Ecosystem state shifts during long-term development of an Amazonian peatland

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1. Graeme T. Swindles, School of Geography, University of Leeds, UK (Corresponding author)
2. Paul J. Morris, School of Geography, University of Leeds, UK
3. Bronwen Whitney, Department of Geography and Environmental Science, Northumbria University, UK
4. Jennifer M. Galloway, Geological Survey of Canada, Calgary, Canada & Department of Geoscience, University of Calgary, Canada
5. Mariusz Galka, Department of Biogeography and Palaeoecology, Adam Mickiewicz University, Poland
6. Angela Gallego-Sala, Geography, College of Life and Environmental Sciences, University of Exeter, UK
7. Andrew L. Macumber, School of Natural and Built Environment, Queen’s University Belfast, UK
8. Donal Mullan, School of Natural and Built Environment, Queen’s University Belfast, UK
9. Mark W. Smith, School of Geography, University of Leeds, UK
10. Matthew J. Amesbury, Geography, College of Life and Environmental Sciences, University of Exeter, UK
11. Thomas P. Roland, Geography, College of Life and Environmental Sciences, University of Exeter, UK
12. Hamed Sanei, Geological Survey of Canada, Calgary, Canada & Department of Geoscience, University of Calgary, Canada
(13) R. Timothy Patterson, Department of Earth Sciences, Carleton University, Canada
(14) Nicole Sanderson, Geography, College of Life and Environmental Sciences, University of Exeter, UK
(15) Lauren Parry, School of Interdisciplinary Studies, University of Glasgow, UK
(16) Dan J. Charman, Geography, College of Life and Environmental Sciences, University of Exeter, UK
(17) Omar Lopez, Panama Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Panamá & Smithsonian Tropical Research Institute, Panama
(18) Elvis Valderamma, Putumayo Cdra. 24, Calle Garcia Calderon 246, Iquitos, Peru
(19) Elizabeth J. Watson, School of Geography, University of Leeds, UK
(20) Ruza F. Ivanovic, School of Earth and Environment, University of Leeds, UK
(21) Paul J. Valdes, School of Geographical Sciences, University of Bristol, UK
(22) T. Edward Turner, School of Geography, University of Leeds, UK
(23) Outi Lähteenoja, School of Life Sciences, Arizona State University, USA

Phone: +44 (0)1133 439127
Email: g.t.swindles@leeds.ac.uk

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Abstract

The most carbon (C) dense ecosystems of Amazonia are areas characterised by the presence of peatlands. However, Amazonian peatland ecosystems are poorly understood and are threatened by human activities. Here we present an investigation into long-term ecohydrological controls on C accumulation in an Amazonian peat dome. This site is the oldest peatland yet discovered in Amazonia (peat initiation c. 8.9 ka BP), and developed in three stages; (i) peat initiated in an abandoned river channel with open water and aquatic plants; (ii) inundated forest swamp; and (iii) raised peat dome (since c. 3.9 ka BP). Local burning occurred at least three times in the past 4,500 years. Two phases of particularly rapid C accumulation (c. 6.6-6.1 and c. 4.9-3.9 ka BP), potentially resulting from increased net primary productivity, were seemingly driven by drier conditions associated with widespread drought events. The association of drought phases with major ecosystem state shifts (open water wetland – forest swamp – peat dome) suggests a potential climatic control on the developmental trajectory of this tropical peatland. A third drought phase centred on c. 1.8-1.1 ka BP led to markedly reduced C accumulation and potentially a hiatus during the peat dome stage. Our results suggest that future droughts may lead to phases of rapid C accumulation in some inundated tropical peat swamps, although this can lead ultimately to a shift to ombrotrophy and a subsequent return to slower C accumulation. Conversely, in ombrotrophic peat domes, droughts may lead to reduced C accumulation or even net loss of peat. Increased surface wetness at our site in recent decades may reflect a shift towards a wetter climate in western Amazonia. Amazonian peatlands represent important carbon stores and habitats, and are important archives of past climatic and ecological information. They should form key foci for conservation efforts.
Introduction

Tropical peatlands are found in Southeast Asia, Central Africa, and Central and South America. They represent globally important terrestrial carbon (C) stores and ecosystems (Page et al., 2011) and contain at least 87 Pg (billion tonnes) of C (Page et al., 2011; Moore et al., 2013), similar to the amount stored in the living aboveground biomass of the entire Amazon rainforest (93 ± 23 Pg C – Malhi et al., 2006; Fauset et al., 2015). There is much concern over the future of tropical peatlands because large areas in Southeast Asia have been severely damaged by burning, logging and conversion to agriculture (Hooijer et al., 2010; Page et al., 2011). In particular, ditch-draining of tropical peatlands to convert them to agricultural use can lead to a rapid destabilisation of their C stores (Baird et al., 2017). Tropical peatlands are under threat from growing resource exploitation and agricultural expansion in developing nations, and their fate under warmer future climates is unknown.

The Pastaza-Marañón foreland basin (PMFB), NW Peru, contains the most C-dense landscape in Amazonia owing to an abundance of peatlands (e.g. Draper et al., 2014), including nutrient-poor ombrotrophic peat domes and river-influenced minerotrophic peat swamps (Lähteenoja & Page, 2011). It has been estimated that peatlands of the PMFB account for 3.5% of the global tropical peatland C stock, cover 35,600 ± 2133 km² and contain 3.14 (0.44-8.15) Pg C (Draper et al., 2014). One peatland type in particular – pole forest peatland – has been identified as the most C-dense ecosystem type in the Amazon Basin (1.391 ± 710 Mg C ha⁻¹) (Draper et al., 2014).

Although much is known about the C dynamics of Amazonian vegetation, including the finding that its ability to store C is diminishing (Brienen et al., 2015), little is known about how Amazonian peatlands developed, including their ecohydrological dynamics through time, C accumulation, and their response to climatic changes. Potential threats to these intact peatlands include hydroelectricity (river damming) projects, road and railway construction, ore, gas and oil exploration, logging and clearance of land, and drainage for agriculture – in particular oil palm plantations (Roucoux et al.,
Over-exploitation of the fruit of the aguaje palm (*Mauritia flexuosa* – commonly found in wetlands) through tree felling is also of increasing concern (Kahn & Mejia, 1990).

Previous research in the PMFB has included preliminary determinations of peat C content, physical properties, and geochemistry (Lähteenoja et al., 2009a,b, 2012; Lähteenoja & Page, 2011), remote sensing of peatland ecosystems (Draper et al., 2014) and palynological studies (Roucoux et al., 2013; Kelly et al., 2017). There have also been studies of the ecology and palaeoecology of testate amoebae (Swindles et al., 2014; Reczuga et al., 2014; Swindles et al., 2016). Watson et al. (2015) reported the presence of microscopic tephra (volcanic ash) in a peat core, tentatively attributed to a source in the Ecuadorian Eastern Cordillera. Here we present an investigation into the long-term controls on C accumulation in the oldest peatland reported in the Amazon basin. We develop a comprehensive, multiproxy palaeoecological dataset to (i) determine the developmental trajectory of the peatland; and (ii) assess the peatland’s response to past climate change.

