



A human role in Andean megafaunal extinction?

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ABSTRACT

A new fossil pollen, *Sporormiella*, and sediment chemistry record from Lake Llaviucu, Ecuador, spanning the period from 16,280–9000 years Before Present, provides a high-resolution record of paleoecological change in the high Andes. The deglacial transition from super-páramo through páramo grasslands, to Andean forest is traced, with near-modern systems being established by c. 11,900 years ago. It is suggested that forest elements probably existed in microrefugial populations close to the ice front. *Sporormiella* is used as a proxy for megafaunal abundance, and its decline to background levels is inferred to indicate a local extinction event at c. 12,800 years ago. About 1800 years prior to the extinction, charcoal becomes a regular sedimentary component in this very wet valley. An early date for human activity in the valley is suggested, with the direct implication of humans in the extinction of the megafauna.

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1. Introduction

The Pleistocene megafauna was filled with charismatic animals, such as sabre-toothed cats (*Smilodon*), elephantids (Proboscideans), and 4-ton sloths (*Megatherium*), but near the end of the last ice age >80% of the large-bodied (>44 kg) mammal species in the Americas went extinct (Barnosky et al., 2004; MacFadden, 2006). The extinction event in South America was even more profound in terms of numbers lost (52 genera), and the proportion (83%) than in North America (34 genera, 72%) (Barnosky and Lindsey, 2010). The leading hypotheses for the causes of the sudden demise of the megafauna are hunting by humans (Martin and Wright, 1967), climate change (Cooper et al., 2015; Grayson and Meltzer, 2003), and ecological cascades (Janzen, 1983; Ripple and Van Valkenburgh, 2010).

To explore the loss of megafauna in South America requires a detailed and accurate picture of environmental changes and human

history during the last deglaciation. A combination of improved tools and archaeological discoveries are fostering a new view of this critical period. Improved calibration techniques in Be-10 analysis are increasing the accuracy of dating moraines and glacial erratics (Heyman et al., 2011), and hence glacial advances and retreat in the Andes (Seltzer, 1990; Rabatel et al., 2013). Similarly, the identification of *Sporormiella*, a dung fungus, as an efficient proxy for detecting the presence of large herbivores provides a tool to determine local megafaunal population trend (Davis, 1987; Gill et al., 2009; Raczka et al., 2018). Lastly, the discovery of archaeological sites in the Andes of Peru and Bolivia provide good evidence of human activity by 12.8 thousands of calibrated ¹⁴C years Before Present (hereafter k cal BP) (Rademaker et al., 2014). Here, we provide a new high-resolution multiproxy record of vegetational change, fire, and megafaunal presence based on a lake sedimentary record from southern Ecuador for the period from 16.28 to 9 k cal BP.

1.1. The last ice-age termination

The peak of the last glaciation can be defined locally or globally. In the Andes, local ice sheets often had their maximal extent prior

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to 40 k cal BP (Clapperton, 1993), followed by an interstadial and substantial ice retreat prior to another advance that took place between c. 32 and 18 k cal BP. This later advance approximates that of the global maximum ice extent and hence is generally referred to as the last glacial maximum (LGM). That this ice advance in the tropical Andes is reported as being at 25.1 ± 7 k cal BP (Bromley et al., 2016), provides an indication of the locally heterogeneous responses to climate forcing. Valley orientation, topographic steepness, precipitation, and seasonality all play a role in determining the extent and duration of ice cover. Typically moraines associated with the LGM lie at c. 3700–3400 m elevation (Clapperton, 1993), but in especially wet locations, glaciers can extend further downslope (Rodbell et al., 2009). In the wet Llaviucu Valley of southern Ecuador, the location of this study, the lowest moraine occurs at c. 2850 m elevation (MBB pers obs.).

