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ORIGINAL PAPER

Peatland carbon stocks and accumulation rates in the Ecuadorian páramo

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Abstract The páramo is a high altitude tropical Andean ecosystem that contains peatlands with thick horizons of carbon (C) dense soils. Soil C data are sparse for most of the páramo, especially in peatlands, which limits our ability to provide accurate regional and country wide estimates of C storage. Therefore, the objective of our research was to quantify belowground C stocks and accumulation rates in páramo peatland soils in two regions of northeastern Ecuador. Peatland soil cores were collected from Antisana Ecological Reserve and Cayambe-Coca National Park. We measured soil C densities and ^{14}C dates to estimate soil accumulation rates. The mean peatland soil depth across both regions was 3.8 m and contained an estimated mean C storage of 1282 Mg ha^{-1}. Peatlands older than 3000 cal. year BP had a mean long-term C accumulation rate of 26 g m^{-2} $year^{-1}$, with peatlands younger than 500 cal. year BP displaying mean recent rates of C accumulation of 134 g m^{-2} $year^{-1}$. These peatlands also receive large inputs of mineral material, predominantly from volcanic deposition, that has created many interbedded non-peat mineral soil horizons that contained 48 % of the soil C. Because of large C stocks in Ecuadorian mountain peatlands and the potential disturbance from land use and climate change, additional studies are need to provide essential baseline assessments and estimates of C storage in the Andes.

Keywords Peatland · Páramo · Carbon · Accumulation rates · Tuberas

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Introduction

The páramo of Ecuador is a humid, high altitude Andean ecosystem with cool temperatures where the landscape has been shaped by glacial activity, tectonic uplift, and an active volcanic history (Balslev and Luteyn 1992). The resulting topography and climate of the páramo is suitable to the formation of wetlands that accumulate thick horizons of organic soil, or "peat", and mineral soils rich in organic carbon (C) (Chimner and Karberg 2008). These mountain peatlands are termed tuberas in the Northern Andes and bofedales in the Central and Southern Andes. The soils are formed from unique páramo vegetation communities (Bosnian et al. 1993; Cooper et al. 2010) that are typically composed of low-stature plants with low aboveground biomass. As a result, almost the entire ecosystem C pool is stored belowground in their soils.

The South American Andean páramo extends north of Ecuador into Colombia and Venezuela and south into the northern reaches of Peru covering a latitudinal range of approximately 11° north to 8° south (Buytaert et al. 2006). The páramo includes an estimated area of 35,000 km^2 and has an altitudinal range from just above the continuous tree line up to the permanent snow line (Balslev and Luteyn 1992). Wetlands throughout the páramo are experiencing greater resource demands including grazing, agriculture, mining, and hydrological diversions (Benavides 2014). Of particular concern is the enormous human consumption of water from the páramo with unknown effects on long-term sustainability (Buytaert et al. 2006; Buytaert and De Bièvre 2012). Furthermore, climate change is predicted to affect precipitation patterns and increase annual mean temperatures throughout the Andes (Buytaert et al. 2006; Michelutti et al. 2015; Vuille et al. 2008). The combined influence of these disturbances on Andean peatlands has the potential to reduce soil water retention, increase soil erosion, change vegetation structure, and cause increased rates of organic soil decomposition (Holden and Burt 2002; Buytaert et al. 2006; Buytaert et al. 2011; Urbina and Benavides 2015). The resulting changes to peatland function will reduce ecosystem services that are essential to the páramo environment and local populations including wildlife habitat, water supplies, native vegetation diversity, and loss of sustainable grazing pasture. Moreover, these activities could threaten the C stability of Ecuadorian peatlands, transforming them from a long-term C sink to a C source. Therefore, to provide a benchmark for studies of contemporary C cycling, it is essential that we evaluate the potential of these peatlands to store and accumulate C over the centuries to millennia since their formation.

Soil C data are sparse for most of the páramo and if collected, typically only quantify the upper surface of well-drained soils (e.g. Farley et al. 2004; Poulenard et al. 2003; Tonneijck et al. 2010). Only a few studies have measured C stocks and rates of C accumulation in tropical mountain peatlands (Chimner and Karberg 2008; Hribljan et al. 2015). Temperate mountain peatlands are known to contain on average 1200 Mg C ha^{-1} with a C accumulation rate of 20–25 g m^{-2} $year^{-1}$ (Chimner 2000; Cooper et al. 2012). In contrast, recent C inventories in lowland Amazonian tropical peatlands have shown they harbor on average greater C pools (1397 Mg ha^{-1}) (Draper et al. 2014) and display faster rates of C accumulation (39–85 g m^{-2} $year^{-1}$) (Lähteenoja et al. 2009). We might expect similarly high rates of C storage and long-term accumulation in tropical mountain peatlands than temperate alpine peatlands, because the perennially cool and wet alpine climate would stimulate year-round production while inhibiting decomposition. However, it is unknown if low temperatures, photosynthetic limits to production, and multiple mineral inputs into tropical mountain peatlands (Chimner and Karberg 2008; Schittek 2014; Cooper et al. 2015; Hribljan et al. 2015) not typical for lowland tropical peatlands might inhibit long-term C accumulation.

Given the limited baseline information and intense human pressures on mountain peatlands in Ecuador, it is important to understand the long-term potential for C storage and accumulation in these ecosystems. This lack of data on Andean peatland C dynamics limits our ability to provide accurate regional and countrywide estimates of C storage in the páramo. In addition, inventorying C stocks, accumulation rates, and spatial distribution of Ecuadorian alpine peatlands will provide essential data that can support efforts to conserve and restore degraded peatlands across the greater páramo complex. The objective of this study was to quantify soil C pools and C accumulation rates in páramo peatland soils in northeastern Ecuador. We asked three questions: (1) What are the C stocks in these ecosystems and how do they compare with other peatlands? (2) What is the age of these peatlands? and (3) What are the long-term rates of C accumulation in these peatlands.

Methods

Study sites

This study was conducted in the páramo ecoregion of northeastern Ecuador. We sampled six peatlands in the Cayambe-Coca National Park (CCNP) (C1–C6) and two peatlands in an area abutting and one within the Antisana Ecological Reserve (AER) (A1–A3) (Fig. 1). Both areas are located in the Eastern branch of the Ecuadorian Andes, at altitudes between 3919 and 4880 m. Between 2007 and 2013, precipitation data for CCNP at 3920 m ranged from 1066 to 1401 mm year^{-1}, with mean daily temperatures of 6.7 °C. The region of AER is slightly drier, with an annual precipitation that averaged 781 mm year^{-1} between 1987 and 2007, and mean daily temperatures of 6.5 °C. Precipitation data does not include horizontal precipitation (cloud or mist interception by vegetation), which can be significant across this region of the páramo.

