# Carbon dioxide and methane fluxes in grazed and undisturbed mountain peatlands in the Ecuadorian Andes

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## SUMMARY

Peatlands are widespread throughout the tropical Andean páramo. Despite the large carbon stocks in these ecosystems, carbon dioxide ($CO_2$) and methane ($CH_4$) flux data are lacking. In addition, cattle grazing is widespread in the páramo and could alter gas fluxes. Therefore, our objectives were to measure $CO_2$ and $CH_4$ fluxes with the static chamber technique in an undisturbed and in an intensively cattle grazed peatland in the mountains of Ecuador. We found that hummocks in the undisturbed site had higher net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (ER), and $CH_4$ fluxes, compared to lawns. In contrast, microtopography at the grazed site did not predict $CO_2$ fluxes, whereas vegetation cover was correlated for all three metrics (NEE, ER, and GPP). At low vegetation cover, NEE was positive (losing carbon). $CH_4$ emissions in the undisturbed site were low (8.1 mg $CH_4$ m$^{-2}$ d$^{-1}$). In contrast, $CH_4$ emissions at the grazed site were much greater (132.3 mg $CH_4$ m$^{-2}$ d$^{-1}$). This is probably attributable to trampling and nutrient inputs from cattle. In summary, the two peatlands differed greatly in $CO_2$ and $CH_4$ exchange rates, which could be due to the variation in climate and hydrology, or alternatively to intensive grazing by cattle.

**KEY WORDS:** cattle, grazing, greenhouse gas flux, páramo, peat

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## INTRODUCTION

Peatlands accumulate thick layers of partially decayed organic matter (peat) that develops by the accumulation of plant material in saturated anoxic soils (Gorham 1991, Rydin & Jeglum 2006). The long-term apparent rate of carbon accumulation (LARCA) of these systems results from an imbalanced carbon (C) cycle favouring C uptake over C loss (Clymo 1984). However, the anoxic conditions in peatlands commonly stimulate production of methane ($CH_4$), a potent greenhouse gas that has a higher global warming potential and radiative forcing than carbon dioxide ($CO_2$) (Myhre et al. 2013).

Peatlands cover only approximately 3 % of the Earth's land surface, but represent 30–40 % of the global soil C pool (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 ~18 % of the global peat stock, with tropical South American peatlands estimated to contain ~ 24 % of the total tropical peatland area (Page et al. 2011). However, recent mapping of peatlands in the South American lowlands provides evidence that there is a considerable amount of C

unaccounted for in regional and global C inventories (Draper et al. 2014). Until recently, C accounting initiatives have focused on lowland peatlands, overlooking the large pools of C in tropical Andean mountain peatlands (Samaniego et al. 1998, Chimner & Karberg 2008, Cooper et al. 2010, Hribljan et al. 2015, Hribljan et al. 2017).

The tropical alpine zone of Venezuela, Colombia, Ecuador, and Northern Perú, ~ 3000–5000 m above sea level (masl) (called the páramo), is cold and wet with high solar radiation (Balslev & Luteyn 1992, Hofstede 2003). Due to its tropical location, the páramo has low seasonal climate variability (Mena & Hofstede 2006), resulting in both year-long plant production and perennially saturated soils. The interaction between climate, geographical location and topographical convergence in the Andes contributes to the formation of numerous peatlands (Buytaert et al. 2005).

Andean peatlands, locally referred to as "turberas" or "bofedales", are common throughout the South American tropics (Chimner & Karberg 2008, Cooper et al. 2010, Maldonado Fonkén 2014, Hribljan et al. 2015, Hribljan et al. 2017). In the Ecuadorian páramo, these peatlands 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 vegetation cover (Bosman *et al.* 1993, Hribljan *et al.* 2017). Peatlands in the Ecuadorian páramo are small but numerous, representing approximately 22 % of the páramo in north-central Ecuador (Hribljan *et al.* 2017). They range in age from 10000 to 100 years, with most initiated between 5000 and 3000 years ago (Samaniego *et al.* 1998, Chimner & Karberg 2008, Hribljan *et al.* 2015, Hribljan *et al.* 2016). Although relatively young, Ecuadorian peatlands have thick peat deposits (regional mean ~ 5–6 m) with mean LARCA values in the range 12–53 g m$^{-2}$ yr$^{-1}$ (Chimner & Karberg 2008, Hribljan *et al.* 2015, Hribljan *et al.* 2016). These C accumulation rates are generally greater than in northern high-latitude peatlands, which have mean LARCA values of ~18 g m$^{-2}$ yr$^{-1}$ (Yu *et al.* 2010), but are comparable to those of Amazonian lowland peat swamp forests whose LARCA value range is 39–85 g m$^{-2}$ yr$^{-1}$ (Lahteenoja *et al.* 2009).

Despite the large C deposits in Andean peatlands, data on the dynamics and environmental factors that control C cycling here are sparse. Studies of the CO$_2$ fluxes of mountain peatlands in temperate regions show distinct seasonal patterns, with a broad range of photosynthetic values during snow-free periods and a significant positive correlation of CO$_2$ emissions with soil temperature, as well as a significant negative correlation of CO$_2$ emissions with water table level (Wickland *et al.* 2001, Chimner & Cooper 2003, Otieno *et al.* 2009). Because CO$_2$ flux data are lacking in the tropical Andean region there is a large knowledge gap on C cycling dynamics and the environmental factors that influence these fluxes.

Studies of CH$_4$ efflux in Andean peatlands provide contrasting results. A study of a cool temperate peatland dominated by aerenchymatous cushion plants in Patagonia found near-zero emissions of CH$_4$ (Fritz *et al.* 2011), which deviates from the finding that aerenchymatous vascular plants are typically associated with higher CH$_4$ emissions (Turetsky *et al.* 2014). Fritz *et al.* (2011) attributed the low CH$_4$ emissions to high levels of soil oxygenation in the rooting zone of aerenchymatous cushion plants supporting aerobic methanotrophs. In support of this, they measured greater CH$_4$ emissions from clipped cushion plant patches, concluding that the cushions suppressed CH$_4$ emissions. At the only tropical Andean site, Teh *et al.* (2014) found that upper montane grasslands in Perú are net CH$_4$ sources. Since CH$_4$ emissions in high-altitude ecosystems have rarely been measured, it is difficult to generalise these patterns to all Andean peatlands.

Microtopography (e.g. hummocks, lawns, and pools) is important in peatlands, providing heterogeneity in microclimate and anoxic conditions, which can in turn modify C cycling and vegetation composition (Rydin & Jeglum 2006). For example, hummocks in temperate *Sphagnum* peatlands are often associated with higher CO$_2$ fluxes, whereas lawns are wetter and typically have greater rates of CH$_4$ emissions (Bubier *et al.* 1992, Johnson *et al.* 2013). Microtopography effects on C exchange in Andean peatlands may be different as many of them are dominated by cushion plants 15–30 cm above the water table (Bosman *et al.* 1993), which could provide direct vascular pathways for trace gas movement. However, we are unaware of any tests of this hypothesis.

In addition to their ecological relevance, Andean peatlands are socio-economically important to local communities and cities, which benefit from their many ecosystem services including hydrological regulation (Suárez 2001, Izurieta 2005, Buytaert *et al.* 2005) and grazing (Izurieta 2005, Young 2009). Since the introduction of hoofed grazing animals to the Andean páramo ~ 200 years ago and the growth of agricultural practices, the vegetation has suffered a significant change in composition and fragmentation (Millones 1982, Molinillo & Monasterio 2002). Of the total land area of páramo in Ecuador (approximately 5 % of the national territory), 40 % is protected in national parks or ecological reserves, and the remaining 60 % has been altered by human intervention or is currently being utilised (Beltrán *et al.* 2009). Grazing is widespread 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 widespread use of cattle, as well as the increasing intensity of grazing, could significantly change the ecological functions of these systems.

Cattle can affect peatlands by trampling, grazing, and altering nutrient cycling (Sjögersten *et al.* 2011). Trampling can cause peat subsidence and changes to bulk density (Rydin & Jeglum 2006). Moreover, trampling can reduce the amount of photosynthetically active biomass by damaging or killing plants, leading to lower plant production (Falk *et al.* 2014, Chimner *et al.* 2016). Furthermore, the addition of nutrients from faecal matter and urine can shift vegetation cover towards a graminoid dominated system, enhance photosynthesis and net ecosystem C uptake (Falk *et al.* 2015), increase above-ground biomass, and accelerate organic matter decomposition (Urbina & Benavides 2015). Changes in the biomass, productivity, and structure of peatland vegetation, with shifts in soil decomposition, can affect net gaseous C exchange

and in some cases transform the peatland to a net source of $CO_2$ (Sjögersten *et al.* 2011, Falk *et al.* 2014).