Tropical Andean deglaciation appears to have begun as early as 22 k cal BP (Smith et al., 2005) and substantial ice retreat had occurred before 18 k cal BP (Seltzer et al., 2002). Glacial re-advances are suggested to have occurred at c. 16.1 k cal BP (Bromley et al., 2016) and between c. 14 and 12 k cal BP, with a peak probability at 12.8 k cal BP (Jomelli et al., 2014). This latter advance is thought to have caused an expansion of glaciers to occupy about half their LGM range in southern Peru and Bolivia (Jomelli et al., 2014). The timing of these re-advances is suggested to match cold periods in Antarctica rather than those of the northern hemisphere (Bromley et al., 2016; Shakun et al., 2015).

The moraines of the Llaviucu valley have not been dated, but a datum relating to local ice retreat in southern Ecuador comes from Lake Pallcacocha in El Cajas National Park, a glacially-formed lake just 15 km from our field site of Lake Llaviucu (Fig. 1). Pallcacocha lies at 4200 m above sea-level (masl) and has sediments with a basal age of c. 15.1 k cal BP (Moy et al., 2002; Rodbell et al., 1999). As this site is over 1000 m higher in elevation than Lake Llaviucu it

would be expected to show a later local deglaciation, thus its age of formation would be a minimum age for deglaciation at Lake Llaviucu. The relative locations of these two lakes could also have influenced their glaciation history. Lake Pallcacocha is windswept and faces northward, while Lake Llaviucu lies in a sheltered valley oriented to trap moisture and heat rising from the Amazonian lowlands.

Upper Andean forests are very diverse ecosystems that support many rare and endemic species, but our knowledge of how these assemblages changed through time is limited, especially in the southern hemisphere (Bush et al., 2005; Niemann and Behling, 2009; Valencia et al., 2010). The peak of the last ice age saw the lowering of many species distributions by 1000–1500 m (Liu and Colinvaux, 1985; Van der Hammen, 1974). The lower limit of grasslands has yet to be established for the LGM, but would be anticipated to be between c. 2000 and 2500 masl. The upslope migration of species in response to deglacial warming is evident across a range of elevations beginning as early as 21 k cal BP (Bush and Silman, 2004; Paduano et al., 2003; Valencia et al., 2010). In the upper Andes, a commonality of many records is that grasslands were invaded by trees (Van Der Hammen and Hooghiemstra, 1995, p. e.g.; Velásquez-R. and Hooghiemstra, 2013). It cannot be assumed that the composition of those ancient grasslands was similar to those of today because plants migrate individually, and floral composition may have been shaped by now-extinct megaherbivores. A common theme between North America and the Andes is that when megafaunal populations collapsed a non-analogue forest flora replaced the previous parkland or grassland signature (Gill et al., 2012, 2009; Rozas-Dávila et al., 2016).

A low-resolution pollen record from Lake Llaviucu showing a transition from pre-glacial grasslands, through páramo to Andean forest was previously published under the alternative site name of Lake Surucucho (Colinvaux et al., 1997). We follow recent precedent in adopting the name Lake Llaviucu (Harden, 2006; Labaj et al., 2016; Michelutti et al., 2016; Rühland et al., 2015) as we provide a detailed paleoecological reconstruction of its deglacial history.

1.2. Megafaunal extinction

Barnosky and Lindsay (2010) reviewed the paleontological evidence for the extinction of South American megafauna. Of the 52 genera thought to have gone extinct, only 14 of those have radiometrically-dated remains indicating that they survived until at least the LGM. The other taxa are known to be of Quaternary age, but their last occurrence is unknown. If many of these animals were rather rare it is not surprising that their remains have not been recovered from a datable context close to the time of extinction (Signor and Lipps, 1982).

Three recent studies from South America have contributed to our understanding of the megafaunal population collapse, if not the final extinction, of megaherbivores. In Patagonia, dates were established on 79 bones and teeth from seven extinct mammal species (Metcalf et al., 2016). Combined with other dated remains from the region the latest survival age for the assemblage was estimated to be 12.3 k cal BP. The authors inferred a period of co-existence with humans for 1–2 millennia and suggested that the population decline was a synergy between changing climates and human-induced hunting pressure (Metcalf et al., 2016). In southeastern Brazil, the fossil *Sporormiella* record from two lakes indicated an abrupt decline in megafaunal populations at c. 12.8 k cal BP (Raczka et al., 2018). The archaeological record from the region near the lakes was rich (Neves and Hubbe, 2005; Neves and Pilo, 2003), but no dated human artifact was older than c. 11.5 k cal BP. Nevertheless, the authors did not rule out human involvement in the megafaunal decline.