Our study site in CCNP is part of the Chacana caldera, a large volcanic complex with a North–South diameter of approximately 50 km. Earliest volcanic activity for this caldera has been dated at 2.5–2.7 million year BP, while the most recent events occurred only 200–300 year BP (Hall and Mothes 2008). The AER is part of the Antisana volcanic complex that also had its latest activity between 200–300 years ago.

Both CCNP and AER have experienced turbulent histories of volcanic activity, especially between 4000 and 1500 year BP, a time when this area was subject to several volcanic eruptions from Cotopaxi, Cayambe, Guagua Pichincha, and Quilotoa volcanoes (Hall et al. 2008). Additionally, these sites were impacted by at least two large recent events. The 800 year BP eruption of Quilotoa that covered large areas of the Northern Ecuadorian Andes with thick deposits of ash and the eighteenth century activity of the Chacana caldera (Mothes and Hall 2008; Hall et al. 2008). In addition to an active volcanic history, both areas (CCNP and AER) were shaped by the last glacial period that carved deep valleys and left countless lakes

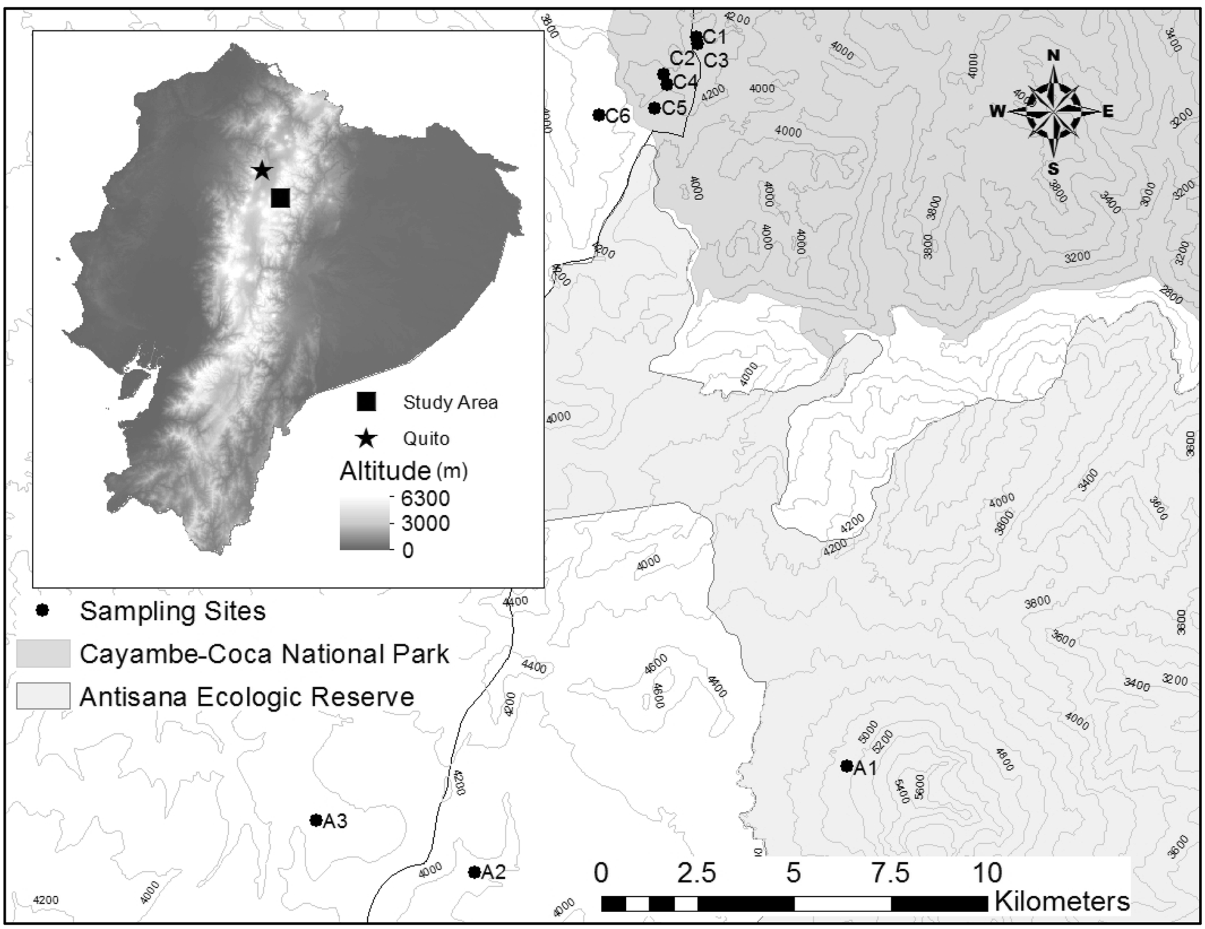


Fig. 1 Peatland core locations in Antisana Ecological Reserve (sites A1–A3) and Cayambe-Coca National Park (sites C1–C6). Inset map shows altitudinal range of Andean mountains in Ecuador and location of study area in relation to the capital, Quito

and ponds, interspersed on a complex topography (Schubert and Clapperton 1990; Jomelli et al. 2009).

Sites were chosen to capture an altitudinal gradient (3900–4800 m) and are distributed across a diverse matrix of páramo vegetation communities that includes grassland, scrublands, wetlands, and small pockets of high Andean forests (Table 1). Páramo ecosystems can display pronounced shifts in ecological form and function across short environmental gradients. All sites sampled in CCNP exhibited negligible signs of human disturbance; however, the two lower sites at AER (A2 and A3) have experienced a long history (>200 year) of cattle grazing, which is evident as bare soil patches, damaged vegetation, and cattle dung. Vegetation communities at CCNP displayed distinctive changes over a narrow altitudinal range. The lower sites (C5 and C6) are dominated by brown mosses and low herbaceous plants (*Disterigma empetrifolium*, *Hypericum lacioides*, *Ranunculus* spp.) interspersed with tussock grasses (*Calamagrostis* sp. and *Cortaderia nitida*), while higher sites (C1–C4) had a larger proportion of cushion plants dominated by *Plantago rigida* (Plantaginaceae) and *Distichia muscoides* (Juncaceae) (Fig. 2). Although our AER sites did not display this altitudinal pattern in vegetation, it is unknown if this difference between the two regions is due to natural environmental factors or cattle grazing.

