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ORIGINAL ARTICLE

Elevation and temperature are strong predictors of long-term carbon accumulation across tropical Andean mountain peatlands

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Abstract

Mountain peatlands are understudied globally, especially in tropical regions such as the Andes. Their high abundance across the landscape and thick carbon (C)-rich soils establish them as regionally important C reservoirs. However, they are at high risk of degradation due to unsustainable land use and climate change. Mitigation of these threats requires detailed inventories of C stocks present and improved understanding of the major drivers of long-term C accumulation in these ecosystems. We cored 24 peatlands located between 3000 and 4800 m elevation across Colombia, Ecuador, Peru, and Bolivia, calculated C storage and long-term and recent apparent rate of C accumulation (LARCA and RARCA, respectively), and tested their relationships to environmental variables (elevation, temperature, precipitation, and solar radiation). The peatlands had a mean thickness of 4.7 m (range, 0.7−11.25 m). The mean age of peatland was 7918 yrs B.P., with a range from 490 to 20,000 yrs B.P. The mean C stock was 1743 Mg ha^{-1} and did not significantly vary by climatic region or basal age but did increase with elevation. LARCA was best predicted by age and elevation, while RARCA was negatively related to mean annual temperature. These findings indicate that peatlands in the tropical Andes store thick deposits of soil C that are likely influenced by temperature, making them vulnerable to changes in climate. To inform climate policy, there is a need for science that will determine the potential for adaptation and mitigation treatments to increase the resilience of these C-rich ecosystems to climate change.

Keywords Mountain peatlands · Carbon · Peat · Andes · Accumulation rate

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1 Introduction

Peatlands are one of the most important reservoirs of carbon (C), storing upwards of ~ 600 Gt of C globally, despite only occupying ~ 3% of global land surface (Yu et al. 2011). They represent > 50% of wetland area worldwide and store twice the amount of C as all the world's forests (Joosten and Clarke 2002; Loisel et al. 2020). However, these estimates are continually changing as newly surveyed areas of extensive peatlands in the tropics are incorporated into global peatland inventories and many additional areas lack sufficient data for their inclusion (e.g., Gumbricht et al. 2017). Mountain peatlands are particularly underrepresented in global surveys (Chimner et al. 2010; Hribljan et al. 2017; Longman et al. 2021), but are likely to be vulnerable to C loss through rising temperatures, changing precipitation patterns, and increasing human pressures (Chimner et al. 2010; Millar et al. 2016). Because they are understudied, the key drivers of C storage in these ecosystems are unknown, making it difficult to predict which changes will most strongly impact their C reservoirs.

Peatlands have the largest areal extent in boreal regions, followed by tropical regions, mostly occurring in low-elevation, low-relief settings. However, peatlands are also numerous across tropical, temperate, and boreal mountains due to higher annual precipitation, cooler temperatures, and higher available water compared to the surrounding lowlands (Cooper et al. 2012). In addition to the tropical Andes, peatlands are also common on many other tropical highlands such as in Hawaii (Chimner 2004), Africa (Grundling and Grootjans 2018), and New Guinea (Hope 2015); as well as in temperate regions, including the Rocky Mountains (Chimner et al. 2010), Sierra Nevada Mountains (Wolf and Cooper 2015), Alps (Tomaselli et al. 2018), and the Himalayas (Khan et al. 2020). Although mountain peatlands are similar in some ways to lowland peatlands, they have many properties that make them unique, including landform positions, vegetation types, steep slopes, large daily temperature variations, high values of sediment and chemical inputs, erosion potential, groundwater dependence, and exposure to UV light. Although topographic limitations mean most mountain peatlands are smaller than lowland peatlands, they can be very numerous (Chimner et al. 2010, 2019; Hribljan et al. 2017). Mountain ecosystems are experiencing some of the most rapid environmental alterations from a changing climate (Valencia et al. 2020). Simultaneously, mountain peatlands are also experiencing land use pressures such as ditching for agriculture or water diversion, cropping, high grazing pressure, mining for minerals, and impacts from recreation (Benavides 2014; Salvador et al. 2015; Sánchez et al. 2017; Chimner et al. 2020; Oyague and Cooper 2020).

The tropical zone of the South American Andes contains extensive areas of peatlands often termed bofedales, turberas**,** or vegas. These peatlands are vastly understudied with only a few reports characterizing peatland types and quantifying their spatial extent, degradation, and C storage (e.g., Hribljan et al. 2017, Chimner et al. 2019, Chimner et al. 2020). Tropical Andean peatlands are unusual compared to their better-studied high-latitude cousins because of their unique vegetation and continuous growing season. These peatlands occur along a climatic gradient from the wetter northern *páramo* to the drier central *puna* climatic zones (Cleef 1979). The *puna* occurs in central Peru, Bolivia, and northern Chile and Argentina (Earle et al. 2003) and is characterized by a distinct wet and dry season. In contrast, the *páramo* of Colombia, Venezuela, Ecuador and Northern Peru are in the humid equatorial region of the Andes that is characterized by cool and wet conditions with negligible variations in annual temperature and smaller contrast between dry and wet seasons (Balslev and Luteyn 1992; Luteyn 1999). While peatlands in the Andes do support the mosses and graminoids typically found in other peatlands, many are dominated by cushion plants, predominantly within the families Juncaceae, Asteraceae, and Plantaginaceae (Cooper et al. 2010; Hribljan et al. 2017; Chimner et al. 2020). These plants are well adapted to arctic and alpine conditions as they trap heat and minimize wind shear because of their low stature (Billings and Mooney 1968). Most peatlands across the *puna* to *páramo* climatic gradient are a mix of cushion, graminoid, and moss vegetation communities with cushion plants becoming more abundant at higher elevations (Chimner et al. 2019).

