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ORIGINAL PAPER

The effect of water table levels and short-term ditch restoration on mountain peatland carbon cycling in the Cordillera Blanca, Peru

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Abstract Many tropical mountain peatlands in the Andes are formed by cushion plants. These unique cushion plant peatlands are intensively utilized for grazing and are also influenced by climate change, both of which alter hydrologic conditions. Little is known about the natural hydroperiods and greenhouse gas fluxes of these peatlands or the consequences of hydrologic alteration for these fluxes. Therefore, our objectives were to assess how carbon dioxide (CO_2) and methane (CH_4) fluxes varied across a hydrological gradient caused by ditching and evaluate how short-term carbon cycling responds after rewetting from ditch blocking in a tropical mountain peatland. The study was carried out in Huascarán National Park, Peru using static chamber methods. Comparing reference to highly drained conditions, mid-day net ecosystem exchange (NEE) was higher (1.07 ± 0.06 vs. 0.76 ± 0.11 g CO_2 m^{-2} h^{-1}), and the light compensation point for CO_2 uptake was lower. Gas fluxes were relatively stable in the rewetted and reference treatments, with small positive responses of NEE to rising water tables. CH_4 emissions averaged 2.76 ± 1.06 mg CH_4 m^{-2} day^{-1}, with negative fluxes at water tables >10 cm below the soil surface, and positive fluxes at higher water levels. Our results indicate that undrained peatlands appear to be carbon sinks, highly drained peatlands were likely carbon sources, and rewetting of moderately drained peatlands increased NEE and the ability to store carbon to undrained reference conditions. Ditching of peatlands will likely increase their susceptibility to negative climate change impacts, and hydrologic restoration could moderate these impacts.

Keywords Bofedales · Carbon cycling · Carbon dioxide · Methane · Andes · Cushion peatlands · Ditch blocking · Light compensation point

Introduction

The majority of peatlands globally are found in low-elevation areas, primarily in boreal and tropical regions (Clymo 1987). However, peatlands are also common in many mountain ranges, including the Andes (Cooper et al. 2012). In the tropical Andes they occur above 3500 m in several climate zones including (1) the northern (peri-equatorial) *páramo* ecoregion (wet year round) of Colombia, Venezuela, and Ecuador (Samaniego et al. 1998; Chimner and

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Karberg 2008; Hribljan et al. 2016), (2) mesic *jalca* ecoregion of northern Peru (Cooper et al. 2010), and (3) the *puna* ecoregion that extends from southern Peru through Bolivia (Cooper et al. 2015; Hribljan et al. 2015) to northern Chile and Argentina (Earle et al. 2003; Preston et al. 2003).

In contrast to *Sphagnum*-dominated northern peatlands, many Andean mountain peatlands are dominated by vascular plants with a cushion life form (Cooper et al. 2010). Common cushion plant species are in the family Juncaceae, Plantaginaceae, and Asteraceae (Cooper et al. 2010; Benavides 2014; Salvador et al. 2014). These plants have a dense, low-statured growth form with long taproots or buried stems with adventitious roots (Cooper et al. 2015). The cushion plant growth form has undergone convergent evolution in several regions as an adaption to arctic and alpine environments (Billings and Mooney 1968). The compact growth form can trap heat and warm plants up to ~ 15° C above the surrounding air temperature and increase vegetation canopy humidity by reducing wind shear and evapotranspiration (Cavieres et al. 2007). In addition, their deep roots can acquire deep soil moisture and increase access to nutrients buried in decomposing tissues as the cushions grow upward. The aerenchymatous tissue of some species' roots can also transport oxygen from the surface to deep layers of peat, causing rhizosphere oxidative activity (Fritz et al. 2011). The physiological and morphological characteristics of cushion plants are vastly different from sedges and *Sphagnum* moss species that dominate most boreal and temperate peatlands (Earle et al. 2003; Fritz et al. 2011; Salvador et al. 2014), which could have consequences for carbon cycling.

Biological processes in peatlands generally have been found to be strongly controlled by water table levels (Chimner and Cooper 2003a; Page et al. 2009; Silvola et al. 2010; Gatis et al. 2016). The water table is a physical barrier to oxygen diffusion from the atmosphere into the peat, limiting microbial activity and slowing decomposition rates (Oechel et al. 1998). A declining water table increases the volume of oxic soil and increases CO_2 production, while decreasing anaerobically produced CH_4 (Silvola et al. 2010).

This relationship between water table level and carbon cycling is modified by vegetation type. For example, *Sphagnum* mosses do not have roots and are sensitive to changes in water tables (Turetsky 2002; Bubier et al. 2003; Vasander and Kettunen 2006). Cushion plant traits could buffer their responses to hydrologic disturbance. Although a recent study examined C cycling impacts of cattle disturbance (Sanchez et al. 2017), no studies have focused on changes in hydrology. Since cushion plants have such different morphology and rooting strategies than plants in northern peatlands and tropical peat swamp forests, it is unclear how cushion plant peatlands will respond to changing water table levels.

CH_4 emissions in peatlands are also strongly modified by vegetation type, with graminoids (e.g., sedges and rushes) having been found to enhance rates of CH_4 emissions because labile root exudates increase CH_4 production (Vasander and Kettunen 2006) and vascular aerenchymatous tissue (air channels in roots) increases CH_4 transport when O_2 flux through roots is insufficient to support high methanotroph (CH_4-oxidizing bacteria) activity (Schütz et al. 1990; Shannon and White 1994; Chanton 2005). In the few studies that have been carried out in intact cushion peatlands, cushion plant peatlands have been found to have very low CH_4 efflux rates, which has been attributed to high oxygen diffusion from cushion plant roots (Fritz et al. 2011; Dullo et al. 2017; Sanchez et al. 2017). However, there is little information on how water table levels control methane efflux and no study has examined the effect of hydrologic alteration on methane efflux in cushion plant peatlands .

Mountain peatlands in the Andes have undergone hydrologic changes from both climate change and pastoral activities. Climate change can be one agent of hydrologic change, as exemplified by rapid Andean deglaciation in recent decades (Bradley et al. 2006), and it is expected that climate change will lead to the loss of carbon from tropical peatlands from drying and warming conditions (Gallego-Sala et al. 2018). The exact sign of climate change impacts on water balance depend on the combined impacts of warming and precipitation, which are predicted to vary along a latitudinal gradient in the Andes (Dangles et al. 2017). For example, the central Peruvian Andes have already experienced a warming and drying trend in the latter half of the twentieth century and future warming is projected to be similar to that of polar regions (Anderson et al. 2011). These changes would likely lead to region-specific trends, with a high likelihood of a general drying trend in peatlands of Peru that are likely to have negative impacts from lowered water tables.

In addition to climate change, many Andean mountain peatlands are also being affected by grazing. Local communities have been raising livestock for hundreds of years, and to facilitate grazing they often dig ditches to drain the peatlands. This has changed the composition and ecosystem functions of the natural vegetation communities (Millones 1982), and could accelerate C loss from cushion peatlands (Sanchez et al. 2017), with expected increases in decomposition of drained peat that are unlikely to be compensated for by increased production. However, the sensitivity of carbon cycling parameters to hydrologic alteration has not been explored in cushion peatlands.

If ditching is causing degradation to Andean peatlands similar to other mountain peatlands (Schimelpfenig et al. 2014; Chimner et al. 2019a), peatland hydrologic restoration could be a good strategy to reverse degradation (Chimner et al. 2017), potentially returning the water table to more natural levels and reduce erosion and improve carbon sequestration (Page et al. 2009; Luan et al. 2018). There are two main techniques to restore hydrology in drained peatlands, ditch-filling and ditch-blocking (Chimner et al. 2017). Filling ditches is a good long-term technique, but can be difficult due to lack of suitable fill material and cost of filling. Blocking ditches is a more common method because it is often easier and less expensive than filling ditches (Chimner et al. 2017). However, it is unclear if this method will be effective in the sloping peatlands with incised channels sometimes found in the central Peruvian Andes.