**Materials and Methods**

**Study site**

Aucayacu (3.927°S, 74.386°W), meaning “water of the natives” or “water of the warriors” in the language of the indigenous people, is a nutrient-poor ombrotrophic peat dome in Peruvian Amazonia (Lähteenoja & Page, 2011; Swindles et al., 2014). We estimate the maximum dimensions of Aucayacu to be 33 km (NW-SE) × 15 km (NE-SW). The vegetation of the site is characterised by pole and dwarf forest (including some palm trees) with an understory of grasses and ferns. The peatland developed between the Aucayacu stream of the Pastaza fan and the Tigre River (Fig. 1). It is situated in the PMFB which formed during the uplift of the Andes Mountains and contains alluvial deposits several kilometres thick that began to accumulate in the Cretaceous period (Räsänen et al., 1990). The PMFB foreland basin is characterised by migrating river channels and avulsions leading to burial and erosion of peats (Lähteenoja et al., 2012). In Iquitos (120 km east of the study site) average
rainfall of up to 3,000 mm yr\(^{-1}\) is typical (Martinez et al., 2011). The average annual temperature at Iquitos is 26°C, with a diurnal range of approximately 10°C (30-32°C daytime temperatures and 21-22°C at night) (Met Office, 2011).

Fieldwork

Aucayacu was visited in 2008 (by O.L.) and a 3.5-km long transect from edge to centre was established (Lähteenoja & Page, 2011; Lähteenoja et al., 2012). Peat thickness was determined using a Russian D-section corer with a 50-cm long chamber (Jowsey, 1966; De Vleeschouwer et al., 2010) across the transect (8 cores). The topography of the site was determined using a method involving two wooden stakes and a 35 m hose filled with water (for further technical details see Lähteenoja et al., 2009). Accelerator mass spectrometry (AMS) radiocarbon dates were obtained from basal peat from the centre of the site (3.5 km from the edge, c. 8.9 ka BP, Lähteenoja et al., 2012). Root remains were removed from the samples before acid-alkali-acid pre-treatment. Dating was carried out in the Laboratory of the Finnish Museum of Natural History, University of Helsinki, Finland.

For the purpose of this study the site was revisited in 2011 (by G.T.S) and peat thickness was determined along an alternative 1.4 km-long transect (11 cores) using a 5 cm diameter Russian D-section corer in the same manner as in 2008 (De Vleeschouwer et al., 2010). Basic core stratigraphy was logged in the field using Troels-Smith (1955). A 5.3-metre core was extracted from the interior of the Aucayacu peatland for a detailed multiproxy analysis. The core was taken from a flat area (‘litter flat’ – see Swindles et al., 2014) between pools. Two additional cores were logged in the central area (20 metres apart) to examine the representativeness of the master core chosen for detailed analyses. Following clearance of vegetation along the narrow transect, the site was surveyed to the river edge using a Leica optical level and staff. Sampling locations were recorded by hand-held GPS. The size and shape of each microform along with the vegetation composition (within an area of 25 m\(^2\)), as well as % litter and vegetation cover were recorded at each location.
Fig. 1 (a) Map of the Amazon Basin showing major rivers (with upstream catchment area >4 km$^2$) derived from HydroSHEDS flow direction data at 30 minute resolution (Lehner et al. 2006). The red box indicates the extent of panel (b). (b) SRTM Digital Elevation Model of the region at 30 m resolution, showing the major rivers, population centres and national borders. The red box indicates the extent of panel (c). (c) False colour Landsat 5 TM image (15/09/2011) of the Aucayacu peatland with bands 4, 5 and 3 assigned to R, G and B respectively. Wetter soil appears darker and the variation of vegetation type and condition is visible as variations in hues (brown, green and orange) and tone. Both (b) and (c) available from the U.S. Geological Survey http://earthexplorer.usgs.gov/. (d) Photograph of the pole forest typical of Aucayacu peatland. (e) Pool microform in the centre of Aucayacu (a 1-m levelling staff is shown for scale).
A hole was augered at each sampling point and water level measured at regular intervals until it equalised to determine depth to water table. Water table measurements were carried out over a three-day period. pH and conductivity measurements were carried out on water samples extracted from the boreholes using calibrated field meters. Litter samples of approximately 5 cm³ were sampled from each point and placed into Ziploc bags. Samples were shipped to the University of Leeds and stored at 4°C prior to further analysis. Approximately one-half of each surface litter sample was weighed, oven dried, burnt in a muffle furnace and re-weighed to determine moisture content and loss-on-ignition. The other half was used for analysis of contemporary testate amoebae (see Swindles et al., 2014).

**Chronology**

AMS ¹⁴C dates were carried out on basal peat samples and throughout the main core. Samples were sieved at 63 µm (retaining the <63 µm fraction) and all rootlets were picked out before acid-alkali-acid treatment. In some horizons hand-picked wood and peat macrofossils were dated (Table 1). ¹⁴C dating was carried out at the UK Natural Environment Research Council’s Radiocarbon Facility (East Kilbride, UK), ¹⁴CHRONO (Queen’s University Belfast) and Direct-AMS (Bothell, USA). All dates are reported as calibrated ages (cal. yrs BP, before present = AD 1950). Calibration was carried out using Calib 7.1 and the IntCal13 calibration dataset (Reimer et al., 2013). ²¹⁰Pb measurements were performed on contiguous 2 cm samples from the upper 50 cm of the Aucayacu core. ²¹⁰Pb methodologies followed modified versions of Ali et al. (2008) and Pratte et al. (2013). ²¹⁰Pb was extracted from 0.5 g of ground, freeze-dried peat, spiked with a ²⁰⁹Pb tracer, using sequential HNO₃–H₂O₂–HCl digestions with interspersed drying. The samples were then recovered in a 0.5M HCl solution and plated to Sterling Silver discs over a 24 hour period. Samples were counted using an Ortec Octête Plus Integrated Alpha-Spectrometry System with Maestro software at the Geography Radiometry Laboratory, University of Exeter. A constant rate of supply (CRS) model was used to assign ages to the raw ²¹⁰Pb activity profile (Appleby, 2001). Microscopic tephra layers have been
reported from Aucayacu (Watson et al., 2015); however, these were not used in the chronology owing
to the current uncertainty of their exact origin and age. Age models based on the $^{14}$C and $^{210}$Pb ages
were constructed using Bacon, a Bayesian piece-wise linear accumulation model, where the
accumulation rate of sections depend to a degree on that of the preceding sections (Blaauw &
Christen, 2011). The a priori accumulation rate was assumed to be 15 yr cm$^{-1}$ and 5-cm thick sections
were used. Markov Chain Monte Carlo (MCMC) iterations estimate the accumulation rate for each
of these sections.