The effects of grazing on $CH_4$ emissions in peatlands vary, with some studies linking grazing to higher emissions (e.g. Aerts & de Caluwe 1999, Fritz *et al.* 2011, Boon *et al.* 2014) and others to lowered or unimpacted emissions (e.g. Sjögersten *et al.* 2011, Falk *et al.* 2015). Higher emissions have been attributed to nutrient inputs (Aerts & de Caluwe 1999, Boon *et al.* 2014) and physical changes (e.g. vegetation removal) (Fritz *et al.* 2011). In addition, reduced net ecosystem exchange (NEE) and gross primary production (GPP) could lead to lower $CH_4$ emissions by reducing substrate availability for $CH_4$ production (Falk *et al.* 2015).

Because of the lack of information on C cycling in tropical Andean peatlands, and the vegetative differences between these peatlands and temperate/boreal peatlands (especially the replacement of *Sphagnum* hummocks with cushion hummocks), our objectives were to measure fluxes of $CO_2$ and $CH_4$ in an undisturbed peatland and an intensively grazed site. We hypothesised 1) that microtopography would affect fluxes, leading to greater $CO_2$ uptake on hummocks and greater $CH_4$ emissions in lawns; and 2) that disturbance by intensive grazing would cause a reduction of NEE and GPP, and an increase in $CH_4$ emissions.

## METHODS

### Study sites

The study was conducted in two peatlands in the Ecuadorian Andes (Figure 1). Cayambe Coca (CC) is situated in the Cayambe Coca National Park and Antisana (AN) is located on a cattle farm that borders
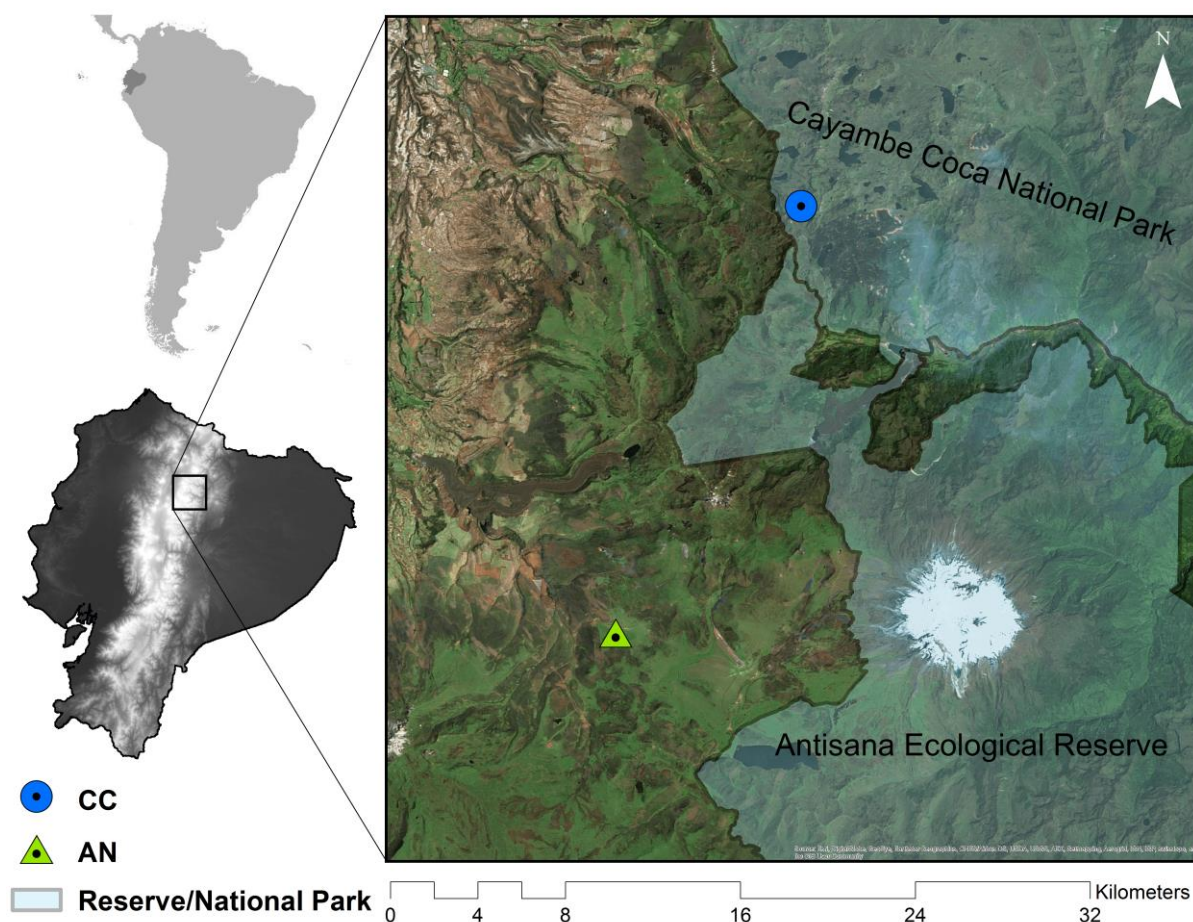


Figure 1. Map of sites in Cayambe Coca National Park (CC) and Antisana Ecological Reserve (AN) located in the Andean mountain region to the east of Quito, Ecuador. Satellite image includes intellectual property of ESRI and its licensors and are used herein under licence. Copyright © [World Imagery, August 2016] ESRI and its licensors. All rights reserved. Ecuador and South America maps: Diva-GIS, GADM Database of Global Administrative Areas, November 2015.

the Antisana Ecological Reserve. The air temperature at these sites varies greatly during the day, due to the high altitudes, but there is minimal seasonality and precipitation occurs almost daily (Suárez 2001).

The CC site (0º 19' 09″ S, 78º 11' 59″ W) is located in the Potrerillos lava flow, which is part of the Chacana Caldera (Hall & Mothes 2008). This level, basin-shaped peatland in a very small catchment is adjacent to a small pond (Figure 2A) with no evidence of human activity or livestock use. Annual precipitation is high due to orographic effects. The site is dominated by the hummock-forming cushion plant *Plantago rigida* (Plantaginaceae), and the lawns are covered by brown mosses interspersed with a few dwarf shrubs, mostly *Disterigma empetrifolium* (Ericaceae). The peat deposit at CC is 3.9 m deep, composed of dense sapric peat with inter-bedding of volcanic ash, and has a basal age of 8036 years (Site C2 in Hribljan *et al*. 2016).

The sloping AN site (0º 29' 41″ S, 78º 16' 35″ W) is adjacent to a stream in the foothills of the Antisana volcano (Figure 2) and is dominated by *P. rigida* and

*Eleocharis albibracteata* (Cyperaceae). In contrast to CC, this site has a long history of cattle grazing (Whymper 1880). Currently, cattle are allowed to range across the greater Antisana region, and this peatland is widely affected. Plant cover varies greatly at the micro-scale due to trampling by cattle, and ranges from 0 to 100 % (Figure 2 B1). The peat deposit is 2.9 m deep, composed of dense sapric peat with ash and other mineral layers interbedded, and has a basal age of 5313 years (Site A3 in Hribljan *et al*. 2016).

Although CC is well protected from disturbance, we do not regard it as a control for the highly impacted AN site because of the differences in geomorphology, altitude and local climatic conditions between the two sites.

