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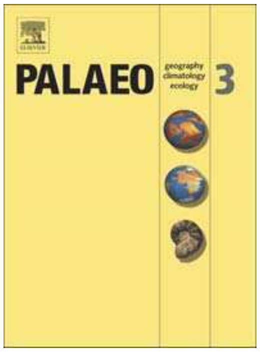

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The vegetation history of an Amazonian domed peatland

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Abstract

The peatland pole forests of the Pastaza-Marañón Foreland Basin (PMFB), Peru, are the most carbon-dense ecosystems known in Amazonia once below ground carbon stores are taken into account. Here we present the first multiproxy palaeoenvironmental record including pollen data from one of these peatlands, San Jorge in northern Peru, supported by an age model based on radiocarbon and ^{210}Pb dating. The pollen data indicate that vegetation changes during the early phases of peat initiation resulted from autogenic succession in combination with fluvial influence. The overall pattern of vegetation change is not straightforward: the record does not reflect a process of unidirectional, progressive terrestrialization, but includes a reversal in the succession and vegetation transitions which omit predicted successional phases. This complexity is similar to that seen in the only other existing pollen record from a PMFB peatland, at Quistococha, but contrasts with peat records from Panama and Southeast Asia where successional patterning appears more predictable. Our dating results provide the first evidence from a PMFB peatland that peat accumulation may have been discontinuous, with evidence for reduced rates of peat accumulation, or a possible hiatus, around 1300–400 cal yr BP. An ecological shift from open lake to palm swamp occurs at this time, possibly driven by climatic change. The pollen data indicate that the present pole forest vegetation at San Jorge began to assemble c. 200–150 cal yr BP. Given this young age it is likely that the pole forest at this site remains in a state of transition.

Key words: pollen analysis, Holocene, geochemistry, pole forest, vegetation change, tropical peatland

Introduction

Lowland tropical peatlands are estimated to cover 441,000 km^2 and to store at least 88.6 Pg C (Page et al., 2011). Recent field exploration has uncovered substantial peat accumulations in Amazonia (Lähteenoja et al., 2009a,b, 2012, 2013; Lähteenoja and Page, 2011; Householder et al., 2012). These peatlands contribute to landscape-scale biodiversity, provide habitats for threatened animal species (Nicholson, 1997), and provide other ecosystem services such as fruit harvests (Kahn, 1988; Vasquez and Gentry, 1989; Gilmore et al., 2013). Lowland peatlands are particularly widespread in the Pastaza-Marañón Foreland Basin (PMFB) of north-east Peru where they occupy an estimated 35,600 ± 1088 km^2 (Draper et al., 2014), with peat up to 7.3 m thick (Lähteenoja and Page, 2011). The total above- and below-ground carbon stock of these peatlands is estimated at 3.14 Pg C, comprising a significant component of regional carbon storage (Draper et al., 2014). Of the three remote sensing peatland vegetation classifications (open herbaceous, palm swamp and pole forest), pole forest peatlands, which are typically domed, are the most carbon dense with 1391 ± 710 Mg C ha^{-1}, most of which is stored below ground (Draper et al., 2014).

Given their role as carbon stores, it is important that we understand how Amazonian peatlands function as, like all peatlands, they have the potential to affect the Earth’s climate system by sequestering carbon and by emitting carbon dioxide and methane to the atmosphere (Page et al., 2002; Li et al., 2007; Sjögersten et al., 2014). A particular priority is to determine their sensitivity to past and future climatic change. Climate model projections vary between different models; while all show increased temperatures across Amazonia, with respect to rainfall there are a range of projected future scenarios for the period from 2071-2100 (Sánchez et al., 2015). Some climate models project pronounced decreases in dry season (June, July, August) rainfall, while others project more moderate reductions, or even increased precipitation (Sánchez et al., 2015). Analysis of recent historical trends indicates that the hydrological cycle in western Amazonia is becoming more intense, with greater differences between dry and wet season rainfall (Gloor et al., 2013).

Domed, ombrotrophic peatlands are likely to be sensitive to climatic change as they receive all of their moisture input from rainfall (Charman, 2002). As such, the environmental information recorded in the peat archive provides an important insight into the sensitivity of peatlands to past climatic change. Domed peatlands in the PMFB frequently host so-called ‘pole’ forests, characterised by closely-spaced slender trees, similar in structure to pole forests known from Southeast Asian peatlands. Morley (1981) produced a pollen record from one of these sites at Sungei Sebangau, Kalimantan which showed that the formation of pole forest vegetation occurred within the top c. 1 m of the peat profile, suggesting that they are a late-successional vegetation type (Morley, 2013).

In this paper, we use pollen analysis and other palaeoenvironmental data to reconstruct, for the first time, the vegetation history of a domed Amazonian peatland. Through comparison with proxy climate and palaeoecological records from the wider region, we seek to understand:

1. The pattern of biotic and abiotic development at our site, with a focus on vegetation change (particularly the formation of the present pole forest) since c. 2300 cal yr BP, the point at which peat initiated.
2. The drivers of peatland development, including consideration of extrinsic factors (such as climate and geomorphological change) and intrinsic factors (ecological succession).

Study Site

The study site of San Jorge, named after the adjacent village, is a domed peatland bordering the Amazon River (Figs. 1 and 2), towards the north-eastern margin of the PMFB (Lähteenoja and Page, 2011). The PMFB, a c. 120,000 km^2 subsiding tectonic basin, is characterized by a mosaic landscape with river systems and floodplains belonging to the Ucayali, Marañón, and Amazon rivers and their tributaries, surrounded by higher, un-flooded, older terraces with different vegetation and underlying geology (Räsänen et al., 1992). The floodplain in this region is highly dynamic, with thousands of hectares of land reworked each year through channel migration (Kalliola et al., 1992; Mendoza et al., 2016). This region is one of the wettest parts of Amazonia, with rainfall > 3000 mm yr^{-1}, and remaining above 100 mm per month even in the dry season (Marengo, 1998). Mean annual temperature is c. 25 ˚C, with high relative humidity of 80–90% throughout the year (Marengo, 1998). The San Jorge peatland was chosen for study because of its shallow domed structure (as confirmed by a topographic survey undertaken by Lähteenoja et al., 2009b), pole forest vegetation, and thick peat, the latter maximising the likelihood of obtaining a long and well-resolved palaeoecological record. The area of pole forest can be clearly seen in Landsat imagery (Fig. 2); the satellite imagery shows an approximately concentric pattern of vegetation, with the central pole forest surrounded by palm swamp areas which we observed in the field. These marginal areas of the peatland are characterised by year-round standing water and Mauritia flexuosa-dominated palm forest (known locally as aguajal). This contrasts with the raised centre of the peatland where there is currently no evidence of annual flooding (Lähteenoja et al., 2009b). The low Ca/Mg ratio of the near-surface peat indicates that the central peatland area is, at present, a dominantly ombrotrophic (rain-fed) system, with low nutrient availability (Lähteenoja et al., 2009b). The Landsat imagery also shows a lake to the west of the coring location with a ring of different, possibly palm swamp, vegetation surrounding it, although we were unable to access this part of the site.

The measured diversity of the pole forest at San Jorge is low, with only ten tree species identified in a 0.5 ha inventory plot (Kelly et al., 2014). Pole forest of this kind is estimated to occupy c. 10% or 3686 km^2 of the total peatland area in the PMFB (Draper et al., 2014). The assemblage is dominated by three species (see Supplementary Information) which make up 83% of the individuals: Pachira aff. brevipes (A. Robyns) W.S Alverson (Malvaceae), Remijia aff. ulei K.Krause (Rubiaceae), and Calophyllum brasiliense Cambess (Clusiaceae). The slender growth form typical of pole or 'dwarf' forest (E. Honorio Coronado, pers. comm.) was exhibited by most tree species (including specimens of M. flexuosa). Some of the species in the plot, including P. brevipes and C. brasiliense, are also commonly found in terra firme white sand forests (Fine et al., 2010), which are also nutrient-poor.

Methods

We undertook a multiple-proxy analysis of a peat/sediment core from close to the centre of the San Jorge peatland. Stratigraphic pollen analysis was used to establish the history of vegetation change, and pollen surface samples were used to assist interpretations. Geochemical analysis was used to reconstruct changes in the trophic status of the peat and other information about its development through time (Shotyk, 1996; Lähteenoja et al., 2009b, Lähteenoja and Page, 2011; Lawson et al., 2014). Additional palaeoenvironmental information was provided by loss-on-ignition (LOI) and magnetic susceptibility, and an age model was established by ^{14}C and ^{210}Pb dating. This is the first time that ^{210}Pb dating has been applied in an Amazonian peatland.

Core collection

The peat in the pole forest at San Jorge was cored during the dry season (July) in 2010 using a 5 cm diameter, 50 cm long Russian-type peat corer (Jowsey, 1966). Each 50 cm core section was wrapped in the field, and stored at 4°C on return to the UK. The core (SJO-2010-1) was taken at 4°03'48" S, 73°11'42" W which is, within the limits of precision of our GPS receiver, the same location as that sampled by Lähteenoja et al. (2009b) for geochemistry and dating.

Pollen analysis

Down-core pollen data were generated at a minimum resolution of 8 cm for the top 240 cm of the sequence, where LOI values reveal pure peat accumulation with little inorganic residue. Sample preparation followed standard methods, including HF digestion where necessary (Faegri and Iversen, 1989). Slides were made using silicone oil as the mounting medium and were sealed using paraffin wax. Pollen, phytolith and charcoal analysis was undertaken using a Leica DMLS binocular microscope, routinely at 1000x. A minimum pollen sum of 300 was counted, although in a single instance (196 cm) low pollen concentrations meant that a pollen sum of only 150 grains was counted. The pollen sum excludes spores of the Pteridophyta and fungi and the pollen grains of aquatic plants. Unknown pollen types were included in the pollen sum. Pollen and phytolith concentrations were calculated through the addition of Lycopodium spike tablets (Stockmarr, 1971). Three pollen surface samples obtained from the pole forest at the site were counted in order to aid interpretations (total aggregated pollen sum: 438).

Identifications were based on pollen reference slides, the pollen atlases of Roubik and Moreno (1991) and Colinvaux et al. (1999), the Neotropical Pollen Database (Bush and Weng, 2006) and other literature (Absy, 1979; Walker and Walker, 1979; Andersson, 1993; Weber et al., 1999; Van Geel, 2001; Nowicke and Takahashi, 2002; Dias Saba, 2007; Burn and Mayle, 2008). Mauritia and Mauritiella are morphologically similar but reference material differs systematically in size between the two genera (Fig. S2; Kelly, 2015), so the size of fossil grains was measured wherever possible. Zonation was carried out manually, informed by the automated statistical techniques implemented in Psimpoll (Bennett, 2007).