**Sedimentology**

Grain-size frequency distribution for 93 different grain-size classes, ranging from 0.4 to 2000 µm,
were determined for sediment samples below the peat using a Beckman Coulter LS 13 320 Laser
Diffraction-Particle Size Analyzer equipped with a Universal Liquid Module. Utilizing a protocol
modified from van Hengstum et al. (2007) and Murray (2002); 30% H$_2$O$_2$ was added to sub-samples
in a 80ºC water bath to oxidize organic matter (OM). HCl treatment was deemed unnecessary owing
to low carbonate content. End-member mixing analysis (EMMA) was performed on the grain size
analysis results to detect grain size variability in sediments beneath the peat at Aucayacu. EMMA
was performed following the procedure of Dietze et al. (2012, 2014) using extensions implemented
in the R package EMMAgeo (Dietze & Dietze 2013). Only robust end members (EMs) were included,
defined as those with non-overlapping, interpretable end member loadings, with the addition of those
in which similar EM loadings occurred in most of the model runs (Dietze et al., 2014). EM scores
were centred and scaled using the ‘decostand’ function in the R package ‘vegan’ (Oksanen et al.,
2013). An Euclidean distance matrix was generated using the ‘dist’ function in the R package ‘stats’
(R Core Team, 2016). The loadings were scaled to be genetically meaningful (scale and unit
according to original data (Weltje, 1997) using a weight transformation after Klovan & Imbrie (1971).
Pollen analysis

Samples measuring 1 cm\(^3\) were processed using standard protocols (Fægri & Iversen, 1989), including sieving at 250 μm to remove large organic fragments and a cold HF treatment to dissolve silicates. Pollen were not sieved at 10 μm because of the presence of *Cecropia* and other pollen types with small grains (< 10 μm). Residues were dehydrated with isopropanol and mounted in silicone oil. 300 pollen grains were identified and enumerated in each sample. Spores and pollen from obligate aquatic plants are not included in the pollen sum. Abundance of all pollen and spores was calculated relative to the pollen sum. Over 185 pollen taxa were differentiated but we present the 13 most important types as determined through Principal Components Analysis. The full palynological dataset will be presented elsewhere.

Plant macrofossils

Plant macrofossils were analysed at 5 cm intervals. Samples were washed and sieved under a warm-water spray using a 0.20-mm mesh sieve. The volume percentages of different vegetative remains (rootlets, leaves, wood fragments) were estimated to the nearest 5% with a stereoscopic microscope. Macroscopic charcoal pieces (> 1 mm) were counted during plant macrofossils analysis. The number of seeds and insects remains were counted separately and expressed as absolute numbers. The volume percentage of amorphous or unidentifiable organic matter (UOM) was estimated to the nearest 5% during sieving and serves as a complimentary indicator of peat decomposition (Galka et al., 2013).

Phytoliths and diatoms

Ashes remaining after loss-on-ignition (see below) were mounted on glass slides and phytolith and diatom total abundance was determined (number of diatoms in 1 cm\(^3\) sample of peat). Phytoliths were classified based on their general morphology.
Testate amoebae and hydrological reconstruction

Full details of the testate amoebae method and analysis are provided in Swindles et al. (2014, 2016). Subfossil testate amoebae were counted under transmitted light at 200-400× magnification and identified using morphology, composition, size and colour to distinguish taxa. The weighted-averaging partial least squares (component 3) transfer function of Swindles et al. (2014) was applied to the subfossil testate amoebae to generate a water-table reconstruction. This model has the following performance statistics: \( r^2_{\text{apparent}} = 0.81; \) RMSE = 3.81; \( r^2_{\text{leave-one-out cross validation}} = 0.65, \) RMSEP = 5.24, water-table depth range = 49 to -12 cm (negative values indicate a water level above the ground surface). Because the transfer function is based on one-time water table measurements, the reconstruction was detrended using linear regression following Swindles et al. (2015).

Peat properties and C accumulation

The main core was subsampled in contiguous 1-cm sections and moisture content and loss-on-ignition (LOI; ash content) were determined using standard methods on 1 cm³ samples of peat (Chambers et al., 2011). Bulk density was calculated by dividing sample mass after freeze-drying by volume (Chambers et al., 2011). The change in sample mass after drying also provided a measurement of moisture content. C and N were measured on a Thermo Scientific Flash 2000 Series CHNS/O Analyser. Peat accumulation rate (mm yr⁻¹), C accumulation rate (g C m⁻² yr⁻¹) and the long-term average rate of C accumulation (LORCA) were calculated following Tolonen & Turunen (1996). Peat humification analysis was carried out through colorimetric measurement of alkaline extracts following Roos-Barraclough et al. (2004). This proxy has come under criticism (e.g. Yeloff & Mauquoy 2006), so we adopt it cautiously here.

Rock-Eval pyrolysis

We used Rock-Eval® 6 pyrolysis to analyze organic constituents of the peats and underlying sediments (Vinci Technologies, Rueil-Malmaison, France; Lafargue et al., 1998). The Rock-Eval® 6
instrument pyrolyses OM under an inert (N$_2$) atmosphere and oxidizes OM at programmed temperature heating of bulk sediments (~20 mg) at a heating rate of 25 °C min$^{-1}$. Rock-Eval® 6 pyrolysis measures total organic C (TOC, wt. %) as well as the quantity of labile, readily degradable hydrocarbon devolatilized at 300°C (S1, mg HC g$^{-1}$), higher molecular weight kerogen-derived hydrocarbon released by thermal cracking of OM at 650 °C (S2, mg hydrocarbon g$^{-1}$), and the amount of carbon dioxide released during pyrolysis of kerogen (S3, mg hydrocarbon g$^{-1}$). Following pyrolysis, the sample is automatically transferred to an oxidation oven where it is heated from 400 °C to 850 °C, incinerating all of the residual carbon in the sample (RC wt. %) The quantity of all OM released during pyrolysis and oxidation heating is the Total Organic Carbon (TOC; wt. %). Analyses of standard reference materials (IFP 160000, Institut Français du Pétrole and internal 9107 shale standard, Geological Survey of Canada, Calgary) show accuracy and precision to be better than 5% relative standard deviation. In near-modern sediments, the S1 fraction of OM mainly consists of readily degradable geolipids and pigments predominantly derived from autochthonous OM (e.g. algal-derived lipids; Carrie et al., 2012). Lipid material consists of the fraction of OM isolated from biological material by extraction with organic solvents (Meyers & Ishiwatari, 1993). Biological lipids undergo degradative alteration as the algae sinks to the bottom of water bodies. After sedimentation, molecular composition is modified diagenetically to various degrees depending on the composition of the parent lipid, resulting in slightly different compounds termed “geolipids” (Meyers & Ishiwatari, 1993). S2 compounds in near-surface sediment are derived from the highly aliphatic biomacromolecule structure of algal cell walls and aquatic biological matter (Sanei et al., 2005; Carrie et al., 2012). The S3 portion of OM is dominated by carbohydrates, lignins, and other remains of terrigenous plant materials (Carrie et al., 2012). Humic and fulvic acids are also represented in the S3 fraction (Albrecht et al., 2015). Residual carbon represents refractory carbon (RC: charcoal, coal, reworked, oxidized OM) that cannot be further modified by bacterial activity in early diagenesis. Oxygen index (OI - the amount of oxygen relative to the amount of organic carbon present in a
sample) and hydrogen index (HI - the amount of hydrogen relative to the amount of organic carbon present in a sample) were calculated as follows: $OI = S3/TOC \times 100$; $HI = S2/TOC \times 100$.