Soil core sampling and carbon analyses

Single full length cores were extracted from each of the nine sites. Coring sites were selected by probing the soil across the peatland in a grid pattern. Coring location should be offset from the deepest area of the mountain basin formation that contains the peatland if substratum lake sediment is detected by probing. An error in dating peatland initiation can result from peat infilling processes because the peatland will start to develop at the edge of the lake. However, all of the sampled peatlands were underlain with mineral sediments; therefore, we cored the deepest section of the peatland. The upper 100 cm of the peatlands was cored with a 6.35 cm diameter open faced gouge auger to avoid compaction of the surface peat (AMS, Inc., American Falls, ID; modified from a stock auger with a larger head stock to create a uniform volume down the length of the auger). Deeper core sections were sampled with either a Russian peat borer (Aquatic Research Instruments, Hope, ID, USA) or for extremely dense peat the gouge auger. Our goal was to sample the full peat profile down to the underlying substratum. Separate holes 25 cm deep were augured (3–4 for each peatland) to measure the mean peatland pore water pH (YSI model 63, Yellow Springs, Ohio, USA).

Once collected, soil was cut into ~5–10 cm sections (thickness varied based on visual evidence of high concentrations of mineral or volcanic material that were isolated) in the field. Core sections were immediately placed in soil tins or whirl-pak bags. Samples were transported to Michigan Technological University Wetlands lab, USA. Soils were dried in a convection oven at 65 °C until a constant mass was obtained. Dry bulk density (g cm^{-3}) was calculated by dividing the oven dried soil mass by the original sample volume determined from the corer/auger volume. Samples were then ground and homogenized to a fine powder with a ball mill (SPEX 8000 M, Metuchen, NJ, USA), re-dried at 65 °C to a constant mass, and stored in airtight plastic whirl-pak bags until C analyses. Soil organic matter content was

Table 1 Site descriptions of peatlands sampled at Antisana Ecological Reserve (A1–A3) and Cayambe-Coca National Park (C1–C6). Vegetation type represents the dominate plant functional group across each peatland

Site	Latitude	Longitude	Elevation (m)	pH	Veg type
A1	−0.480641	−78.157162	4881	5.3	Cushion
A2	−0.505500	−78.244067	4064	5.9	Cushion
A3	−0.493453	−78.281074	3920	n.a.	Cushion
C1	−0.310410	−78.192390	4270	5.7	Cushion
C2	−0.319160	−78.200011	4270	n.a.	Cushion
C3	−0.312090	−78.192260	4254	5.5	Cushion
C4	−0.321430	−78.199300	4250	5.4	Cushion
C5	−0.327000	−78.202100	4136	5.1	Graminoid
C6	−0.328749	−78.215196	3919	6.2	Graminoid

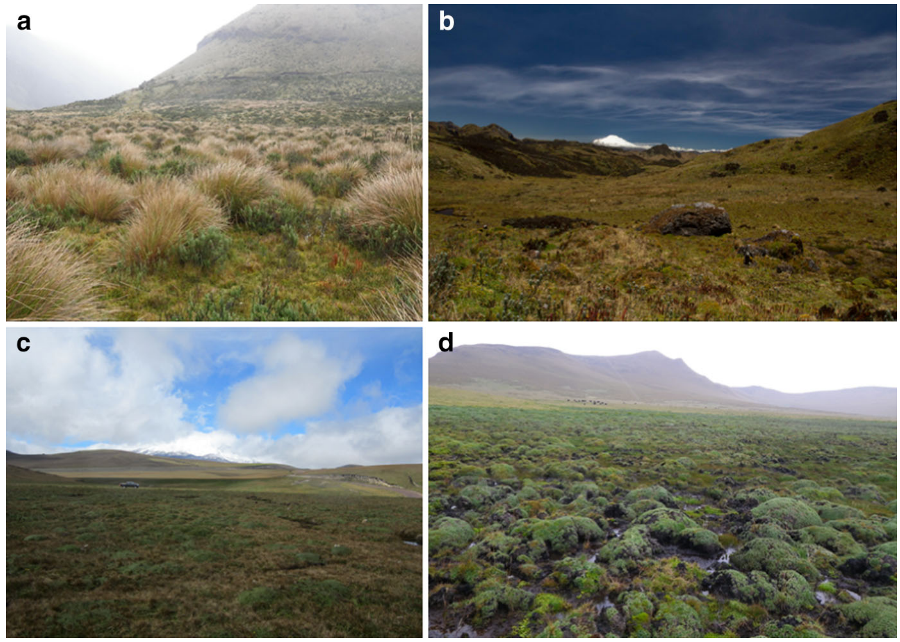


Fig. 2 Andean high altitude peatlands in the páramo of northeastern Ecuador with low-stature vegetation. **a** A graminoid dominate peatland (site C6) and **b** a cushion plant peatland (site C3) in Cayambe-Coca National Park. **c**, **d** Cushion plant peatlands in Antisana Ecological Reserve (sites A2 and A3, respectively). Picture of site A3 (**d**) shows intensive disturbance to the surface of the peatland from cattle use. (Color figure online)

determined on a ~1 g subsample of the ground soil for all core sections by loss on ignition (LOI) at 550 °C for 5 h (Chambers et al. 2011). A subset of 400 samples was analyzed for C with an elemental analyzer (Costech 4010, Valencia, CA, USA and Fisons NA 1500, Lakewood, NJ, USA). The line equation C (%) = (0.5324 × LOI (%)) − 0.9986 ($R^2 = 0.989$; $p < 0.001$) was developed on the relationship between LOI and C to calculate C content in the remaining samples not analyzed by elemental analysis. Carbonates are reported to be absent in páramo volcanic soils, therefore, total soil C is assumed to equal soil organic C content (Tonneijck et al. 2010). The cores contained many sections that are below the general guidelines of peat that is defined as soils containing a % C content greater than 12 % C when clay is not present (Soil Survey Staff 1975). Regression lines for the mineral and peat soil samples did not have significantly different slopes so were combined to develop the C to LOI relationship. Carbon density for each core section was calculated as the product of dry bulk density, sample length, and sample % C. Total peatland C stock (Mg ha^{-1}) was estimated by scaling up the sum of all individual soil samples in the entire core profile. We report the C content in the mineral and peat soils and the contributions of each to the overall belowground C stocks in the peatland. In addition, where coring was continued below the base of the peatland, estimates are presented for C stocks in the substratum soils.