Sedimentological and geochemical analysis

Peats and sediments were described following Troels-Smith (1955). Volumetric magnetic susceptibility (κ, dimensionless; Hatfield and Stoner, 2013) measurements were made at 2 cm intervals using a Bartington MS-2 meter and MS-2C loop sensor. Background measurements were made before and after each core section to account for sensor drift. LOI analysis followed Heiri et al. (2001). Bulk density estimates were made using 1 cm^3 samples; samples were taken using a volumetric sampler, weighed, and then dried at 105 ºC overnight before being re-weighed.

The concentration of Ca and Mg was determined using inductively coupled plasma optical emission spectroscopy (see Hou and Jones, 2000). Solid samples were subjected to a chemical extraction using pure aqua regia (conc. HCl and 6M HNO_3) following British Standard BS 7755 (British Standards Institute 1995).

For carbon and nitrogen analyses, samples of 1 cm^3 were dried at 105˚C and milled to ensure that the sample was thoroughly homogenised. Each sub-sample was then weighed into a tin cap and analysed using a Eurovector Turboflash CNS combustion analyser. Vanadium pentoxide was used as a catalyst. The peat standard NJV942 was used with all sample batches. The experimental values for carbon and nitrogen were within 95% of the certified value for NJV942 for all sample runs.

Dating

Samples of 5 or 6 cm^3 of peat were taken from contiguous 2 cm thick slices from the uppermost 50 cm of the sequence (i.e. 25 samples in total), dried for two days at 50˚C, and weighed in order to estimate their dry bulk density. Samples were chemically treated with aqua regia and H_2O_2 in order to extract ^{210}Pb and remove organic matter before the extract was transferred to silver plates. The ^{210}Pb content of the samples was then determined indirectly through counting alpha particle emissions from the decay of its granddaughter isotope ^{210}Po (Appleby, 2001). A spike of ^{209}Po was added to each sample to determine whether there was any loss of ^{210}Po during the preparation (Le Roux and Marshall, 2011). Measurements were made using a combination of ‘TENNELEC TB 3LB’ and ‘ORTEC OCTÊTE-Plus Integrated Alpha-Spectroscopy System’ emission counters, with a measurement time between 70 and 285 hours. The ^{210}Pb activity of the samples was converted into real ages using a constant rate of supply (CRS) age model, after Appleby (2001).

Five radiocarbon dates were obtained from the peat above 240 cm (Fig. 3, Table 1). We did not date the underlying more mineral-rich sediments, for which a lowermost date of 2880–3010 cal yr BP at 560–570 cm was obtained from a separate core from the same site by Lähteenoja et al. (2009a). Peat samples 1-2 cm^3 in volume were prepared for radiocarbon dating by sieving at 180 μm to remove as much root material as possible. The δ^{14}C and δ^{13}C content of the samples was determined through accelerator mass spectrometry at the NERC Radiocarbon Facility in East Kilbride and at the ^{14}Chrono Radiocarbon Laboratory, Queen’s University Belfast. A Bayesian age-depth model incorporating all of the ^{210}Pb and ^{14}C dates was produced using the BACON package (Blaauw and Christen, 2011) in R (R Core Team, 2015).

Results

Peat stratigraphy and geochemistry

The basal sediments in the core from 600 to 640 cm (Fig. 4) consist of inorganic sandy silts with a minor clay component, and are characterised by high magnetic susceptibility (>30) and bulk density (>1.25 g cm^{-3}), and low LOI (1.4–3.4%). Single measurements indicate low carbon concentration (0.3 wt%), nitrogen concentration (0.05 wt%), C/N (6.0), and Ca/Mg (0.46) ratios.

From 560 to 600 cm the core contains a higher proportion of clay and less silt than the unit below, and bulk density declines (from 1.3 to 0.4 g cm^{-3}), as does magnetic susceptibility (to 0.9 at 560 cm), while carbon and nitrogen both increase to 8.4 and 0.5 wt% respectively at 560 cm. Ca/Mg ratios remain low (0.49–0.73).

From 240 to 560 cm, the core consists of a variable mixture of clay and organic matter, with pieces of wood observed in places (297–301 cm, 352–354 cm), and intact leaves at 465 cm. Bulk density remains low relative to the basal sediments (mostly <0.25 g cm^{-3}), but some sections with higher bulk density (up to 0.68 g cm^{-3}) occur in association with increased clay content. LOI values are variable (3.4–90wt%), averaging 51wt%. Carbon and nitrogen concentrations vary together in step with changes in organic content, while Ca/Mg ratios vary but remain below 20 throughout.

From 0 to 240 cm the core consists of fibrous peat, with abundant small roots and twigs. The contact with the underlying clay and organic matter (‘clayey-peat’ in Lähteenoja et al., 2009a) is gradational: from 240 to 244 cm, LOI values increase from 58 to 93wt%, and remain above 91wt% with only minor fluctuations thereafter to the top of the sequence. Carbon concentration is high throughout the top 240 cm of the core, peaking at 61.3wt% at 208 cm. Nitrogen concentrations are also high, reaching a peak for the record of 2.4wt% at 32 cm. C/N ratios vary between 22.5 and 46.4. Ca/Mg ratios are much higher than elsewhere in the record between 128 and 240 cm, peaking at 78.6 at 145 cm, then falling towards the top of the core.

Pollen stratigraphy

The pollen record is presented in Fig. 5. Pollen preservation is good throughout the record, with indeterminable damaged pollen <10%, and pollen concentration values (excluding spores and pollen from aquatic taxa) between 13,900 and 980,000 grains cm^{-3} (Tables S2 and S3). Local pollen assemblage zones are defined and described in detail in Table 1. In outline, the pollen stratigraphy consists of a zone dominated by Cecropia pollen (SJ-1), followed by a zone with abundant herbaceous (Poaceae, Cyperaceae) and shrub (Asteraceae) taxa, and a short-lived peak in Mauritia-t. pollen (SJ-2). Zone SJ-3 is overwhelmingly dominated by the pollen of Pistia stratiotes. This is followed by zone SJ-4, which is dominated by Mauritia-t. with Euterpe-t. and Ilex pollen as significant constituents, and finally by SJ-5, where Mauritia-t grain sizes increase and Alchornea pollen peaks. Peak pollen concentrations occur in the basal pollen zone (SJ-1), but a second peak in pollen concentration occurs at 96 cm (667,000 grains cm^{-3}), close to the base of zone SJ-5. The surface pollen sample results are shown in Fig. S1.

Spinulose phytoliths (produced by members of the Arecaceae) are found in all of the zones, but are most abundant in zones SJ-4 and SJ-5 where the concentrations exceed 200,000 phytoliths cm^{-3} in every sample, peaking at 1,200,000 cm^{-3} at 80 cm in SJ-4. Microcharcoal fragments (5–180 µm in size) are infrequent in the pollen samples, the most found in an individual sample being seven (Table S2).

Dating

The ^{210}Pb dating results indicate a ^{210}Pb inventory of 7275 Bq m^{-2} and an annual ^{210}Pb flux (the supply rate) of 226.5 Bq m^{-2} yr^{-1} (Table S1). The observed decline in ^{210}Pb activity with depth in our core is approximately exponential, with the exception of the near-surface samples (0–2 and 2–4 cm) and the sample from 14–16 cm.

The ^{14}C dates are shown in Table 2. From the lowermost date (SUERC-54422, 238-240 cm, 2120-2306 cal yr BP) the calibrated ages decrease steadily upwards to 114 cm; however, between sample

UBA-20285 (90–92 cm; 299-425 cal yr BP) and SUERC-54417 (112–114 cm; 1416-1564 cal yr BP) a large age difference indicates a period of slow accumulation.

Chronology

The annual ^{210}Pb flux estimated for the San Jorge record (226.5 Bq m^{-2} yr^{-1}) lies towards the upper end of values collated for wetlands of the world by Preiss et al. (1996). The ^{210}Pb supply rate is generally thought to correlate with rainfall (Preiss et al., 1996), so a high flux rate is to be expected in a wet region such as western Amazonia. The observed exponential decline in ^{210}Pb activity with depth in our core is consistent with the post-depositional decay process (Appleby, 2001). A slight ‘flattening’ or relative fall in the ^{210}Pb activity curve near the peat surface, as exhibited in our data, has been observed in many peat profiles in different countries (e.g. Malmer and Holm, 1984; MacKenzie et al., 1998; Olid et al., 2008). Given the high hydraulic conductivity (K) of the peat at San Jorge (Kelly et al., 2014), a likely cause is movement of ^{210}Pb in the near surface. Although Pb is present in insoluble forms under anoxic conditions, it can form soluble $PbSO_4$ where oxygen is at least intermittently available, as in the upper layers of a domed peatland (Damman, 1978).

The dating results suggest a period of slow, nil or negative accumulation between dates UBA-20285 and SUERC-54417. In developing an age model using BACON (Fig. 3) we chose to specify a hiatus at a depth of 100 cm, between these dates. The resulting age model indicates that peat sensu stricto (with LOI values >90%) began to accumulate at San Jorge between 2160 and 2370 cal yr BP. The average apparent peat accumulation rate (i.e. the net effect of accumulation and subsequent decomposition: sensu Tolonen and Turunen, 1996) is 1.4 mm yr^{-1} between 240 and 112 cm, 0.4 mm between 112 and 90 cm, and 2.0 mm yr^{-1} between 112 and 0 cm. The temporal resolution of the pollen record is typically 58, 206, and 39 years in these intervals respectively.

Environmental Reconstruction

Below the pollen record: 240–632 cm (2950–2290 cal yr BP)

The silts and sands towards the base of the recovered sequence, between 600 and 632 cm, are typical of deposition in a moderately high-energy environment and indicate fluvial sedimentation, probably by an active channel of the Amazon. Below 592 cm, the low C/N ratios low (<8) indicate a substantial contribution from aquatic plants (Meyers 1994).

The 3.5 m of clay-dominated sediments that overlie the basal silts and sands, alternating with organic-rich layers, are indicative of low-energy depositional environments such as floodplain swales and lakes where the suspended sediment load of the Amazon River is deposited (Irion et al., 1997). The change to clayey sediments above 600 cm therefore indicates that the site had become cut off from the main channel but continued to be flooded frequently, under low-energy conditions, by sediment-laden water from the Amazon. The increase in C/N ratios above c. 592 cm is consistent with a shift to more terrestrially-influenced depositional environment (Meyers, 1994). The presence of intact leaves supports sub-aqueous deposition in a permanently inundated back swamp or swale: intact leaves are rarely found in the near-surface peats at San Jorge or other sites in the region (Draper 2015; Kelly 2015). The large wood fragments observed, some of which were sections of logs that exceeded the diameter of the corer, are likely also to be locally derived.

