditions in the grazed site could be increasing the CH₄ fluxes. The presence of cattle could have profound consequences not only for the physical characteristics of the peatland but also for their biogeochemistry. Given that the undisturbed site shows less CO₂ storage over the gradient of disturbance intensity and higher CH₄ emissions, intensive grazing practices are likely to reduce or reverse greenhouse gas benefits from mountain peatlands. The importance of that effect depends on the intensity and extent of grazing impacts in these ecosystems.

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FIGURES

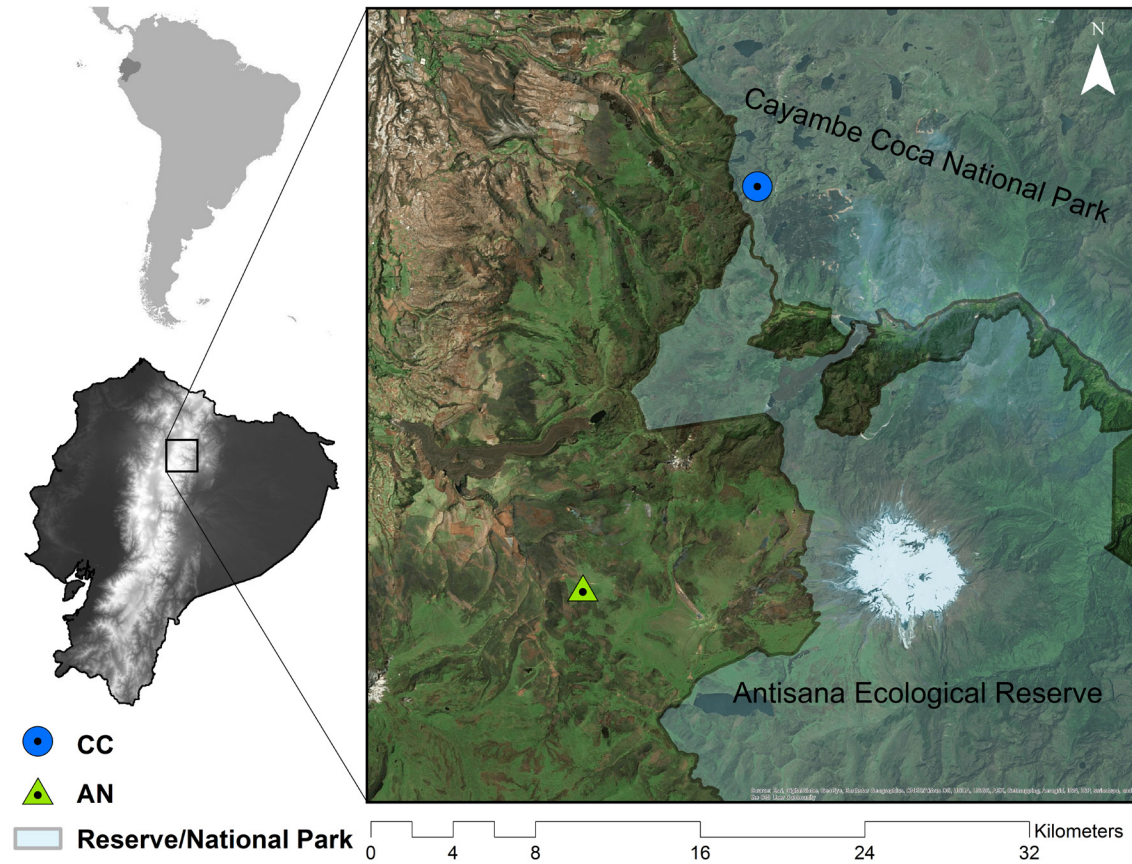


Figure 1. Map of sites in Cayambe Coca National Park (CC) and Antisana Ecological Reserve (AN) located in the Andean mountain region, East of Quito, Ecuador. Satellite image includes intellectual property of Esri and its licensors and are used herein under license. Copyright © [World Imagery, August 2016] Esri and its licensors. All rights reserved. Ecuador and South America maps: Diva-GIS, GADM Database of Global Administrative Areas, November, 2015. See Appendix A.2 for documentation on terms of use.