Peatland age and accumulation rates

Peatland basal soil samples and samples from multiple depths from each core were analyzed for bulk ^{14}C dating. Bulk soil samples were graphitized in preparation for ^{14}C measurement at the Carbon, Water & Soils Research Lab in Houghton, Michigan. After grinding, samples were dried, weighed, and placed into quartz tubes and sealed under vacuum. Samples were combusted at 900 °C for 6 h with cupric oxide (CuO) and silver (Ag) in sealed quartz test tubes to form CO_2 gas. The CO_2 was then reduced to graphite through heating at 570 °C in the presence of hydrogen (H_2) gas and an iron (Fe) catalyst (Vogel et al., 1987). Graphite targets were then analyzed for radiocarbon abundance using an accelerator mass spectrometer (Davis et al., 1990) at Lawrence Livermore National Lab and corrected for mass-dependent fractionation using measured $\delta^{13}C$ values according to Stuiver and Polach (1977). The radiocarbon dates were calibrated to calendar dates (cal. year BP, BP = 1950) (Stuiver and Reimer, 1993 (version 5.0) using a southern hemisphere correction curve (McCormac et al. 2004).

The ca. modern ^{14}C date from the A1 core of depth 45–50 cm was calibrated with CALIBomb (Hogg et al. 2013) using a southern hemisphere correction (Hua et al. 2013). Median value of the 2σ calibration range for each date is reported and used in calculating accumulation rates (Table 2).

The peatland long-term apparent rate of C accumulation (LARCA) (g m^{-2} $year^{-1}$) for the peat soils and the entire core (peat and mineral soils), soil mass, and thickness for each core were determined from the line slopes (not forced through zero) of each parameter plotted versus the ^{14}C dates (minimized sum of squares of differences). For peatlands that are younger than 500 year we designated them as exhibiting a recent rate of C accumulation (RERCA).

Results

The peatlands had large amounts of non-peat material throughout the cores. Peat was present at the top of all cores, but most sites had many layers of non-peat soils and peat intermixed down the core profile (Figs. 3, 4). The heterogeneous soil horizons throughout the cores made identifying the bottom of the peatlands difficult. Our working definition of the bottom of the peatland is when we encountered a rock substratum or there was a noticeable change in the trajectory of the long-term rate of C accumulation. Carbon accumulation rates in some of the sites showed abrupt changes from a slow rate in substratum soils to considerably faster rates in the overlying peatland confirming the bottom of the peatland.

Two cored peatlands, A1 and C1, were very young (<500 cal. year BP) and shallow with thicknesses of 100 and 70 cm, respectively (Table 3). Thickness varied between 294 and 605 cm across the rest of the sites (Fig. 5), with basal ages ranging between 3412 and 8270 cal. year BP. The mean vertical growth rate across all sites was 1.65 mm $year^{-1}$ (0.45–8.05 mm $year^{-1}$) with a mean soil accumulation rate of 0.85 kg m^{-2} $year^{-1}$ (0.13–5.46 kg m^{-2} $year^{-1}$). As a result, the peatlands have a mean soil mass of 1468 kg m^{-2} (98–2994 kg m^{-2}) (Table 3; Fig. 5).

The C content of peat varied across sites, ranging between 19.1 and 30.0 %, with a mean of 23.1 % (Table 3). Mineral soil C content also varied across the sites, ranging between 3.1 and 8.3 %, with a mean of 6.0 %. Mean dry bulk density of the peat was 0.21 g cm^{-3} (0.14–0.27 g cm^{-3}), while the mean dry bulk density of the mineral soil was 0.58 g cm^{-3} (0.46–0.91 g cm^{-3}).

Total C stored in the peat layers (excluding interbedded mineral horizons) was low in the two youngest, shallow sites (A1 = 128 Mg ha^{-1}, C1 = 245 Mg ha^{-1}) (Table 3) and averaged 898 Mg ha^{-1} (535–1347 Mg ha^{-1}) in the sites >3000 cal. year BP. Total C stored in the interbedded mineral layers of the peatlands averaged 610 Mg ha^{-1} (151–1118 Mg ha^{-1}). Total soil C (peat + interbedded mineral soil) averaged 1282 Mg ha^{-1} (245–2025 Mg ha^{-1}). Sites A1 and C1 have RERCA values of 224 and 43 g m^{-2} $year^{-1}$, respectively. The mean LARCA across all peatlands older than 3000 cal. year BP is 26 g m^{-2} $year^{-1}$.

Discussion

Peatland thickness and carbon stocks

This is the first study to characterize peatland depth, age, and C accumulation rates across multiple geographic regions and altitudes in the Ecuadorian high altitude páramo. The mountain peatlands we sampled in the northeastern region of Ecuador have deep and dense soils with large C pools. The mean peatland soil depth across both regions (CCNP and AER) for sites older than 3000 cal. year BP was 4.6 m and contained an estimated mean C storage of 1573 Mg ha^{-1}. We were unable to core the full depth of the C4 and C6 peatlands because of impenetrable soil horizons; therefore, these data represent conservative estimates of belowground C pools. In comparison, mountain peatlands in Colorado, USA are on average 8000 years old and have an average soil C storage of 1200 Mg ha^{-1} (Chimner 2000; Cooper et al. 2012). The youngest peatlands (A1 and C1) with ages of less than 450 cal. year BP are less than 1 m deep and have accumulated 279 and 245 Mg C ha^{-1} respectively in their soils.

These data indicate that peatlands are the largest C sink on a per area basis recorded for any ecosystem type in the Ecuadorian páramo (Farley et al. 2004; Tonneijck et al. 2010). However, the contribution of tuberas to páramo and total Andean C stocks awaits

Table 2 Radiocarbon ages (^{14}C) corrected for mass-dependent fractionation using measured $\delta^{13}C$ and calibrated ages (cal. year BP, BP = 1950) for cores A1–A3 and C1–C6. Median value of the 2σ calibration range for each calibrated date is reported