Because there is little fundamental information on carbon cycling in hydrologically intact cushion peatlands, and even less is known about how cushion plant peatlands in the Andes respond to drainage or restoration, the goals of this study were to test: (1) how carbon cycling varies along a water table gradient caused by ditching, and (2) how does carbon cycling change in the short-term (months to a year) after ditch restoration in a cushion plant peatland. We hypothesized that (1) changes in water table will affect CO_2 fluxes, by increasing ecosystem respiration (ER) at lower water table levels, and increasing net ecosystem exchange (NEE) at higher water table levels. We also hypothesized that (2) CH_4 emissions will increase with high water table levels in the cushion plant dominated areas. In terms of the restoration, we hypothesized that (3) rewetting the area will bring the CO_2 fluxes rates closer to those in the reference (hydrologically unaltered) areas.

Methods

Study sites

The study took place in Huascarán National Park (HNP), in the humid *puna* (Troll 1968, Josse et al. 2011) ecoregion in the central Andes of Peru (Fig. 1a). This 340,000-ha park covers an elevation range of 2500 to 6768 masl with mountain peatlands occupying ~ 6% of the park area (Fig. 1b: Chimner et al. 2019b). These HNP's ~ 660 glaciers and 300 water bodies of glacial origin feed the main hydrological basins in north-central Peru. The mean annual precipitation of nearby Huaraz (elevation 3050 masl) is 632 mm and the mean annual temperature is 13.5 °C. The wet season typically occurs between October and April and has a mean temperature of 13.8 °C and mean precipitation of 83 mm/month. The dry season occurs between May and September and has a mean temperature and precipitation of 13.1 °C and 10.4 mm/month (climate-data.org).

The research occurred in two groundwater fed cushion plant peatlands in the Tambillos region (Fig. 1C). The main site (peatland 1) is a peatland complex of approximately 7 ha at ~ 4200 masl, (S 9°41′21.80″, W 77°14′18.40″). Peat depth in this peatland is ~ 400 cm, has a basal date of 9340 year BP, with an average specific conductivity of 112 μS cm^{-1} and pH 5.9 (Hribljan et al. unpublished data). The peatland slopes down into and along the valley bottom and is bordered by a road on the one side and has a ditch near the road that drains part of the peatland (Fig. 1c). Although the ditch construction date is unknown, local residents confirmed that it has been there for over 10 years. The ditch is 30–50 m length and varies between 2–3 m width and 50–100 cm depth.

Most sampling occurred for 5 months before any restoration occurred that allowed some pre-restoration data to be collected. In October 2015, at the beginning of the wet season, ~ 120 m of the ditch was blocked by hand with 22 wooden check dams that ranged in size from 1–4 m wide, and 0.4–1.5 m high by

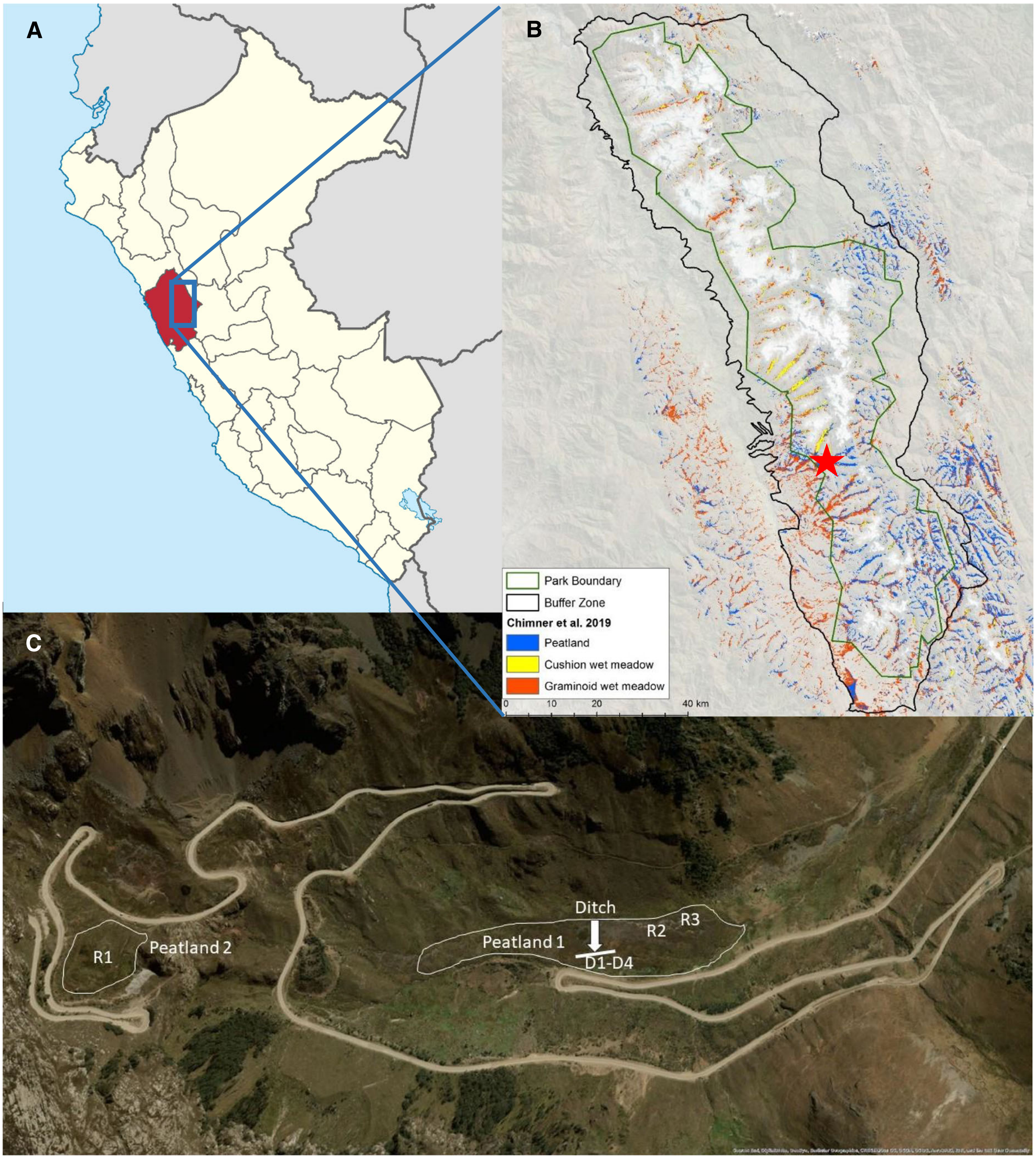


Fig. 1 **a** Location of Huascaran National Park in Peru; **b** location of study sites (star) on a wetland map (Chimner et al. 2019b) of Huascaran National Park; **c** map of study sites superimposed on aerial image of Tambillos Valley, Huascaran National Park, Peru. R1–R3 refer to location of reference plots and D1–D4 indicate location of plots associated with the ditch. See Fig. 2 for detailed locations of D1–D4