**Experimental setup**

Polyvinyl chloride (PVC) collars (diameter 40.6 cm, height 10 cm, wall thickness 0.5 cm) were placed in pairs in adjacent hummocks and lawns. The hummocks consisted mostly of *P. rigida* cushions
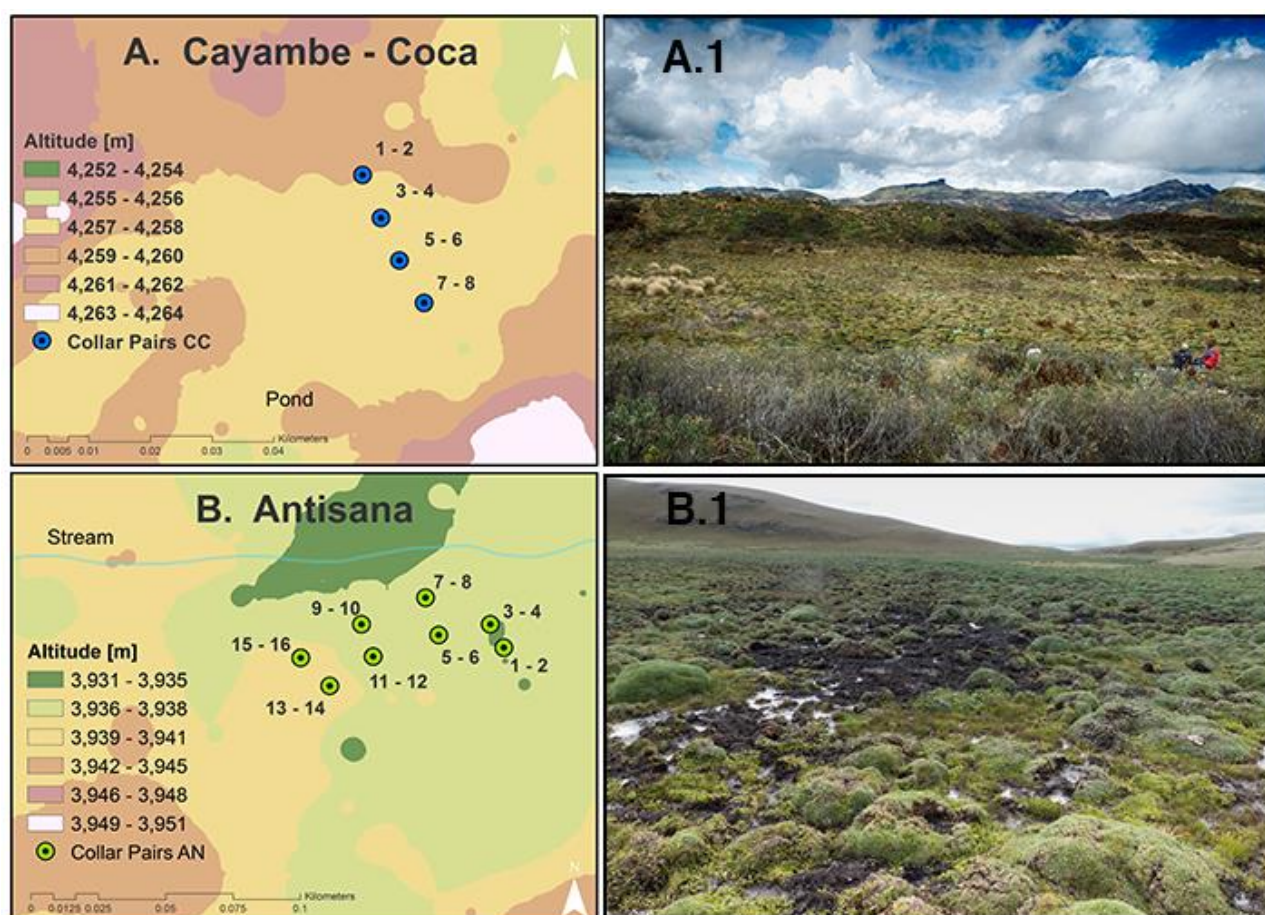


Figure 2. Left: topography of the study sites, Cayambe Coca (A) and Antisana (B). Each circle represents a collar pair. Right: photographs of the study sites Cayambe Coca (A.1) and Antisana (B.1) with vegetation dominated by cushion plants. There is evidence of cattle disturbance at Antisana.

and the lawns consisted mainly of a mix of *E. albibracteata* and *D. empetrifolium*. Each pair of collars was separated from other pairs by approximately 3 m, and the distance between the collars of each pair was approximately 1 m. 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 were left in place for the entire study. At CC, eight collars (four pairs) were laid along a transect that bisected the peatland (Figure 2A). At AN, 16 collars (eight 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, and the other half were placed in more disturbed areas with vegetation cover that varied from 0 to 95 % (Figure 2B). Movable boardwalks were constructed at both sites to prevent disturbance of the peatland while measuring CO₂ and CH₄ fluxes. To create supports for the boardwalks, four PVC pipes (10.2 cm diameter × 50 cm long) were installed in the soil adjacent to each pair of collars, and left in place throughout the study.

## CO₂ flux measurements

An EGM-4 Infrared Gas Analyzer (IRGA; EGM-4; PP Systems, Amesbury, USA) connected to a custom-made clear acrylic chamber (diameter 40.6 cm, height 59 cm, volume 76533 cm³; Hutchinson & Mosier 1981) was used to measure CO₂ fluxes. The chamber was equipped with a detachable top, mixing fan, vent valve, and a photosynthetically active radiation (PAR) sensor. The IRGA had a closed path system with a constant pump flow rate of approximately 350 cm³ min⁻¹. The IRGA was zeroed through a soda lime scrubber and calibrated *in situ* every sampling campaign with a 400 ppm calibration CO₂ standard (Mesa, USA). Calibration of the IRGA was problematic because the sites were above 3,900 masl with atmospheric pressure 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 confirm IRGA stability at these altitudes, a curve of volumetric concentration (ppm) *versus* altitude was fitted. Tests of the IRGA along an altitudinal gradient from 3500–4100 masl with a 400 ppm calibration standard revealed a measured CO₂ concentration that was offset from the real standard gas concentration and linearly increased as pressure decreased with altitude. Therefore, CO₂ standards (300, 400, 500, and 600 ppm) were measured at the field sites to prepare a curve for posterior (subsequent) slope

correction. Standards were prepared using 400 and 10000 ppm CO₂ calibration standards (Mesa, USA), 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 $R^2 = 0.96$) and did not differ significantly between dates. From the mean slope of the curves ($0.70 \pm 0.08$), a correction factor of 1.43 was created for adjusting the IRGA CO₂ measurements.

To perform a CO₂ measurement, the acrylic cylinder was placed on the collar and the chamber/collar seam was sealed with a rubber gasket. After the chamber had equilibrated briefly, the acrylic lid was closed and also sealed with a rubber gasket. To measure NEE, clear chamber measurements were taken first under a range of light conditions, capturing the net effect of photosynthetic CO₂ fixation plus plant and microbial respiration. Next, ecosystem respiration (ER) was measured as follows: the chamber lid was opened briefly to re-equilibrate the chamber with ambient conditions, then closed, sealed, and covered with a white opaque cloth to block sunlight and prevent photosynthesis. Measured PAR was always equal to zero under the cloth. The CO₂ flux into the chamber ($\Delta C/\Delta t$; µmol mol⁻¹ s⁻¹) was calculated from the slope of a quadratic fit of the CO₂ concentration (ppm) curve over a sampling period of 124 seconds with CO₂ concentration recorded every 4.8 seconds. To convert the flux from volumetric to mass basis we used the following equation:

$$F_{CO_2} = \frac{3600\Delta C}{10^6 \Delta t} \times \frac{P}{1013} \times \frac{273.15}{(273.15+T)}$$

$$\times \frac{44.009}{22.414} \times \frac{V_c}{A_c} \times 10^3 \quad [1]$$

where: $F_{CO2}$ is the mass flux in g CO₂ m⁻² h⁻¹, $\Delta C$ is the change in CO₂ concentration in µmol mol⁻¹, $\Delta t$ is time in s, 3600 is a conversion factor from s to h, $10^{-6}$ is the conversion factor from µmol to mol, $P$ is ambient pressure in mbar, $T$ is ambient temperature in °C, 44.009 is the molar mass of CO₂ in g mol⁻¹, 22.414 is the molar volume of an ideal gas at STP in L mol⁻¹, $V_c$ is the chamber plus collar volume in m³, $A_c$ is the cross-sectional area of the collar in m², and $10^3$ is the conversion factor from L to m³. GPP was calculated as the difference between NEE and ER. In this study, we use the flux sign convention where positive values indicate a release of CO₂ from the ecosystem to the atmosphere, and negative values represent an uptake of CO₂ by the ecosystem from the atmosphere. Chamber measurements were taken on

dry days only, between 09:00 and 16:00 hrs, and the measurement order was randomised across collars. Data collection was performed in eleven campaigns for CC and nine for AN, at intervals of approximately 1–2 months from July 2014 to February 2016.