	[a]CAMS #	Depth (cm)	$\delta^{13}C$	^{14}C age	±	Cal. year BP	Median −2σ	Median +2σ
A1	165246	45–50	−25.03	>Modern	–	1955[b]	1956[b]	1955[b]
A1	165247	95–100	−24.40	165	30	118	1	153
A2	164730	45–50	−25.98	140	25	96	1	145
A2	164731	65–70	−25.01	790	30	686	649	734
A2	168744	110–115	−25.20	1375	25	1269	1258	1301
A2	164733	145–150	−26.28	2305	35	2252	2159	2271
A2	164734	175–180	−25.22	2485	25	2497	1605	1740
A2	164736	245–250	−25.30	3300	25	3485	3397	3568
A2	164737	295–300	−25.43	4065	25	4484	4419	4571
A2	164738	345–350	−25.80	4970	30	5654	5597	5731
A2	164739	430–435	−25.00	5915	40	6694	6561	6792
A2	164740	445–450	−25.44	6115	25	6931	6842	7012
A2	168473	505–510	−25.30	6520	30	7380	7313	7459
A2	164741	535–540	−25.75	6965	25	7747	7680	7829
A2	164742	580–585	−24.59	9515	30	10,715	10,584	10,793
A3	168485	295–305	−25.20	4635	25	5313	5275	5330
C1	168474	65–70	−24.20	460	30	490	448	521
C1	168475	295–300	−23.40	4625	25	5302	5269	5327
C2	168483	51–60.2	−25.00	790	30	685	655	729
C2	168746	145.4–147	−24.90	2285	25	2235	2159	2272
C2	168747	234–244	−25.90	3740	25	4036	3961	4101
C2	168484	376–386	−24.80	7270	30	8036	7968	8076
C3	168748	170–180	−24.60	1000	30	857	797	926
C3	168749	300–310	−23.80	1510	30	1348	1305	1384
C3	168486	490–500	−26.50	3215	25	3412	3343	3480
C4	168745	340–350	−25.20	3365	25	3550	3466	3635
C5	165219	45–50	−25.84	430	30	466	438	507
C5	165220	75–80	−26.56	875	30	739	682	798
C5	165221	95–100	−26.65	1020	25	860	802	874
C5	165222	145–150	−26.18	1365	30	1241	1185	1296
C5	165224	260–265	−26.73	2570	30	2605	2489	2645
C5	165225	295–300	−26.13	2720	30	2784	2747	2850
C5	165226	345–350	−26.97	3340	35	3524	3446	3633
C5	165227	390–395	−26.40	4035	35	4481	4406	4584
C5	165228	445–450	−26.33	4460	40	5007	4863	5074
C5	165230	495–500	−26.02	5540	45	6299	6208	6400
C5	165232	595–600	−26.07	7490	60	8270	8161	8393
C5	165233	635–640	−26.51	9550	90	10,837	10,567	11,152
C6	168476	40–50	−26.60	275	30	292	272	327
C6	168477	80–90	−25.70	785	25	679	657	724
C6	168478	255–260	−25.60	3285	30	3466	3388	3561
C6	168479	398–400	−26.20	5385	25	6123	6000	6212
C6	168480	615–620	−25.70	7005	30	7792	7693	7865

[a] The CAMS# is the sample reference number from the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory

[b] Values expressed in cal. yr. AD due to the fact that the sample could be younger than 1950 AD. One sigma values were selected for this sample using the age of the peat below to constrain the most probable age of the stratum