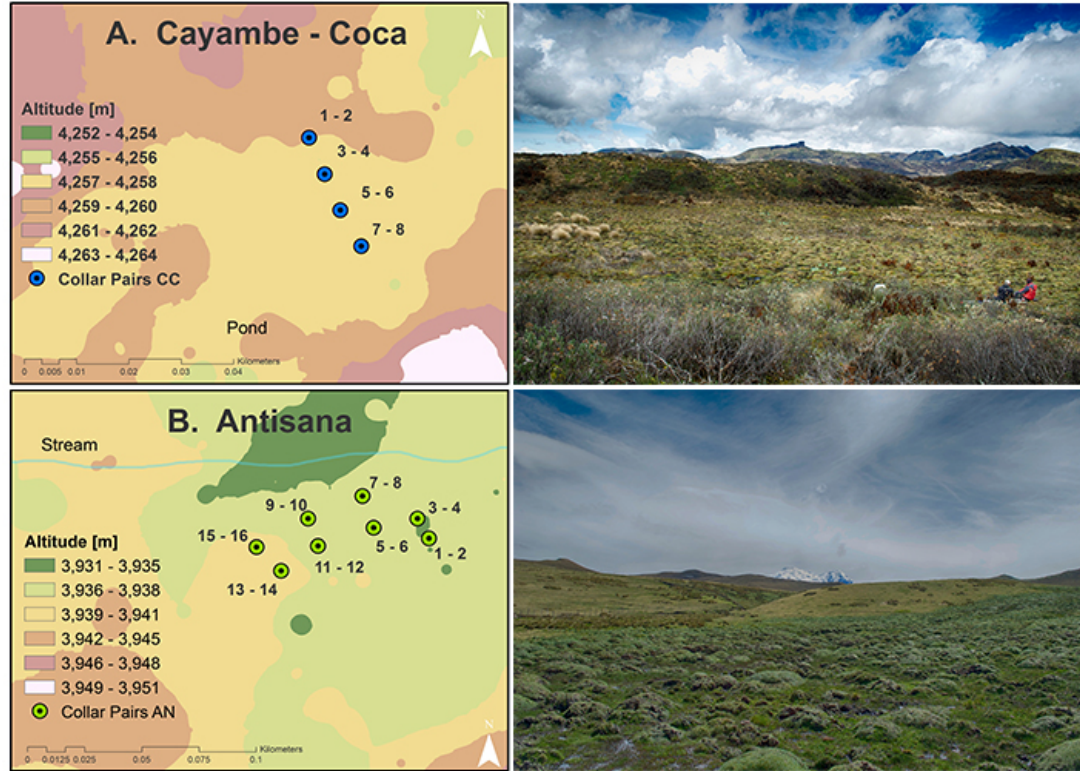


Figure 2. Study sites' topography (A. Cayambe Coca: CC, and B. Antisana: AN), circles represent each collar pair. Pictures of each site with vegetation dominated by cushion plants on the right. AN shows evidence of cattle disturbance.