Statistical analysis

Fossil pollen data were zoned using stratigraphically (depth)-constrained cluster analysis by incremental sum of squares (CONISS). Three statistically significant zones were identified using the broken stick model (Bennett, 1996). These zones were marked onto the proxy diagrams and used to interpret the main phases of peat development. CONISS was carried out on the full pollen dataset and also the 13 most important types - identical results were obtained. CONISS was also used to determine contemporary vegetation zones using distance along transect as the constraining variable. Non-metric multi-dimensional scaling (NMDS) analysis using the Bray-Curtis distance was applied to contemporary vegetation data to help determine the main communities. Statistically significant ($p < 0.05$) environmental variables were fitted using Envfit, which is a routine for fitting an environmental vector onto an ordination. CONISS was also undertaken on the EMMA results to determine variability in the EM scores. Statistical analyses were carried out using PAST (Hammer et al., 2001) and the Rioja (v. 0.9) and Vegan (v. 2.3) packages in R v. 3.2 (Juggins, 2015; Oksanen, 2016).

Climate data and modelling

Full details on climate data and modelling procedures including hindcasts and future scenarios used here are provided in Methods S1.

Results

Site characteristics

Hydrology, plant communities and geochemistry are highly variable along the contemporary transect (Fig. 2). Microforms are present in the peatland including pools containing standing water, hollows, litter flats, and litter hummocks/ridges (see Swindles et al., 2014). Sometimes litter hummocks were
anchored on tree roots and were termed ‘tree hummocks’. The microforms are characterised by different water-table depths (Fig. S1). pH and conductivity suggest that Aucayacu is currently a nutrient-poor system and topographic survey data shows that the site is clearly domed (Fig. 2).

The most abundant trees include Alibertia sp., Iryanthera ulei, Oxandra euneura, Virola pavonis and Zygia sp. The most commonly occurring palm trees are Mauritia flexuosa and Oenocarpus mapora. The understory is dominated by the fern Trichomanes pinnatum and grass Pariana sp. Six vegetation zones occur across the site (Fig. S2). Beginning at the river edge and working towards the peatland interior, the vegetation zones comprise: A1 dominated by Oxandra euneura, Parahancornia peruviana, Lacmellea oblongata and Eschweileria sp. 1; A2 dominated by Zygia sp. 1, Oxandra euneura, Mauritia flexuosa and Trichomanes pinnatum; A3 dominated by Iryanthera ulei, Zygia sp. 1, Alibertia sp. 1 and Oenocarpus mapora; A4 dominated by Iryanthera ulei, Zygia sp. 1 and Alibertia sp. 1; A5 dominated by Mauritia flexuosa, Zygia sp. 1, Virola pavonis and Iryanthera ulei; and A6 dominated by Iryanthera ulei, Brosimum sp. 1 and Euterpe precatoria. The major environmental controls on vegetation distribution along the transect appear to be distance from the river and peat depth (Fig. S3).

Peat initiation

We found progressively younger dates from the centre to the edge of the peatland: c. 8.9 ka BP in the centre (7.5 m peat thickness; Lähteenoja et al., 2012), c. 7.7 and 7.1 ka BP midway (~3.0 m peat thickness), and c. 5.6 ka BP at the edge (1.2 m peat thickness).
Fig. 2 Topographic and stratigraphic profile of the Aucayacu peatland with environmental variables and ecological data (plant families and plant functional types) recorded along the transect. Data are plotted against distance from the Aucayacu stream. The shape (“hollow and pool morphology”) and calculated area of individual hollow and pool microforms are also shown (“microform area”). Vegetation zones are illustrated (see Fig. S2).
Core stratigraphy

Peat depth across the transect varies from <1 to >3 m (Fig. 2). Further to the northeast, peat depths of ~7.5 m have been recorded (Lähteenoja et al., 2012). The stratigraphy of the three logged cores is similar and contains alternating bands of humified peat with occasional wood and wood peat (Fig. S4). There is a horizon of increased minerogenic material in the middle of the peat units in all three cores. Underlying the peat are sediments dominated by silt and clay, in turn overlying very coarse silt with fine sand.

Sedimentology

Results from EMMA are provided in Fig. S5-9 and Tables S1-3. EMMAgeo identified that the maximum number of EMs was 7. Values of the weight transformation that explained the most variance ranged from 0.00-0.26, with 0.00-0.06 performing the best. We chose a model using a weight transformation of 0 and consisting of 4 robust EMs. The EMMA model explained 78 ± 18% of the mean total variance across subsamples and 82 ± 15% of the mean total variance across the grain size distribution (GSD). Significant breaks occur between 497 and 498 cm and between 492 and 493 cm. The first break represents the disappearance of EM-070, while the second break represents the disappearance of EM-112. The core displays a fining-upward succession that is consistent with the interpretation of progressive isolation from the main channel flow over time as EM-012 and EM-05 can only be deposited in quiet-water conditions. The basal section of the core represents a depositional environment dominated by very coarse silt and fine sand where finer sediments were not deposited. This is interpreted as a relatively higher energy environment than the depositional setting where finer sediments were deposited.