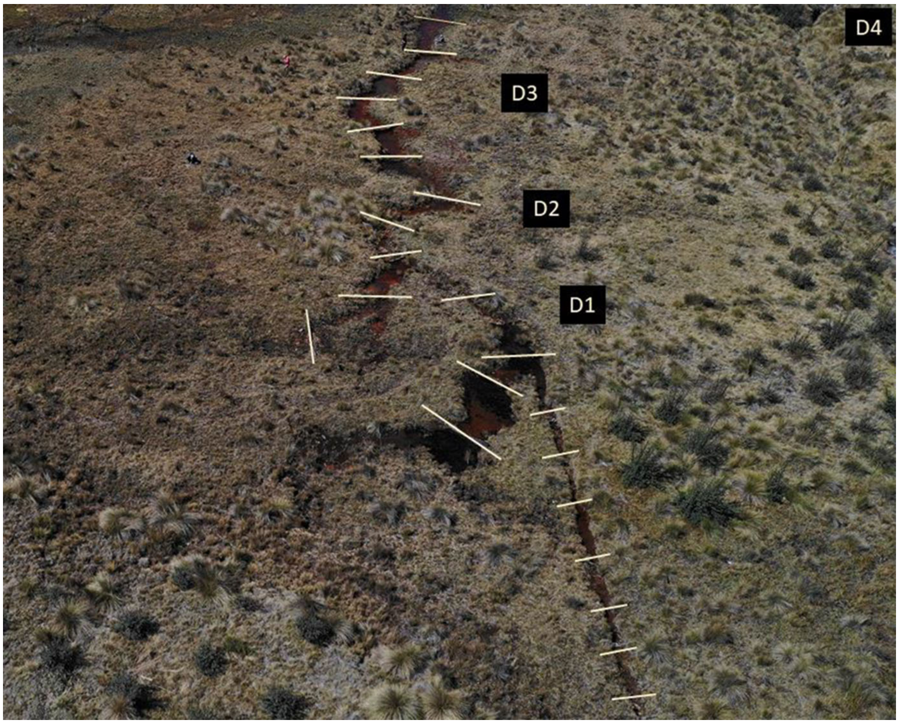


Fig. 2 Drone image from August 2019 (late dry season) of ditch at Peatland 1in Tambillos Valley showing ditch plug locations. Yellow lines were drawn over the ditch plugs to make plugs easier to see. Plot locations indicated by D1–D4

researchers and local community members (Figs. 2 and 3).

We established seven plots in total. Three plots were established along the length of the ditch (D1–D3) and were sampled before and after ditch restoration (referred to hereafter as *moderately drained* before restoration and *rewetted* after). One sampling plot (D4) was isolated from the ditch blocking by another ditch and the road and was not restored (referred to hereafter as *highly drained*).

Other locations in the main peatland complex had low levels of grazing and received groundwater inputs from the valley slopes opposite the road and ditches, so were hydrologically unaltered. We used two locations (R1 and R2: Fig. 1) in these areas as reference locations (referred to hereafter as *reference*). We also created an additional reference plot (R3) in a small peatland (~ 4 ha) located near the top of the watershed (~ 4400 masl: S 9°41′14.51″, W 77°14′54.25″: Fig. 1) that had no ditching and little or no grazing impacts. The depth of peat at this site is ~ 415 cm (basal date of 8365 year BP) and has a similar specific conductivity (180 μS cm^{-1}) and pH (5.8) as the main site (Hribljan et al. unpublished data).

Water table levels

At each of the seven plots we installed a polyvinyl chloride (PVC) well to measure the water table. The wells were 6.3 cm in diameter and 1–2 m long. All wells were perforated, covered with a fine mesh, and capped to exclude infiltration from rain. Water table depths were measured manually once a month for 17 months, from June 2015 until August 2016 and then again in December 2016 and May 2017.

CO_2 flux measurements

Daytime net ecosystem exchange (NEE) and ecosystem respiration (ER) were measured using a chamber-based method (Hutchinson and Mosier 1981) at all 7 well locations once a month starting in June 2015 until August 2016 and again in December 2016. Before flux measurements began, we inserted 4 PVC collars per well (diameter 40.6 cm, height 10 cm, and wall


A
B
C
D
E

◀**Fig. 3** Ditched areas in páramo peatland site 1. Two ditch sections shown before (**a** and **b**) and after (**c** and **d**) ditch blocking. Reference area (R1) shown in photo E

thickness 0.5 cm) ~ 5 cm into the peat at ~ 1 to 3 m distance from each groundwater monitoring well as a fixed base for the chamber measurements. Fluxes were measured with a PP Systems EGM-4 infrared gas analyzer (IRGA; PP Systems, Amesbury, USA) attached to a custom built clear acrylic cylindrical chamber (diameter 40.6 cm, height 59 cm, volume 76,383 cm^3) equipped with a detachable lid, a fan and a vent valve (Sanchez et al. 2017).

To measure NEE, the clear chamber was placed carefully on the collar, without damaging the vegetation inside, and the collar-chamber joint was sealed using a cylindrical cut section of rubber tire inner tubing. With the fan on and the lid off, the chamber was flushed before each measurement, and then closed and sealed to conduct the measurements. The measurements were taken over a 124 s period. The same method was used to measure ER, except we placed a lightproof white cloth cover over the chamber to prevent light from entering the chamber. All measurements took place between 10:00 and 16:00, and collars were measured in random order to avoid any systematic bias.

We measured several additional environmental parameters during flux measurements including water table level, time of the measurement, air temperature, soil temperature, relative humidity, barometric pressure using a barometer, and photosynthetically active radiation (PAR) using a PAR sensor. Some of these measurements, such as time of measurement, relative humidity, and barometric pressure were already recorded by the IRGA; however, we measured them manually as a backup. PP Systems soil temperature probe (STP) was inserted into the soil next to the chamber at 5 cm during the light measurements and at 20 cm depth during the dark measurements, while an additional small temperature probe was also inserted into the soil, at the same depths as PP Systems STP, to compare values. The PAR sensor started to fail in September 2015 and was replaced in January 2016, leaving a gap of approximately 4 months in our PAR measurements.

Light response experiment

We developed a light response experiment to quantify the light compensation point for CO_2 uptake, and to understand if the light compensation point (LCP) differed along the water table gradient. The light compensation point for net ecosystem exchange is the x intercept of the light response curve, i.e., the point when instantaneous rates of GPP and ER are equal, and NEE is zero. To develop light response curves, we used shade cloths of different mesh sizes to reduce light. This experiment followed the methods of Whiting et al. (1992) and Bubier et al. (1998), using a clear chamber, an IRGA, and shade cloths that provided 100%, 90%, 80%, 70%, 60%, 50%, 40% and 30% shade.

The measurements took place in May and June 2016, from 9:00 to 13:00 when wells were in direct sunlight and the sky was clear. We used the chamber-based methods described above. Six well areas were measured: two in the reference area (R1 and R3), three in the moderately drained/rewetted area (1, 2, and 3), and one in the highly drained area (4). For logistical reasons, we only measured light response curves on one collar per well, picked at random. As with the regular NEE and ER measurements, we also included other environmental variables and observations. The measurements were done alternating shade cloths from low light to high light levels, sometimes starting and other times ending with 100%/0% shade pair, otherwise in the order: 90%, 30%, 80%, 40%, 70%, 50%, 60% shade.

CH_4 flux measurements

We measured CH_4 flux at two collars per well (picked at random from the four collars at each well) at the same seven wells as for NEE for 3 months. CH_4 sample collection took place at the end of the wet season in May 2016, at the middle of the dry season in July 2016, and near the end of the dry season in August 2016. We prepared field CH_4 standards in the MTU wetlands lab before going to Peru in order to test for any effects of sample transport. We filled nine 10 ml exetainers with 10 ppm CH_4 standard and another nine 10 ml exetainers with 100 ppm CH_4 standards, and sealed them with silicone caulk to act as tests for transport loss. These showed no evidence of any loss.

We used two closed CH_4 chambers (diameter 40.6 cm, height 31 cm, volume 40,133 cm^3) to collect gas samples (Hutchinson and Mosier 1981; Sanchez et al. 2017). CH_4 chambers were placed on the same collars installed for CO_2 measurements. Each chamber was equipped with a narrow vent tube (to minimize pressure differentials) and a fan. Samples were collected every 15 min for a period of 45 min per collar using a 60 ml syringe and needle. Gas samples were taken from the chamber's port without pumping the syringe to minimize changes in pressure inside the chamber. Prior to affixing the chamber, a sample of ambient air was taken over the vegetation of each collar to use later to correct fluxes. Ambient barometric pressure, humidity, temperature, dew point, soil moisture and soil temperature from a temperature probe inside the collar were recorded at the beginning and end of each measurement. We injected ~ 20 ml of gas in the exetainers to keep the vial pressurized. The syringe was flushed 2–3 times before taking the next sample. Both chambers were used concurrently on neighboring collars. CH_4 samples were analyzed in the laboratory using a flame ionization detector (FID) installed in a gas chromatograph (Varian CP- 3800, Palo Alto, CA, USA).