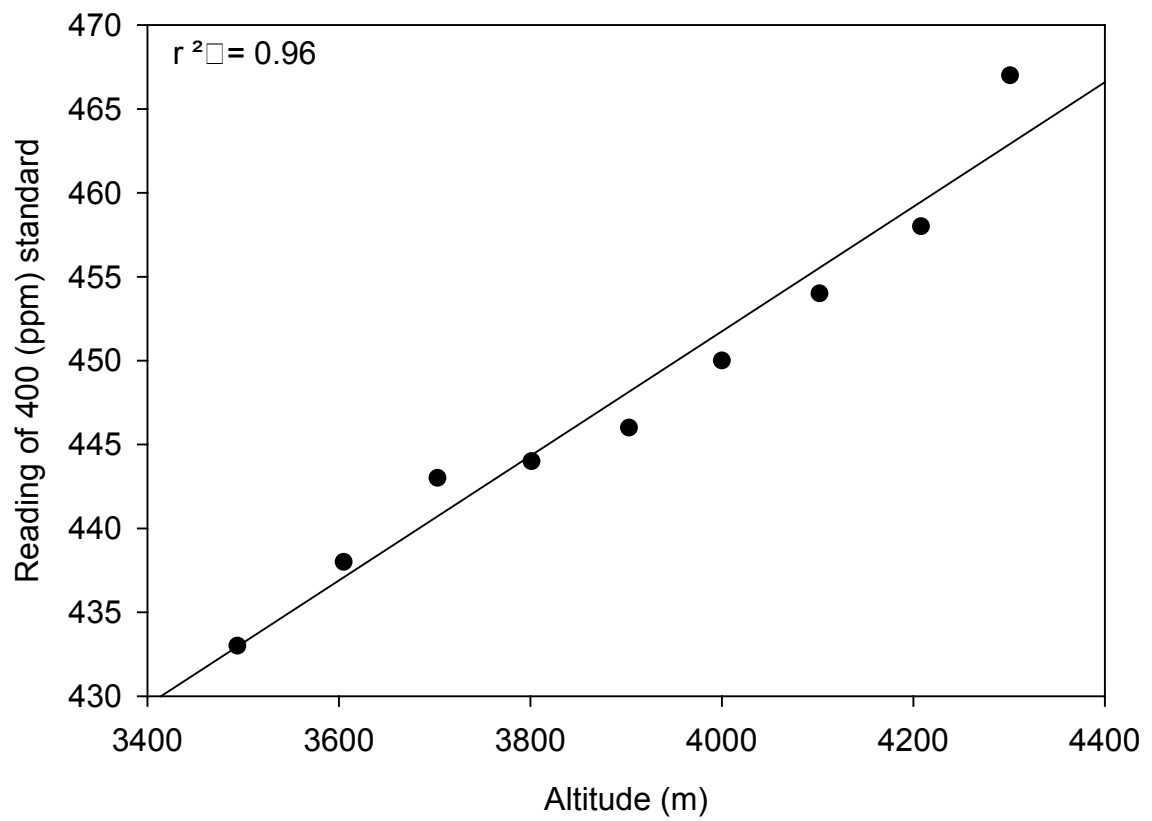


Figure 3. EGM-4 reading of a 400 ppm standard vs altitude (m)