To provide protection for C rich ecosystems, countries can qualify for international C offset programs such as the REDD+ mechanism, which seeks to fight climate change by reducing carbon emissions caused by deforestation and forest degradation (Nasi et al. 2011). These types of programs provide monetary incentives to protect C-rich ecosystems from environmental degradation by fostering conservation and sustainable management of C stocks in plant biomass. However, these programs typically only apply to forested systems and have completely overlooked C-rich tropical Andean peatlands characterized by low stature vegetation cover (e.g., graminoids, mosses, and shrubs) and large C stocks. This study is a first attempt to expand our knowledge on the extent of belowground C storage in Andean peatlands and explore the environmental factors that control its variation across a broad latitudinal range of the tropical Andes. It is a remote area characterized by a rugged landscape shaped by many geological events including a combination of volcanic activity, glacial cycles, and tectonic movement. In addition, the Andes have a history of multifaceted and highly disruptive land use activities (e.g., grazing, mining, water diversions, and agriculture) that are coupled with the current concerns of a rapidly changing climate that is altering historic mean annual temperatures and precipitation patterns. These multiple stressors raise serious concerns regarding the sustainability of current land use management practices for high elevation ecosystems and highlight the urgent need to gather baseline ecological data to inform government policy and management initiatives. This study aims to answer the following questions:

1) What is the belowground C storage per unit area for Andean peatlands?
2) Are there differences in C storage between peatlands in the northern and southern climatic ecozones (*páramo* and *puna*) of the tropical Andes?
3) Which environmental variables (elevation, temperature, precipitation, solar radiation) best predict longer-term C accumulation rates in tropical Andean peatlands?

2 Methods

2.1 Study region

Our study covers a large latitudinal gradient from −18 to +5 degress latitude, including the countries of Bolivia, Peru, Ecuador, and Colombia. We sampled peatlands at 25 sites over an elevation gradient from 3000 to 4800 m above sea level spanning the *páramo* and *puna* climatic ecozones of the tropical Andes (Fig. 1).

2.2 Carbon stocks

To estimate peatland C storage, peat cores were extracted from 24 peatlands across the tropical Andes. The upper 100 cm of the majority of the peatlands were cored with a

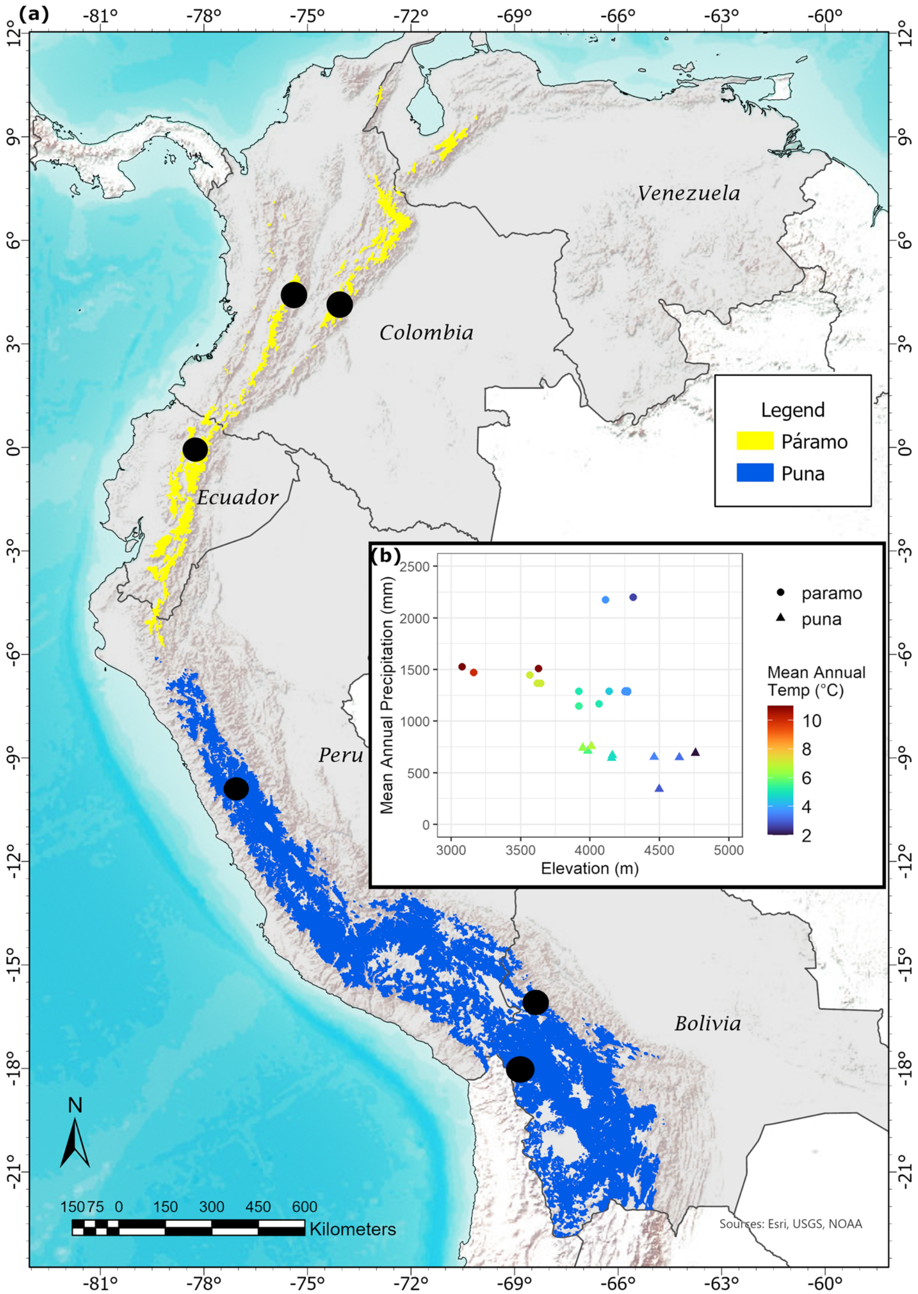

Fig. 1 Map of the Andean region showing sampling locations (circles) and area of *páramo* (yellow) and *puna* (blue) derived from (Romano 2017). Inset: elevation (m), mean annual precipitation (mm), and mean annual temperature (°C) for each core in the *páramo* (circles) and *puna* (triangles)

6.35-cm diameter × 100-cm-long open-faced stainless steel gouge auger to avoid compaction of the surface peat (AMS, Inc., American Falls, ID, USA; 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 stainless steel Russian peat borer with a 5-cm diameter × 50-cm-long core tube (Aquatic Research Instruments, Hope, ID, USA) or for extremely dense peat the open-faced gouge auger. The peat borer cover plate width was reduced to facilitate insertion into dense peats. A slide hammer (AMS, Inc., American Falls, ID, USA) was deployed to drive the sampler into especially dense peats and the sampler was retrieved with a hydraulic jack. Coring was performed to depth of refusal or until basal non-peat substratum sediments were sampled. The entire length of the peat cores for all sites was cut into ~ 5−10cm sections in the field (the thickness varied based on visual evidence of mineral-rich layers that were sampled separately), placed in plastic bags, and transported to the USDA Forest Service Northern Research Station lab in Houghton, MI, USA.