Core chronology and peat accumulation rates

Information from 14C dates and 210Pb determinations on the central Aucayacu core are provided in Table 1 and Fig. S10. The 14C dates were in stratigraphic order apart from one date at 200 cm:
SUERC-59691 (Table 1). The Bayesian age-depth model is shown in Fig. 3 and illustrates changes in peat accumulation rate through time. Peat accumulation rate varies between 0.05 and 18.2 mm yr\(^{-1}\) (mean = 1.88 mm yr\(^{-1}\)) (Fig. 4). A phase of extremely slow peat accumulation, possibly a hiatus, is apparent between 50 and 60 cm, and phases of rapid accumulation occur at 244-265 cm, 109-137 cm, and above 40 cm. The apparent rapid accumulation rate in the uppermost 40 cm reflects the larger proportion of fresh, undecomposed litter at the top of the peat profile (Fig. 3 & S1).

### Table 1. \(^{14}\)C dates from Aucayacu including as transect of basal ages and the main multiproxy core.

<table>
<thead>
<tr>
<th>Laboratory code</th>
<th>Depth (cm)</th>
<th>Distance from river (m)</th>
<th>(^{14})C age 1σ error</th>
<th>Material dated</th>
<th>Material dated</th>
<th>(^{13})C (per mil)</th>
<th>Calibrated range 2σ (cal. yr BP)</th>
<th>Calibrated median age (cal. yr BP)</th>
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<td>Wood and leaf microfossils</td>
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<td>2372</td>
<td>23</td>
<td>Sieved peat, roots removed</td>
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### Pollen analysis

Changes in pollen and spore abundance over time reflect three phases of peat development: open water wetland (310-270 cm), forest swamp (270-95 cm) and raised peat dome (above 95 cm) (Fig. 5). The open water wetland phase is dominated by arboreal pollen, with consistently high abundances of Moraceae/Urticaceae (23-24%), particularly *Pseudolmedia*, *Brosimum* and *Helicostylis* types, likely derived from floodplain forest communities surrounding slow-moving open water, most likely an oxbow lake or backwater pond that was permanently inundated. The abundance of Poaceae (4-19%) and Cyperaceae (5-16%) pollen reflects an open water wetland environment that supported
semi-aquatic species of these families, rather than terrestrial forms (Burn et al., 2010). This is supported by the absence of other terrestrial herb pollen types.

**Fig. 3** Bayesian age-depth model of the Aucayacu core. On the right-hand panel, the top plot shows that both MCMC runs were stable, the middle plot show the prior (curves) and posterior (filled histograms) distributions for the accumulation rate (yr cm$^{-1}$), and the bottom plot show the prior (curves) and posterior (filled histograms) for the dependence of accumulation rate between sections. The large plot shows age distributions of calibrated $^{14}$C dates and $^{210}$Pb, and the age-depth model (grey-scale). Dark grey areas indicate precisely dated sections of the chronology, while lighter grey areas indicate less chronologically secure sections. The $^{210}$Pb age model is also shown (insert).
The presence of evergreen tree pollen in this zone indicates a closed-canopy forest around the water body. Similarly, trees from the genus *Cecropia* (12-51%) require light gaps, can tolerate flooded conditions, and frequently occupy low- to mid-level communities in floodplain forests, especially várzea forest (Worbes, 1997; Nebel et al., 2001). Clay content in this phase (as observed in the pollen slides and loss-on-ignition data) is higher than in successive zones, suggests a low-energy depositional environment not likely directly connected to the river occurred at this time.

The forest swamp phase is characterised by an increase in *Mauritia/Mauritiella* pollen, likely reflecting the high water level of a floodplain environment. *Mauritia flexuosa* is adapted to flooded conditions and has pneumatophores and other anatomical adaptions to enable gas exchange in inundated ground surface conditions (Junk, 1989). The abundance of *Cecropia* pollen in this zone suggests that although the water level was relatively shallow, seasonal flooding was common because *Cecropia* seedlings will not establish under permanent inundation (Junk, 1989) and trees of this genus are most common in mid-level floodplain plant communities (Worbes, 1997; Nebel et al., 2001).

Pollen of Combretaceae/Melastomataceae is most abundant in this phase (4-30%). Although this pollen type encompasses a large number of species from two ubiquitous Neotropical families, a comparison of pollen signatures from a range of Amazonian forest formations shows that seasonally-inundated rainforest is characterised by this pollen morphotype (Burn et al., 2010). The forest swamp phase characterized by this pollen type therefore likely reflects a seasonally inundated floodplain forest. The depositional environment likely contained no permanent water body, as indicated by the decline in Poaceae and Cyperaceae pollen at the boundary between this zone and the previous zone.

*Mauritia/Mauritiella* (10-42%) and more than ten additional undifferentiated Arecaceae pollen types dominate the assemblages above 95 cm, indicating the transition to the final peat dome phase. The transition from seasonally-inundated floodplain forest to a nutrient poor peatland, as.
Combretaceae/Melastomataceae and Cecropia pollen (reflective of seasonally-inundated floodplain forest) decline in this zone. Other abundant taxa include Alchornea/Aparisthmium (Euphorbiaceae) (2-15%) and Virola (Myristicaceae) (4-22%), species of which produce hypertrophic lenticels and adventitious rooting systems (Junk, 1989; Lopez et al., 2003) in response to low oxygen conditions caused either by inundation and/or burial by sediments or peat. Virola pollen is indicative of peatland in the Neotropics (Ledru, 2001). Pollen and LOI data (Fig. 4 & 5) suggest that in this phase the peatland mostly functioned as an ombrotrophic dome; however, the occasional influence of high-magnitude floods cannot be discounted.

Peat composition and macrofossils

An analysis of macrofossils shows considerable variation in the proportional contributions of roots, wood, UOM and leaf epidermis (Fig. 6). Major shifts in root-dominated to wood-dominated peats are apparent during the forest swamp phase. Occasional seeds and insect remains are also present, and quartz grains were found in the bottom of the profile. Macroscopic charcoal occurs in the uppermost 20 cm of the core, at 73 cm and at 123 cm. Phytoliths are also common. In particular, an increase in spinulose palm phytoliths (produced by members of the Arecaceae family) occurs in the peat dome phase. Diatoms are present in three depths in the core and may suggest wetter conditions at these times (Fig. 6).

Testate amoebae

The most common testate amoebae in the profile include Hyalosphenia subflava, Trigonopyxis arcula, Phryganella acropodia and Centropyxis aculeata. Preservation down-core is variable and concentrations of testate amoebae in general were very low (see Swindles et al., 2016). The horizon 50-60 cm (peat dome phase) was barren of testate amoebae.
Fig. 4 Peat properties and carbon and nitrogen data from the Aucayacu core, plotted by depth and age. Interpretative zones are shown on the right hand side of the diagram.
Fig. 5 Percentage pollen data from the Aucayacu core, plotted by depth and age. Interpretative zones are shown on the right-hand side of the diagram.
A contemporary training set from Aucayacu (Swindles et al., 2014) shows that *C. aculeata* is an indicator of surface water; an abundance of this taxon in the early part of our record indicates persistent standing water and provides evidence to support the open water depositional environment interpreted from pollen analysis. Fluctuations in palaeohydrological conditions during the subsequent forest swamp phase, and a trend towards dryness followed by a wet shift (at c. 50 cm) in the peat dome phase are identified from the testate amoeba-based reconstruction (Fig. 7).