Zone SJ-1: 220–240 cm (2150–2290 cal yr BP)

The gradual increase in LOI from 58–93% between 244 and 240 cm marks another change in the depositional environment at the core site: sediment-bearing flood-waters ceased to arrive at the site. The water table must have remained high, since peat requires year-round water-logging to accumulate, and a high water table is likely to have been maintained by inputs from rainfall and groundwater. The high Ca/Mg ratios (>40) imply that there was some continuing input of Ca and other cations from floodwater or groundwater. If seasonal or more sporadic flooding still occurred, it now deposited little clay at the site; the main channel of the Amazon may have migrated further away, reducing its influence on the floodwater at this point within the perirheic zone (Mertes 1997).

During this period Cecropia pollen exceeds 90%, and is therefore likely to have been abundant in the vicinity of the core site (values of 15-20% occur even where it is not locally dominant: Weng et al. 2002; Gosling et al., 2005, 2009). Cecropia is genus of light-demanding pioneer trees that typically colonize floodplain areas following disturbance (Salo et al., 1986; Kalliola et al., 1991; Parolin, 2002). Although Cecropia rapidly forms a closed canopy, each tree lives for only c. 20 years, and low-diversity Cecropia stands are quickly replaced by more diverse vegetation unless the forest is subjected to continued disturbance (Parolin, 2002). Thus, this interval is interpreted as reflecting the early stages of riparian succession, with Cecropia colonising recently exposed (and frequently disturbed) land surfaces in the vicinity of the core site.

Zone SJ-2: 188–220 cm (1920–2150 cal yr BP)

Peat continued to accumulate rapidly (c. 1.44 mm yr^{-1}) through the interval represented by zone SJ-2, indicating that the water table remained high. Ca/Mg ratios >60 indicate continued importance of ground water and/or fluvial inputs. High LOI values show that sediment input continued to be minimal. High C/N ratios (>35) and the presence of wood fragments indicate that the peat was mostly terrestrial in origin.

The pattern of increases in herbaceous pollen that marks this interval is consistent with the early stages of a riparian succession. Asteraceae (subfamily Asteroideae) pollen becomes abundant at the base of this zone; most Asteraceae in Amazonia are herbaceous (Gentry, 1993), but the shrub Tessaria integrifolia (Asteraceae; Asteroidea), for example, is a common coloniser of recently exposed river sediments (Salo et al., 1986). Within c. 150 years, the vegetation at the core site became dominated by Poaceae and Cyperaceae, with accessory taxa that mostly represent herbs and shrubs (e.g. Begonia, Asteraceae). Poaceae and Cyperaceae are commonly found forming marginal lake-side and floating mat vegetation, either or both of which may have been present at the site during this interval. Representation of Cecropia pollen drops to less than 15%, which implies limited local presence (Weng et al., 2002; Gosling et al., 2005, 2009). At the top of the zone, Mauritia-t. pollen increases to 60% which, on the basis of pollen grain size measurements (Fig. 5a), indicates local colonisation by Mauritiella either at or close to the core site (Mauritia-t. pollen has poor transport potential: Rull, 1998). The ecology of Mauritiella implies that the flood amplitude was likely greater than 1–2 m during this period of peatland development (Junk et al., 2015). The concentration of Mauritia-t. is lower than in the upper Mauritia-dominated zone (SJ-5); Pteridophyte spores are extremely abundant, e.g. Nephrolepis, a gap coloniser (Tuomisto and Ruokolainen, 1994) reaches 75%; and the pollen of other herbaceous, light-requiring taxa such as Begonia and Cyperaceae (>8%) is common. The pollen of trees such as Ilex and Euterpe-t. is present but in small quantities (<3%). Hence, this assemblage is probably not indicative of a closed canopy forest, but of one or a few individuals of Mauritiella at (or close to) the core site in an otherwise herbaceous assemblage.

Similarly brief spikes of Mauritia-t. pollen occur in the lower parts of other pollen records from Amazonia. At Quistococha (Roucoux et al., 2013), 30 km northwest of San Jorge, a two-sample Mauritia spike was interpreted as indicating a short-lived change from deep seasonal flooding to permanently waterlogged (but not deeply-flooded) conditions. At Lago Calado in Brazil (Behling et al., 2001), a Mauritia-t. peak was interpreted as indicating a Mauritia swamp which formed along the river margin and, as at San Jorge (see below), it was followed by an increase in aquatic pollen types demonstrating the formation of a lake system. At Lago Calado, this transition was inferred to have been caused by waterlogging related to the increase in eustatic sea level during the early Holocene (Behling et al., 2001), a scenario which cannot be invoked at San Jorge, which is more than 2500 km from the coastline and which formed well after major adjustments to eustatic sea level prior to c. 7000 cal yr BP (Stanford et al., 2011).

Zone SJ-3: 100–188 cm (650–1920 cal yr BP)

Mauritia-t. pollen all but disappears at the start of this period represented by this zone, replaced by Cyperaceae and Poaceae, indicative of marginal and/or floating mat vegetation (as in SJ-2). The most striking feature of this zone is a pronounced increase in the pollen of Pistia stratiotes, a free-floating aquatic plant common in the Amazon floodplain (Kalliola et al., 1991), frequently found alongside Cyperaceae and Poaceae (Kalliola et al., 1991; Piedade et al., 2010). Pistia is uncompetitive in nutrient-poor water (Junk and Piedade, 1997), so its abundance in SJ-3 indicates some input of nutrient-rich water, an inference supported by a peak in Ca/Mg at the points (144 and 152 cm) where Pistia pollen is most abundant. Pistia pollen has not been recorded in such abundance in other Amazonian pollen records.

The spores of Spirogyra (Zygnemataceae), a genus of freshwater alga, are consistently found in small quantities for the first time throughout this period (a single spore was found in SJ-2) and provide evidence for the presence of open, oxygen-rich water (Van Geel, 2001). Spirogyra was most abundant at the start of this period and may have declined as P. stratiotes became established and began to compete for light and nutrients. This would be consistent with the C/N values (mean: 36.6), which are higher than would be expected if algal material were the dominant component of the sediment (Meyers, 1994). The sediments accumulated during this period are similar in terms of C/N values and texture to modern marginal lake sediments at Quistococha, where macrophytes (Poaceae and Cyperaceae) and terrestrial vegetation appear to be contributing detrital organic matter to the lake sediment (Kelly, 2015; Patterson et al., 2015).

The increase in abundance of pollen grains of Mauritia, Mauritiella, and other Arecaceae towards the top of zone SJ-3 from 104 to 128 cm indicates the beginnings of the establishment of palm swamp at the site. This is accompanied by a decline in the Ca/Mg ratio from 78.6 at 145 cm to 16.0 at 113 cm, indicating reduced nutrient input.

Zone SJ-4: 52–100 cm (200–650 cal yr BP)

The dating results indicate that the change from Cyperaceae- and Pistia-dominated (marginal fen/open shallow water) assemblages to tree-dominated (swamp forest) assemblages at the boundary between SJ-3 and SJ-4 occurs across a period of slow peat accumulation. There is a marked peak in the pollen and spore concentration, followed by a peak in the palm phytolith concentration; these peaks are likely to be the result of the decrease in peat accumulation rate and thus may indicate locally drier conditions. The increase in Mauritia-t., Euterpe-t., Alchornea sp. and Ilex is indicative of the establishment of a palm-dominated swamp forest at the core site, analogous to the ‘aguajals’ found today across Amazonia (Rull 1998; Roucoux et al., 2013; Gilmore et al., 2013; Aguajal Project Database, 2015). Small quantities of Malouetia pollen, representing a genus of c. 24 species found mostly in seasonally inundated forests (Endress, 2004), indicates that there may have been infrequent flooding of the site.

Since Pistia continues to be present as palm pollen increases at the top of zone SJ-4, the core site itself probably remained in a lake-marginal position during this period while palm swamp established nearby. Pistia is beetle pollinated and of low stature (Gibernau, 2003), and hence the pollen is unlikely to be blown in from neighbouring areas. The increase in peatland taxa such as Mauritia alongside Pistia at the top of SJ-4 could also indicate that the peatland was encroaching on a shrinking lake.

Zone SJ-5: 8–52 cm (AD 1990–AD 1750)

In zone SJ-5, Alchornea pollen abundance increases markedly, above the levels seen throughout the rest of the record. Alchornea is widely known as a pioneer taxon (Marchant et al., 2002; Rondon et al., 2009), and its high abundance here could be interpreted to represent the development of secondary forest. However, it is also a common constituent of floodplain vegetation and palm swamps (Roucoux et al., 2013; Aguajal Project, 2015), and given the context and co-occurring taxa, it is these wetland species of Alchornea which are most likely to have been present during this period.

The earliest appearance of the present pole forest vegetation is not immediately evident in the pollen record since the dominant pole forest tree species (e.g. Pachira brevipes) are poorly represented in the modern pollen rain and they tend to be swamped by the presence of even a few Mauritia flexuosa individuals (as shown by palynological analysis of surface samples from the site: Fig. S1). We would anticipate this difficulty given that the main pole forest tree species are all insect pollinated. Although it is not possible to conclusively identify the start of the present vegetation in this record, five lines of evidence allow us to identify the point at which the vegetation began to take its present form. Firstly, in zone SJ-5 (below 52 cm) the pollen assemblage contains higher percentages of Euterpe-t. than above. Euterpe palms are not present in the modern vegetation, but E. precatoria occurs in the marginal palm swamp areas at San Jorge today (E. Valderama, pers. comm., 2012). Secondly, the Mauritia-t. grain size data indicate a change from mixed Mauritia and Mauritiella to pure Mauritia flexuosa pollen at this point (Fig. 5a). Mauritiella is rare the modern pole forest census plot (Kelly et al., 2014) so, like the disappearance of Euterpe pollen, this change represents an increase in similarity to the present day vegetation composition. It also points to a change in flood amplitude to a situation closer to present conditions at the core site since in other parts of the Amazon, Mauritia flexuosa replaces Mauritiella when flood amplitudes decline to 1–2 m (Junk et al. 2015). Thirdly, the presence of Bombacaceae-type pollen grains in low abundance could be attributed to Pachira brevipes (placed in the Bombacaceae family in Roubik and Moreno, 1991, the taxonomy used here). Fourthly, other minor pollen types also indicate a change in composition from SJ-4 to SJ-5 that is consistent with a change in ecology towards the situation we see at the site today; Malouetia, while present throughout SJ-4, is almost absent from SJ-5, which supports the interpretation that the transition was associated with a reduction in flood amplitude (Endress, 2004), and Malvaceae pollen is also most abundant in SJ-5. Fifthly, the decline in Ca/Mg ratio around the SJ-4 – SJ-5 boundary indicates a shift to more ombrotrophic conditions. Hence, we conclude that the changes recorded by the palaeoecological record at 52 cm depth (dated to between 200 and 150 cal yr BP) indicate the maximum age of the pole forest at the site.