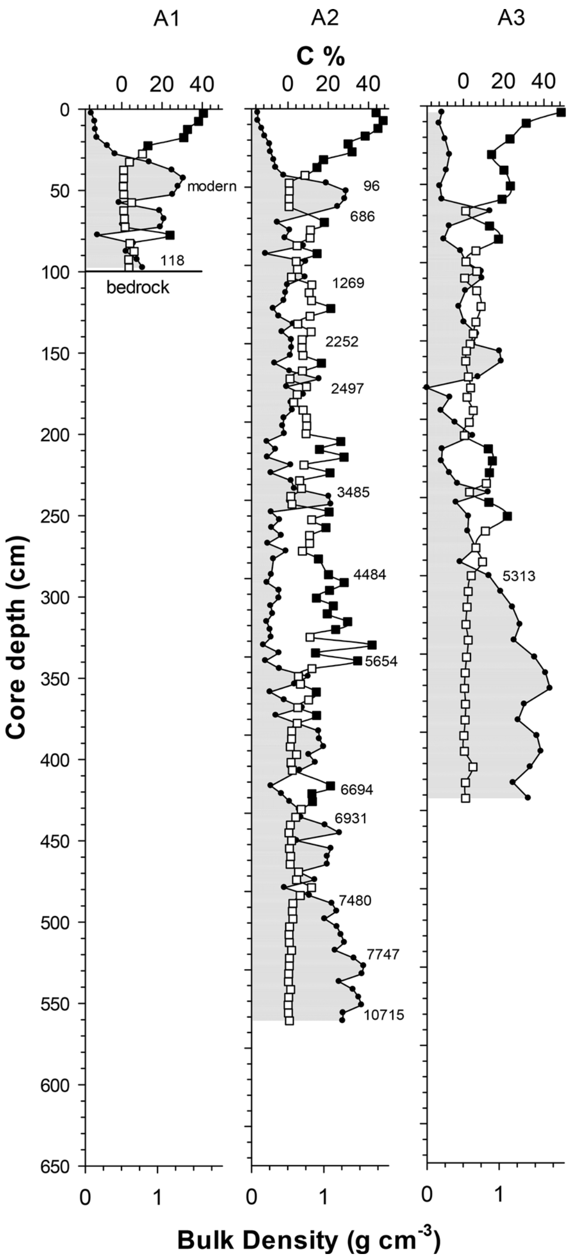


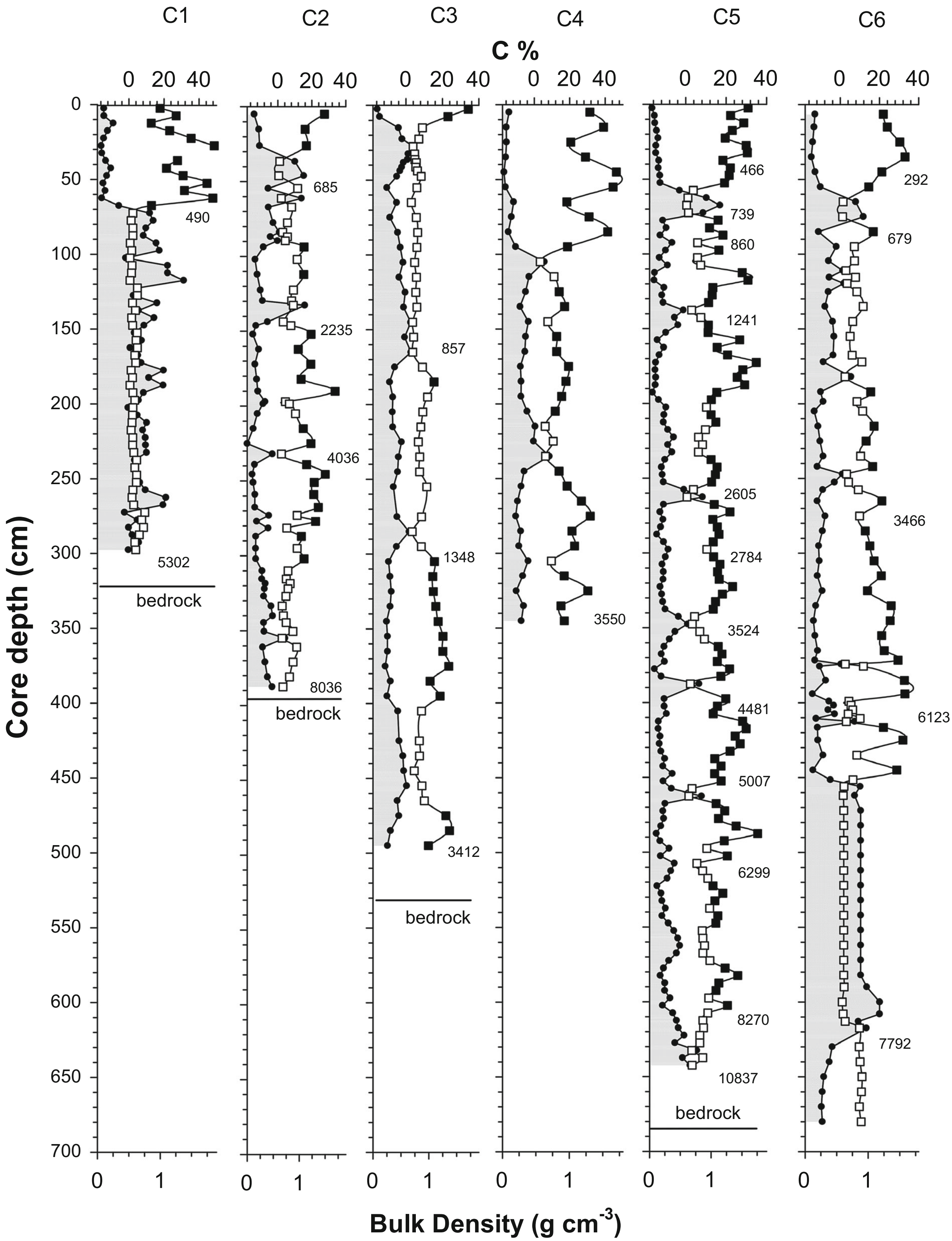
Fig. 3 Soil carbon concentration (C %) for the organic (*black squares*) and mineral (*white squares*) horizons and soil dry bulk density (g cm^{-3}) (*shaded grey*) in peatland cores from Antisana Ecological Reserve (sites A1–A3). Ages of dated soil horizons (cal. year BP) are placed next to each core

additional research quantifying C stocks in the diverse upland and wetland ecosystems, scaling C stocks to peatland basin morphology (Hribljan et al. 2015), and their spatial distribution across the Andes. Furthermore, mountain peatland C stocks represents an underreported C pool in the tropics and should be included with peat swamps (Draper et al. 2014) and coastal mangrove forests (Donato et al. 2011) in an effort to greatly improve our ability to provide accurate C accounting for future tropical wetland C inventories.

Initiation dates and accumulation rates

Peatlands in the Ecuadorian Andes are accumulating C at surprisingly fast rates (Fig. 5). We measured a mean C accumulating rate of 26 g m^{-2} year^{-1} for all the sites over 3000 year old. We classified the two <500 year old sites (A1 and C1) as exhibiting recent rates of C accumulation (RERCA) because of their young age making them not directly comparable to the LARCA's calculated from the older sites. The fastest long-term C accumulation rates were from the cushion plant dominated peatlands C3 and C4 in CCNP that had LARCA's of 50 and 38 g m^{-2} year^{-1}, respectively. These rates are similar to our previous estimates based on fewer sites from the Ecuadorian páramo (Chimner and Karberg 2008). However, these two peatlands (C3 and C4) had core basal dates that were considerably younger (3412 and 3550 cal. year BP) than the other peatlands sampled with ages older than 5000 cal. year BP. It is unknown if the C3 and C4 peatlands will continue on the same steep LARCA trajectories. The data from our study suggest that LARCA values in these páramo peatlands decline with age. Peatland LARCA values are known to decrease as peat accumulates, because of decomposition of organic matter throughout the peat column as the peatland ages (Clymo 1984). Interestingly, peatlands in the Ecuador páramo, can display long-term C accumulation rates as great as 50 g m^{-2} year^{-1} (peatlands older than 3500 cal. year BP) that is comparable to Amazonian peat swamp forest that are reported to accumulate 39–85 g C m^{-2} year^{-1} (peatlands ages 715–2300 cal. year BP) (Lähteenoja et al. 2009). These peatland LARCA rates for the páramo are surprising given the high altitudes, cold temperatures, and large mineral inputs of the mountain environment and are an indication of the uniquely adapted and productive peatland vegetation (Cooper et al. 2015).

We measured a broad range of ages (118–8270 cal. year BP) for peatland initiation in


C1
C2
C3
C4
C5
C6
C %
0 20 40
Core depth (cm)
Bulk Density (g cm-3)
bedrock
490
5302
685
2235
4036
8036
857
1348
3412
3550
466
739
860
1241
2605
2784
3524
4481
5007
6299
8270
10837
292
679
3466
6123
7792

◀**Fig. 4** Soil carbon concentration (C %) for the organic (*black squares*) and mineral (*white squares*) horizons and soil dry bulk density (g cm^{-3}) (*shaded grey*) in peatland cores from Cayambe-Coca National Park (sites C1–C6). Ages of dated horizons (cal. year BP) are placed next to each core

the Ecuador páramo. Core C1 began peat production only 490 cal. year BP directly on top of a 50 cm thick layer of volcanic ash. In contrast, site A1, which is positioned at the base of the Antisana glacier, has accumulated 1 m of C dense soil within only 118 years on a lithic substrate and has recently started peat production in the upper 25 cm. During the last glacial maximum most or all of our study area was above the snowline (Smith et al. 2005). The timecourse of deglaciation set the upper limit for peatland age, after which peatland formation was started by changes in site hydrology promoting the establishment of wetland vegetation and subsequently peat production. The broad range of peatland ages documented from our soil cores demonstrates that these alpine peatlands in the páramo of Ecuador are continuously forming as the dynamics of the mountain environment changes and site conditions become favorable for peat formation.