**Methane flux measurements**

Methane fluxes were measured using the static chamber technique (diameter 40.6 cm, height 31 cm, volume 40133 cm$^3$; Hutchinson & Mosier 1981). The custom-made chamber was opaque, and equipped with a vent tube for pressure equilibration together with a fan. A portable flame ionisation detector (FID; INFICON-Photovac MicroFID II, New York, USA) was used to determine CH$_4$ concentrations. We have used this unit directly plumbed to our chamber at lower altitudes, but this was not possible here because a minimum of 17 % effective oxygen is required to start the hydrogen flame (INFICON 2012) and the effective percent oxygen at both study sites was around 13 %. Therefore, gas samples from the chambers were analysed the same day on the FID at a lower altitude (~ 2,400 masl) in a laboratory at the Universidad San Francisco de Quito. For each collar, a sample of ambient air was taken from above the vegetation using a gas-tight syringe. Next, the chamber was placed over the collar, tightly sealed with a rubber gasket placed over the chamber/collar seam, and the syringe was used to extract 500 ml of headspace gas through a septum on the side of the chamber and then injected into a Tedlar gas bag that was pre-flushed with nitrogen (zero grade 99 %; Mesa, USA). An air sample was taken from the chamber immediately after it was closed (i.e. at 0 min), then at 15, 30, and 45 min. In the laboratory, the FID was calibrated using a two span calibration (zero air, 10 ppm and 100 ppm CH$_4$; Mesa, USA). The CH$_4$ concentration in each of the Tedlar bags was measured by connecting the bag to the FID and measuring until readings stabilised (~ eight seconds). CH$_4$ volumetric fluxes ($\Delta C/\Delta t$; μmol mol$^{-1}$ s$^{-1}$) were calculated as the slope of the linear relationship of CH$_4$ concentration (ppm) over the 45 min sampling period and converted to a mass basis using the molar mass of CH$_4$ (16.043 g mol$^{-1}$) in Equation 1. A headspace correction was calculated to adjust CH$_4$ volumetric fluxes to account for chamber gas dilution when a gas sample was taken from the chamber, assuming the removed 500 ml of headspace gas was replaced *via* the vent tube with ambient air at the CH$_4$ concentration measured at the beginning of the measurement period (LI-COR Doc # 979-08937). The CH$_4$ emissions were scaled to mg m$^{-2}$ d$^{-1}$. The difference between the CH$_4$ flux calculated with and without the headspace correction was less than 2.7 %.

We did not consider or apply any corrections for ebullition events. Data collection was performed in eight campaigns for CC and six for AN, on dry days at intervals of approximately 1–2 months from November 2014 to February 2016.

**Environmental factors and vegetation cover**

Ambient air temperature, peat temperature at 5 cm depth, and barometric pressure were recorded during each gas flux measurement. In addition, a three sensor logging thermometer (1-Wire Digital Thermometer DS18B20, Dallas Semiconductor, Maxim Integrated, San Jose, USA) was inserted into the peatland to record peat temperature at three different depths (0, -5, and -10 cm) every four hours within each collar. Peat temperature data were recorded from June 2014 to March 2015 for CC and from October 2014 to May 2015 for AN. Reported peat temperature data are averages of temperatures at the three depths. Due to equipment malfunction and unforeseen loss of some data, the data presented for peat temperature at AN are for hummocks only. Vegetation cover was estimated visually for each collar, as the percent cover of each species or genus.

Precipitation data for CC were obtained from the Fondo de Agua para Quito (FONAG) Virgen Papallacta station, which is located approximately 4 km from the study site (3920 masl). Precipitation data for AN came from the Mica Presa station of Empresa Pública Metropolitana de Agua Potable y Saneamiento (EPMAPS) approximately 6.5 km from the study site (3957 masl).

Water table levels (cm) were measured at each site in a 1 m long × 6.3 cm diameter PVC slotted pipe covered with a fine nylon mesh, inserted into a pre-cored hole, flushed several times to clear the well of sediment from installation, and capped. A water level datalogger (Levelogger Model 3001, Solinst, Canada) was placed inside each well. In addition, a barometric pressure datalogger (Barologger Model 3001, Solinst, Canada) was placed in a PVC pipe on a drier section of the peatland. Atmospheric pressure correction was made to the Levelogger values and daily measurements of water table level were obtained for each site. Manual well measurements were also conducted over the course of the sampling season to confirm the accuracy of the Levelogger. Each manual well measurement was conducted by dipping a ruler inside the well, aligning the 0 cm mark with the peatland surface and measuring the distance to the water level. If the water table was above the peatland surface a positive value was registered, and if it was below the surface a negative value was recorded. A single pH measurement was made for each site in March 2015.

**Statistical analyses**

For $CO_2$ fluxes, 84 measurements were included for CC and 124 for AN, taken on eleven and nine dates, respectively. For $CH_4$ fluxes, 64 measurements were used for CC and 49 for AN, taken on eight and six dates, respectively. At AN, the $CH_4$ measurements were taken consistently only in lawns due to logistical constraints. A few data points were omitted for both sites due to equipment problems (for $CO_2$ fluxes, data from five collars and one date were omitted at CC, and data from 20 collars and five dates were omitted at AN; for $CH_4$, data from seven collars and two dates were omitted). The potential effect of microtopography (hummocks *versus* lawns) on peat temperature was analysed with a paired t-test. Proc Mixed software (SAS version 9.4, Cary, NC, USA) was used to perform a repeated measures analysis with mixed effects, collars as subjects, the collar pairs as a block effect, and microtopography as a group effect. $CH_4$ and $CO_2$ were the dependent variables with GPP, NEE and ER analysed separately for $CO_2$. For AN, the effects of the explanatory variables (vegetation cover and microtopography) on $CO_2$ fluxes, and the effects of vegetation cover on $CH_4$ fluxes, were analysed. For CC, the effects of microtopography on $CH_4$ and $CO_2$ fluxes were analysed. Residuals were checked for normality and that homogeneity of variance assumptions were met. Data were prepared for presentation as arithmetic means $\pm$ SE, and significance was determined at an alpha value of 0.05. At both sites PAR was regressed against GPP to assess the possible impact of cloud cover on our results. The data were fitted with an exponential rise to the maximum, single, three parameter model in SigmaPlot 12.5 (Systat Software Inc., San Jose, USA). The equations were then used to calculate the PAR value for 95 % saturation of GPP.

**RESULTS**

**Environmental factors and hydrology**

During the study period, both sites were very wet with frequent, almost daily precipitation that led to relatively stable water tables until an El Niño event started in October 2015. This reduced precipitation leading to lowered water tables in January–February 2016 (Figure 3). Prior to the El Niño event, water table levels typically ranged from around 3 cm above to 5 cm below the soil surface at CC and from around 0 cm to 20 cm below the soil surface at AN (Figure 3 and Table 1). Peat temperature ranged from 0.5 to 17.5 °C at CC and from -3.5 to 41.5 °C at AN

(Table 1). The daily minimum and maximum peat temperatures typically occurred at approximately 02:00 and 14:00 hrs, respectively. For CC, a paired t-test showed a significant difference between the daily mean peat temperatures of hummocks (M = 6.3 °C, $s^2$ = 1.9) and lawns (M = 6.8 °C, $s^2$ = 1.5), (t(278) = 27.8; $p < 0.001$), with higher temperatures in lawns. For AN, a paired t-test showed a significant difference between the daily mean peat temperatures of hummocks with 100 % cover (M = 8.7 °C, $s^2$ = 0.7) and less than 100 % cover (M = 8.4 °C, $s^2$ = 0.5), (t(221) = 11; $p < 0.001$), with higher temperatures in 100 % cover collars.

**Carbon dioxide and methane fluxes**

Mean GPP for the undisturbed site (CC) was -1.35 g $CO_2$ m⁻² hr⁻¹, and for the grazed site (AN) -2.87 g $CO_2$ m⁻² hr⁻¹ (Table 2). Mean NEE was -0.69 g $CO_2$ m⁻² hr⁻¹ at the undisturbed site and -1.25 g $CO_2$ m⁻² hr⁻¹ at the grazed site, and mean ER was 0.66 and 1.62 g $CO_2$ m⁻² hr⁻¹ for the undisturbed and grazed sites, respectively.