Discussion

Here we first consider the pattern of vegetation change recorded at San Jorge and compare it with records from other tropical peatlands. We then discuss the possible causes of slow or nil peat accumulation between c. 1300 and 400 cal yr BP, the subsequent re-commencement of peat accumulation, and development of the current pole forest vegetation. Finally, we discuss the implications of our study for understanding carbon accumulation and community ecology in domed peatlands in the PMFB.

Peatland successional pathways

Although peatland successions have been described for Southeast Asian and Panamanian peatlands (Anderson, 1961; Anderson and Muller, 1975; Phillips et al., 1997; Morley, 2013), the developmental context for western Amazonian peatlands – on the floodplains of some of the world’s largest rivers – is fundamentally different (cf. Lähteenoja et al., 2012; Dommain et al., 2014). In contrast to Southeast Asia and Panama, dynamic fluvial processes are more important in Peru and the influence of sea level change on peat initiation is far less significant. Kalliola et al. (1991) used modern ecological observations to infer the typical succession, from open water to palm swamp, on floodplains in the PMFB (although pole forests were not included in their study). Roucoux et al. (2013) presented the first palaeoecological study of floodplain succession from the region at the Quistococha palm swamp.

The new record from San Jorge, the first from an Amazonian peatland pole forest, offers an opportunity to test whether different Amazonian peatlands follow similar long-term plant successional pathways.

Figure 6 summarises plant successional pathways hypothesised from field observations of peatland vegetation and its position on the floodplain, remote sensing observations (e.g. using Landsat imagery), previous studies of floodplain successions (e.g. Kalliola et al., 1991), and the existing pollen records from Quistococha and San Jorge. Differences between the trajectories of vegetation development at the two sites are immediately apparent. The record at San Jorge lacks the ‘shrub swamp’ and seasonally flooded forest phases (known locally as *tahuampa* in black water contexts) seen at Quistococha, instead transitioning directly from an open aquatic phase to *aguajal*.

However, despite their differences, the Quistococha and San Jorge records share some important features. Both pollen records begin with a *Cecropia*-rich zone (which precedes rather than accompanies peat initiation at Quistococha). Abundant *Cecropia* pollen is also found in the basal pollen zones of other records from Amazonian wetland sites in Colombia (Urrego, 1997; Urrego et al., 2006). *Cecropia*-dominated phases are common in floodplain pollen records in Amazonia mainly because *Cecropia* pollen is wind-transported, and because *Cecropia* readily colonizes recently exposed land surfaces in the floodplain.

In both the Quistococha and San Jorge pollen records, the peak in *Cecropia* is followed by a transition to a herbaceous assemblage. At Quistococha, the precise interpretation of this herbaceous assemblage is difficult because both floating mats and rooted marginal vegetation often contain abundant Poaceae and Cyperaceae. At San Jorge, it seems unlikely that the vegetation represented in pollen zone SJ-2 was fully aquatic, given the presence of Asteraceae pollen and the lack of algal colonies seen, for example, in SJ-3. Instead, SJ-2 probably represents a grounded herbaceous fen, perhaps with scattered *Mauritiella* trees. Although the stochastic character of fluvial action on the floodplain means that the early history of peatland sites is likely to vary from site to site, the palaeoecological records support the view that open herbaceous vegetation (either grounded, semi-aquatic, or floating) may form a part of the early succession in many peatlands.

Both the San Jorge and Quistococha records exhibit reversals in the succession, i.e. a return to wetter and/or more open conditions. At San Jorge a herbaceous fen with scattered palms transitions to an ‘earlier’ successional phase with floating aquatic vegetation (Fig. 6). At Quistococha, there is a change from palm swamp to tahuampa flooded forest which represents a re-commencement of deep (up to 5 m) seasonal flooding. There also appears to be a common trajectory with regard to the development of the aguajal following its establishment at the two sites. At San Jorge, following the increase in Mauritia-t. at 96 cm, Euterpe t. becomes common along with Ilex, which is also found in the early phases of palm swamp development at Quistococha (e.g. zone QT-5b in core QT-2010-1). These elements then decline and are replaced by a pure Maurita-t. assemblage. A similar pattern can be seen in the wetlands of the Chocó in Colombia (sites at San Martin and Villaneuva); Euterpe oleracea occupies more poorly drained and frequently flooded areas than Mauritiella macroclada, and in the stratigraphic records Euterpe precedes Mauritiella (Urrego et al., 2006). In the Caquetá floodplains of Colombia, Euterpe precatoria is also more common in annually flooded sites than Mauritia flexuosa (Duivenvoorden, 1995). The abundance of Euterpe and Ilex during the early, but not later stages of aguajal development at San Jorge and Quistococha may therefore reflect a common successional pattern in Amazonian peatlands.

At Quistococha, there is no clear relationship between the temporal succession and the modern distribution of plants across the site. For example, earlier vegetation phases reconstructed from the pollen record include mixed Euterpe and Mauritia palm swamp, and flooded forests with abundant Myrtaceae, neither of which occur at the site today. At San Jorge the vegetation distribution across the whole site has not been studied in the field, but satellite imagery (Fig. 2) and field observations along a transect both indicate an approximately concentric zonation of vegetation, with the pole forest being surrounded by palm swamp. This spatial pattern apparently mirrors the stratigraphic transition in SJ-5 from palm swamp to the present pole forest vegetation at the core site; the down-core geochemical data presented here suggest that this transition follows a trend towards increasing ombrotrophy, i.e.

reduced importance of flooding relative to aerosols and precipitation as a source of nutrients, which would be expected to accompany the upward growth of a peat dome. At San Jorge we have not observed analogues for the vegetation in SJ-1 to SJ-3 in the field, although satellite imagery indicates that other vegetation types and a lake occur further inland from the river. Further investigation of the relationship between spatial and temporal patterns in vegetation using multiple cores would help to explain the distribution of vegetation at San Jorge and in other PMFB peatlands.

Peat accumulation rates

The radiocarbon dates presented here, indicating a period of slow pea accumulation (or a possible hiatus) between c. 1300 and 400 cal yr BP, constitute the first evidence that Holocene peat accumulation at a site in the PMFB may not have been constant over time. This is potentially important because it implies that, even in the wet climate of our study region, carbon sequestration may be sensitive to site-specific processes (e.g. fluvial erosion or geomorphological change more generally) and/or to climatic change. Identifying the cause of the slow-down in peat accumulation at San Jorge is important because it has implications for the future stability of PMFB peatlands and their carbon stocks. However, the data presently available leave room for differing explanations including: (i) contamination during coring; (ii) introduction of young carbon from plant roots into the uppermost radiocarbon sample, (iii) peat erosion/removal, (iv) reduced litter inputs (e.g. through a reduction in vegetation productivity), and (v) increased decomposition (either due to alteration of the local hydrology or regional climatic change). Sample contamination cannot be ruled out, but is unlikely given that a closed-chamber corer was used and that visible roots were removed from the dated material, and given that the uppermost radiocarbon date is consistent with the ^{210}Pb-based age model for the peats above it. There is no sedimentological evidence for peat removal by fluvial erosion, which would likely have left traces in the core, such as silt layers. Tip-up events, where a treefall displaces the peat around the roots of the tree, can also create gaps in a peat sequence (Dommain et al., 2015). However, the pool left behind by a tip-up typically quickly fills with leaf litter, which is not evident in the San Jorge record. Tip-up pools are also thought to result in a pulse of increased peat accumulation (Dommain et al., 2015), differing from the pattern seen here where steady peat accumulation both precedes and follows the period of slow accumulation. The high concentration of pollen and palm phytoliths indicate that litter continued to be laid down (particularly by Mauritia and Mauritiella palms) but that high decomposition (not physical erosion) removed most of the organic matter, leaving only recalcitrant particles behind. This eliminates reduced litter production as a possible explanation, while supporting the final possible explanation for the apparent decrease in peat accumulation rate, an increase in decomposition.

Three hydrological scenarios could lead to a lowering of the local water table, stimulating aerobic decomposition. The first relates to the migration of the Amazon across its floodplain. If a river channel migrates closer to the centre of a peatland, it can increase the hydraulic gradient and cause increased drainage, and therefore a fall in lake level or peat water table (Anderson et al., 2003; Glaser et al., 2004). However, in a simulation of the effects of marginal drainage on the water table, using hydraulic conductivity values measured at San Jorge, Kelly et al., (2014) found that, even during a simulated 90-day drought, significant water loss from subsurface flow occurred only within c. 100 m of the peatland margin. As such, the river would have to have been close to the core point to have a significant effect on the water table. The presence of thick peat accumulations across the c. 3 km from the core site to the river margin (Lähteenoja et al., 2009b) make it unlikely that the river could have been in such close proximity to the core site in the recent past (c. 400 cal yr BP).

The second possible scenario is that a natural hydrological barrier was removed by fluvial erosion. Householder et al. (2012) found that river levees help to maintain waterlogged conditions in peatlands in Madre de Dios (S. Peru). If the Pistia- and Cyperaceae-dominated lake at San Jorge was originally contained by a levee, and that levee was removed by lateral movement of the river channel, rapid drainage could result. There is evidence that the river was close to the core site at San Jorge from c. 2200 to 800 cal yr BP, in the form of high Ca/Mg ratios (characteristic of minerotrophy; Shotyk, 1996), and the pollen of floating aquatic plants (which require high nutrient input; Junk and Piedade, 1997). However, direct evidence in support of this scenario (e.g. the remains of an eroded levee) has not been observed, although such evidence would be unlikely to be preserved.