Gas flux calculations

CO_2: We used the sign convention in which negative values signify ecosystem release of CO_2, and positive values signify ecosystem uptake of CO_2. Gross primary production (GPP) was calculated as the difference between NEE and ER. We used Excel (Vers. Xxx, Microsoft Corporation) to plot linear regressions for each CO_2 measurement and estimate the R^2 and slope of the line to quality-control the data. All dark measurements with an R^2 lower than 0.8 were excluded. For the light measurements, for logistical reasons we measured even on partly cloudy days. Variable PAR over the course of measurements often led to lower R^2 values. Therefore, we examined the regression fits with R^2 lower than 0.8. Those with noise in the data unrelated to variation in PAR were excluded. In total, 8 measurements were excluded due to poor fit.

CH_4: We calculated a headspace correction to account for the gas dilution when taking samples from the chamber. The difference between the gas concentration with and without the headspace correction was negligible (0.02% on average). We used the ideal gas law equation to estimate CH_4 fluxes using Microsoft Excel:

$$F_{CH_4} = \frac{\Delta C}{\Delta t} \times \frac{P}{1013} \times \frac{273}{273+T} \times \frac{16.043\ \mathrm{kg}}{22.4414\ \mathrm{m}^3} \times \frac{Vc}{Ac} \times \frac{\mathrm{mol}}{10^6\ \mu\mathrm{mol}} \times \frac{86400\ \mathrm{s}}{\mathrm{day}} \times \frac{10^6\ \mathrm{mg}}{\mathrm{kg}} \quad (1)$$

where F_{CH_4} is the CH_4 efflux (mg m^{-2} day^{-1}), $\Delta C/\Delta t$ is the change in CH_4 with time (µmol mol^{-1} s^{-1}), P is the barometric pressure (atm), T is the air temperature at soil surface (°C), 16.043/22.4414 is the molar mass of CH_4 over the molar volume of a gas at standard temperature and pressure (expressed as kg/m^3), Vc is the volume of the chamber when placed on top of the collar (m^3), and Ac is the area of the chamber (m^2).

Because these are instantaneous daytime measurements, without considering nighttime respiration, they do not directly reflect ecosystem C balance. To gain some insight into possible impacts of water table on ecosystem C balance, we used a daytime GPP:|ER| ratio (Law et al. 2002; Amiro et al. 2010) plot. A value of two for this ratio is considered to be a *very rough* approximation of a zero net carbon balance on a 24-h basis, on the assumption that nighttime respiration is roughly equal to daytime respiration. This of course does not account for other factors such as day-night air temperature difference that would lower nighttime respiration relative to daytime, the difference between daytime and nighttime dark respiration rates (Heskel et al. 2013) that would have an opposite effect, and shoulder effects on GPP which would lower the cumulative GPP, all of which were beyond the scope of the present study and would shift the position of the zero-carbon balance line.

Vegetation survey

We took pictures of each collar at the beginning, middle and end of the study period to characterize plant communities. We recorded the plant communities inside of each collar, and estimated the percent cover of the cushion plants, non-cushion plants, as well as the percent bare ground for each collar. Then we averaged the four collars around each well to estimate percent cushion plant cover, non-cushion plant cover, and bare ground cover around the well.

We also estimated cushion plant production using the modified cranked wire method (Clymo 1970; Gunnarsson and Rydin 2000; Cooper et al. 2015), In each collar with cushion plants we inserted one to ten 20 cm long, metal wires in the cushion plants, the number of cranked wires inserted depended on the cover of cushion plants present in the collars. Every wire, which had bristles to keep it in place, was inserted into the cushions, allowing 5 cm to extend vertically above the cushion surface. Wires were installed on February 2016 and growth was measured in May, August and December 2016. In December 2016, we took 6 core samples of cushion plants near the collars in the reference area and 15 in the moderately drained/moderately drained/rewetted area. Cores were taken without altering their density and volume. Each core was 2 cm in diameter and 8 cm in length and included the live vegetation. We cut them into four 2 cm increment subsamples to relate organic carbon content with height gain. Samples were oven dried at 65 °C to a constant weight, then combusted in a muffle furnace to calculate organic matter content of each sample. Next, we followed the method described in Cooper et al. (2015) to estimate organic carbon production in cushion plants. To estimate cushion plant production in plots with cranked wires but lacking core samples, we estimated a linear regression of height growth versus biomass for the cored plots, and used the average bulk density of the same cushion plant species in the same treatment to estimate biomass production.

Statistical tests

We used linear regression in Sigmaplot 13 (Systat Software, San Jose, CA) to quantify the relationships between water table and NEE, ER, GPP, and GPP/ER, using the average of all four wells per plot per date in the analysis. We plotted the relationships separately for the drained collars and moderately drained/rewetted collars because they responded differently to changes in water table. We plotted the cleaned data for CO_2 and CH_4 against water table levels, and used simple linear regression to describe the data. Light response curves were fitted with an exponential rise to the maximum function. We tested production differences between cushion plant species in reference and rewetted areas using a t-test in JMP Pro 13 statistical package.

Results

Water table

Water table levels in the reference areas were relatively stable throughout the year, with a mean of − 4.6 ± 0.4 cm depth during the wet season, and − 7.6 ± 0.6 cm depth in the dry season (negative values indicate depth below the soil surface; Fig. 4a). During the dry season, the moderately drained/rewetted area had an average of − 69.4 ± 7.3 cm depth before the restoration and − 38 ± 11.3 cm depth after the restoration. The moderately drained/rewetted area had an average of − 6.1 ± 2.2 cm depth during the wet season after the restoration. The highly drained area had a mean water table level of − 108.5 ± 3.1 cm depth in the wet season, and − 154 ± 4.2 cm depth in the dry season.

Vegetation survey and plant productivity

We identified 28 plant species, including cushion plants, graminoids, mosses, and other vascular plants. Reference and moderately drained/rewetted areas had the greatest number of species while the highly drained area had fewer species (Table 1). Plant community composition changed across the water table gradient. The reference area had the lowest percentage of bare ground (3%) and the greatest cover (46%) of cushion plants, including two *Distichia* species as well as *Oreobolus obtusangulus* Gaudich. The moderately drained/rewetted areas had the highest percent cover of bare ground (18%) and a lower percent cover of cushions (11%), all *O. obtusangulus*. The non-cushion plants found were mostly sedges (*Carex* sp.) and grasses (*Calamagrostis* sp.). The highly drained area had a low percent bare ground (3%), no cushions, and a plant community dominated by a trailing herb that is common in disturbed non-wetland areas (*Lachemilla orbiculata* Ruiz & Pav) and an invasive grass *(Agrostis breviculmis* Hitchc).

When production (estimated via the cranked wire analysis) was examined separately for the two genera within the reference area, *Distichia* production (4.5 ± 2.5 g C m^{-2} day^{-1}) and *Oreobolus* production (2.5 ± 2.2 g C m^{-2} h^{-1}) were not significantly different ($p = 0.31$). However, cushion plant production in the reference area (3.2 ± 2.5 g C m^{-2} h^{-1}) was greater than in the moderately drained/rewetted