The $CO_2$ fluxes at CC were significantly different between hummocks and lawns (Figure 4). GPP was approximately five times greater on hummocks (-2.28 $\pm$ 0.13 g $CO_2$ m⁻² hr⁻¹) compared to lawns (-0.43 $\pm$ 0.06 g $CO_2$ m⁻² hr⁻¹; $p = < 0.0001$). ER was four times greater on hummocks (1.08 $\pm$ 0.07 g $CO_2$ m⁻² hr⁻¹) than on lawns (0.24 $\pm$ 0.03 g $CO_2$ m⁻² hr⁻¹; $p = < 0.0001$). NEE was six times higher on hummocks (-1.19 $\pm$ 0.12 g $CO_2$ m⁻² hr⁻¹) compared to lawns (-0.19 $\pm$ 0.04 g $CO_2$ m⁻² hr⁻¹; $p = 0.0009$). $CH_4$ efflux was not significantly different between hummocks (10.15 $\pm$ 2.06 mg $CH_4$ m⁻² d⁻¹) and lawns (6.07 $\pm$ 1.01 mg $CH_4$ m⁻² d⁻¹; $p = 0.3207$). In contrast, at the grazed site (AN) there was no significant effect of microtopography on any of the fluxes. There was, however, a linear relationship for NEE, GPP and $CH_4$ flux *versus* percent vegetation cover (Figure 5).

Gas emissions were modified by temperature, with GPP, ER, and NEE all generally increasing with increasing temperature (Figure 6). There was no discernable pattern with $CH_4$ and temperature. GPP was also influenced by PAR, but the effects of microtopography on light response curves differed between sites. In CC the light response curve showed a marked difference between hummocks and lawns (Figure 7 and Table 3). The lawns in CC showed a non-significant equation, whereas the hummocks showed a significant response function with a 95 % saturation point at around 2500 µmol m⁻² s⁻¹. In AN, the light response curves (generated using collars with 100 % vegetation cover only) showed no clear differences between hummocks and lawns, but the 95 % saturation point was around 3000 µmol m⁻² s⁻¹.
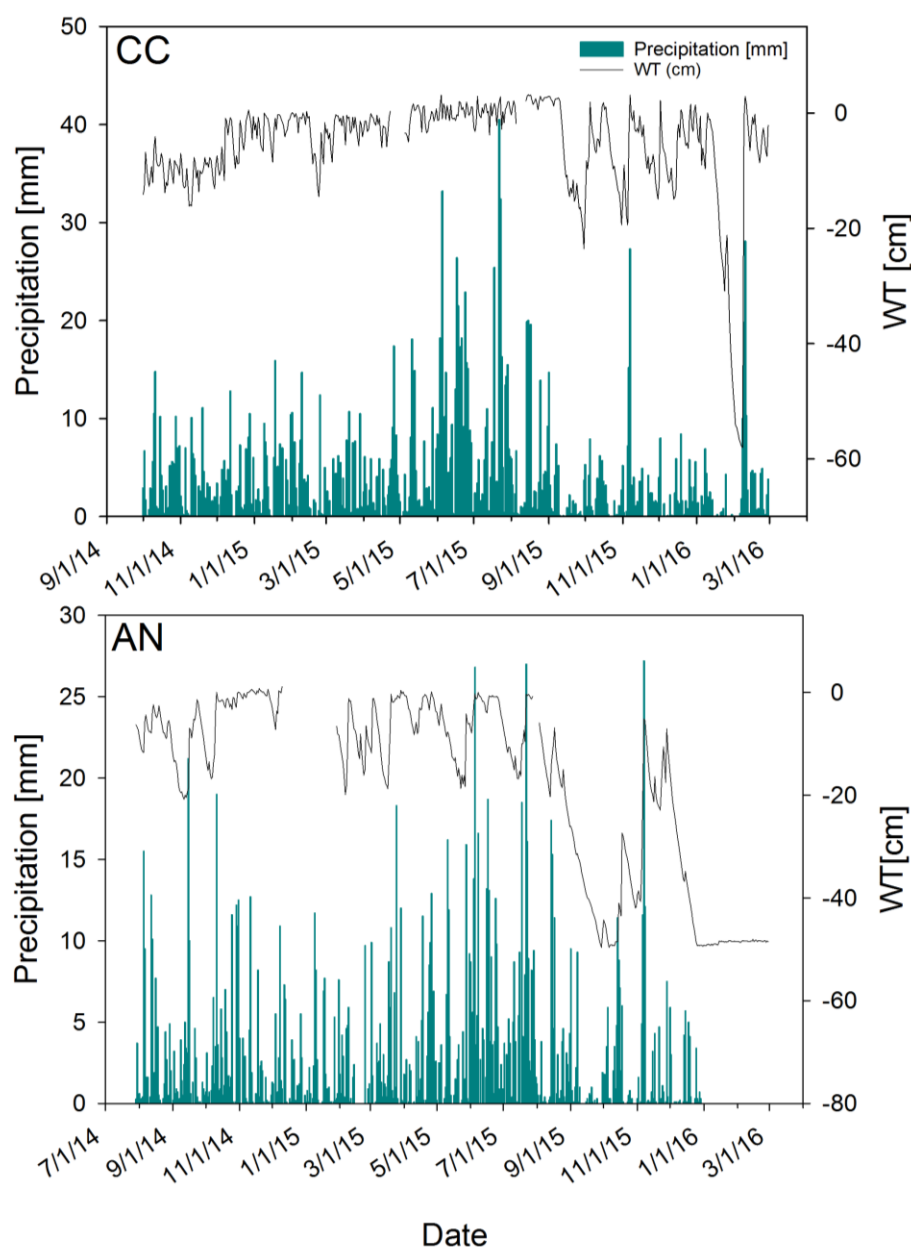
Figure 3. Water table levels (cm) for Cayambe Coca (CC) and Antisana (AN). Negative values indicate water level below the peatland surface. No precipitation data were available for AN in 2016, but the steady line for water table level suggests a long period of reduced precipitation.

## DISCUSSION

### CO$_2$ fluxes

Despite the high altitude (> 3200 masl) and the cold and cloudy conditions of the páramo, plant production appeared to be high in these peatlands. Our results for mean GPP in both the undisturbed and the grazed site were greater than those reported for *Sphagnum* dominated low-altitude temperate peatlands (-0.71 and -1.03 g CO$_2$ m$^{-2}$ hr$^{-1}$; Carroll & Crill 1997, Johnson *et al*. 2013, Ballantyne *et al*.

2014), but within the range of values reported for sedge-dominated mountain ecosystems in temperate regions (-0.01 and -6.32 g CO$_2$ m$^{-2}$ hr$^{-1}$; Wickland *et al*. 2001, Otieno *et al*. 2009, Millar *et al*. 2016). These results show that, despite the harsh conditions (high UV, potential for frosts and snow on any day) of growing at high altitudes (> 3500 m), some plant communities in these peatlands have high productivity throughout the year, which allows them to accumulate considerable amounts of peat (Hribljan *et al*. 2016).

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

| Attribute | CC | AN |
|---|---|---|
| Altitude (masl) | 4258 | 3940 |
| Co-ordinates (longitude, latitude) | -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 | 5.4 | 5.2 |
| Mean daily water table (cm) | -5.8 (-58.0, 3.2) | -24.2 (-50.0, 1.1) |
| Mean daily peat temperature (°C) | 6.5 (0.5, 17.5) | 8.7 (-3.5, 41.5)[d] |
| Age of peatland (yr) [e] | 8036 | 5313 |
| Mean peatland soil depth (m) | 3.9 [e] | 2.9 [f] |
| Carbon storage (Mg ha$^{-1}$) [e] | 1037 | 1046 |

[a] between the years 2009–2015 at Virgen Papallacta station; 3920 masl and 4 km distant 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 distant from the study site (EMAPS, personal communication July 2016)

[c] between the years 2000–2010 at Mica Presa station (EPMAPS, personal communication July 2016)

[d] peat temperature for hummocks only on AN

[e] (Hribljan *et al*. 2016)

[f] (Comas *et al*. 2017)

Table 2. Summary of carbon gas flux data from the Cayambe Coca (CC) and Antisana (AN) sites. Net ecosystem exchange (NEE), ecosystem respiration (ER) and gross primary production (GPP) are expressed in g CO$_2$ m$^{-2}$ hr$^{-1}$, and positive values represent release by the ecosystem. Methane (CH$_4$) flux is expressed in mg CH$_4$ m$^{-2}$ d$^{-1}$, and positive values represent loss from the ecosystem. Note that these data represent daytime-only values; carbon dioxide (CO$_2$) flux would be higher if night-time respiration were considered. The mean values represent averages of collars.

| | 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 |
| **Standard error** | 0.08 | 0.06 | 0.12 | 1.17 | 0.13 | 0.07 | 0.17 | 34.22 |

* lawns only

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 g CO$_2$ m$^{-2}$ hr$^{-1}$; collar averages) are greater than those reported for *Sphagnum*-dominated temperate peatlands (-0.005 and -0.5 g CO$_2$ m$^{-2}$ hr$^{-1}$; Carroll & Crill 1997, Riutta *et al*. 2007, Johnson *et al*. 2013, Ballantyne *et al*. 2014), but within the range of those reported for grass and moss dominated mountain peatlands in southern Germany (-0.79 and -1.58 g CO$_2$ m$^{-2}$ hr$^{-1}$; Otieno *et al*. 2009) and sedge dominated peatlands in the Colorado Rocky Mountains (-1.08 g CO$_2$ m$^{-2}$ hr$^{-1}$;

Millar *et al*. 2016).