The third hydrological scenario that could explain the decrease in apparent peat accumulation rate at San Jorge is that climatic drying caused a lowering of the peatland water table and an increase in the rate of litter and peat decay. Other authors have invoked climatic change as a possible explanation for the features of palaeoecological records in Amazonia. For example, Roucoux et al. (2013) commented that the establishment of the palm swamp at Quistococha c. 1000 cal yr BP would be consistent with reduced flooding (i.e. a drier climate). Weng et al. (2002) suggested that the demise of a Mauritia swamp recorded in their Maxus 4 core in northern Ecuador could be due to climatic drying. Further afield, in the central Amazon near Manaus, Brazil, Piperno and Becker (1996) invoked climatic drying to explain soil charcoal evidence for large natural fires between 1700 and 780 cal yr BP. Elsewhere there is independent evidence that the context for the development of the San Jorge sequence during the last c. 2000 years was one of climatic variability. For example, in the Andes, following a period of relative stability, some proxy records for lake level, snowfall chemistry, and glacial extent suggest substantial variability that may reflect variations in rainfall and runoff (Fig. 7; Thompson et al., 1995; Bird et al., 2011; Stansell et al., 2013). However, a consensus on the regional palaeoclimatology is still lacking (Flantua et al., 2016a). For example, pollen records from northern Ecuador, including Anañgucocha, Lago Agrio, Limoncocha, and Lago Santa Cecilia (Frost, 1988; Colinvaux et al., 1988), have been interpreted as recording a period of increased rainfall and flooding c. 1100 cal yr BP (albeit with chronological uncertainties: Flantua et al. 2016b). Similarly, several isotopic records of rainfall in Andean ice cores show no clear anomaly during this period (Thompson et al., 1986, 1995, 2013).

At San Jorge, the peat accumulation rate increases again after c. 400 cal yr BP. This is difficult to account for without invoking an increase in the available moisture, and as the site was receiving most of its water from rainfall at this time (as inferred from low peat Ca/Mg ratios), this most likely means that rainfall increased and/or evapotranspiration decreased. This period is associated with higher percentages of Ilex and Euterpe-t. pollen; species such as Ilex inundata are typical of black water flooded forests (tahuampa) in Amazonia (Gentry, 1993), and in the Caquetá region of Colombia Euterpe precatoria (also present in the modern forest at Quistococha and San Jorge; E. Valderama, pers. comm., 2012) is most common at flooded sites (Duivenvoorden, 1995). These palynological changes are therefore also consistent with a shift to wetter conditions, potentially a shorter or less severe dry season as peat accumulation rates are likely to respond more to dry season than wet season rainfall (Page et al., 2004; Kelly et al., 2014).

In summary, it is possible (though not proven) that climatic change played a role in the accumulation of peat and the dynamics of vegetation at San Jorge, given the growing (but still inconclusive) body of evidence for climatic variability in the region. In this context the striking similarity in some aspects of the palynostratigraphy of the San Jorge and Quistococha records, particularly the curves for Mauritia-t. (Fig. 7), superficially suggests a climatic link, but the two sites could equally be reflecting the same, stochastically-driven changes in river course (they are only 30 km apart on the same floodplain). Testing this hypothesis requires further records, particularly from ombrotrophic sites in the PMFB: of all the processes set out above, only a strong role for climatic change would lead to synchronous changes in age models, palaeoenvironments, and palynology at many hydrologically-independent sites.

After 200 cal yr BP: the history of the present pole forest

PMFB peatland pole forest has only been described at a limited number of sites, although a programme of ecological census is in progress (Kelly et al., 2014; Draper, 2015). The San Jorge pollen record provides the first long-term record of a PMFB peatland pole forest site. As discussed above, the establishment of the present vegetation is inferred on four lines of evidence to have occurred within the last 200–150 cal yr BP. The possibility that peatland plant assemblages are still developing and potentially far from equilibrium with the prevailing conditions needs to be taken into account in discussions of their biodiversity and community ecology. Modelling of peatland hydrological fluctuations has shown that responses to climate change may begin immediately, but can continue over the course of centuries, and that homeostatic behaviour can create disconnections between climate and peatland behaviour (Swindles et al., 2012; Morris et al., 2015).

The transition from palm swamp to pole forest may represent a purely intrinsic, autogenic development, such as the gradual raising of the peatland dome leading to increasing ombrotrophy. However, there is circumstantial evidence that regional climatic drying could be involved. A dry period can cause a shift to ombrotrophy, as it can serve to isolate the vegetation from nutrients in the substrate and groundwater through a lowering of the water table (Hughes and Barber, 2003). At San Jorge, a dry period could have accelerated an ongoing autogenic transition.

As in earlier intervals, there are numerous palaeoclimate proxy records that indicate variation in climate within the last 200 years (Fig. 7), but as yet no consensus on the pattern of change in western Amazonia. The few well-dated pollen records from lowland Amazonia are either equivocal or indicate no measurable climatic change during the last few centuries (Flantua et al. 2016a), though this may reflect a lack of sensitivity in the sites studied up to now. Any link between climatic variability and peatland ecosystem development therefore remains speculative at this stage, but deserves further attention due to the implications for future change in Amazonian peatland ecosystems. For example, climatic drying or interference in the flood pulse of the Amazon River (e.g. through hydroelectric schemes; Roucoux et al., in review) could result in an expansion of existing peatland pole forest areas. The young age of the present pole forest (less than 200 years) shows that a change in forest composition may be rapid.

Conclusions

The palaeoecological record from San Jorge presented here is the first from a domed peatland in Amazonia. It shows that autogenic succession and geomorphological change were important drivers of vegetation change during the early stages of peatland inception, and were also important for creating the conditions necessary for peat accumulation. The early successional pattern bears some similarity to that seen in the record from the Quistococha peatland 30 km to the northwest, but also features important differences such as the lack of a tahuampa phase. Vegetation development at San Jorge, as at Quistococha, is not a straightforward process of progressive terrestrialization, but includes abrupt changes taking less than a century, and apparent returns to wetter conditions interrupting the overall trajectory of terrestrialization.

This study has provided the first evidence that peat accumulation in the PMFB may have declined or stopped entirely as there is a hiatus c. 1300–400 cal yr BP at this site. This result is potentially important because it indicates that below-ground carbon storage in the PMFB may be vulnerable to climatic (and/or geomorphological) change. The pollen record shows a sharp change across this interval, which implies that changes in the conditions controlling peat accumulation may also have consequences for the vegetation.

The palaeoecological record from San Jorge provides the first insight into the origins of a peatland pole forest in Amazonia. The ecosystem at this site is at most only a few tree generations in age, having formed since c. 200–150 cal yr BP, and indeed a transition may still be underway.

The high carbon density (by area) of the PMFB peatlands makes them a priority for conservation through schemes such as the UN-backed Green Climate Fund (Draper et al., 2014; Roucoux et al., in review), and their full value in terms of biodiversity and other ecosystem services remains to be explored. They also represent a regionally significant resource for palaeoecology: there is much scope to exploit their pollen and macrofossil archives to improve our understanding of vegetation assembly patterns and processes in Amazonian floodplain ecosystems, and in particular to understand the balance between intrinsic (autogenic, successional) and extrinsic (allogenic; geomorphological and climatic) drivers of ecosystem change.

Supporting information

Additional supporting information can be found in the online version of this article.

Table S1: ^{210}Pb activity determinations for the top 50 cm of the San Jorge peat core (SJO-2010-1).

Table S2: Palaeoenvironmental data for the San Jorge core (SJO-2010-1): Loss on ignition, magnetic susceptibility, bulk density, C and N values, Ca and Mg values, pollen concentration and charcoal abundance.

Table S3: Pollen data for the San Jorge core (SJO-2010-1): raw counts and percentage data.

Figure S1: Comparison of the pollen assemblage in surface samples with the forest plot inventory data for San Jorge peatland (plot data from Kelly et al., 2014). Three surface samples were analysed (total pollen = 438).

Figure S2: Histograms showing collected pollen size data (grain diameter and echinae length) for Mauritiella armata (n = 100) and Mauritia flexuosa collections (n = 601). Measurements were undertaken on pollen grains taken from herbarium materials treated using standard methods outlined in the article (no HF treatment) and mounted in silicone oil.

Modern ecological census data for the pole forest at San Jorge were collected in 2010 by Euridice Honorio et al., and are archived and available at http://www.forestplots.net/.

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Tables

Table 1: Radiocarbon age determinations for the San Jorge peat core (SJO-2010-1). AMS radiocarbon dates were obtained from the NERC facility at East Kilbride (SUERC prefix), and at the ^{14}Chono radiocarbon laboratory (Queen's University Belfast; UBA prefix). Calibration was undertaken using the INTCAL13 curve. All samples are the <180 µm peat fraction. Sample UBA-20285 was a humic acid extraction.

Laboratory code	Depth (cm)	^{14}C age (yrs BP)	Error (1 s.d.)	δ^{13}C	Calibrated age (cal yr BP)
UBA-20285	90—92	282	± 22	-31.8	299—425
SUERC-54417	112—114	1,623	± 41	-29.0	1416—1564
SUERC-54418	144—146	1,759	± 41	-28.9	1610—1720
SUERC-54419	192—194	1,990	± 40	-28.8	1897—1989
SUERC-54422	238—240	2,173	± 41	-29.5	2120—2306

Table 2: Summary descriptions of pollen assemblage zones for record SJO-2010-1. Zonation was undertaken using optimal splitting by sum-of-squares in Psimpoll (Bennett, 2007). A summary of the palm phytolith data has also been provided. Indications of abundance refer to the maximum phytolith concentrations in a given zone, where 'abundant' corresponds to >200,000 phytoliths cm^{-3}, 'present' corresponds to >5,000 phytoliths cm^{-3}, and 'rare' corresponds to <1000 phytoliths cm^{-3}. Phytoliths were not absent from any of the zones.