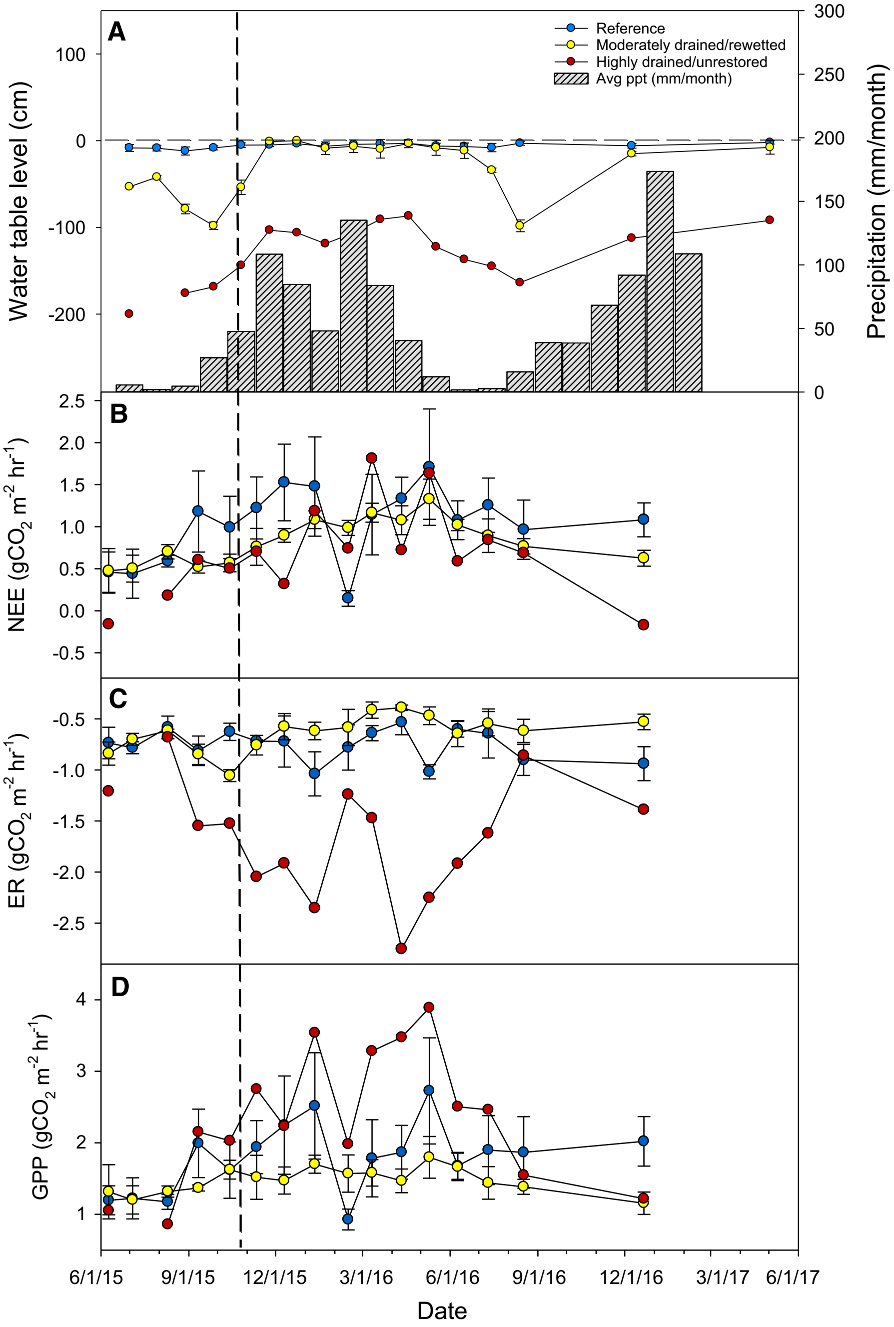


Fig. 4 **a** Average precipitation (mm/month) from four meteorological stations near the study area—Milpo, Chavin, Recuay, and Santiago Antunez de Mayolo (grey bars)—and the fluctuation in water table levels from the different treatments (lines) during the study period. Water table is averaged by treatment per month, error bars show standard error (SE). Note that the reference area is an average of both sites (1 and 2). Dashed line shows when the check dams were installed (October 2015). Changes in CO_2 fluxes in the Tambillos valley during the wet and dry seasons by water table treatment. **b** net ecosystem exchange (NEE), **c** ecosystem respiration (ER), and **d** gross primary production (GPP). Symbols are averages of fluxes by treatment, error bars show standard error (SE)

area (0.4 ± 0.3 g C m^{-2} h^{-1}; $p = 0.005$). This difference remained even when comparing within a single genus: *Oreobolus* had higher production in the reference areas (2.5 ± 2.2 g C m^{-2} h^{-1}) than in the moderately drained/rewetted area (0.4 ± 0.32 g C m^{-2} h^{-1}; $p = 0.028$).

CO_2 fluxes

CO_2 fluxes varied among treatments and through time (Fig. 4). Throughout the study period, all treatments had a mean daytime CO_2 uptake by the ecosystem (i.e., positive NEE), except for 2 months in the highly drained area (Fig. 5a). The reference areas had the

Table 1 Plant abundance for species with average cover > 5% and percent cushion and non-cushion and bare ground cover at each plot (R1–R3, D1–D4). Each cover value is the mean of all four collars per plot over the three sampling dates

Species	Functional type	R1 (Ref.)	R2 (Ref.)	R3 (Ref.)	D1 (Rew.)	D2 (Rew.)	D3 (Rew.)	D4 (H. drained.)
Sphagnum spp.	Moss	2	6					
Distichia spp.	Cushion	36	11					
Oreobolus obtusangulus	Cushion	7	7	17	12	13	3	
Plantago tubulosa	Cushion		46	14	2	3		
Agrostis breviculmis	Graminoid							9
Calamagrostis spp.	Graminoid	13	1	12	10	6	14	6
Carex spp.	Graminoid			6	17	21	4	
Zameioscirpus sp.	Graminoid		18					
Lachemilla spp.	Herbaceous							65
Oritrophium limnophilum	Herbaceous	25	4	5	1	14	6	
Werneria nubigena	Herbaceous			10	7	21	6	
Total cushion (% cover)		43 ± 11.3	64 ± 6.6	31 ± 14.1	14 ± 12.5	16 ± 8.6	3 ± 12.9	0
Non-cushion (% cover)		66.8 ± 11.3	35.2 ± 6.6	43.0 ± 7.1	35 ± 14.4	62 ± 0.6	30 ± 10.7	80 ± 2.5
Bare ground (% cover)		8.0 ± 6.5	0	0	5.3 ± 0.8	33.3 ± 2.1	16.7 ± 6.1	2.5 ± 2.5

highest ecosystem uptake of 1.07 ± 0.06 g CO_2 m^{-2} h^{-1}, but was highly variable despite having a stable WT, likely related to variation in PAR. The moderately drained/rewetted area had an average ecosystem uptake of 0.86 ± 0.04 g CO_2 m^{-2} h^{-1} while the highly drained area had the lowest average fluxes (0.76 ± 0.11 g CO_2 m^{-2} h^{-1}). The moderately drained/rewetted area had an average ecosystem uptake of 0.55 ± 0.1 g CO_2 m^{-2} h^{-1} in the pre-restoration dry season, compared to 1.00 ± 0.24 g CO_2 m^{-2} h^{-1} in the post-restoration dry season. In the moderately drained/rewetted area, NEE generally increased when water table levels were closer to the soil surface ($R^2 = 0.25$, $p = 0.028$), approaching the reference area values (Fig. 5a). NEE also showed a marginally significant increase with increasing water table level in the highly drained area ($R^2 = 0.18$, $p = 0.065$). ER responded oppositely to increasing water tables by increasing in the highly drained area ($R^2 = 0.33$, $p = 0.015$) and decreasing in the rewetted areas ($R^2 = 0.20$, $p = 0.046$) (Fig. 5b). GPP response to water table also differed between the highly drained and rewetted areas, with a positive response to increasing water table ($R^2 = 0.38$, $p = 0.009$) in the former, and no significant trend in the latter (Fig. 5C).

Water table had a strong positive relationship with the GPP/|ER| ratio in the moderately drained/rewetted area (Fig. 6). Within the reference treatment, we found the highest values for GPP/ER and also high variation in the GPP:|ER| ratio despite stable water tables (Fig. 6). Water table had a strong positive relationship with the GPP/|ER| ratio in the moderately drained/rewetted plots and also showed a similarly high ratio and high variation when water table level was above ~ 20 cm depth, likely related to PAR—see next section. The highly drained area did not show a significant increase in its GPP:|ER| ratio with changes in water table.