Soils were dried in a convection oven at 65 °C to a constant mass. Dry bulk density (g cm^{-3}) was calculated by dividing the oven dried mass by the original sample volume determined from the cross-sectional area of either the peat corer or gauge auger multiplied by sample length. Organic matter content for each section was determined by loss on ignition (LOI) at 550 °C for 4 h (Chambers et al. 2011) using ~ 1 g homogenized subsamples ground to a fine powder with a ball mill (SPEX 8000M, Metuchen, NJ, USA). A random subset of 400 samples that spanned the entire range of measured organic matter content were selected from the cores and analyzed for % C concentration with an elemental analyzer (Costech 4010, Valencia, CA, USA and Fisons NA 1500, Lakewood, NJ, USA). The linear equation C (%) = (0.5324 × LOI (%)) − 0.9986 ($R^2 = 0.99$; $p < 0.001$) was developed to calculate C concentration in the remaining samples analyzed only by LOI (Hribljan et al. 2015). Carbon stock for each core section was calculated as the product of dry bulk density (g cm^{-3}), sample length (cm), and sample % C resulting in Mg ha^{-1}. We used the definition of a peatland as containing soils with a C concentration of greater than 12% and a combined peat thickness of at least 40 cm in the upper 80 cm of the peatland (Soil Survey Staff 2014).

Total belowground peatland C stock per unit area (Mg ha^{-1}) was calculated for each peatland by summing C stock per unit area of all individual samples in the entire core. All cores contained layers falling below the general definition of peat (> 12% C content) for non-clay soils (Soil Survey Staff 2014). The total peatland C stock estimates combined the C content of these interbedded mineral layers and peat horizons. Total C stock calculations for the two Bolivian peatlands were adjusted for basin morphology based on depth profiles from tile probing transects following a bathymetric approach (Hribljan et al. 2015). The total C stock estimates for the peatlands from Colombia, Ecuador, and Peru are calculated without basin morphology adjustments as that information was not available.

2.3 Carbon dating

Peat samples from the peatland base and multiple depths from each core were analyzed for bulk ^{14}C dating. Selection of peat layers for dating was informed by an analysis of bulk density and % organic matter. Transitions in peat physical properties were used as key locations to age throughout the peat cores since they have been correlated to climate, volcanic activity, land use change, and C accumulation rates (Tolonen and Turunen 1996; Xing et al. 2015; Ratcliffe et al. 2020). Peat material for dating was carefully extracted from the center of each core section to avoid contamination that could be present on the exterior surface. Bulk peat samples were graphitized in preparation for ^{14}C measurement at the US Forest Service Carbon, Water & Soils Research Lab in Houghton, Michigan. After grinding, samples were dried, weighed into quartz tubes, sealed under vacuum, and combusted at 900 °C for 6 h with cupric oxide (CuO) and silver (Ag) 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 using CALIB v. 5.0 (cal yr B.P., B.P. = 1950, Stuiver and Reimer 1993) and the SHCal04 and IntCal04 atmospheric curves (McCormac et al. 2004; Reimer 2004) depending on their latitude. Median value of the 2σ calibration range for each date is reported and used in calculating accumulation rates. The peatland long-term apparent rate of C accumulation (LARCA), peat mass, and thickness for each core was determined from the line slopes (not forced through zero) of each parameter plotted versus the ^{14}C dates (see Hribljan et al. 2016 for more detailed methods).

2.4 Carbon accumulation rates

In order to compare C accumulation rates over a similar time period among peatlands of different ages, recent apparent rates of C accumulation (RARCA) were also calculated. This method allows for better comparison of C accumulation rates across peatlands which would otherwise be masked by large differences in decomposition of the older and larger versus younger and smaller peat columns. Thus, we avoid comparing apparent rates of accumulation from different time periods which has been appropriately identified as problematic in previous work such as Dylan et al 2021. First, the ages of all sampled sections of each core that were not dated were estimated based on the known ages of the dated sections and the minimum depth of each section using linear interpolation. Then the C accumulation rate (total C/maximum age) was calculated using the same method as for LARCA above, for all sections of each core younger than the segment with the age closest to the desired age (either 2500 years or 700 years) and within +/− 200 years (with the exception of a single core which had a basal age of 490 years but was retained in both calculations). Differences between *paramo* and *puna* ecotypes were calculated by *t*-tests performed in R version 4.0.4 (R Core Team 2021).

2.5 Environmental variables

To assess the role of environmental factors in determining RARCA and LARCA, mean values from the last 30 years of environmental variables for each site were downloaded from the WorldClim database (Fick and Hijmans 2017) at 30 second resolution (corresponding to an area of ~ 1 km^2). Variables in the WorldClim database are the result of thin-plate spline interpolation at 1 km^2 resolution from weather station data modified with covariates from MODIS satellites (see Fick & Hijmans 2017 for details) and have been used broadly for modeling and large-scale soil C assessments (e.g., Zhou et al. 2021; Cong et al. 2022; Fairman et al. 2022) as well as climate vulnerability assessments for Andean plant communities (Valencia et al. 2020). Linear regressions were performed in R version 4.0.4 (R Core Team 2021) to assess the relationship between independent environmental variables (elevation, mean annual temperature (MAT), mean annual precipitation (MAP), precipitation seasonality, and total annual solar radiation) and the dependent variables describing peat C accumulation rates (LARCA, RARCA700, and RARCA2500). Corresponding figures were created using ggplot2 (Wickham 2016).

3 Results

Sampled peatlands (Fig. 2) ranged in thickness from 0.7 to 11.25 m, with an average of 4.7 m (± 0.53 standard error of the mean–SE, Table 1; see Supplementary Table S1). Peatlands in the *puna* averaged 5.2 m (± 0.99 SE) while the *páramo* peatlands averaged 4.4 m (± 0.63 SE), but these were not significantly different ($p = 0.5$). *Páramo* peatlands sampled were on average at slightly lower elevations (3889 m, $p = 0.01$) and experienced slightly higher mean annual temperatures (5.9 °C) than those in the *puna* (4290 m, 4.4 °C), though the temperature difference was only marginally significant ($p = 0.10$). Elevation was a strong predictor of mean annual temperature ($p < 0.001$, $r^2 = 0.85$) but these two factors did not equally predict all peatland characteristics and therefore are reported separately.