Zone (depths)	Summary of pollen assemblage zone characteristics
SJ-5 (8-52 cm)	Six samples. Mauritia-t. declines to c. 31% at the base of the zone before increasing again to >60% at the top of the record. Average Mauritia-t. grain size increases notably at the base of the zone and consistently remains above 42 µm for the first time. Alchornea sp. peaks in this zone (60%), but declines to <3% at the top of the record. **Spores:** Not abundant in this zone. Trilete spores most abundant type (≤ 11%), monolete spores <3% throughout. Selaginellaceae Type 4 reaches its peak abundance in the top 50 cm (3.3%). **Palm phytoliths:** Abundant
SJ-4 (52–100 cm)	Six samples. Mauritia-t. peaks in this zone (85%), as do Ilex sp. (20%), and Euterpe-t. palm pollen (17%). There is a second peak in Cecropia sp. mid-way through this zone (38%). **Spores:** Less abundant throughout this zone than in SJ-4. Nephrolepis sp. is abundant at the base of the zone (71%) but declines rapidly to low values. **Palm phytoliths:** Abundant; peak concentration for the record occurs at 80 cm.
SJ-3 (100–188 cm)	Eleven samples. There is a pronounced increase in Pistia stratiotes pollen, which peaks in this zone (93%), and along with Cyperaceae (max. 50%) is the dominant pollen type. Moraceae pollen (29%), and Malouetia-t (21%) also peak in this zone. Begonia sp. peaks (max. 30%) and Poaceae is common (max. 15%), especially above 1.30 m depth. Alchornea sp. is persistently present but remains a fairly minor constituent (<9%). Mauritia-t. (max. 25%) and other Arecaceae (<3%) increase in abundance towards the top of the zone. Trema aff. micrantha, Coussapoa sp., Piper sp. and Brosimum sp. are all minor constituents (<5%) but are most abundant in this zone. **Spores:** Extremely abundant; Nephrolepis sp. varies from <5% to 74%. Spirogyra sp. (Algae) rare but present throughout this zone. **Palm phytoliths:** Present
SJ-2 (188–220 cm)	Five samples. This zone is dominated by the pollen of Cyperaceae (max. 44%), Poaceae, which peaks in this zone (35%) and Asteraceae, which also peaks in this zone (39%). Begonia sp. is moderately abundant towards the top of the zone (13%). Cecropia sp. declines significantly from its peak values in SJ-1 to <15%. Mauritia-t. increases towards the top of the zone (65%) **Spores:** Abundance of spores increases markedly from low values in SJ-1; Monolete spores reach their peak abundance (32%), and Nephrolepis reaches its peak abundance at the top of the zone (75%). **Palm phytoliths:** Present
SJ-1 (220–240 cm)	Three samples. This zone is dominated by the pollen of Cecropia sp., which peaks at 92%. Mel./Comb. are less abundant but also peak in this zone (8%). Malouetia is common at the top of this zone (10%), and Cyperaceae begins to increase (6%). Low percentages of various other taxa such as Moraceae (max. 9%) are also present. **Spores**: Low in abundance (no taxa exceed 7%). **Palm phytoliths:** Rare

Figure Captions

Figure 1: Location of sites discussed in the text. (a) Location of the main study area, part of the Pastaza Marañon Foreland Basin. (b) Map indicating the location of the two PMFB peatland sites for which palaeoecological data are available, Quistococha (Roucoux et al., 2013) and San Jorge (present study). The point marked for San Jorge shows the location of core SJO-2010-1, taken c. 3 km west of the main Amazon channel. The town of Tamshiyacu and city of Iquitos (filled circles) have also been shown for reference. Darker shading shows land over 120 m above sea level, inferred from Shuttle Radar Topography Mission (SRTM) data (http://srtm.csi.cgiar.org).

Figure 2: Landsat satellite map (false colour) of the peatland at San Jorge (image processed following Lähteenoja et al. 2009: band 4 = red, band 5 = green, band 7 = blue). The core point has been marked with a white circle. Red areas generally correspond to peatlands and palm swamps with lighter red/orange areas generally corresponding to pole forest. Pure green areas mostly correspond to terra firme rainforest. The blue/grey areas mark open areas, the town of Tamshiyacu (top right), and other disturbed land associated with roads, agriculture, and fluvial sediments. Arcuate features on the margins of the river indicate ridge-and-swale topography associated with channel migration.

Figure 3: a) ^{210}Pb activity (Bq kg^{-1}) in the top 50 cm of the San Jorge profile (left), and the resulting constant-rate-of-supply age model (right). Errors refer to the analytical error (1 s.d.) only (see Table S1). **b)** Bayesian age-depth model for the San Jorge peat core (SJO-2010-1). The enclosed area indicates the 95% probability interval of the model. The dashed line indicates the best-fit (most probable) age-depth relationship. A 'hiatus' at 100 cm depth was incorporated into the model run, and the ^{210}Pb dating results were used for the uppermost 39 cm. The core lithology is also shown following Troels-Smith (1955).

Figure 4: Geochemical and compositional data for San Jorge core SJO-2010-1. Core lithology is shown alongside organic content (LOI), bulk density, magnetic susceptibility, total carbon, total nitrogen, C/N ratio, Ca, Mg, and Ca/Mg ratio. A single Ca/Mg ratio value has been omitted at 172 cm as it was unrealistically high, a result of low Mg values (likely due to low recovery). Radiocarbon dates and pollen assemblage zones (PAZ) are shown for reference. For Ca and Mg, the line with marker circles indicates the measured values, and the plain line shows the values exaggerated 10x for clarity.

Figure 5a: Pollen percentage diagram for the main taxa (present at >5%) for core SJO-2010-1, plotted against depth. An age scale, radiocarbon dates, lithology, selected concentrations, the pollen sum, and pollen assemblage zones (PAZ) are also shown. Average Mauritia-t. grain diameters are shown to the right of the diagram (bars indicate one standard error). Mel.-Comb. = Melastomataceae and Combretaceae pollen (undiff.).

Figure 5b: Pollen percentage diagram (continued from Fig. 5a): minor taxa (present at <5%) and Pteridophyte spores.

Figure 6: Diagram illustrating the differing vegetation successions at Quistococha (Roucoux et al., 2013) and San Jorge (this paper). The pathways shown in the two records have been superimposed onto a successional framework based on field observations of present-day peatland/floodplain vegetation (e.g. Kalliola et al., 1991), remote sensing imagery, studies of plant succession in the Amazonian floodplain, and the two records themselves. Starting points for peatland successions are shown in ellipses, quasi-stable assemblages are shown in rectangles, and palynologically-indistinguishable plant assemblages are enclosed in dashed ellipses. Hypothetical transitions (in the sense that they have not been directly observed in palaeoecological records, but are inferred from the study of modern vegetation) are shown as dashed arrows, while transitions observed in the palaeoecological records are shown as solid numbered arrows.

Figure 7: Mauritia-type percentage pollen curves and pollen assemblage zones for the pollen records from San Jorge and Quistococha (Roucoux et al., 2013), together with selected climate

proxy data from Andean Peru: the Pumachocha $\delta^{18}O$ lake record (Bird et al., 2011); the Huascarán ice core $\delta^{18}O$ record (Thompson et al., 1995); and the record of glacier advance and retreat from Queshquecocha (Stansell et al., 2013).

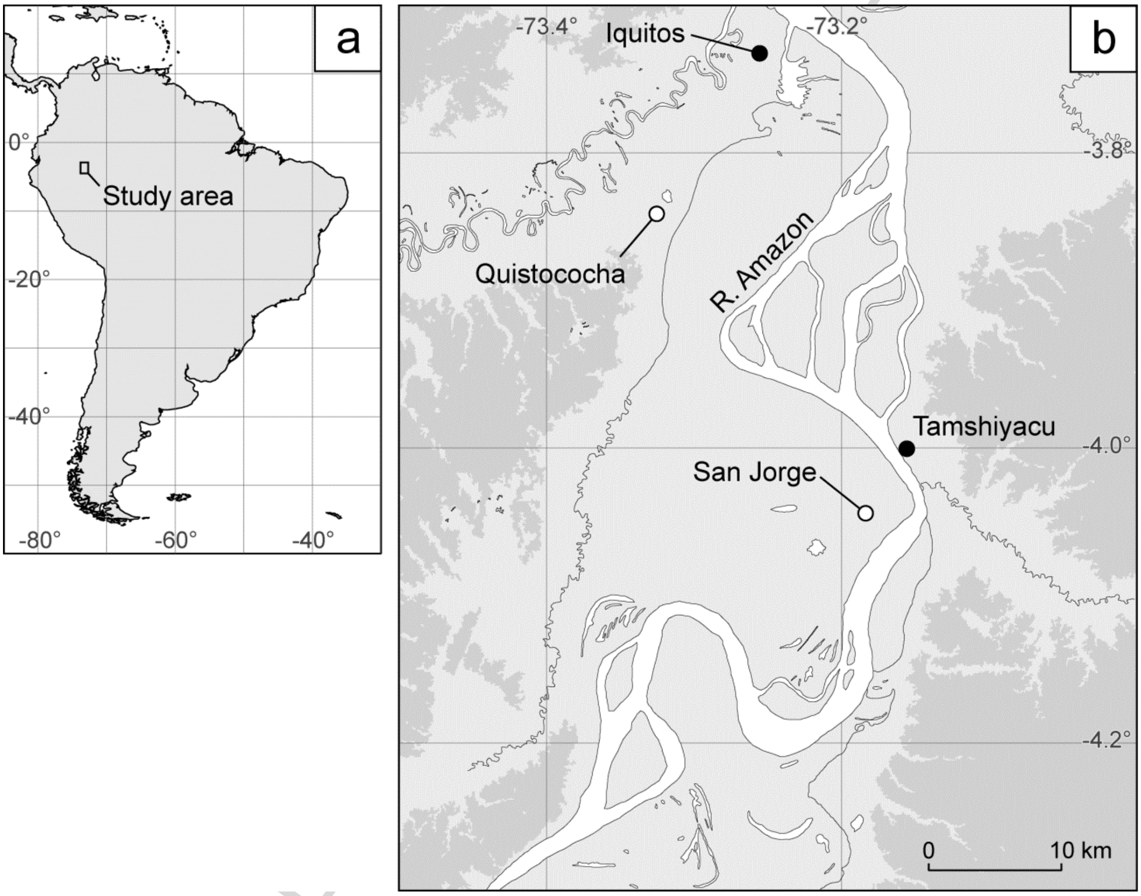
a
0°
-20°
-40°
-80°
-60°
-40°
Study area
b
-73.4°
-73.2°
Iquitos
-3.8°
Quistococha
R. Amazon
Tamshiyacu
-4.0°
San Jorge
-4.2°
0
10 km