Light response curves

For the pooled data from all dates and collars, light levels were a strong predictor of NEE, explaining over 30% of the variation in rates, with rates saturating (95% of maximum) at ~ 1900 and an overall ecosystem light compensation point of ~ 300 μmol CO_2 m^{-2} s^{-1} (Fig. 7a). For the light response curve experiment, we could not estimate a light saturation point (LSP) because we did not have enough points at the high end of the curve (Fig. 7b); however, we could

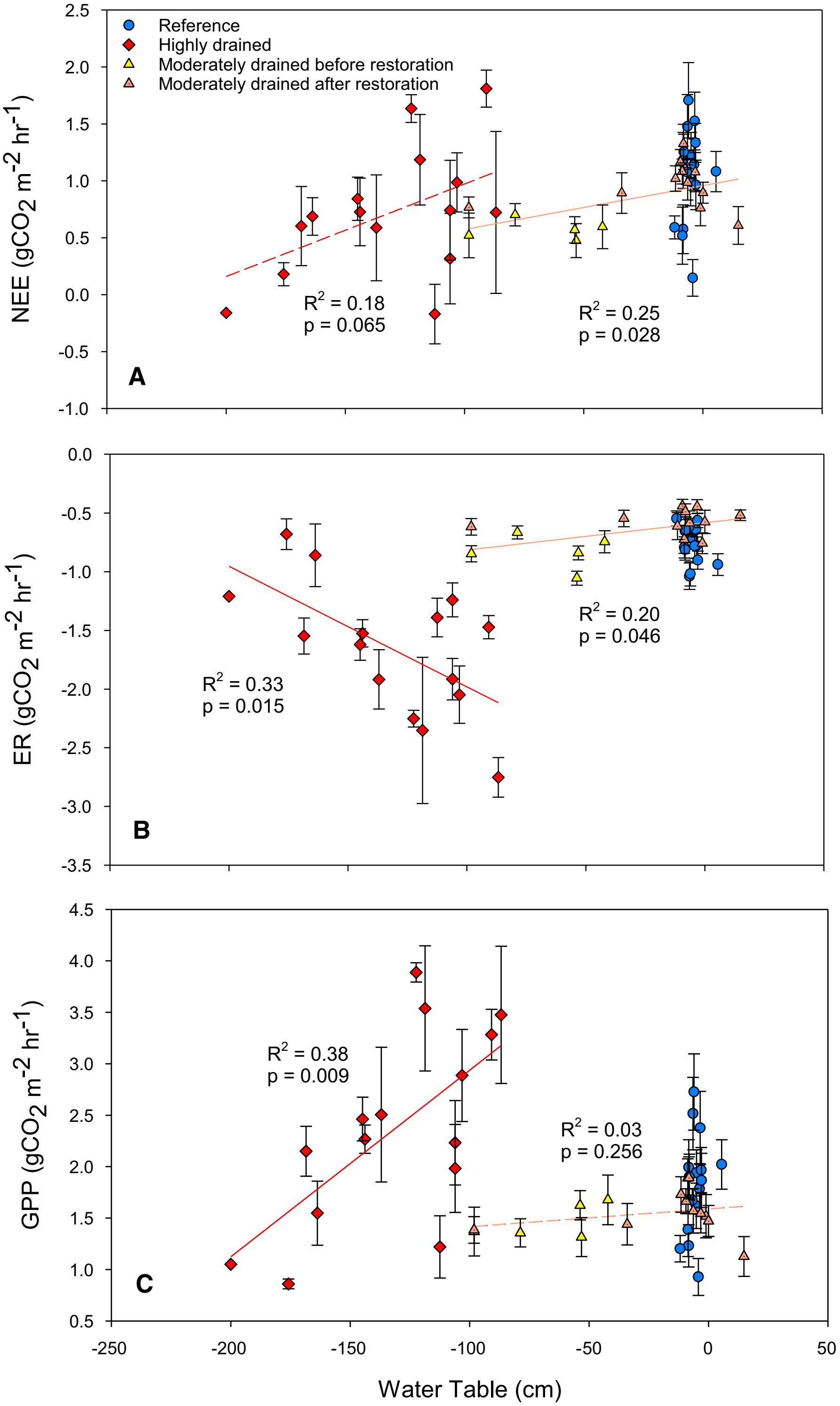


Fig. 5 Daytime CO_2 fluxes in relation to water table and drainage treatment: **a** NEE, **b** ER, and **c** GPP. Means are averages of fluxes by treatment and error bars represent standard error (SE). Regression lines show the relationship between CO_2 fluxes and water table for the unrestored (red line) and rewetted (orange line) treatments. Solid and dotted lines represent significant and non-significant regressions, respectively

estimate the light compensation point (LCP) by creating an equation using the NEE values for each collar, and solving for the PAR at which NEE = 0. We found that LCP was lowest in the reference and

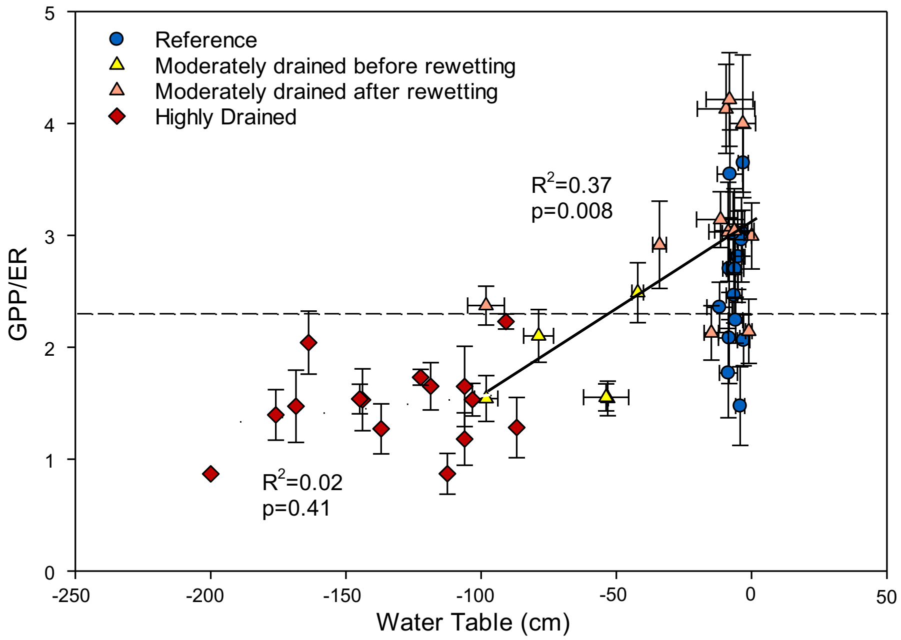


Fig. 6 Changes in instantaneous daytime GPP/ER ratio at different water table levels by treatment. Blue circles represent the averaged fluxes of the reference areas, yellow triangles the rewetted area before the restoration and the orange triangles the rewetted area after the restoration. Red diamonds represent the unrestored area. Error bars represent standard error (SE). Simple regression lines for the unrestored (dotted red line), and rewetted (solid orange line) treatments

moderately drained/rewetted areas, with a mean of 184 ± 117 and 324 ± 60 µmol CO_2 m^{-2} s^{-1} respectively while the highly drained area with lower water table levels had the highest light compensation point, 710 µmol CO_2 m^{-2} s^{-1} (Fig. 7c).

CH_4 fluxes

We measured very low CH_4 fluxes overall, averaging 2.76 ± 1.06 mg CH_4 m^{-2} day^{-1} across all dates and treatments. However, there appears to be a water table threshold at approximately − 10 cm above which CH_4 fluxes increase (Fig. 8). Below − 10 cm water table depth, the average CH_4 flux is − 0.07 ± 0.784 mg CH_4 m^{-2} day^{-1} and above − 10 cm water table depth, the average CH_4 flux is 5.58 ± 9.18 mg CH_4 m^{-2} day^{-1}.