Microtopography had a large influence on CO$_2$ fluxes at the undisturbed site, with higher NEE, GPP, and ER values on hummocks than on lawns. Other studies have observed this pattern in low-altitude peatlands at higher latitudes (e.g., Strack *et al*. 2006, Sullivan *et al*. 2008). These increased values of NEE, GPP, and ER in hummocks result in a heterogeneous CO$_2$ exchange pattern. In contrast, at the fully vegetated collars of the grazed site, hummocks and lawns showed no significant differences for NEE, GPP, and ER mean values, which might suggest that
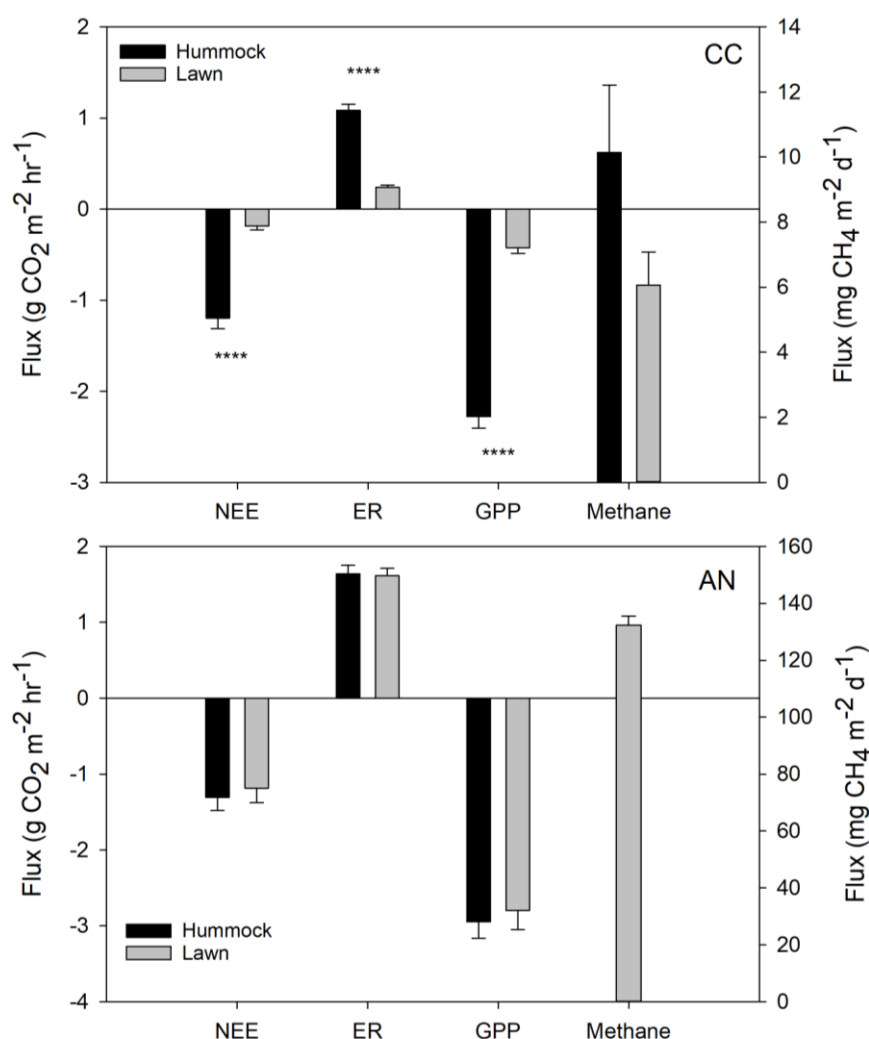
Figure 4: Mean net ecosystem exchange (NEE), ecosystem respiration (ER), gross primary production (GPP) and methane flux by microtopography (hummock and lawn) for all plots at Cayambe Coca (CC) and Antisana (AN). Error bars indicate one standard error. Asterisks indicate significant differences between hummock and lawn. For carbon dioxide ($CO_2$) components (g $CO_2$ m$^{-2}$ hr$^{-1}$), negative values represent uptake by the ecosystem. For methane (mg $CH_4$ m$^{-2}$ hr$^{-1}$), positive values represent loss from the ecosystem. No data shown for $CH_4$ fluxes in hummocks at AN.

the influence of grazing reduces the heterogeneity of $CO_2$ flux patterns in peatlands dominated by cushion plants. Alternatively, the differences in plant community and depth to water table might also drive these patterns.

The mean GPP and NEE values measured for fully vegetated collars are approximately two and a half times greater at AN than at CC. The higher GPP and NEE at AN could be due to environmental differences, such as higher temperature, lower cloud cover, lower precipitation, sloping basin morphology that alters the hydrology between the sites, and greater nutrient inputs because of the larger upslope catchment. Lower cloud cover does not explain the entire pattern because the light response functions saturated at a higher GPP for AN than for CC. Moreover, AN is approximately 2.2 °C warmer and has lower water tables which minimises flooding stress, both of which could have contributed to increased production. However, these differences in flux might also be caused by grazing. Light to moderate grazing can lead to increased density of vascular plants, an increased net ecosystem uptake of $CO_2$ (Falk *et al.* 2015), and fertilisation by cow manure and urine can lead to higher plant productivity (Boon *et al.* 2014). This pattern was found by a study conducted in cushion plant dominated peatlands in the Andes of Colombia, where above-ground biomass was greater in grazed plots (Urbina & Benavides 2015).
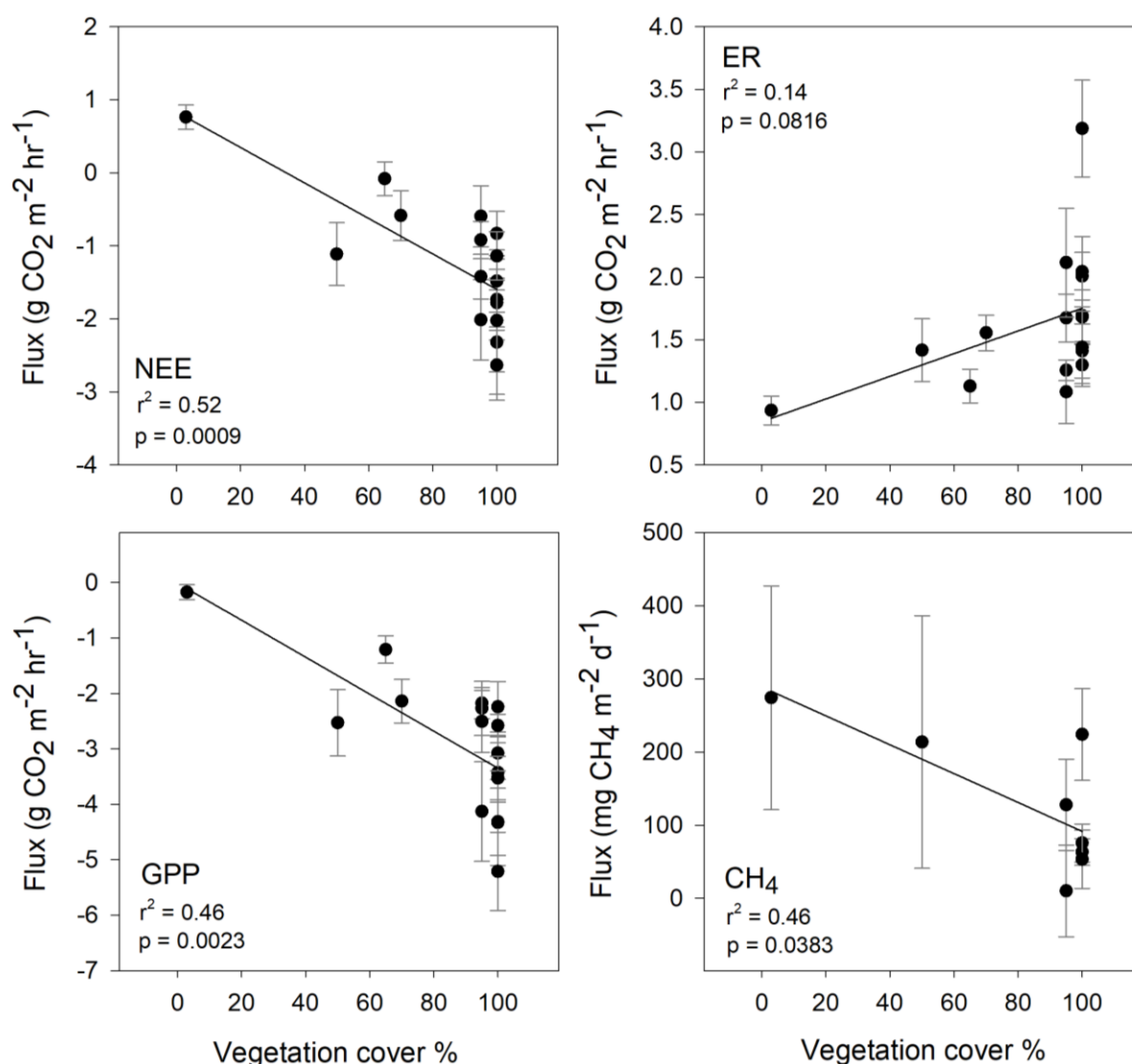
Figure 5. Mean net ecosystem exchange (NEE), ecosystem respiration (ER), gross primary production (GPP), and methane (CH$_4$) flux by percent vegetation cover at Antisana. Error bars indicate one standard error. For carbon dioxide (CO$_2$) components (g CO$_2$ m$^{-2}$ hr$^{-1}$), negative values represent uptake by the ecosystem. For CH$_4$ (mg CH$_4$ m$^{-2}$ hr$^{-1}$), positive values represent loss from the ecosystem. CH$_4$ values are shown only for lawns. Linear fit for all graphs. Normality assumption not met for ER.