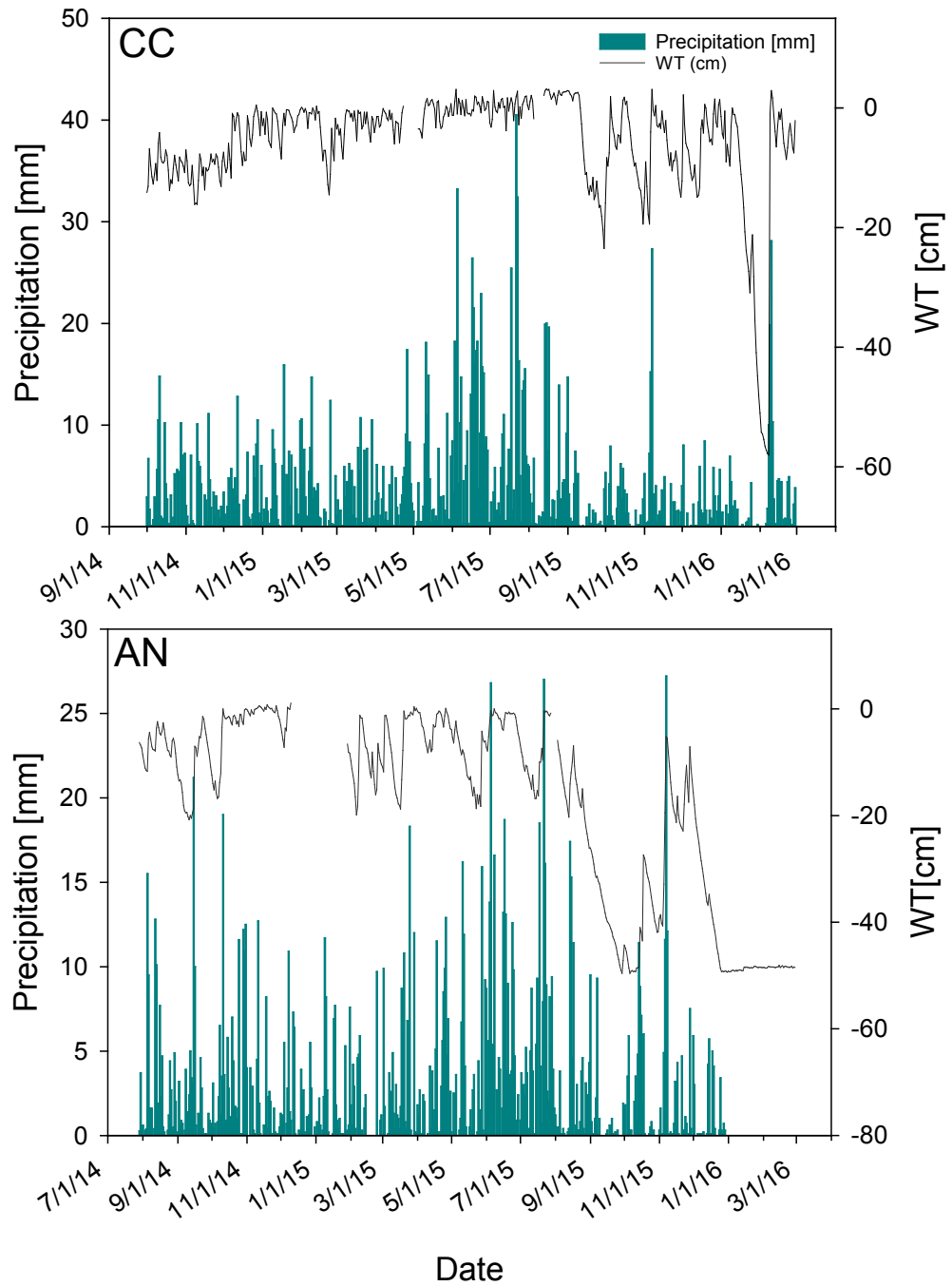


Figure 4. Water table levels for each study site measured with a Solinst logger. Precipitation data for CC is from “Virgen Papallacta” station from FONAG, at 3920 masl and 4 km away from the study site. Precipitation data for AN is from “Mica Presa” station from EPMAPS at 3957 masl and 6.5 km away from the study site. Negative values of WT are below the surface. No precipitation data were available for the year 2016 in AN.