The mean age of basal peat was 8124 yrs B.P. (± 946 SE) ranging from 490 yrs B.P. to 20,466 yrs B.P. (Table 1; see Supplementary Table S2). Basal age did not statistically vary between *páramo*/*puna*. Basal age was weakly predicted by elevation and temperature, with younger peatlands generally occurring at significantly higher elevations (Table 1, Fig. 2b, p = 0.04, $r^2 = 0.14$) and cooler mean annual temperatures (Fig. 2e, p = 0.02, $r^2 = 0.17$). Increased peat thickness was not well predicted by basal age, but was predicted

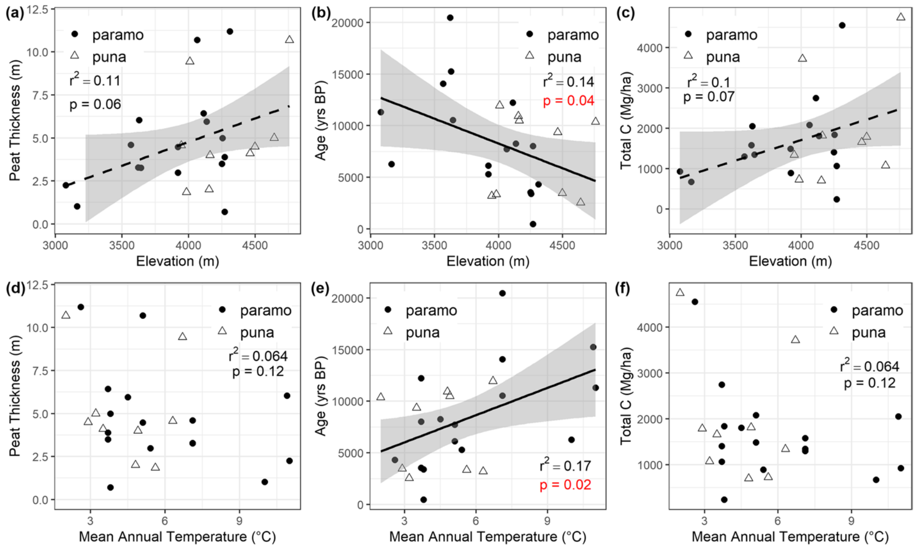

Fig. 2 Relationship between elevation and **a** peat thickness (m), **b** peat age (yrs BP), and **c** total C (Mg/ha) and relationship between mean annual temperature (°C) and **d** peat thickness (m), **e** peat age (yrs BP), and **f** total C (Mg/ha). Filled circles: *páramo* sites, and open triangles: *puna* sites. Listed *p* values and r^2 are for linear regressions of all site types. Shaded areas show 95 % confidence intervals

Table 1 National and overall averages of characteristics for sites and cores, precipitation, elevation, peat thickness, bulk density (D_b), percent C, C density (D_C), total C stocks in peat layers (soil with a % C content > 12 %), total C stocks (including peat and mineral layers), age, and long-term apparent rate of carbon accumulation (LARCA). All ^{14}C reported ages are the median calibrated calendar age

Country	Precipitation (mm yr^{-1})	Elevation (m)	Depth (cm)	D_b (g cm^{-3})	C (%)	D_C (kg m^{-3})	C in peat layers (Mg ha^{-1})	Total C (Mg ha^{-1})	Age (yrs BP)	LARCA (g m^{-2} yr^{-1})
Colombia (8 cores)	1633	3640	491	0.2	31.6	52.6	1752	1900	11810	23.8
Ecuador (8 cores)	1256	4135	392	0.4	15.4	47.6	817	1355	5368	30.9
Páramo average (16 cores)	**1445**	**3888**	**442**	**0.3**	**23.5**	**50.1**	**1285**	**1628**	**8589**	**27.3**
Peru (7 cores)	764	4201	514	0.3	25.4	52.8	1550	2008	8127	26.6
Bolivia (2 cores)	640	4358	478	0.2	31.0	48.7	1596	1815	7332	28.6
Puna average (9 cores)	**650**	**4290**	**524**	**0.2**	**28.9**	**48.6**	**1592**	**1952**	**7298**	**30.6**
Overall average (25 cores)	**1159**	**4033**	**472**	**0.3**	**25.4**	**49.6**	**1395**	**1744**	**8124**	**28.5**

Bold values indicate averages for páramo (Colombia and Ecuador), *puna* (Peru and Bolivia), and overall (all four countries) with marginal significance and low explanatory power by increasing elevation (Fig. 2a, p = 0.06, $r^2 = 0.11$) and decreasing mean annual temperature (Fig. 2d, p = 0.06, $r^2 = 0.12$).

The mean bulk density and percent C of all sites did not differ significantly across *páramo*/*puna*, elevation, or basal age of peatland (Table 1; see Supplementary Table S1). However, both did vary between mineral and peat layers, with mineral layers having an average bulk density of 0.46 g cm^{-3} (± 0.04 SE) and an average % C of 6.7% (± 0.57 SE) while peat layers had an average bulk density of 0.18 g cm^{-3} (± 0.02 SE) and an average % C of 30.0% (± 1.74 SE) (Fig. 3). The average total C stock of 1745 Mg ha^{-1} (± 225 SE) did not differ significantly between *páramo*/*puna* or basal age (Table 1). Total C did tend to increase with increasing elevation (Fig. 2c, p = 0.07, $r^2 = 0.1$) and, to a lesser degree, decreasing mean annual temperature (Fig. 2f, p = 0.12, $r^2 = 0.06$) but these relationships were only marginally significant and weakly explanatory.