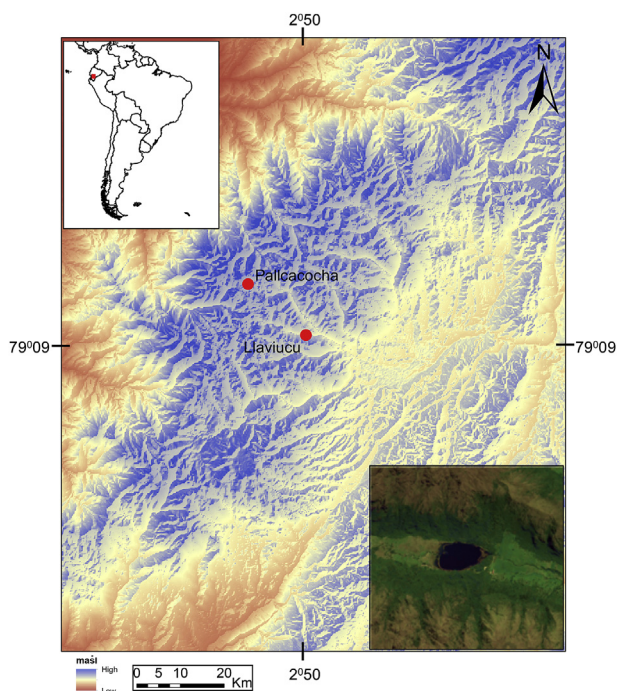


Fig. 1. Map of the study area showing South America and the location of Lake Llaviucu and Lake Pallcacocha (red circles). Digital elevation model is from the Shuttle Radar Topography Mission (STRM) w250 m. At the bottom right corner is a Google Earth image of Lake Llaviucu showing the lake in detail situated in a valley system. Images of Llaviucu are Figs. S1–3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

At Lake Pacucha in the Peruvian Andes, fossil *Sporormiella* suggested a two stage decline in megafaunal population abundance with one event occurring at c. 21 k cal BP, which was followed by a recovery, before the functional extinction at c. 15.8 k cal BP. The distinction between functional and final extinction is important, as very low numbers of a species may linger long after they have almost no ecological impact (functional extinction *sensu* Davis, 1987). Between 15.8 k cal BP and 13 k cal BP, *Sporormiella* were present in the sediments of Lake Pacucha at much lower densities, not reaching the 2% of the pollen sum often used to indicate a functional extinction (Davis, 1987; Davis and Shafer, 2006; Gill et al., 2012). In the Andes, however, where camelids and deer survived the extinction, the 2% threshold could be misleading, as the extant megafauna could provide these background amounts of *Sporormiella* or, alternatively, there could have been low densities of megafauna still present in the landscape until c. 13 k cal BP.

Although some criticism has challenged the use of *Sporormiella* as a proxy for megafauna abundance in sedimentary archives (Etienne et al., 2012; Fiedel, 2015), new data from modern calibration studies (Bakker et al., 2016; Gill et al., 2012; Raczka et al., 2016; Raper and Bush, 2009) have reinforced the validity of this approach. Analysis of *Sporormiella* is a demonstrably robust tool to evaluate mega-herbivore abundance whether it is to evaluate extinctions in the terminal Pleistocene or human introductions of livestock (Burney et al., 2003; Gill et al., 2009; Halligan et al., 2016; López-Sáez and López-Merino, 2007; López-Sáez et al., 2018; Perrotti, 2017; Raczka et al., 2018; Robinson et al., 2005; Rozas-Dávila et al., 2016; van der Kaars et al., 2017; van Geel et al., 2003).

1.3. Human entry

The timing of human entry into South America is actively debated (see Borrero, 2016 for a recent review) and sites are so sparse that data must be treated as providing minimum occupation ages. The earliest credible record comes from Monte Verde in Chile, which places people in southern South America by c. 18.5 k cal BP (Dillehay et al., 2015). The Monte Verde data have progressively pushed back the earliest occupation of South America by about 7000 years compared with the state of knowledge before that site was excavated.