Figure 1

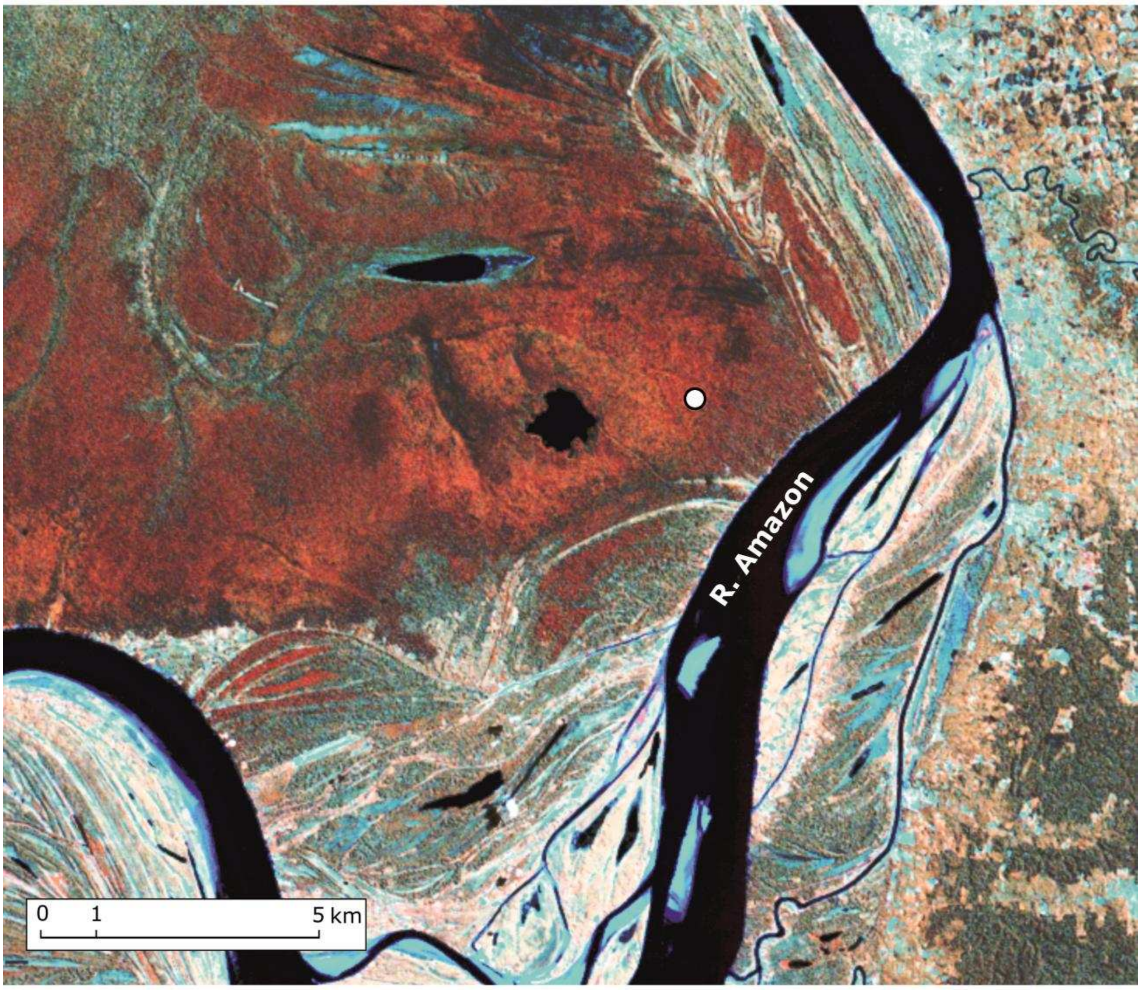

Figure 2

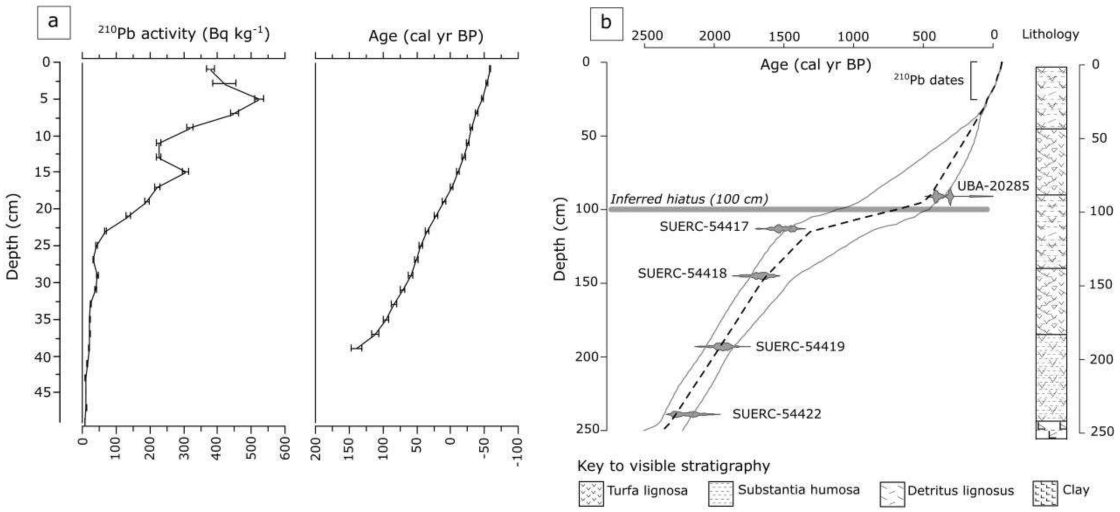
a
^{210}Pb activity (Bq kg^{-1})
Age (cal yr BP)
Depth (cm)
0
5
10
15
20
25
30
35
40
45
0
100
200
300
400
500
600
200
150
100
50
0
-50
-100
b
2500
2000
1500
1000
500
0
Lithology
Age (cal yr BP)
^{210}Pb dates
Depth (cm)
0
50
100
150
200
250
UBA-20285
Inferred hiatus (100 cm)
SUERC-54417
SUERC-54418
SUERC-54419
SUERC-54422
Key to visible stratigraphy
Turfa lignosa
Substantia humosa
Detritus lignosus
Clay

Figure 3

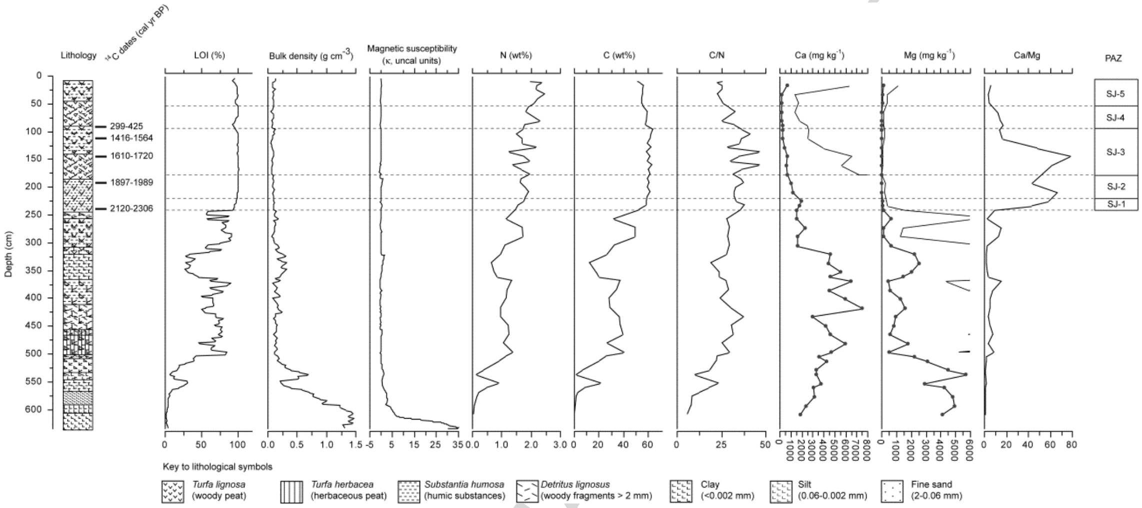
Lithology
¹⁴C dates (cal yr BP)
LOI (%)
Bulk density (g cm-3)
Magnetic susceptibility (κ, uncal units)
N (wt%)
C (wt%)
C/N
Ca (mg kg-1)
Mg (mg kg-1)
Ca/Mg
PAZ
Depth (cm)
0
50
100
150
200
250
300
350
400
450
500
550
600
299-425
1416-1564
1610-1720
1897-1989
2120-2306
SJ-5
SJ-4
SJ-3
SJ-2
SJ-1
0 50 100
0.0 0.5 1.0 1.5
-5 5 15 25 35
0.0 1.0 2.0 3.0
0 20 40 60
0 25 50
0 1000 2000 3000 4000 5000 6000 7000 8000
0 1000 2000 3000 4000 5000 6000
0 20 40 60 80
Key to lithological symbols
Turfa lignosa (woody peat)
Turfa herbacea (herbaceous peat)
Substantia humosa (humic substances)
Detritus lignosus (woody fragments > 2 mm)
Clay (<0.002 mm)
Silt (0.06-0.002 mm)
Fine sand (2-0.06 mm)

Figure 4

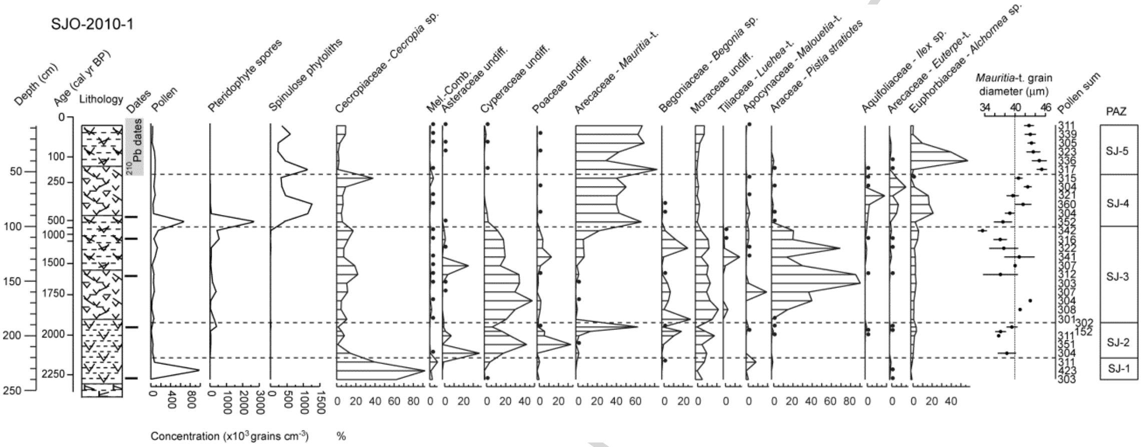
SJO-2010-1
Depth (cm)
Age (cal yr BP)
Lithology
Dates
^{210}Pb dates
Pollen
Pteridophyte spores
Spinulose phytoliths
Cecropiaceae - *Cecropia* sp.
Mel.-Comb.
Asteraceae undiff.
Cyperaceae undiff.
Poaceae undiff.
Arecaceae - *Mauritia*-t.
Begoniaceae - *Begonia* sp.
Moraceae undiff.
Tiliaceae - *Luehea*-t.
Apocynaceae - *Malouetia*-t.
Araceae - *Pistia stratiotes*
Aquifoliaceae - *Ilex* sp.
Arecaceae - *Euterpe*-t.
Euphorbiaceae - *Alchornea* sp.
Mauritia-t. grain diameter (µm)
34 40 46
Pollen sum
PAZ
0 50 100 150 200 250
0 100 250 500 1000 1500 1750 2000 2250
0 400 800
0 1000 2000 3000
0 500 1000 1500
0 20 40 60 80
0 20 40 60
311 339 305 323 336 317 315 304 321 360 304 352 342 316 322 341 307 312 303 307 304 308 301 302 152 311 351 304 311 423 303
SJ-5
SJ-4
SJ-3
SJ-2
SJ-1
Concentration (x10^3 grains cm^{-3})
%