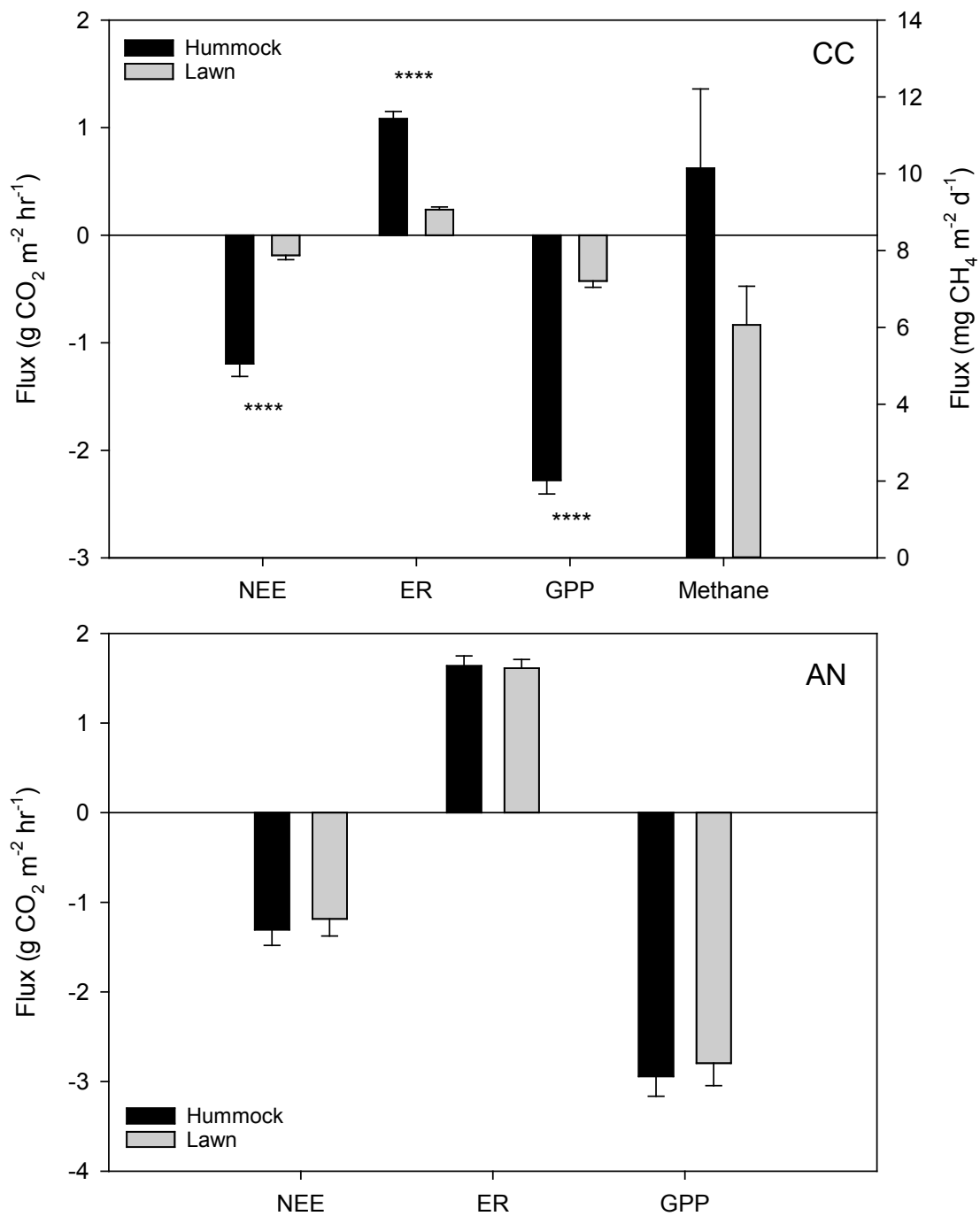


Figure 5. Mean NEE, ER, GPP and methane flux by microtopography (hummock and lawn). Cayambe Coca (CC) top and Antisana (AN) bottom for all plots. Error bars indicate one standard error. Asterisk indicates significant differences between microtopography. For CO₂, negative values represent uptake by the ecosystem. For CH₄, positive values represent loss from the ecosystem. No information for CH₄ in hummocks at AN.