The mean LARCA was 28.5 g m^{-2} yr^{-1} (± 4.4 SE) (Table 1). We did not detect any significant difference in LARCA between *páramo* and *puna*. LARCA was significantly greater with increasing elevation and decreasing mean annual temperature across the entire dataset (Fig. 4a, d) as well as in the *páramo* (elevation $p < 0.001$, temperature $p = 0.001$), but not in the *puna* (elevation $p = 0.34$, temperature $p = 0.5$), where there was a narrower range of both temperatures and elevations. Total C stocks also increased significantly with increasing LARCA, though the relationship depended on peatland age (Fig. 5). As expected, LARCA was strongly predicted by age, with higher LARCAs found in younger peatlands ($p = 0.003$, $r^2 = 0.30$). This is a normal pattern caused by slow decomposition across the entire peat column causing a reduction in the measured apparent accumulation rate as peatlands get older (Clymo et al. 1984). To control this effect, we also investigated drivers of RARCA. The mean RARCA for the last 2500 years (RARCA2500) was 32.8 g m^{-2} yr^{-1} (± 4.55 SE) and for the last 700 years (RARCA700) was 37.8 g m^{-2} yr^{-1} (± 4.75 SE). Neither RARCA was well predicted by MAP, precipitation seasonality, or total annual solar radiation. Elevation (Fig. 4b, c) and MAT (Fig. 4e, f) were both significant predictors of RARCA, with MAT a slightly stronger predictor of log transformed RARCA 2500 (Fig. 4e, $r^2 = 0.46$, $p < 0.001$) and RARCA700 (Fig. 4f, $r^2 = 0.44$, $p < 0.001$).

4 Discussion

4.1 Carbon stocks

These data form the first large-scale survey of C stocks and accumulation rates in tropical mountain peatlands in South America and provide critically needed information to increase our overall understanding of global mountain peatland C storage. In all four countries we sampled, peatlands displayed a large potential for belowground C sequestration. Although the % C content of Andean peat is substantially lower than in other areas because of mineral admixture, the C accumulation rate, C density, and depth of peat are some of the highest reported for peatlands across the globe, resulting in large belowground C stocks (Table 2). Our reported Andean peatland mean C storage of 1745 Mg ha^{-1} is the greatest reported in the region, exceeding the average of 1037 Mg ha^{-1} across the Pastaza Marañón Foreland Basin (the largest known peatland complex in the Amazon basin), as well as the average of 1363 Mg ha^{-1} estimated for pole forest peatlands, the most C dense peatland type found in the Peruvian Amazon (Table 2, Draper et al. 2014; Bourgeau-Chavez et al. 2021). Average C stocks of Andean peatlands are lower than lowland peatlands in other

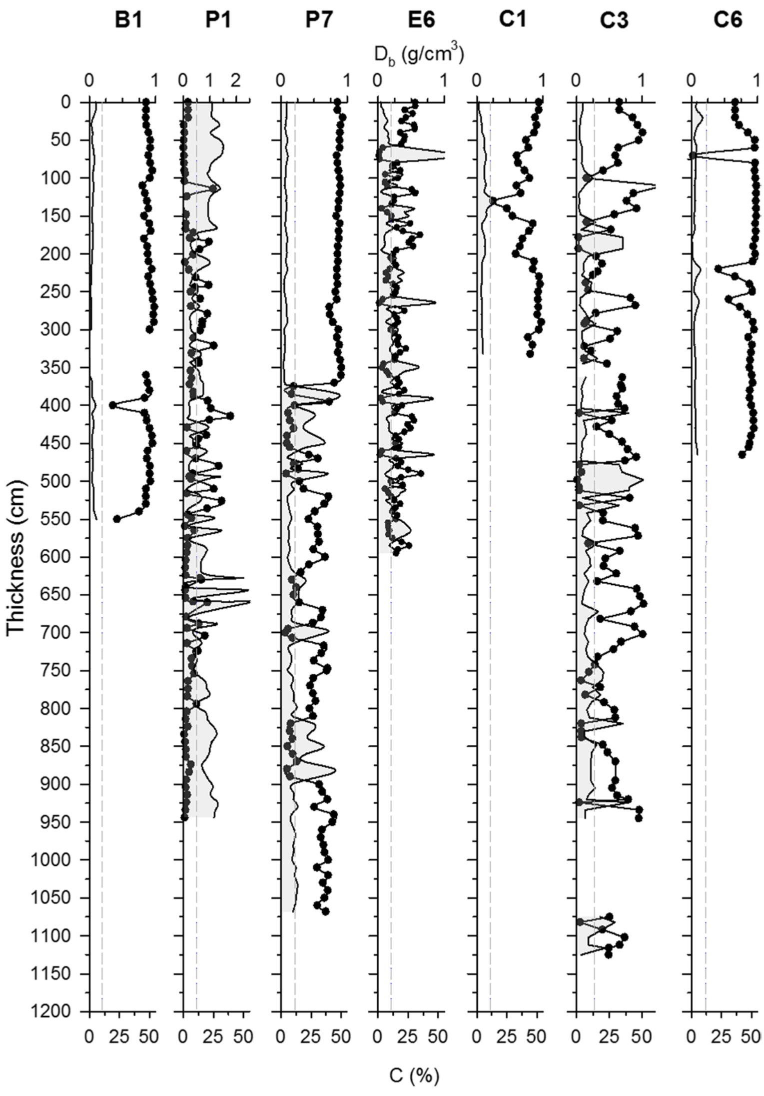

Fig. 3 Depth profiles from seven cores representing the broad range of bulk density (top axis, D_b, g/cm^3) and C (bottom axis, %) measurements from peatlands in: Bolivia (B1; see supplemental table 1 for core ID designations), Peru (P1; P7), Ecuador (E6) and Columbia (C6; C1; C3). Gray filled areas: soil bulk density, black dots: % C, and the vertical dashed line represents the 12% C threshold for peat classification. The missing section (300−350 cm) in core B1 was a non-soil water horizon. Core C3 has gaps in the depth profile because those sections were not sampled. Mineral intrusions are discernable, particularly in cores P1, P7, E6, and C3 where % C drops and D_b increases

tropical regions such as Indonesia and the Central Congo Basin which have average C stocks of 2514 Mg ha^{-1} and 2690 ha^{-1} respectively (Page et al. 2011; Dargie et al. 2017). In comparison, high-latitude Arctic and subarctic peatlands, which are famous for their high C stores, average 1275 Mg ha^{-1} (Loisel et al. 2014) and midlatitude temperate Great Lakes peatlands average and 554 Mg ha^{-1} (Ott and Chimner 2016).