Figure 5A

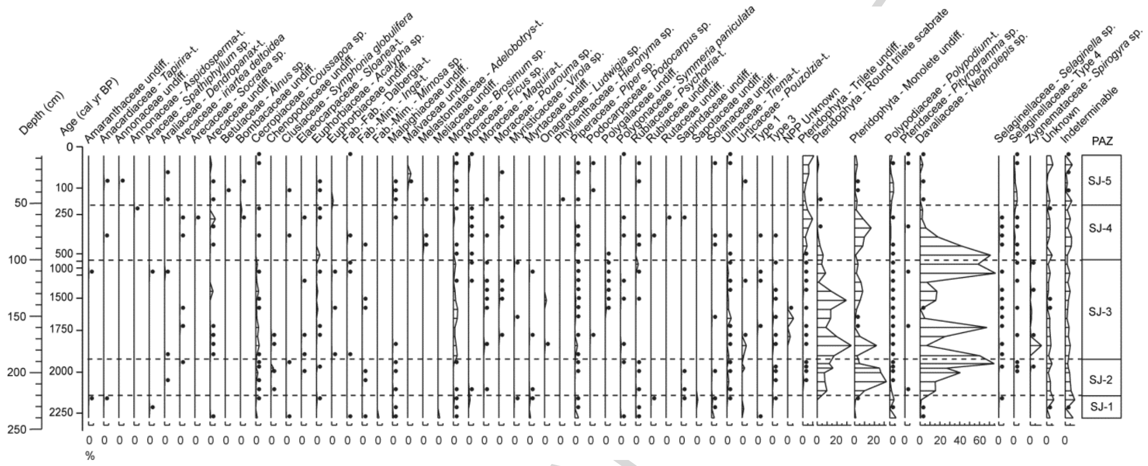
Depth (cm)
Age (cal yr BP)
Amaranthaceae undiff.
Anacardiaceae - Tapirira-t.
Annonaceae undiff.
Annonaceae - Aspidosperma-t.
Araceae - Spathiphyllum sp.
Araliaceae - Dendropanax-t.
Arecaceae - iriartea deltoidea
Arecaceae - Socratea sp.
Arecaceae undiff.
Betulaceae - Alnus sp.
Bombacaceae undiff.
Cecropiaceae - Coussapoa sp.
Chenopodiaceae undiff.
Clusiaceae - Symphonia globulifera
Elaeocarpaceae - Sloanea-t.
Euphorbiaceae - Acalypha sp.
Euphorbiaceae undiff.
Fab.-Fab. - Dalbergia-t.
Fab.-Mim. - Inga-t.
Fab.-Mim. - Mimosa sp.
Malpighiaceae undiff.
Malvaceae undiff.
Melastomataceae - Adelobotrys-t.
Meliaceae undiff.
Moraceae - Brosimum sp.
Moraceae - Ficus sp.
Moraceae - Maquira-t.
Moraceae - Pourouma sp.
Myristicaceae - Virola sp.
Myrtaceae undiff.
Onagraceae - Ludwigia sp.
Phyllanthaceae - Hieronyma sp.
Piperaceae - Piper sp.
Podocarpaceae - Podocarpus sp.
Polygalaceae undiff.
Polygonaceae - Symmeria paniculata
Rubiaceae - Psychotria-t.
Rubiaceae undiff.
Rutaceae undiff.
Sapindaceae undiff.
Sapotaceae undiff.
Solanaceae undiff.
Ulmaceae - Trema-t.
Urticaceae - Pouzolzia-t.
Type 1
Type 3
NPP Unknown
Pteridophyta - Trilete undiff.
Pteridophyta - Round trilete scabrate
Pteridophyta - Monolete undiff.
Polypodiaceae - Polypodium-t.
Pteridaceae - Pityrogramma sp.
Davaliaceae - Nephrolepis sp.
Selaginellaceae - Selaginella sp.
Selaginellaceae - Type 4
Zygnemataceae - Spirogyra sp.
Unknown
Indeterminable
PAZ
SJ-5
SJ-4
SJ-3
SJ-2
SJ-1
0
50
100
150
200
250
0
100
250
500
1000
1500
1750
2000
2250
0
20
40
60
%

Figure 5B

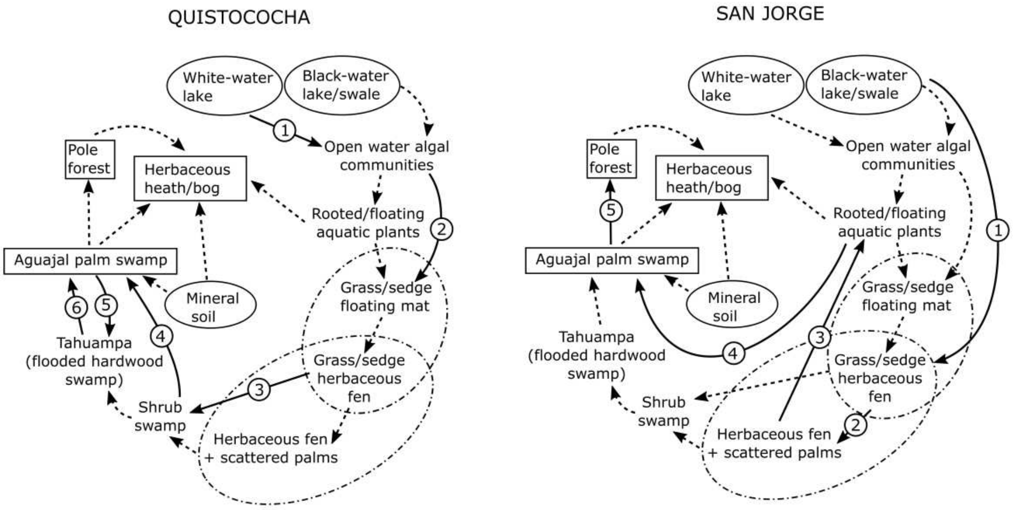
QUISTOCOCHA
White-water lake
Black-water lake/swale
Open water algal communities
Pole forest
Herbaceous heath/bog
Rooted/floating aquatic plants
Aguajal palm swamp
Grass/sedge floating mat
Mineral soil
Tahuampa (flooded hardwood swamp)
Grass/sedge herbaceous fen
Shrub swamp
Herbaceous fen + scattered palms
1
2
3
4
5
6
SAN JORGE
White-water lake
Black-water lake/swale
Open water algal communities
Pole forest
Herbaceous heath/bog
Rooted/floating aquatic plants
Aguajal palm swamp
Grass/sedge floating mat
Mineral soil
Tahuampa (flooded hardwood swamp)
Grass/sedge herbaceous fen
Shrub swamp
Herbaceous fen + scattered palms
1
2
3
4
5

Figure 6

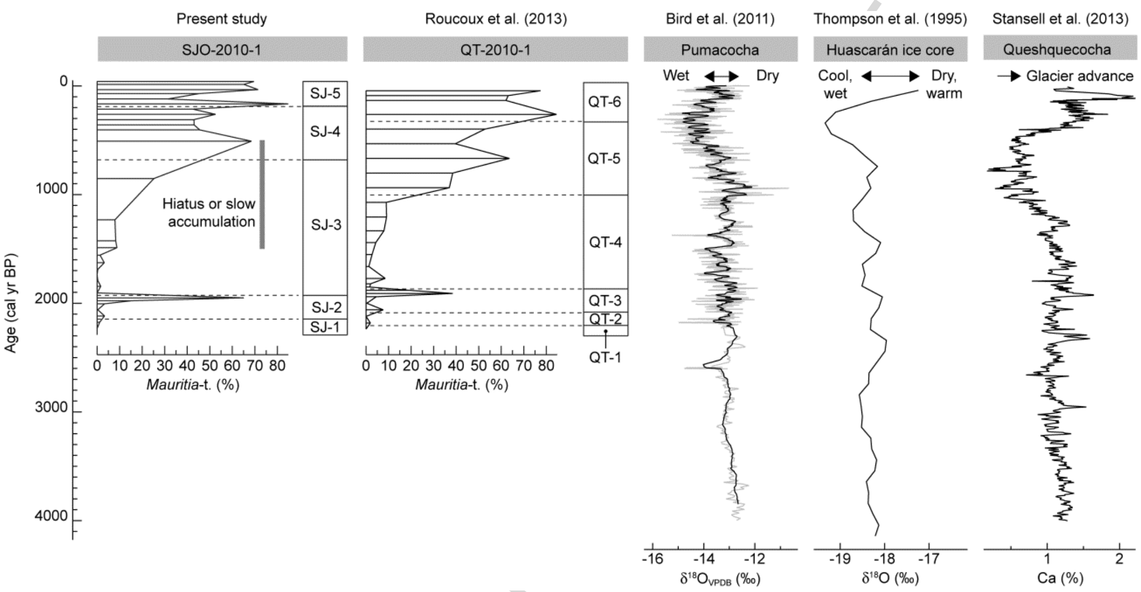
Present study
SJO-2010-1
Roucoux et al. (2013)
QT-2010-1
Bird et al. (2011)
Pumacocha
Thompson et al. (1995)
Huascarán ice core
Stansell et al. (2013)
Queshquecocha
Age (cal yr BP)
0
1000
2000
3000
4000
SJ-5
SJ-4
SJ-3
SJ-2
SJ-1
Hiatus or slow accumulation
0 10 20 30 40 50 60 70 80
Mauritia-t. (%)
QT-6
QT-5
QT-4
QT-3
QT-2
QT-1
Wet
Dry
Cool, wet
Dry, warm
Glacier advance
-16 -14 -12
δ18OVPDB (‰)
-19 -18 -17
δ18O (‰)
1 2
Ca (%)

Figure 7

Highlights

1. We present the first pollen record from an ombrotrophic domed peatland in Peruvian Amazonia

2. An age model presents the first evidence for discontinuous peat accumulation in this region

3. Spatial vegetation patterning at the site today is not clearly reflected down-core

4. The pole forest formed in the last 200 years after several other vegetation phases

5. Some vegetation changes in the record can be correlated with regional climatic events