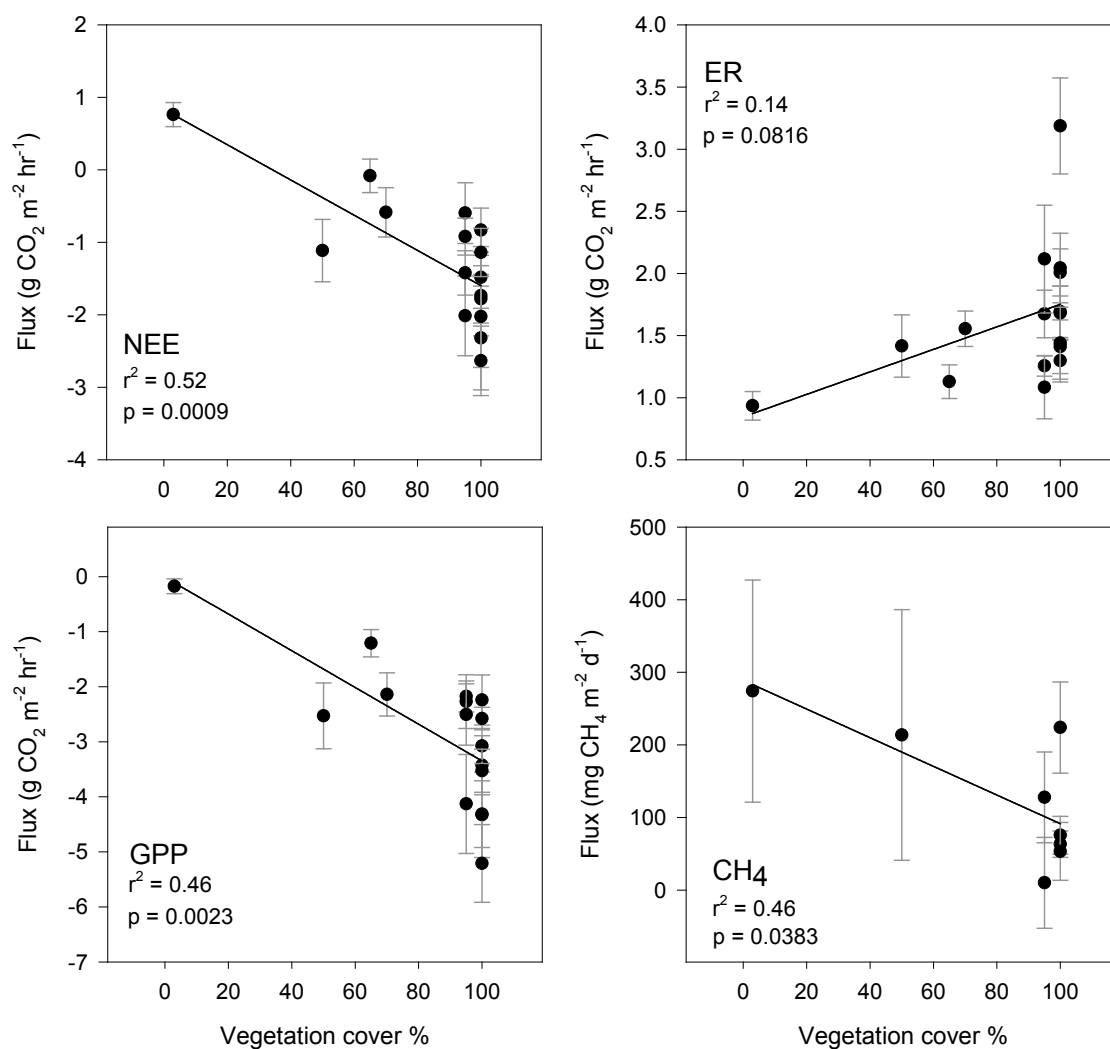


Figure 6. Mean NEE, ER, GPP ($\text{g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$), and methane ($\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) flux by percent vegetation cover in Antisana (AN). Error bars indicate one standard error. For CO_2 , negative values represent uptake by the ecosystem. For CH_4 , positive values represent loss from the ecosystem. AN values for CH_4 are only for lawns. Linear fit for all graphs. Normality assumption not met for ER.

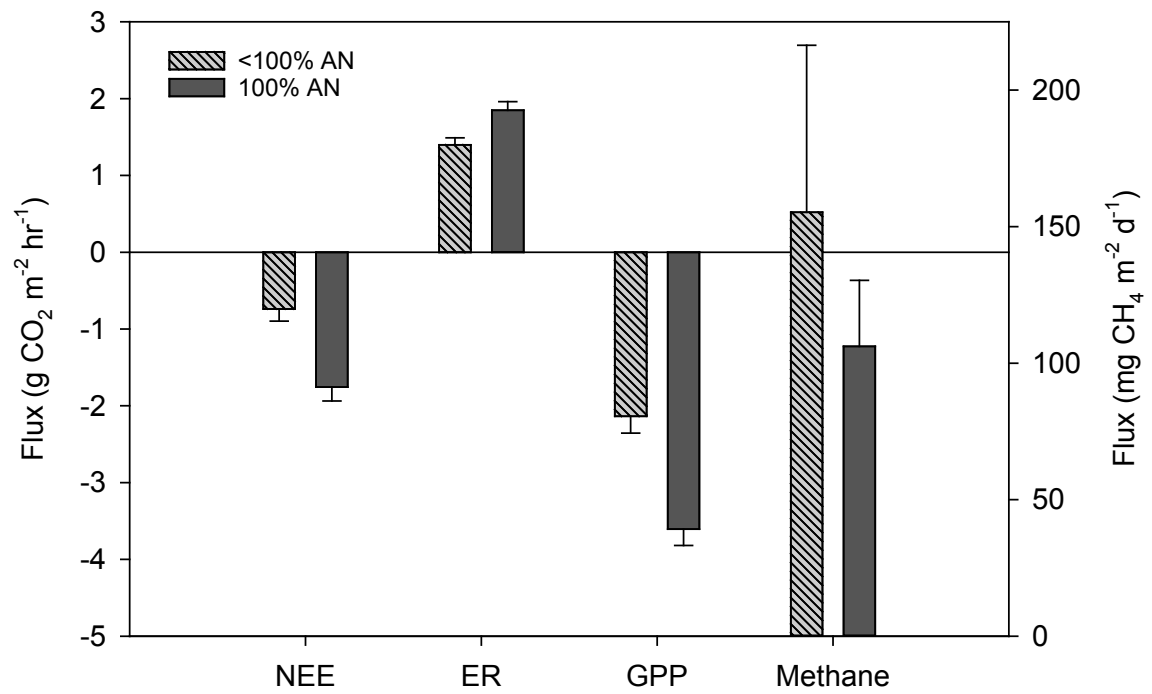


Figure 7. Mean NEE, ER, GPP, and methane flux by the degree of disturbance (<100 and 100% plant cover) in Antisana (AN) site. Error bars indicate one standard error.