However, intensive grazing and trampling can expose the peat and reduce the photosynthetically active biomass. Other studies have shown a relationship between NEE and plant biomass, reporting a decrease in NEE with grazing in arctic mires (Sjögersten *et al.* 2011, Falk *et al.* 2014). Our low NEE values and proportionally higher ER values at trampled locations indicate that areas with less than ~ 90 % vegetation cover are likely to be net sources of CO$_2$ if night-time respiration is taken into account. Thus, the combination of the positive effects of fertilisation and the negative effects of trampling might lead to a peaked relationship between herbivore disturbance intensity and NEE in these ecosystems.

## CH$_4$ fluxes

There is a stark contrast between the low CH$_4$ emissions in the undisturbed site (10.1 mg CH$_4$ m$^{-2}$ d$^{-1}$ for lawns) and the greater CH$_4$ emissions at the grazed site (132.3 mg CH$_4$ m$^{-2}$ d$^{-1}$ for lawns). In a global review, Turetsky *et al.* (2014) found that average CH$_4$ emissions for pristine boreal and temperate peatlands were in the range ~ 50–200 mgCH$_4$ m$^{-2}$ d$^{-1}$ and developed equations for calculating CH$_4$ emissions based on mean annual temperature. Using the mean annual air temperature of both our sites (5 °C) and Equation 2 in Turetsky *et al.* (2014), we calculated a mean flux of ~ 45 mg CH$_4$ m$^{-2}$ d$^{-1}$, which is several times greater than the values we measured at the undisturbed site but lower than
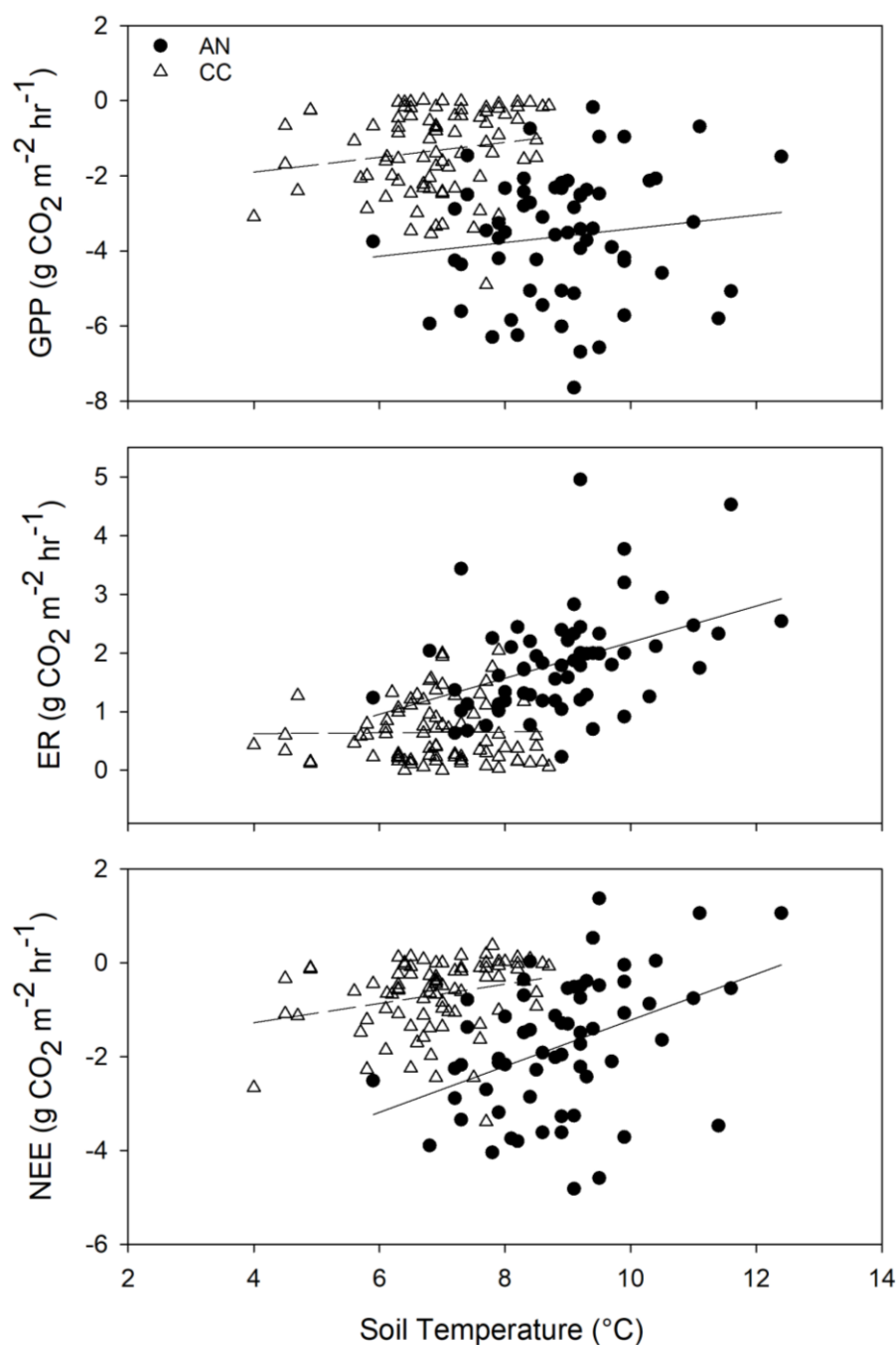
Figure 6. Correlations between gross primary production (GPP) (top), ecosystem respiration (ER) (bottom) (g $CO_2$ m$^{-2}$ hr$^{-1}$) and soil temperature (°C) at 5 cm depth for Cayambe Coca (CC) and Antisana (AN). Note that AN values only included collars with 100 % vegetation cover.

the values we measured at the grazed site. It is important to realise that the low growing season rates measured in this study do not accurately reflect differences in annual flux rates due to differences in seasonality between the tropics and temperate-boreal zones (Chimner 2004). Most peatlands in temperate-boreal regions have low CH₄ emissions during winter and much higher rates during the growing season (Dise 1992, Alm *et al.* 1999, Huth *et al.* 2012), which

suggests that annual CH₄ emissions at our study sites could be closer to the mean reported for the temperate and boreal zones. Indeed, the mean annual values measured in the undisturbed site (3 g CH₄ m$^{-2}$ yr$^{-1}$) are close to the annual rates reported for nutrient-poor boreal peatlands ~ 4 to 15 g CH₄ m$^{-2}$ yr$^{-1}$ (Wilson *et al.* 2016).