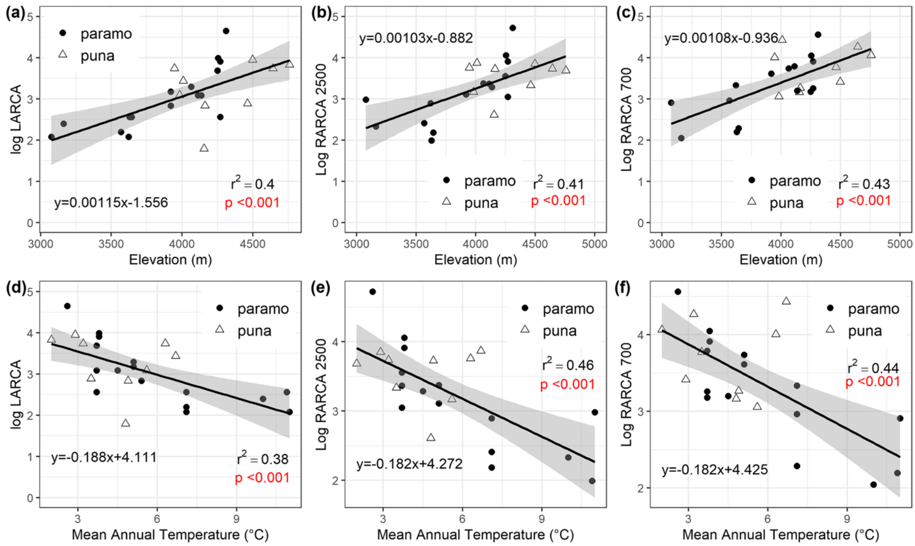

Fig. 4 Top row: relationship between elevation and **a** log long-term apparent rate of carbon accumulation (log LARCA), **b** log recent apparent rate of carbon accumulation over the last 2500 years (Log RARCA2500), **c** log recent apparent rate of carbon accumulation over the last 700 years (Log RARCA700). Bottom row: relationship between mean annual temperature (°C) and **d** log LARCA, **e** log RARCA2500, and **f** log RARCA700. Filled circles: *páramo* sites, and open triangles: *puna* sites. Listed p values and r^2 are for linear regressions (equations shown) of all site types. Shaded areas show 95% confidence intervals

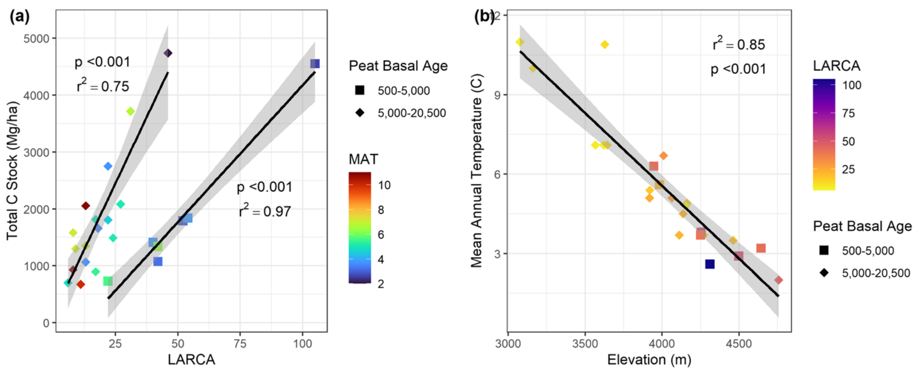

Fig. 5 **a** Total C stock (Mg/ha) as explained by long-term apparent carbon accumulation rate (LARCA) for peatlands with maximum measured age between 2000 and 5000 years old (squares) and peatlands between 5000 and 12,500 years old (diamonds). Slopes for the two age groups are significantly different (ANCOVA interaction p = 0.004). Points are color coded by mean annual temperature (MAT) values. **b** Relationship between elevation (m) and mean annual temperature (°C) does not differ by peatland age group (squares and diamonds). Points are color coded by LARCA values. Shaded areas show 95 % confidence intervals

Andean peatlands follow a large-scale latitudinal trend in which tropical peatlands display a greater mean peat depth and faster C accumulation rates when compared to high latitude peatlands. Andean peatlands average 4.5 m in thickness and tropical New Guinea

Table 2 Age range and mean peat properties (long-term apparent rate of carbon accumulation (LARCA), peat thickness, % C, bulk density (D_b), C density (D_C), and total C stocks) and for peatlands from different geographic regions as compared to tropical Andean peatlands ordered from lowest to highest C stocks. Values for C per area in italic were calculated based on reported mean thickness, % C, and D_b of peat and therefore could be unreliable in areas where peatlands contain measurable mineral intrusions

Region	Age range (kyr BP)	LARCA (g m^{-2} yr^{-1})	Thickness (m)	C (%)	D_b (g cm^{-3})	D_c (kg m^{-3})	C stocks (Mg ha^{-1})	Citation
Peruvian Amazon	0.5–6.5	52	3.0	46	0.11	51	1037	Lähteenoja et al. 2012
Arctic/Boreal	9–11	23	2.3	47	0.11	52	1275	Loisel et al. 2014
Colorado Mountains	5–12	21	1.2	30	0.25	75	1289	Chimner 2000, Chimner et al. 2010
Eastern Europe	4–12	50	4.7	43	0.16	–	–	Longman et al. 2021
Peruvian Amazon Pole Forest	–	–	3.2	44	0.08	35	1391	Draper et al. 2014 & Bourgeau-Chavez et al. 2021
Tropical Andes	**0.5–20.5**	**28**	**4.7**	**25**	**0.26**	**66**	**1745**	**This study**
Tropical Indonesia	7–21	31	4.7	57	0.11	63	2514	Page et al. 2011 & Dargie et al. 2017
Central Congo Basin	7–10.5	24	2.4	59	0.19	112	*2690*	Dargie et al. 2017

Measurements from this study are in bold mountain peatlands have a thickness range between 4 and 8 m (Hope 2015). Moving pole-ward, mountain peatlands contain less C, with the Colorado Rockies and the Sierra Nevadas averaging 1.5 m (Chimner et al. 2010) and ~ 1 m in depth (Wolf and Cooper 2015), respectively. The predominant factor proposed to be driving the differences between tropical peatlands and temperate high-latitude peats (Table 2) is faster C accumulation rates in the tropics due to a longer growing season (Cooper et al. 2015). The short growing season in high-latitude regions limits total solar radiative input and reduces the annual photosynthetic C input. In comparison, tropical areas experience year-round growing seasons with a higher cumulative radiative input that sustains organic matter production and high C accumulation rates.