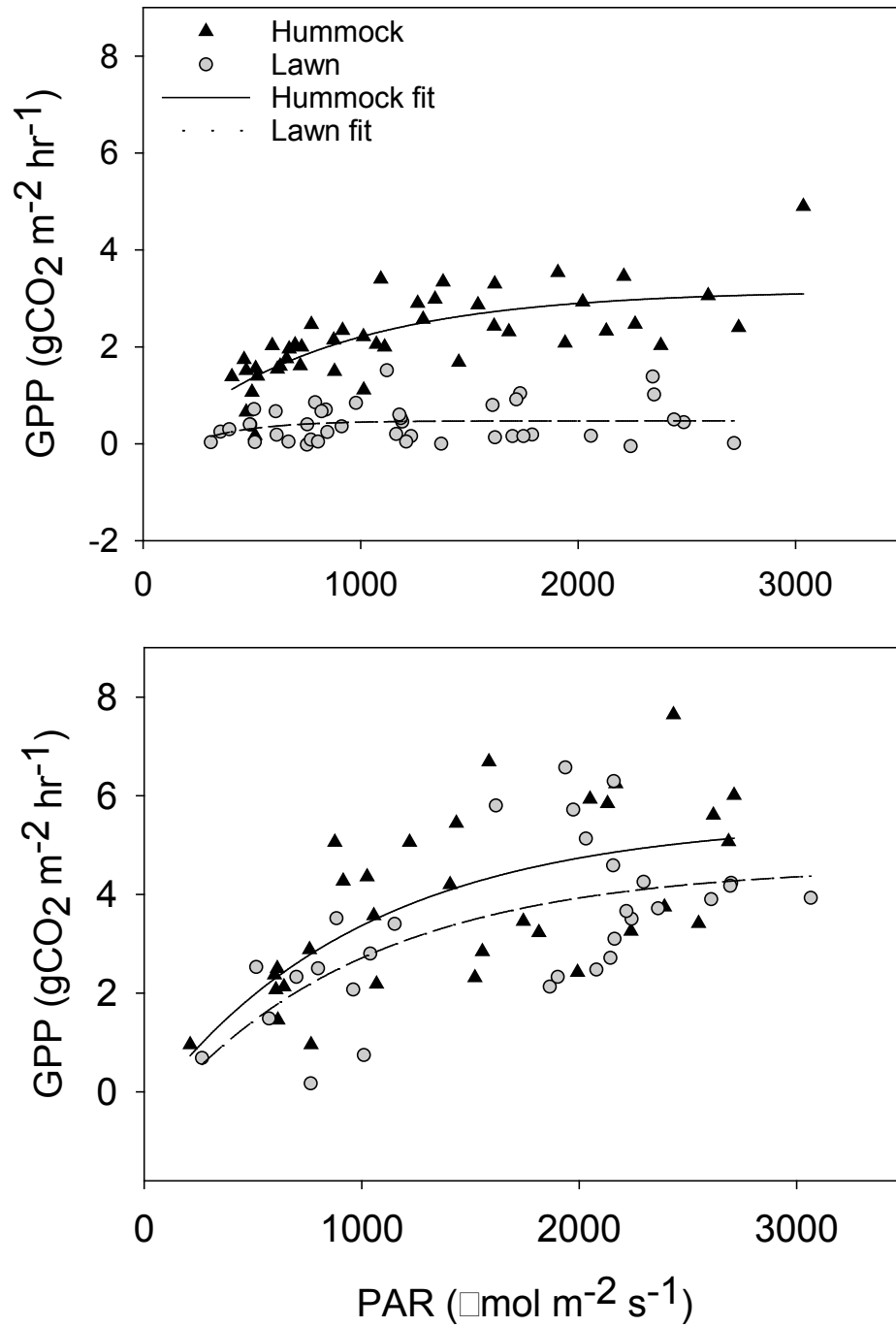


Figure 8. Light response curves, GPP ($\text{gCO}_2 \text{ m}^{-2} \text{ hr}^{-1}$) vs. mean PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) by microtopography (hummock and lawn). We used the inverse sign for GPP in these light response curves. Cayambe Coca (CC) top and Antisana (AN) bottom. Only 100% vegetated collars considered for AN. Equation fit exponential rise to the maximum, single, 3 parameter: $f=y_0+a(1-\exp(-bx))$

TABLES

Table 1. Descriptions of peatlands sampled at Cayambe Coca National Park (CC) and Antisana Ecological Reserve (AN). Precipitation and ambient temperature values are presented as mean (minimum, maximum)

Parameter	CC	AN
Altitude (masl)	4258	3940
Coordinates (Lon , Lat)	-78.199753 , -0.319114	-78.276429 , -0.494660
Mean annual precipitation (mm yr ⁻¹)	1375 (635 , 2667) ^a	828 (558 , 1168) ^b
Mean daily ambient temperature (°C)	5.2 (0.94 , 9.98) ^a	5.7 (0.4 , 7.7) ^c
pH	5.38	5.2
Age of peatland (yr) ^d	8036	5313
Mean peatland soil depth (m)	3.9 ^d	4.5 ^e
Carbon storage (Mg ha ⁻¹) ^d	1037	1046