Although CH₄ emissions in CC were low compared to northern peatlands in temperate and

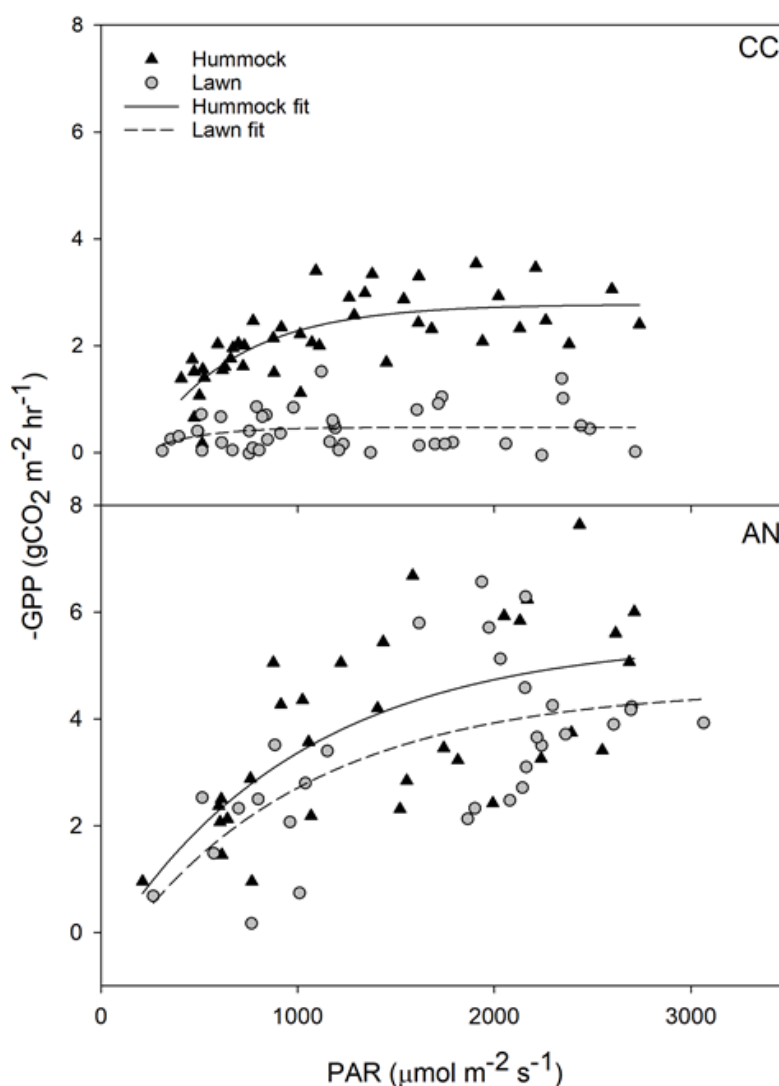Figure 7. Light response curves, gross primary production (GPP; g CO$_2$ m$^{-2}$ hr$^{-1}$) *versus* photosynthetically active radiation (PAR; μmol m$^{-2}$ s$^{-1}$) by microtopography (hummock and lawn) for Cayambe Coca (CC) and Antisana (AN). The inverse sign for GPP was used in these light response curves. Note that AN values only included collars with 100 % vegetation cover. The equation fitted is exponential rise to the maximum, single, 3 parameter: $f = y0 + a(1 - exp(-bx))$.

boreal zones, they are not zero. This contrasts 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 climate (the Fritz *et al.* 2011 study was conducted at 40 masl in a temperate zone), and/or associated plant communities (Turetsky *et al.* 2014).

To explore the influence of plant communities further, we can look at the effect of microtopography on CH$_4$ emissions at the undisturbed site. Microtopography seems to be an important control on CH$_4$ emissions in CC, with higher CH$_4$ emissions for hummocks than for lawns. A number of studies have found that CH$_4$ efflux derives from greater

photosynthetic activity, which in turn leads to an elevated supply of root exudates as a substrate for CH$_4$ production, and subsequently enhanced CH$_4$ emission through aerenchymatous tissues (Whiting & Chanton 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). However, increased CH$_4$ efflux by aerenchymatous plants depends on whether the rhizospheres are sufficiently oxygenated by radial oxygen loss from roots. Fritz *et al.* (2011) attribute the absence of CH$_4$ emissions to oxygenation of the rooting zone of densely growing cushion plants. The plant species in our study may have different oxygen

Table 3. Light response curve equation coefficients and adjusted R$^2$ for the Cayambe Coca (CC) and Antisana (AN) sites by microtopography (hummock and lawn). Note that AN values only included collars with 100 % vegetation cover. The equation fitted is exponential rise to the maximum, single, 3 parameter: $f = y0 + a(1 - \exp(-bx))$.

| | CC | | | | AN | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hummock** | | **Lawn** | | **Hummock** | | **Lawn** | |
| **R$^2$** | 0.5120 | | -0.0084 | | 0.3863 | | 0.3606 | |
| | Coefficient | P | Coefficient | P | Coefficient | P | Coefficient | P |
| **y0** | -1.5263 | 0.4154 | -0.5436 | 0.8212 | -0.4081 | 0.8367 | -0.7327 | 0.7366 |
| **a** | 4.3013 | 0.0175 | 1.0172 | 0.6668 | 5.9232 | 0.0003 | 5.3219 | 0.0023 |
| **b** | 0.0022 | 0.0199 | 0.0037 | 0.5236 | 0.0010 | 0.1634 | 0.0010 | 0.2274 |

transport characteristics, as porosity values for roots with aerenchyma have been found to differ among plant species and even between genotypes (Colmer 2003). The presence of these cushion plants at our site may enhance CH$_4$ emissions from the anoxic rooting zone *via* aerenchymatous tissues (Joabsson *et al.* 1999). The influence of vegetation on gas flux is also evidenced by the strong positive association of graminoids with CH$_4$ emissions (Turetsky *et al.* 2014). In the Andes, this is consistent with a study by Teh *et al.* (2014) who reported CH$_4$ emissions of 15.6 mg m$^{-2}$ d$^{-1}$ for montane grasslands in Perú, which is roughly double the emission rate reported for the undisturbed site in this study.

The higher CH$_4$ emissions from the grazed site equate to an annual emission of 48 g CH$_4$ m$^{-2}$ yr$^{-1}$ which is 16 times greater than for the undisturbed site, in the upper range of values reported for pristine peatlands in northern regions, and higher than those reported for nutrient-rich boreal peatlands (Turetsky *et al.* 2014, Wilson *et al.* 2016). Because many grazed peatlands are drained, studies conducted in these grazed drained peatlands have often found lower rates of CH$_4$ emissions due to the absence of saturated conditions (e.g. Nykänen *et al.* 1995, Turetsky *et al.* 2014) rather than to grazing *per se*. Thus, CH$_4$ emissions from enclosures of muskox grazing in an undrained high arctic mire in Greenland were 44 % lower than in grazed controls (Falk *et al.* 2015). Although not directly comparable, the undrained and often saturated conditions of AN provide a perfect environment for the production of CH$_4$ (Rydin & Jeglum 2006). In addition, the presence of cattle at AN may lead to increased CH$_4$ emissions due to the constant input of cattle urine and manure. Nutrient additions could increase CH$_4$ emissions, as it has been shown that ammonium (NH$_4^+$) may inhibit an enzyme in CH$_4$ oxidising bacteria and boost CH$_4$ production (Dobbie & Smith 1996, Aerts & de Caluwe 1999, Boon *et al.* 2014), and manure can also provide a labile substrate for methanogens (Lai *et al.* 2014). In addition, we estimated that the reduction of vegetation cover by grazing and trampling may increase CH$_4$ emissions by approximately 50 %. This hypothesis is supported by Fritz *et al.* (2011), who found that emissions from clipped cushion plants were higher than those reported for intact cushions.

**CONCLUSIONS**

This article is the first to report both CO$_2$ and CH$_4$ emissions in Andean mountain peatlands, providing knowledge of C gas fluxes in an understudied ecosystem type. The two peatlands we studied differed greatly in CO$_2$ and CH$_4$ exchange patterns, which could be due to differences in climate and hydrology, or alternatively to cattle disturbance at AN. Given that the grazed site shows lower NEE values and higher CH$_4$ emissions with increasing disturbance intensity, intensive grazing practices that lead to physical disturbance of the vegetation are likely to reduce or reverse greenhouse gas benefits from mountain peatlands. These intensive grazing practices will also cause loss of peat and, consequently, a decline in the many other ecosystem services that peatlands provide.

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