Total belowground C stocks in tropical Andean peatlands can only be roughly estimated since robust mapping efforts of their areal extent are still ongoing. However, based on current estimates, and assuming a constant ratio between Chimner et al. (2019) and the national ecosystem map (MINAM Mapa Nacional de Ecosistemas del Perú n.d.), Peru may hold as much as 1,617,455 ha of mountain peatlands. Assuming the national average of 2007 Mg C ha^{-1} measured here, this would predict 3.25 Pg of C in Andean peatlands in Peru alone. Country-wide peatland mapping efforts for Ecuador have estimated the nation may contain 169,700 ha of mountain peatlands (Hribljan et al. 2017), which, assuming the average of 1355 Mg C ha^{-1} estimated here, would result in a total of 0.23 Pg C. Mapping of ecosystem cover in Colombia suggests it may contain 148,000 ha of mountain peatlands (Josse et al. 2009) which, with a national average of 1900 Mg C ha^{-1} would result in 0.28 Pg C. This would result in a total of 3.76 Pg C in Andean peatlands in these three countries alone based on preliminary estimates. This is an amount equal to 86 % of the 4.36 Pg C currently estimated to be stored in Peru's Pastaza–Marañón foreland basin (Draper et al. 2014; Bourgeau-Chavez et al. 2021) and 12.6 % of the 30.3 Pg C estimated to exist in the central Congo basin (the largest know tropical peatland complex in the world, Dargie et al. 2017). More refined estimates await the production of national maps of mountain peatlands that are presently in preparation, combined with more extensive sampling across the range of latitudes and elevations.

4.2 Mineral content

The high bulk density and low % C that is common in Andean peatland soils is due to high mineral content, a common characteristic of mountain peatlands. These peatlands often occur on mountainsides or the bottoms of valleys (Cooper et al. 2010) whose steep eroding side slopes can be a large source of alluvial, colluvial, or aeolian sediment into the peatlands. Some mountain peatlands also occur in volcanic regions and receive large ash and pumice inputs (Chimner and Karberg 2008; Hribljan et al. 2016). These depositional events result in high input of mineral material to these peatlands that lowers the % C concentration and increases peat bulk density. Mountain peatlands of New Guinea, Colorado, and this study had an average of 23, 30, and 29 % C, respectively. Colorado and this study had bulk densities of 0.20–0.25 g cm^{-3} and 0.26 g cm^{-3}, respectively (Hope 2015, Chimner et al. 2010). In contrast, lowland peatlands in Indonesian and temperate-boreal *Sphagnum* peatlands often have C concentrations greater than 45% and bulk densities ranging from 0.08 to 0.16 g cm^{-3} (Table 2; Page et al. 2011; Loisel et al. 2014; Ott and Chimner 2016).

In some cases, peatland mineral content is sufficiently elevated that it lowers the % C value below the current accepted definition for peat (Soil Survey Staff 2014). Due to the high mineral inputs to these peatlands, we found that on average 25% of the total C was attributed to mineral horizons in the peat column. Andean peats are commonly embedded with mineral material as well as many interbedded soil horizons from only a few millimeters thick to deposits over 1 m in thickness. Most peat classification systems were originally developed in flat landscapes with little sediment input, or were created for peat industries, so a high C content was an appropriate indicator. Current peat classification systems do not account for the large mineral inputs that can occur in mountain peatlands or in lowland minerotrophic peatlands developed in flood plains of rivers, e.g., the Amazon River basin. Despite their high mineral content, these systems still function as peatlands with fast and long-term organic matter accumulation rates and C dense peat that contribute to large belowground C storage. However, in high-elevation peatlands, care needs to be taken to not confuse peatlands with adjacent wet meadows typified by mineral soils. In contrast with peatlands, wet meadows typically have seasonally saturated soils and do not accrete thick highly organic soil layers (Cooper and Merritt 2012). The distinction between the two can be blurred when a peatland receives high mineral deposition contributing to peats that fall below the current recommended % C guidelines for peat classification. Because a high abundance of wet meadows are present across the tropical Andes (Cooper et al. 2010; Chimner et al. 2019), misclassification with peatlands can significantly affect peatland mapping products and determinations of peat volume and carbon stocks.

The influence of mineral inputs and lithology on Andean peatland C accumulation rates and C storage warrants further investigation (Yang et al. 2020). Volcanic deposition and substrate lithology could influence peat accumulation (e.g., through effects on nutrient availability and/or alteration of organic matter decomposition processes). Carbon stabilization in organo-mineral complexes has been reported for andic soils high in volcanic material (Matus et al. 2014). Given the geological heterogeneity of the Andes, further inquiry into the possible relationship between geological setting and C storage could provide additional insights into mechanisms and patterns of mountain peatland C accumulation rates and storage. Furthermore, the large latitudinal gradient from Colombia to Bolivia represents significant differences in geomorphic setting and environmental conditions that might not be fully represented by our coring campaigns. This landscape heterogeneity needs to be further investigated and sampled to expand upon our understanding of the effects of climate, land use change, and elevation on Andean peat accumulating systems.

4.3 Carbon accumulation rates

Despite large contrasts in precipitation patterns between peatlands from the two bioregions (*páramo* and *puna*), we found no significant differences between their mean peat depth, C storage, LARCA, or RARCA. This may be explained if the effect of the difference in moisture availability is seen in the areal coverage rather than the C accumulation of *páramo* and *puna* peatlands. Mapping work in Ecuador using multi-date and multi-sensor remote sensing techniques found that peatlands represent ~ 22% of the Ecuadorian *páramo* in north-central Ecuador (Hribljan et al. 2017). Peatlands were abundant in this region and were found in basins, valleys, and in large sloping systems. Identical mapping techniques used to map peatlands in the *puna* of Peru (Huascarán National Park: Chimner et al. 2019) found that ~ 11% of the total mapped area was peatland with most found in large mountain valleys. Although not mapped, even cursory review of remote imagery reveals that peatlands are even rarer in the *puna* of Bolivia. It appears that the wet conditions of the *páramo* allow for more peatlands to form across a greater variety of terrain while peatland formation is more restricted in the drier *puna*.