**Peat properties and C accumulation**

Loss-on-ignition (LOI) data clearly show first peatland initiation at ~300 cm (Fig. 4). Relatively lower LOI values during the forest swamp phase provide clear evidence for episodes of minerogenic input during the forest swamp phase. Within the peat (0-300 cm) the maximum LOI is 98.4%, and the minimum is 48.3% (mean = 88.6%). Above 96 cm (the peat dome phase) the maximum LOI is 98.4%, and the minimum is 88.5% (mean = 93.9%). However, ash content above 96 cm is related to the high abundance of silica phytoliths rather than minerogenic material (see Fig. 6). The bulk density of the peat varies between 0.02 and 0.16 g cm\(^{-3}\) (mean = 0.08 g cm\(^{-3}\)). Several shifts in peat humification are apparent with major excursions to lower humification at 264-280 cm, 156-199 cm and above 40 cm (Fig. 4). These may relate to either wetter episodes where peat humification was reduced or changes in peat composition (e.g. shift from root and wood-dominated to UOM-dominated peat – Fig. 6). The C/N (% mass) varies between 16.2 and 94.1 (mean = 44.9). The large increase in %N in the uppermost 40 cm of the profile reflects the oxic zone, where peat has not yet fully decomposed. A decrease in %C in the forest swamp phase reflects the incorporation of minerogenic material within the peat.
Fig. 6 Peat composition data (plant macrofossils) and other microfossils found in the Aucayacu core, plotted by depth and age. Interpretative zones are shown on the right hand side of the diagram.
Fig. 7 Subfossil testate amoebae diagram from Aucayacu (data are expressed as percentages). Richness, Shannon Diversity Index values and the water-table reconstruction (plotted with errors derived from bootstrapping and as detrended values) are also shown.
C accumulation rates mirror peat accumulation rates, with a phase of extremely slow accumulation at 50-60 cm, and phases of rapid accumulation at 244-265 cm, 109-137 cm and above 40 cm. C accumulation rates vary between 1.8 and 495.7 g C m$^{-2}$ yr$^{-1}$ (mean = 70.8 g C m$^{-2}$ yr$^{-1}$). LORCA is 15.96 g C m$^{-2}$ yr$^{-1}$, which is lower than the 39 g C m$^{-2}$ yr$^{-1}$ found by Lahteenoja et al. (2012) on the longer core (7.5 m) taken 2.1 km to the northeast.

Rock-Eval pyrolysis

S1 C displays a decreasing trend down-core, which most probably relates to diagenesis of labile OM as S1 C is the most readily degradable fraction of organic C (Fig. 8). Both S1 and S2 C increase during the early open water wetland phase. This is likely attributable to the relative increase in wetter conditions that promoted primary production and enhanced preservation of OM. Increases in S3 C during the lower part of the open water wetland phase likely represent increased delivery of terrestrially-derived OM from increased runoff or more frequent floods. The shifts in S1, S2, S3, and C/N ratio during the open water wetland phase (Figs 4 and 8) suggest a transition to more lacustrine conditions, reflecting the isolation of the water body through time. S1/S2 illustrates selective diagenesis of S1 relative to S2. RC/TOC shows relative decline in proportion of refractory C during the open water wetland phase and in the uppermost peat. This is attributed to a relative increase in proportion of more labile, liptinitic-rich and autochthonous OM (S1 and S2). RC/TOC remains relatively constant throughout the forest swamp phase, with around 70% of the TOC being refractory due to humification occurring in the uppermost layers of the peatland.
Fig. 8 Rock-Eval pyrolysis data plotted by depth and age. Interpretative zones are shown on the right hand side of the diagram. S1 = the free hydrocarbons present in the sample before thermal pyrolysis (in milligrams of hydrocarbon per gram of sample); S2 = the volume of hydrocarbons that formed during thermal pyrolysis of the sample; S3 = the amount of CO₂ (in milligrams CO₂ per gram of sample) produced during pyrolysis of kerogen (in milligrams CO₂ per gram of sample); TOC = total organic carbon (%); RC = residual carbon (%); HI = hydrogen index; OI = oxygen index; MINC = mineral carbon (%).
Fluctuations in HI and OI profiles during the open water wetland phase reflect the shift in depositional environment from one that accumulated under more terrestrial conditions (Type III OM, OI of ~140 and HI of ~200) to one that accumulated more autochthonous, liptinitic-rich C (Type II OM, HI 300 to 400 and OI of less than 50). In the uppermost 50 to 100 cm of peat, HI is elevated relative to deeper peats, although OI remains more or less constant. This suggests that the relative increase of HI is due to higher deposition of liptinitic-rich OM and little change in the proportion of terrestrially-derived OM input. This shallow section may also reflect active humification that targets liptinitic-rich OM.

The ratio RC/TOC shows downward enrichment of refractory OM as the more labile, hydrogen-rich, liptinitic fraction is degraded due to humification. In the uppermost 40 cm, the marked rise in OI is likely associated with the oxic zone and accumulation of humic and fulvic acids along with a labile geolipid fraction (S1).

**Discussion**

Our contemporary vegetation analysis suggests that water-table depth is not a strong control on modern vegetation distribution, illustrating that vegetation across the site is zoned at the meso-macro scale with distance from the river, unlike many northern peatlands that are commonly characterised by vegetation patterning at the microform level (e.g. Baird et al., 2016). Our multiproxy palaeoenvironmental dataset illustrates the long-term dynamics of the oldest known peatland in the Amazon basin. The modern peat dome has developed in several distinct phases, and its dynamics were driven by a combination of autogenic (vegetation succession, vertical and lateral expansion) and allogenic (climatic, floodplain) influences on millennial and multi-centennial time-scales.

**Allogenic and autogenic controls on peatland development**

Our multi-proxy dataset suggests a relatively simple and unidirectional succession from open water wetland (c. 7.8-6.6 ka BP), through inundated forest swamp (c. 6.6-3.9 ka BP), to raised peat dome (since c. 3.9 ka BP) (Fig. 9).
Fig. 9 Summary diagram from Aucayacu illustrating the main phases of peatland development. Key climate events and GCM hindcasts (see text) are also illustrated.
This is in contrast to the palynological study of Kelly et al. (2017) on another Amazonian ombrotrophic peat bog (San Jorge), which suggested a much more complex trajectory with reversals to former states. The fining-upwards succession in the mineral sediments underlying the peat is consistent with the isolation of a river channel segment into an oxbow lake or a backwater following eastward migration of the river channel, which subsequently allowed peatland development.