Discussion

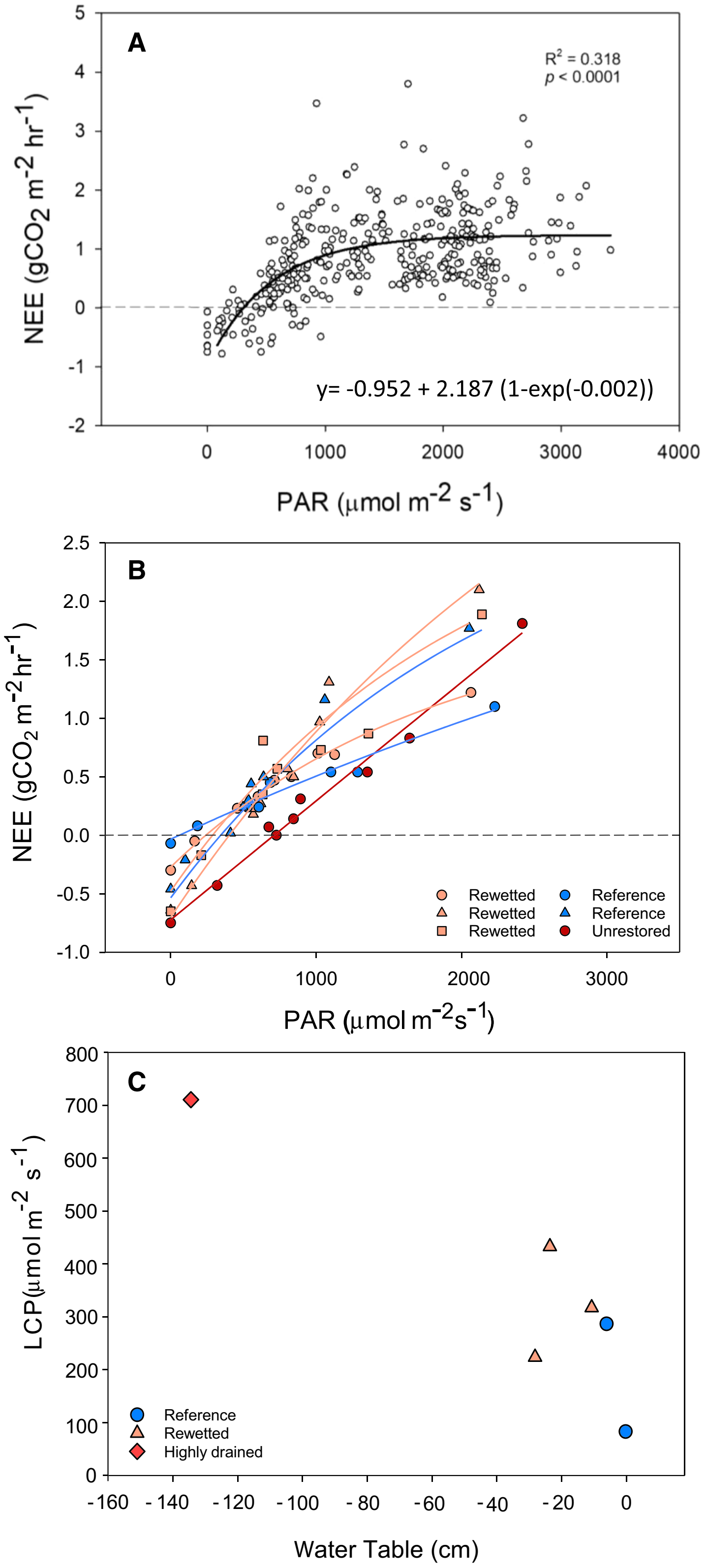
Hydrologically undisturbed sites

Even though there were large differences in precipitation amounts between the wet and dry seasons, the water table levels in the reference sites were high and stable. The stable water table levels, in combination with a moderately high pH of ~ 5.8 and specific conductivity of 146 µS cm^{-1} indicates that these are groundwater fed peatlands, or fens. Fens are the most common peatland type in mountains with bogs being limited to very high rainfall areas (Cooper et al. 2012). These results are similar to other studies that have found that undisturbed mountain fens have perennially stable water table levels (Cooper et al. 2012; Chimner et al. 2019a).

Our CO_2 flux values are the first measured in a mountain peatland in the humid *puna* ecoregion. At the reference sites average fluxes were 1.05 (NEE), 1.82 (GPP), and − 0.76 (ER) g CO_2 m^{-2} h^{-1}, slightly greater than reference conditions measured in an Ecuadoran *páramo* cushion plant of 0.69, 1.35, − 0.66 g CO_2 m^{-2} h^{-1}, respectively (Sanchez et al. 2017). However, our values are lower compared to mountain sedge fens in Colorado, which had greater NEE and GPP (1.74 g CO_2 m^{-2} h^{-1} and 2.85 g CO_2 m^{-2} h^{-1}), but lower ER (− 0.63 g CO_2 m^{-2} h^{-1}) (Schimelpfenig et al. 2014). Although our GPP values are lower than those found for temperate sedge fens, the growing season for temperate peatlands lasts ~ 4 months, whereas plants in the tropics grow all year long, so annual carbon fluxes would be relatively greater in the tropical peatlands.

CH_4 emissions in the wet undisturbed areas were very low (7.06 ± 3.42 mg CH_4 m^{-2} day^{-1}), comparable to the findings of Sánchez et al. (2017) in a

Fig. 7 Peatland net ecosystem exchange of CO_2 in response to light. **a** Light response curve for net ecosystem exchange of CO_2 for all plots during the study period, except September 2015 to January 2016 when PAR sensor was not working. **b** Light response curves of each of the collars assessed in the light response experiment for three months in the dry season. **c** Light compensation point for net ecosystem exchange of CO_2 estimated in the light response experiment versus water table



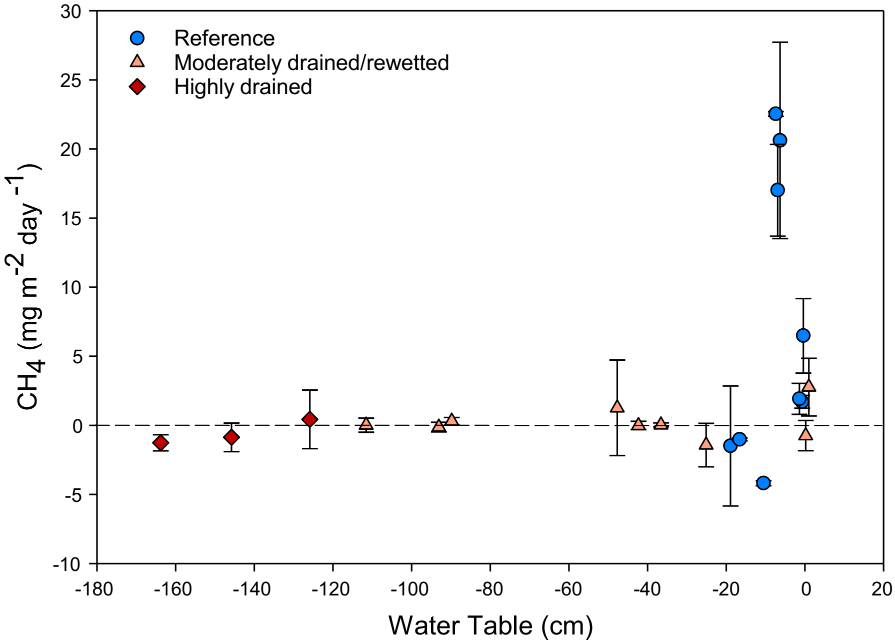


Fig. 8 CH_4 fluxes versus water table from May 2016, July 2016 and August 2016 in all treatments in a peatland carbon cycling experiment in the páramo of Peru

cushion peatland in Ecuador (8.1 ± 1.17 mg CH_4 m^{-2} day^{-1}). These rates are lower than those reported for northern temperate and boreal peatlands (Turetsky et al. 2014; Abdalla et al. 2016; Strack et al. 2016), but higher than those of Fritz et al. (2011) in a temperate cushion peatland in Patagonia where they found zero CH_4 emissions. Low CH_4 fluxes might be explained by vegetation communities present in the area, especially cushion plants and sedges, which have deep roots that transport oxygen deep in the soil, making it available to oxidize the CH_4 produced by methanogens (Fritz et al. 2011).