Occupation of the High Andes was once thought to have been delayed for many thousands of years due to physiological hurdles associated with hypoxia (Aldenderfer, 2008, 2003). Several sites in Peru and Bolivia, however, provide dated evidence of human presence by c. 12.8 k cal BP (Capriles and Tripcevich, 2016; Rademaker et al., 2014). These finds pushed back the occupation of the Andes by at least 1000 years from prior estimates. In northern Florida, a parallel is evident in the recent discovery of a mammoth tusk showing human-made cut marks. The tusk dated to 14.5 k cal BP, almost 3000 years older than prior records of people in Florida (Halligan et al., 2016; Perrotti, 2017). It is clear that we do not have a firm grasp on the timing of earliest human occupation of any of these settings.

Arising from these recent studies we raise the following research questions:

What was the timing of megafaunal extinction at Lake Llaviucu and did it coincide with the onset of burning and no-analogue floras?

1.4. Site description

Lake Llaviucu lies at 2° 50' 35" S, 79° 08' 46" W at an elevation of 3150 m (Fig. 1). The lake (length 475 m, breadth 385 m) is dammed by a glacial moraine. A feeder stream enters the western end of the lake after flowing through a small marsh. A single small stream

leaves the eastern end of the lake and lake level is maintained by a small weir, probably raising lake level by about 2 m.

The valley in which the lake lies is U-shaped with peaks flanking the lake reaching as high as 3815 masl. The flat bottom of the valley extends upslope about 1 km offering a relatively flat section of c. 50 ha up-valley that is currently used by grazing animals. A small herd (6–10 animals) of Llama graze the area (see supplemental information for photographs), and scratches on trees indicate the presence of Andean bear.

The annual average temperature of the region is about 11–12 °C with annual rainfall in excess of c. 1050 mm (Michelutti et al., 2016). Rainfall is increased by cloud interception as the area commonly has low-lying cloud, resulting in an effective precipitation in excess of 2000 mm (Cajas National Park). During the driest time of the year, which lasts from June to September, rainfall decreases to 50–100 mm per month.

The modern vegetation is a diverse, wet Andean woodland rich in *Weinmannia*, *Alnus*, *Podocarpus*, Rubiaceae, *Hedyosmum*, Urticaceae, *Chusquea*, and *Myrsine* (Mosblech, 2012). *Fuchsia*, Ericaceae, Melastomataceae, Rubiaceae, and Solanaceae grow around disturbed forest edge settings. Trees support lush growths of epiphytic mosses, bromeliads, and orchids. The Andean forest gives way to páramo ecosystems, occurring at altitudes above cloud, c. 3400 masl. The marsh in the valley bottom is a mixture of grasses and forbs such as *Lupinus*, *Rumex*, and assorted Asteraceae.

The maximum water depth in the lake is c. 16 m. A deltaic feature causes the western end of the lake to be relatively shallow, but the eastern half of the lake has a gently sloping bottom creating an average water depth of c. 14 m.

1.5. Prior study of the site

A low-resolution fossil pollen record with sample intervals of about 300 years was based on a 12.3 m-long sediment core (Llav89) raised in 1989 by MBB, as part of Paul Colinvaux's research team. That record provided evidence of glacial-age, low-productivity grasslands, with a transition from páramo vegetation to Andean woodland about 13 k cal BP (Colinvaux et al., 1997). The dating at the base of the 1988 core was uncertain as there were a number of age reversals in the bulk carbon ¹⁴C assays. This uncertainty led to the suggestion of alternate chronologies one with a c. 30 k cal BP lake formation and the other with a c. 15 k cal BP formation. The chronologies converged about 12 k cal BP where the ages became more reliable.

In anchoring the platform in 2009 we found an abandoned anchor line cut by MBB in 1989. The line was found floating just beneath the surface near the 2009 coring site, showing that the new sediment record was within a few metres of the original one.