Our four basal dates suggest that the peatland underwent a rapid lateral expansion (~2.0 m yr\(^{-1}\)) from a central nucleus, before slowing down after c. 7.7 ka BP (~0.7 m yr\(^{-1}\)), and again after c. 7.1 ka BP (~0.4 m yr\(^{-1}\)) (Fig. S11). Alternatively, the peatland may have emerged in a more complex manner from several initiation centres that coalesced over time. Both of these point-initiation and simultaneous initiation development pathways have previously been suggested for Northern peatlands (Belyea & Baird, 2006; Foster & Wright, 1990; Glaser et al. 2004). However, our four basal dates become monotonically younger from centre to margin, which is consistent with a point initiation and subsequent lateral expansion (Fig. 1 & S11). As vegetation developed, peat accumulated and the system transitioned into an inundated forest swamp. After sufficient vertical accumulation of peat, the peat surface became hydrologically disconnected from the influence of river flooding, and the ecosystem transitioned into an ombrotrophic peat dome with less pronounced cycles between dry and flooded conditions. The timing of the first appearance of the contemporary pole forest is ambiguous in the pollen record because many of the characteristic trees of this vegetation type are insect pollinated and are thus commonly poorly represented in sedimentological records (e.g. Kelly et al., 2017). Furthermore, the pollen rain in pole forests is often overwhelmed by the presence of a relatively small number of *Mauritia flexuosa* trees (e.g. Kelly et al., 2017). However, the presence of *Mauritia* pollen may also suggest the persistence of palm swamp vegetation disconnected from the influence of pronounced river flooding. The presence of charcoal in the core shows that these ecosystems have been affected by fire on at least three occasions in the last 4,500 years, most probably related to anthropogenic activity (see McMichael et al., 2012). This is in contrast to other published
records from peatlands in Peruvian Amazonia in which no charcoal has been found (see Roucoux et al., 2013; Kelly et al., 2017).

Although there are many uncertainties over the Holocene climate history of western Amazonia (see Flantua et al., 2016; Kelly et al., 2017), some climatic events for which independent evidence exists may have been recorded in the peat record at Aucayacu. During the forest swamp phase we identify two distinct dry phases at c. 6.6-6.1 (henceforth drought phase A) and c. 4.9-3.9 ka BP (drought phase B), as evidenced by a lack of aquatic testate amoebae and increased peat humification. In addition, an apparent hiatus in peat accumulation occurred between c. 1.8 and 1.1 ka BP. Hiatuses in peat accumulation may occur in response to tree fall and tip-up events (Dommain et al., 2015), although high phytolith concentrations and a complete absence of preserved testate amoebae around the hiatus at Aucayacu suggest that it is more likely to reflect increased peat decomposition. This hiatus overlaps with the beginning of a similar hiatus identified at the San Jorge peatland 150-200 km away (c. 1.3 to 0.4 ka BP; Kelly et al., 2017). Timings of drought phases A and B and the hiatus at Aucayacu are temporally consistent with known drought phases in Peru (Fig. 9). For example, major drought phases have been identified in Lake Sauce in Peruvian Amazonia at c. 4.9-3.5 ka BP and c. 1.9-1.3 ka BP (Correa-Metrio et al., 2010). Although the nature of strength of any teleconnection across the Andes is unclear, it is interesting to note that a major lowstand of Lake Titicaca occurred also between c. 7 and 4 ka BP (Baker et al., 2005).

Drought is thought to have been widespread across both upland and lowland Amazonia during the early-mid Holocene (Mayle & Power, 2008). A dry event is also recognised in other lakes of Peruvian Amazonia around the city of Puerto Maldonado between c. 7.2 and 3.3 ka BP (Bush et al., 2007). Phases of reduced South American Summer Monsoon (SASM) rainfall have been dated at c. 7-5 ka BP and c. 1.5-0.9 ka BP (Bird et al., 2011). Therefore, we interpret the hiatus as potentially reflecting a third drought phase (drought phase C). It is also interesting to note that Drought phase B (c. 4.9 to
3.9 ka BP) is contemporaneous with the well-documented and possibly global c. 4.2 ka BP climate event (Booth et al., 2005; Davis & Thompson, 2006; Roland et al., 2014), which itself is correlative with Bond Event 3 (Bond et al., 1997, 2001), although the mechanisms for global climatic teleconnection remain poorly understood.

The palaeoecological study of Peruvian Amazonian lake sediments by Bush et al. (2007) suggests that dry conditions during the mid-Holocene were followed by a period of increasingly wet conditions beginning between c. 4.2 and 2.5 ka BP. A similar wet signal can be seen in our palaeohydrological reconstruction from Aucayacu, immediately following drought phase B. Drought phase C is also chronologically consistent with dry phases found in several other proxy records from Amazonia and other sites in South America (Piperno & Becker, 1996; Weng et al., 2002; Roucoux et al., 2013).

We observe differential effects of these droughts on peat and C accumulation regimes (Fig. 9 & 10). During the forest swamp phase, drought phases A and B led to increased peat and C accumulation, whereas during the subsequent peat dome phase, drought phase C caused a collapse in peat and C accumulation. This apparent hiatus may be explained by recent research into the C dynamics of tropical peatlands. Hirano et al. (2012) investigated the C balance of drained and near-natural ombrotrophic tropical peatlands using eddy correlation. For a near-natural site, they found that gross primary production ($P_G$) showed a quadratic relationship with water-table depth. $P_G$ was lowest at deep water-table levels (c. 0.9 m below the ground surface), highest at intermediate water-table depths of c. 0.3 m, and lower again (but not as low as for the deepest water tables) as water tables became shallower and the peatland surface became inundated. Ecosystem respiration ($R_E$ – the sum of plant respiration and peat decay) also varied with water-table depth, being highest for deep water tables (0.9 m) and declining monotonically to inundation depths of up to 0.2 m, with the rate of decline increasing in the latter part of the water-table range.
Many other studies have shown how depth-integrated decay of peat (usually the dominant component of $R_E$) increases as the water table deepens (see Baird et al., 2017). The combined $P_G$ and $R_E$ data from Hirano et al. (2012) show that net rates of peat accumulation are highest when a tropical peatland is at its wettest and lowest when it is at its driest. Specifically, the data from Hirano et al. (2012) suggest that net accumulation of peat only occurs when water tables are shallower than $c. 0.3-0.2$ m, while deeper water-tables lead to a net loss of peat.