Despite the differences in peatland age, altitude, geographic region, and vegetation cover, all the peatlands we sampled are displaying a consistent site-specific rate of soil C accumulation (Fig. 5b). The peatlands do not show any abrupt changes in their long-term trends of C accumulation indicative of major shifts in soil C production that could result from fluctuations in climate, vegetation changes, or disturbance (Belyea and Malmer 2004; Page et al. 2004). This is quite surprising given the multiple layers of volcanic ash that have been deposited on these peatlands throughout their development. We have cored through ash and pumace layers several centimeters thick without any apparent impact on long-term rates of C accumulation. Furthermore, vertical soil accretion rates were also extremely linear despite the deep heterogeneous soils in the peatlands (Fig. 5c). As a peatland grows in height it can potentially extend above the ground water table, drying the upper surface and slowing down the processes of peat production (Belyea and Baird 2006; Hilbert et al. 2000). The geomorphic position of Ecuadorian alpine peatlands in their mountainous terrain provides ground water connectivity and coupled with the humid and wet climate keeps their soils perennially saturated and provides space for vertical growth. The steady long-term C and soil accumulation rates attest to the ecological resilience of these systems to natural disturbances over several millenia. However, it is uncertain how accumulation rates and C stocks will be affected by the increased anthropogenic land use pressures and climate change on these alpine peatlands (Buytaert et al. 2011).

We attribute the high belowground C stocks and fast accumulation rates in Ecuadorian Andean peatlands to two factors: vegetation that is ideally suited to the alpine environment, and saturated soil conditions that slows organic matter decomposition. Despite the cool temperatures in the páramo the tropical climate allows plants to remain photosynthetically active throughout the year (Beck 1994). Therefore, vegetation is able to provide continual inputs of organic rich material for peatland growth and C sequestration (Squeo et al. 2006). We found two distinct peatland vegetation communities across our sites that were dominated either by cushion plants or graminoids (Fig. 2). Cushion plant peatlands were located at higher elevations and became uncommon below 3900 m. Cushion plants are well suited to the harsh high altitude alpine environment due to their compact growth form (Cavieres and Badano 2007). The two lowest altitude sites in CCNP (C5 and C6) were the only graminoid dominated peatlands sampled. Although these two peatlands had distinctly different graminoid dominated vegetation communities in comparison to the higher altitude cushion plant dominated peatlands they had similar peat accumulation rates and C storage.

Mineral inputs into páramo peatlands

Ecuadorian peatlands in the páramo can contain a substantial input of allochthonous material that is incorporated into their soils. This is well represented by the dense soils in the peatlands we sampled in Antisana and Cayambe-Coca (Table 3). The large deposition of mineral and ash material into the peatlands results in a highly variable soil C content and dry bulk density (Chimner and Karberg 2008). Moreover, the high soil mineral content can lower soil C content below the standard (12 %) typically used for characterizing soil as peat. Many of the peatlands we

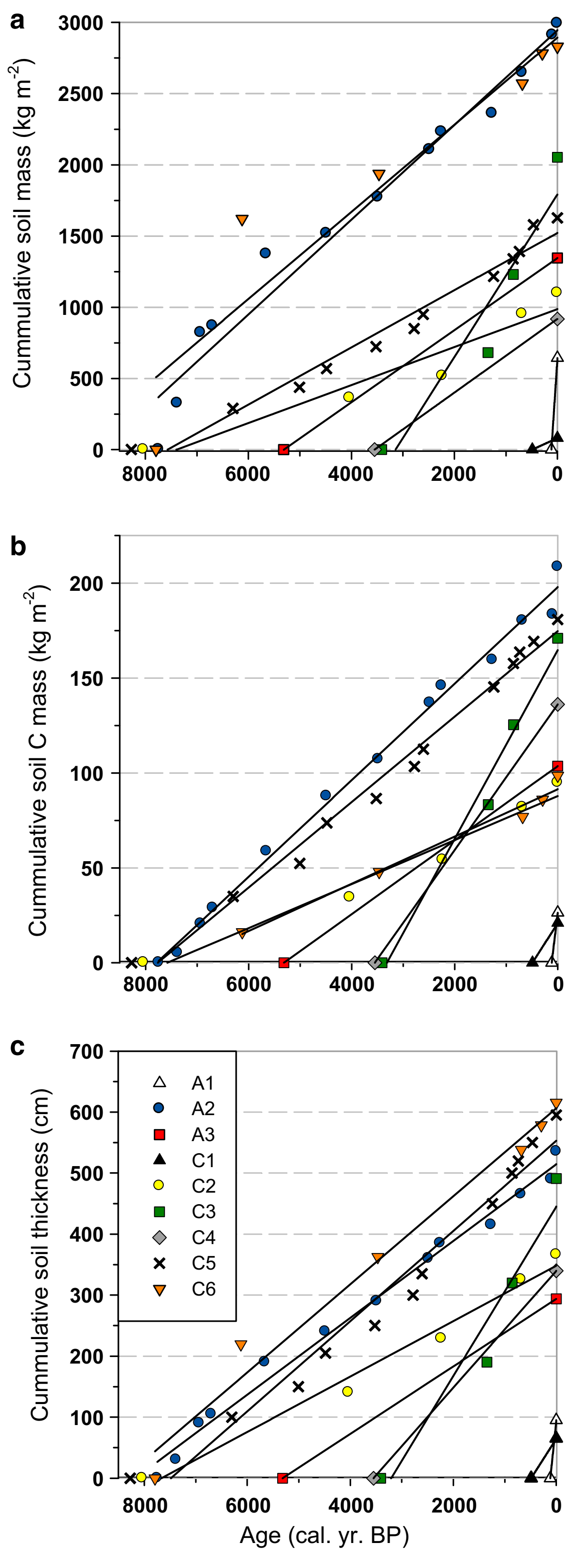
Table 3 Peatland core depth (cm), basal age (cal. year BP), total soil mass (kg m^{-2}), total carbon (C) stocks (Mg ha^{-1}) and long-term accumulation rates [thickness (mm $year^{-1}$), soil mass (kg m^{-2} $year^{-1}$), and for C contained in the peat soils and the entire peatland core including mineral soils (g m^{-2} $year^{-1}$)] for each site sampled at Antisana Ecological Reserve (A1–A3) and Cayambe-Coca National Park (C1–C6). Peatland core data is also partitioned between the "peat soil" and interbedded "mineral soil" horizons (mean values for entire core are presented for soil dry bulk density (D_b, g cm^{-3}) and C concentration (C %)