We observed no ecologically relevant difference in the elevation at which peatlands were found in the *páramo* and the *puna*. We sampled peatlands between 3000 and 4800 m in elevation. Sampled peatland elevations averaged 4290 m in the *puna* and 3885 m in the *páramo*. Mapping in the Peruvian *puna* within the Huascaran National Park showed that peatlands were most abundant between the elevations of 3750−4850 m, with 97% of all mapped peatland area occurring within this elevation zone and the highest mapped peatland at 5000 m (Chimner et al. 2019). The elevation range is very similar to mapping results from the Ecuadorian *páramo* that showed peatlands also occurred between 3800 and 4800 m (Hribljan et al. 2017). However, mapping activities from Hribljan et al. (2017) were constrained to sites above 3500 m and hence did not capture peatlands that are known to occur below this elevation. Nonetheless, our data revealed elevation was a significant driver of peatland RARCA and LARCA across our sites (Fig. 4), with peatlands at higher elevation sites accumulating C significantly faster than peatlands at lower elevations (Figs. 2 and 4), with this trend likely driven by temperature (Fig. 5).

The strong relationship we found between temperature and RARCA and LARCA in the tropical Andes suggests inhibition of peat decomposition from cool temperatures may be an important mechanism determining C storage. The potential temperature dependent rate of decomposition in mountain peats is in contrast to lowland tropical peatlands that are exposed to higher annual air and soil temperatures that should promote greater rates of decomposition. Low-elevation tropical peats have formed from substantial inputs of difficult to degrade recalcitrant organic material predominantly from woody vegetation that is proposed to drive C storage from reduced microbial activity (Hodgkins et al. 2018). In contrast, the temperature inhibition rather than substrate constraints of microbial processing of tropical mountain peats may explain the fast rate of belowground C storage that is comparable to their tropical lowland counterparts. The high-elevation peatlands we sampled had an average LARCA of 28.5 g m^{-2} yr^{-1} and RARCA over the last 2500 years of 32.8 g m^{-2} yr^{-1}. This would put Andean peatlands towards the top end of the range of C LARCA measured for low-latitude peatlands and in the middle of the distribution for temperate low-elevation peatlands, which generally have the fastest LARCA (Gallego-Sala et al. 2018). In addition, in our analyses, temperature declined with elevation as expected, consistent with the explanation that reduced microbial processing of organic soil at our higher elevation sites contributed to the greater rates of C accumulation (Fig. 5).

Our observations regarding the relationship between temperature and the rates of C accumulation are subject to two important caveats. First, the relationship of climatic patterns in the Andes has not been constant for the past 10,000 years—the period over which most of these peatlands formed—and current climatic patterns (last 30 years) are not fully representative of this period. Paleoclimatic reconstructions for the Northern Andes suggest that climate in the region has been heterogeneous (Jantz and Behling 2011; Flantua et al. 2016; Frederick et al. 2018), experiencing several cold-warm phases. However, the current relative ranking of the peatlands has not changed over time, i.e., lower elevation sites that are relatively warmer than high-elevation sites now were relatively warmer in the past. Second, it is interesting to note that the relationships that we found between the rates of apparent C accumulation and temperature are largely driven by our *páramo* sites (Fig. 4d, f). This pattern could be driven by the fact that our *puna* sites are located over a narrower altitudinal gradient, or by other environmental factors that we have not considered (e.g., geomorphology, paleoclimate), but suggest that additional studies are needed to ascertain the relative contribution of different environmental factors to the rates of C accumulation in *puna* and *páramo* ecosystems.

4.4 Risks to Andean C stocks

Unfortunately, strong temperature dependence does not bode well for C storage in Andean peatlands under a changing climate. If mean annual temperature is indeed the driver of the C accumulation rates in Andean peats, we can expect the colder, high-elevation peatlands currently accumulating C at the fastest rates to slow down as temperatures increase in the Andes (Chimborazo et al. 2022). The warmer, lower elevation mountain peatlands may have C accumulation rates reduced even to the point of ceasing to be C sinks as has been predicted for other mountain peat areas (Millar et al. 2016). However, it is not clear the extent to which the temperature effects on peat RARCA and LARCA are mediated by direct temperature effects or indirectly by increasing the rate of evapotranspiration and lowering water tables. Another concern is that certain land management activities that are widely practiced, e.g., peat drainage, can reduce rates of C accumulation in Andean mountain peatlands (Planas-Clarke et al. 2020). Hence, the effects of climate warming and drainage could be additive in driving increased C loss from mountain peatlands. In contrast, land management strategies, such as peatland restoration that include ditch blocking to keep these peatlands wet, could minimize C losses (Planas-Clarke et al. 2020, Suarez et al. 2022), increasing their resilience to climate warming. In combination with accurate maps quantifying peatland area and condition, peatland restoration could provide opportunities for including peatlands in international agreements to minimize climate change, e.g., nationally determined contributions (NDCs) to the Paris Climate Accord and financial mechanisms to reduce greenhouse gas emissions, such as payments for ecosystem services. For example, Peru is in the process of developing NDCs for lowland peatlands of the Amazon basin, but because of the absence of accurate maps of mountain peatland distribution at a national scale, cannot yet develop NDCs for mountain peatlands.

5 Conclusions

High-elevation mountain peatlands in South America contain thick peats with an exceptional ability to sequester large amounts of C, but may be highly vulnerable to increasing temperatures under a changing climate. When current peatland mapping efforts are finished across the tropical Andes, we expect that these peatlands will be found to hold a large pool of C that has been overlooked in global wetland C accounting and Earth system models (Loisel et al. 2020). Hydrological restoration of mountain peatlands could provide a powerful and effective tool to mitigate the increasing pressures of shifting land use and a changing climate on these ecosystems, ensuring that the ecosystem services provided by these peatlands will be sustained for ecological and sociological health throughout the Andes.

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Data availability Soil physical properties of bulk density, % C, and % organic matter for all 25 peat cores can be accessed at the CIFOR Database of tropical wetlands carbon survey: Soil (https://data.cifor.org/dataverse/swamp-soil/).

Declarations

Competing interests The authors declare no competing interests.

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