The increase in rates of peat accumulation during drought phases A and B (forest swamp phase) is the opposite of what occurs during drought phase C (peat dome phase). One possibility is that a reduction in water levels causes a sharp up-step in productivity of the swamp vegetation – growth rates of the component species of this vegetation may normally be inhibited by the deep water-logged conditions that usually prevail – without a corresponding or matching increase in rates of peat decay, which may be expected if water levels are still mostly near the peatland surface. Other possibilities can be conjectured, but what is needed is research on current swamp systems to see how they respond.

**Fig. 10** Peat accumulation rate (mm yr$^{-1}$) plotted on a (natural) logarithmic scale with the three drought events and developmental phases illustrated.
in terms of $P_G$ and $R_E$ during multi-year droughts. Different ‘rules’ almost certainly apply to swamp
and peat dome conditions given their different plant communities and the likely differences in the
nutrient status of peat pore water, both of which will affect $P_G$ and $R_E$. (e.g. DeBusk & Reddy, 2005;
Rydin & Jeglum, 2006). It has also been shown that droughts can affect productivity in Amazonian
forest communities in different ways (e.g. changes in biomass, autotrophic respiration, photosynthesis
and tree mortality), and that they do not always cause a decrease in productivity (Doughty et al., 2015;
Feldpausch et al., 2016). Such variations may offer an alternative explanation for our observations
during the different drought phases.

A further observation is that drought phase A coincides with an ecosystem state shift from open water
wetland to forest swamp (c. 6.6 ka BP); and drought phase B with a shift from forest swamp to raised
peat dome (c. 3.9 ka BP) (Fig. 9-10). GCM hindcasts of annual average precipitation also suggest a
slight drying trend between the open water wetland and forest swamp phases, and suggest reduced
effective precipitation during drought phases B and C (Fig. 9). Drought phase A may have caused
sufficient drying in the open-water phase to stimulate productivity in hitherto limnic conditions,
leading to rapid terrestrialisation and infilling with litter (driving the conversion from open water
wetland to forest swamp). This is consistent with the increase in S3 C observed in the Rock-Eval
pyrolysis data (Fig. 8). Drought phase B potentially drove the conversion of the forest swamp into an
ombrotrophic peat dome, again by stimulating productivity in a previously seasonally-flooded
landscape. The resumption of peat accumulation after drought phase C also adds further weight to the
-growing body of evidence for the resilience of peatland ecosystems to recover from severe
disturbances (e.g. Morris et al., 2015; Waddington et al., 2015; Swindles et al., 2016). The shift to
ombrotrophic peat dome at c. 3.9 ka BP is contemporaneous with the increased El Niño-Southern
Oscillation (ENSO) activity identified from ~4.0 ka BP (Haug et al., 2001; van Breukelen et al.,
2008), which may suggest climate variability played a role in stimulating the ecosystem state shift,
alongside any autogenic mechanisms.
Gloor et al. (2013) suggested that there has been intensification of the Amazonian hydrological cycle over the last two decades and a marked increase in precipitation in north-western Amazonia (up to 80 mm month\(^{-1}\) from the period 1980-1990 to 2000-2009). Climate re-analysis data also show that there has been a recent shift to higher temperatures and increased precipitation at Aucayacu across all seasons (Fig. S12). The recent increase in wetness shown in our testate amoeba record (Fig. 9) is consistent with a progressively wetter climate, although the effects of better test preservation in the uppermost peat cannot be discounted. The CMIP5 climate model ensemble projects that this region will continue to warm over the next ~80 years, with the wet season in particular becoming wetter (Fig. S12). Held & Soden (2006) and Wang et al. (2017) also suggested that rainfall in the Amazon lowlands is likely to increase, alongside the intensification of wet and dry phases (including more pronounced droughts).

**Implications and uncertainties**

Our multiproxy dataset and conceptual model provide an important step in improving understanding of Amazonian peatland ecosystems. However, uncertainties remain over the relative controls of autogenic (e.g. peat growth and ecohydrology, plant succession) and allogenic (e.g. climate, floodplain processes) controls on Amazonian peatland development. Mathematical models of peatland development (e.g. Baird et al., 2011; Swindles et al., 2012; Kurnianto et al., 2015; Morris et al., 2015) may prove useful tools for investigating the behaviour of Amazonian peatlands and the vulnerability of their C stores to climate change and human impacts. However, new data on the ecohydrological properties of these systems (e.g. plant communities, above and below-ground litter production and decomposition, and permeability) are needed for accurate parameterisation of these models. Detailed down-core studies of peat properties, C content, decomposition, palaeohydrology and vegetation types, such as we present here, provide a crucial yardstick for testing model-based simulations of tropical peatland development.
A diversity of peatland types have been found in the PMFB (see Lähteenoja & Page, 2011). Future work should focus on understanding the developmental history of these different peatland types and whether there are developmental or successional pathways between them. Amazonian peatlands are important in terms of biodiversity, ecosystem services, and C storage, and they represent important archives of past climatic, ecological and other environmental information (e.g. volcanic ash). Several infrastructure projects are planned in the PMFB including a proposal for constructing an electricity transmission line and service track through the Aucayacu peatland (Dourojeanni, 2016; Roucoux et al., 2017). We contend that policies should focus on the conservation and protection of these vulnerable ecosystems.

Conclusions

1. A multiproxy palaeoecological dataset shows that the oldest peat dome yet discovered in Amazonia developed in three distinct phases: (i) peat initiated in an abandoned river channel or backwater with standing open water and aquatic plants; (ii) inundated forest swamp; and (iii) raised peat dome (after c. 3.9 ka BP). The presence of charcoal in the core shows that these ecosystems have been affected by fire on at least three occasions in the last 4,500 years.

2. Two phases of rapid carbon accumulation (c. 6.6-6.1 and c. 4.9-3.9 ka BP) potentially resulting from increased net primary productivity were seemingly driven by drier conditions during widespread drought events. A switch to ombrotrophy occurred after the c. 4.5-4.2 ka BP drought phase suggesting a possible climatic control on tropical peatland developmental trajectories and ecosystem state shifts. A third drought phase at c. 1.8-1.1 ka BP led to a collapse in carbon accumulation (potentially a hiatus), relating to increased decomposition from deeper water tables and/or lower net primary productivity during the ombrotrophic peat dome phase.

3. Our results suggest that future droughts will lead to phases of rapid carbon accumulation in some inundated tropical peat swamps, although this can lead ultimately to a shift to ombrotrophy and a
subsequent return to lower carbon accumulation rates. Conversely, drought phases may lead to a collapse in carbon accumulation in ombrotrophic peat domes.

4. Amazonian peatlands are important in terms of biodiversity and carbon storage, and represent important archives of palaeoenvironmental information. Policies should focus on the conservation of these ecosystems.

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