^a between the years 2009- 2015 at “Virgen Papallacta” station, 3920 masl and 4 km away from the study site (FONAG, *Personal communication, July 2016*)

^b between the years 1987-2015 at “Mica Presa” station, 3957 masl and 6.5 km away from the study site (EPMAPS, *Personal communication, July 2016*)

^c between the years 2000-2010 at “Mica Presa” station (EPMAPS, *Personal communication, July 2016*)

^d (Hribljan *et al.* 2016)

^e (Comas *et al.* In preparation)

Table 2. Mean daily water table and peat temperature measurements in Cayambe Coca National Park (CC) and Antisana Ecological Reserve (AN). Values are presented as mean (minimum, maximum)

Parameter	CC	AN
Water table (cm)	-5.8 ± 0.41 (-58.0 , 3.2)	-24.2 ± 0.76 (-50.0 , -1.1)
Peat temperature (°C)	6.5 ± 0.04 (2.4 , 11.9)	8.75 ± 0.04 (4.3 , 16.5)

Table 3. Summary of Cayambe-Coca CC and Antisana AN sites C flux data. NEE, ER, and GPP are expressed in $\text{gCO}_2 \text{ m}^{-2} \text{ hr}^{-1}$, and positive values represent release by the ecosystem to the atmosphere. CH_4 is expressed in $\text{mgCH}_4 \text{ m}^{-2} \text{ d}^{-1}$, and positive values represent loss from the ecosystem. Mean, minimum and maximum are measured across all collars and all dates. SE represents one standard error.

	CC				AN			
	NEE	ER	GPP	CH ₄	NEE	ER	GPP	CH ₄ *
Mean	-0.69	0.66	-1.35	8.10	-1.25	1.62	-2.87	132.25
Maximum	0.37	2.04	0.02	-6.79	1.41	4.96	0.24	-322.75
Minimum	-3.39	0.00	-4.90	38.15	-4.81	0.19	-8.16	1136.89
SE	0.08	0.06	0.12	1.17	0.13	0.07	0.17	34.22

* lawns only

Table 4. Light response curve equation coefficients and adjusted R^2 for CC and AN by microtopography (hummock and lawn). Equation: $f=y_0+a(1-\exp(-bx))$. All models significant ($p = < 0.001$), except for lawns in CC.

CC					AN			
Hummock			Lawn		Hummock		Lawn	
Adj	0.4962		-0.0084		0.3863		0.3606	
R²								
	Coefficient	P	Coefficient	P	Coefficient	P	Coefficient	P
y0	-0.2695	0.7971	-0.5436	0.8212	-0.4081	0.8367	-0.7327	0.7366
a	3.4347	0.0001	1.0172	0.6668	5.9232	0.0003	5.3219	0.0023
b	0.0013	0.0578	0.0037	0.5236	0.0010	0.1634	0.0010	0.2274

APPENDIX

A.1

Table A1. Dates of measurements performed on each site. X denotes if measurements of either CO₂ or CH₄ were taken.

Cayambe Coca CC			Antisana AN		
Date	CO ₂	CH ₄	Date	CO ₂	CH ₄
10/1/2014	x		7/29/2014	x	
10/8/2014	x		11/14/2014	x	
10/27/2014	x		12/5/2014		x
11/17/2014	x		12/10/2014	x	
11/26/2014		x	1/29/2015	x	x
12/8/2014	x	x	3/31/2015	x	x
12/15/2014	x	x	4/30/2015	x	x
1/26/2015	x	x	7/9/2015	x	x
3/16/2015	x	x	11/27/2015	x	x
5/19/2015	x	x	2/5/2016	x	
11/13/2015	x				
11/25/2015	x	x			
2/2/2016		x			

A.2

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GADM - DIVA-GIS

GADM database of Global Administrative Areas

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The current version is 2.8 (November 2015).

The current version of GADM delimits 294,430 administrative areas.

The data are available as shapefile, ESRI geodatabase, RData, and Google Earth kmz format. Shapefiles can be used for most mapping and "GIS" software. You can download a free program such as Q-GIS or DIVA-GIS. The RData files can be used in R with the 'sp' package loaded.

You can download the data by country or for the whole whole world.

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