Response to water table drawdown

The water table level was correlated with ER. The maximum ER occurred when the water table was ~ 1–1.5 m below the soil surface and was lowest when the water table was near the soil surface. The higher ER at lower water table levels is likely due to unsaturated peat allowing increased oxygen diffusion, increasing microbial activity and decomposition (Jaatinen et al. 2008). This pattern is commonly seen in ditched or hydrologically altered peatlands (Chimner and Cooper 2003b; Strack et al. 2006; Riutta et al. 2007; Makiranta et al. 2009; Schimelpfenig et al. 2014). ER also decreased as the water table further dropped to ~ 2 m below the soil surface. This pattern is likely caused to the peat becoming too dry and suppressing plant and microbial respiration. Although this phenomenon has not been explored previously in mountain peatlands, a study conducted in a forested peatland in Alaska discovered that microbial activities decreased up to 50% after a prolonged drought (Allison and Treseder 2008).

Lower water table levels in the drained areas likely resulted in a change in plant species and GPP. Specifically, cushion plants were most abundant in the wetter areas and were absent in the driest areas. In the reference and moderately drained areas, GPP was lower at lower water table levels. However, GPP was greater in the highly drained area due to conversion to non-wetland plants.

Although we did not attempt to develop a full carbon budget to assess if these peatlands were storing or losing carbon, the results do indicate that despite the higher GPP in the highly drained area, the reference sites have a more positive carbon balance (i.e., either gained more, or lost less carbon) than the drained treatments, as indicated by lower NEE and the GPP:ER ratio and the light compensation point analysis. Although our results are based on daytime flux rates, the low GPP:ER ratios of the drained area suggest that this area is more likely than the other locations to be a net carbon source when considered on a 24-h basis.

CH_4 emissions were lower at lower water table levels, confirming our hypothesis. However, the steep threshold in the water table-CH_4 relationship deviates from the pattern shown in a global analysis of CH_4 emissions from lowland peatlands (Turetsky et al. 2014). This could be because dry conditions during the CH_4 measurement period (May-August 2016) led to drying of the surface peat, favoring methanotrophy over methanogenesis. Alternatively, cushion plants have deep aerenchymatous roots that transport oxygen to the deep peat and could also stimulated CH_4 oxidation. Consistent with this hypothesis, Fritz et al. (2011) found zero emissions of CH_4 at a water table level of ~ − 12 cm. For cushion plants to be the cause of such a dramatic effect, they should have demonstrably higher radial oxygen loss rates than sedges, which often stimulate CH_4 efflux. Lastly, it is possible that the lower temperatures in high Andean cushion peatlands favors methanotrophs over methanogens.

Response to water table restoration

Ditching, which is common in many mountain fens (Cooper et al. 1998; Patterson and Cooper 2007; Hartman et al. 2016), lowers the water table causing subsidence, peat oxidation (Schimelpfenig et al. 2014), increases in dissolved organic carbon export (Hribljan et al. 2015), and altered vegetation composition (Cooper et al. 1998). Mountain fens are particularly susceptible to ditching because they are often sloping and dominated by groundwater inputs (Chimner et al. 2019a). Blocking ditches can be an effective restoration method in mountain peatlands as the water table level typically increases after installation of ditch plugs and can match reference water table depths (Patterson and Cooper 2007; Cooper et al. 1998; Schimelpfenig et al. 2014; Chimner et al. 2019a). Although blocking ditches on sloping fens is more complicated than in low gradient peatlands (Chimner et al. 2017), it can be successful if done correctly (Schimelpfenig et al. 2014; Hartman et al. 2016; Green et al. 2017; Chimner et al. 2019a). However, determining the effect of restoration was complicated in this study by the co-occurrence of the initiation of the restoration treatment with the beginning of the wet season and the logistical constrain of not having a long enough pre-monitoring period. However, it did appear that ditch blocking was successful in raising the water table. During the wet season, water flowing down the ditch backed up behind the plugs and rewet the peat near the ditch. The restoration also appeared to rewet conditions in the dry season as water tables post-restoration were ~ 30 cm higher than they were pre-restoration. A supplemental visit to the site in August of 2019 (almost 4 years after ditch blocking) showed that the ditch plugs were intact and still functioning as designed. Water table levels in the reference sites, highly drained site, and the moderately drained/rewetted area were all very similar to measurements in 2016. We were not however able to bring the water table levels up in the ditched area during the dry season to match the reference conditions. We hypothesize that the local hydrology in this section of the fen was also being modified by the construction of the nearby road since a large area of this side of the fen, even away from the ditch, had very low water table levels compared to the sections of the fen on the opposite side of the valley. Peatlands, and especially mountain peatlands, can be susceptible to hydrological alteration from roads (Patterson and Cooper 2007, Chimner et al. 2017), and further investigation into the effects of the road are needed to document changes. The ditch plugging was also successful in slowing down the water in the ditch, which will help with long term erosion which is important since the ditch was downcutting into 4 m thick peat.

Re-wetting by ditch blocking has also been found to restore carbon cycling and improve carbon accumulation rates (Strack et al. 2014; Munir et al. 2014; Laine et al. 2019). Our results indicate that rewetting increased NEE and the ability to store carbon to near reference conditions. This was also found in Colorado mountain fens that were restored as NEE increased from 1.3 to 2.2 g CO_2 m^{-2} h^{-1} after ditch plugs were installed (Schimelpfenig et al. 2014). Although our study was short-term, in the long-term re-wetting the site will hopefully lead to changes in vegetation, reflecting the new wetter conditions (Cooper et al. 1998). However, not all ecosystem processes are quickly restored. For instance, soil physical structure (e.g., bulk density, hydraulic conductivity) may take decades or longer to recover after ditch restoration (Schimelpfenig et al. 2014). Given the short-term nature of the study, conclusions about long-term impacts of restoration await future studies.

Light response implications for climate interactions with drainage

Instantaneous light compensation points were fairly high, even in the reference areas. Additionally, drainage appeared to increase the light compensation point for NEE, making ecosystems especially sensitive to changes in cloud cover and insolation. Hence changes in cloud cover could have a significant effect on carbon balance, independent of effects on water tables. It is possible that climate change could drive shifts in cloud cover. Cloud cover appears to be increasing in the northern tropical Andes, but decreasing in the southern tropical Andes. However, increases in cloudiness in the northern (Colombian) Andes are mostly at lower elevations, with decreases at higher elevations (Carrascal et al. 2011). These climate change mediated shifts in cloud cover and precipitation could lead to shifts in peatland carbon balance, with potential positive impacts in areas with decreasing cloud cover such as southern Peru and Bolivia, as long as climate effects on hydrology do not negate those effects. Wetland area has actually increased in the Bolivian Andes, attributed to changes in precipitation intensity and glacier melt additions of water (Dangles et al. 2017), although neither insolation nor cloud cover was considered in their analysis. Thus, all things being equal increased insolation should have positive impacts on carbon balance. However, given the climate trend in central Peru, increased insolation is likely to be accompanied by lower water tables and greater water stress, exacerbating drainage effects on carbon balance and plant communities.

Conclusions

In conclusion, our results indicate that Andean cushion plant fens, similar to other mountain fens, are sensitive to changes in hydrology, but restoration has the potential to shift carbon cycling toward reference conditions. Ditch blocking partially restored hydrology and C cycling, suggesting that it can be useful as one of a suite of tools for restoration in this ecosystem type. Additionally, the high light compensation points, and the sensitivity of light response functions to water table, point to a strong sensitivity of Andean mountain peatland carbon balance to combined effects of change in cloud cover and hydrology. Hence, climate-change effects on insolation and water table are likely to exacerbate impacts of drainage on these ecosystems, especially in areas where cloud cover increases, highlighting the increasing importance of hydrologic restoration to the long-term viability of Andean mountain peatlands.

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