	Peatland				Peat soil			Mineral soil			Accumulation rates			
	Depth (cm)	Age (year)	Mass (kg m^{-2})	Total C (Mg ha^{-1})	D_b (g cm^{-3})	C (%)	Total C (Mg ha^{-1})	D_b (g cm^{-3})	C (%)	Total C (Mg ha^{-1})	Thickness (mm $year^{-1}$)	Mass (kg m^{-2} $year^{-1}$)	C (g m^{-2} $year^{-1}$)	
													Peat soil	Peatland
A1	100	118	684	279	0.16	29.9	128	0.91	3.1	151	8.05	5.46	219	224[b]
A2	535	7747	2994	2025	0.27	23.9	963	0.71	5.4	1062	0.63	0.33	15	25
A3	294	5313	1372	1046	0.27	20.3	598	0.61	4.6	448	0.55	0.25	10	20
C1	70	490	98	245	0.14	30.0	245	-	-	-	1.33	0.17	43	43[b]
C2	390	8036	1206	1037	0.17	19.3	535	0.46	6.2	502	0.45	0.13	9	12
C3	491	3412	2243	1840	0.26	19.1	723	0.49	6.8	1118	1.39	0.57	21	50
C4	340	3550[a]	946	1409	0.21	23.8	1111	0.48	8.3	298	0.96	0.26	30	38
C5	605	8270	1654	1849	0.18	19.5	1347	0.46	6.9	501	0.74	0.20	16	23
[c]C6	565	6675[a]	2015	1807	0.19	22.1	1006	0.51	6.4	800	0.72	0.31	13	15
Mean	377	4970	1468	1282	0.21	23.1	740	0.58	6.0	610	1.65	0.85	42	50

[a] Dates do not represent basal peat

[b] Because of the young age (<500 cal. year BP) the values do not represent LARCA values, but are more indicative of a recent rate of carbon accumulation (RERCA)

[c] Peatland depth for core C6 does not include the dense volcanic horizon of 465–585 cm



◀**Fig. 5** **a** Cumulative soil mass (kg m^{-2}), **b** carbon mass (kg m^{-2}), and **c** thickness (cm) of the dated cores (cal. year BP) for peatlands from Antisana Ecological Reserve (A1–A3) and Cayambe-Coca National Park (C1–C6). (Color figure online)

sampled had soil horizons with a high mineral content that were below this 12 % C threshold for large sections of the core and are thus not conventionally considered peats. We propose that the mineral horizons are part of the peatland accretion process and should be included in the calculations for overall peatland growth and C accumulation. Visual examination of the mineral soils in the peatlands revealed a considerable quantity of plant material contained in the mineral layers that is well preserved due to the highly anoxic soils. It appears that plant growth has been sustained though time even with the large allochthonous contributions to the peatland soils. This is reflected not only in the steady C accumulation rates (Fig. 5), but also the high C densities in the peat and also the mineral soils (Table 3). We propose that as allochthonous inputs (alluvial, fluvial, and volcanic) are deposited into the peatland the mineral rich material becomes embedded around the vegetation and plant production is able to continue throughout the depositional periods. Volcanic activity is particularly common throughout the páramo and has resulted in multiple layers of ash and pumice deposited onto the peatlands, which is incorporated into the peats throughout their development (Chimner and Karberg 2008). However, there are horizons of volcanic ash and mineral rich soils present in our cores that have C densities comparable to those measured in the peat layers. Only during times of substantial mineral inputs will you see large decreases in soil C densities.

Several of the peatlands we sampled (A1, A2, C1, and C3) contained more than half of their belowground C in the soil horizons classified as mineral (Table 3). This is especially well highlighted by peatland C3 in Cayambe-Coca that has 61 % of its soil C contained in mineral soils. However, this peatland has an incredibly fast C accumulation rate (50 g m^{-2} $year^{-1}$) and is storing 1840 Mg C ha^{-1}. Therefore, for some of these turbaras the current definition of a peatland and peat soils does not encapsulate their unique peat forming abilities. Peatlands in the Ecuador páramo are extremely resilient ecosystems that are well adapted to the harsh conditions of the mountain environment. Detailed dating of páramo peatlands could give addition insights on the influence that allochthonous material has on plant productivity and therefore peat production in these peatlands. Furthermore, the lack of a common and well established name or classification for peat accumulating systems across the Andes points to the limited attention that these important C accumulating ecosystems have received.

Carbon storage in peatland substratum soils

In addition to the high C stocks contained within Ecuadorian mountain peatlands we also measured substantial C storage in substratum soils under some of the peatlands we cored. This pool of C is often overlooked in C inventories, but could be a significant contribution to wetland C budget calculations. Peatlands commonly form on saturated soils that were previously flooded aquatic systems or wet meadows that have slower soil and C accumulation rates. The change from a non-peat accumulating wetland to a peatland is suggested to be depicted in the abrupt shift for C accumulation rates we measured at sites A2 (1.4 g m^{-2} $year^{-1}$, from 10,715 to 7747 cal. year BP changing to 25 g m^{-2} $year^{-1}$ from 7747 cal. year BP to present) and C5 (5 g m^{-2} $year^{-1}$ from 10,837 to 8270 cal. year BP changing to 23 g m^{-2} $year^{-1}$ from 8270 cal. year BP to present). Peatland C1 contained a mean of 182 Mg C ha^{-1} for every 100 cm depth in the substratum. The thickness of the substratum soils and their overall C content were undetermined. We were unable to sample the full depth of the substratum soils due to difficulties of coring in the extremely dense mineral soils. Carbon storage in substratum soils warrants additional research.

Conclusion

The Ecuadorian páramo contains peatlands that have been accumulating C in their soils for over 7000 years. The age and C dense soils in these peatlands has produced the highest C storage per area basis currently reported for any ecosystem type in the Ecuadorian páramo. Furthermore, these tropical alpine peatlands are demonstrating rapid C accumulation rates that are surprisingly stable from their time of inception to the present. However, the local hydrology and regional climate that has supported their existence through millennia is facing increasing pressure from land use change and shifts in the Andean climate. Additional research is needed not only on current C dynamics in these peatlands, but also on the effects of anthropogenic disturbance on their tremendous capacity as a long-term C sink.

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