The most recently published studies on the lake have centered on near-modern changes in the diatom flora. Short (60 cm) cores raised by Michelutti et al. (2016) documented the rapid rise of importance of *Discotella stelligera* and attributed it to climate change altering the thermal structuring of this lake and many other lakes in the region.

Here, we provide a description of the palaeoecological changes associated with the deglacial period between 16.2 and 9 k cal BP.

2. Methods

A sediment core, Llav09, was raised using a Colinvaux–Vohnout piston sampler (Colinvaux et al., 1999) from 15 m water depth in June 2009. Tubes were capped and sealed in the field before being shipped to Florida Institute of Technology where they were stored in a cold room at 4 °C. Afterwards, the tubes were opened and the core split into working and archive halves. Subsamples of 0.5 cm³

were removed for fossil pollen and charcoal analysis. In 2016, a 1 cm-wide, U channel sample was removed from the length of the archive half and shipped to Woods Hole Oceanographic Institute for XRF analysis (X ray fluorescence spectrometry). This non-destructive technique was performed to evaluate the geochemical changes in the Llavivucu sediments.

Fossil pollen samples were prepared following standard protocols (Faegri and Iversen, 1989) that included the addition of exotic *Lycopodium* spores (Stockmarr, 1971) to facilitate calculation of pollen concentrations. Spores of *Sporormiella* and *Isöetes* were excluded from the pollen sum but are expressed as a proportion of it. Pollen and spores were counted on a Zeiss Axioskop photomicroscope at x630 and x1000 magnification. Identifications were made using the modern pollen reference collection at Florida Institute of Technology that contains ~7000 Neotropical types, and the Neotropical pollen database (Bush and Weng, 2007) until a total of 300 pollen grains was reached. Fossil pollen data from the older Llav89 core were used in the bottom section between 7.45 m and 12.1 m as these had previously been shown to be of low pollen abundance and diversity. Data from the section were overlapped and cores cross-correlated with data from Llav09 to ensure consistency. *Sporormiella*, XRF and charcoal data were derived entirely from the Llav09 core. Fossil pollen data were ordinated using Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980) in the R-studio package Vegan (Oksanen et al., 2013). The DCA was run on the commonest 47 pollen types, i.e. those occurring at > 2% in at least one sample, for the depth interval from 12.1 to 4.55 m We performed a Bayesian change point analysis (BCP) to establish the last major change in vegetation associated with *Sporormiella* abundance using the package 'bcp' in R (Erdman and Emerson, 2012; R Core Team, 2015).

Subsamples for charcoal analysis were disaggregated in warm 10% sodium pyrophosphate and then filtered using a 180 µm mesh. Particles retained on the mesh were transferred to a petri dish for identification and quantification. Charcoal counts were completed using an Olympus stereoscope at x20 magnification. Charcoal fragments were imaged and the surface area calculated using ImageJ software (Rasband, 1997).

X-Ray fluorescence (XRF) analyses were conducted on U-channel samples using a Cox Analytical's ITRAX XRF micro-scanner for measuring bulk geochemistry, digital X-radiography and photography at the Woods Hole Oceanographic Institution (Bertrand et al., 2015). Counts for up to 25 elements were recorded at 1 mm intervals along the u-channel using a Mo or a Cr X-ray source. All data were normalized by total counts per second, before 50-year running means were calculated. Of the XRF data, Si, Ti and Rb/Sr are reported as proxies for terrigenous erosion (Croudace and Rothwell, 2015). The ratio of incoherent to coherent scattering (inc/coh) is reported as a proxy for sedimentary organic content (Liu et al., 2013) and supported by loss-on-ignition data. Principal Components Analysis was run on the z-scores for all elements (Olsen et al., 2012).

Loss-on-ignition (LOI) was performed following the procedures in Dean (1974) with modifications made by (Heiri et al., 2001) on 0.5 cm³ subsamples at 2 cm intervals. Subsamples were heated at 550 °C for 4 h to estimate the organic content, and at 950 °C for 2 h to quantify carbonate content.

The chronology of the Lake Llavivucu record was based on nine bulk sediments samples submitted for AMS (accelerator mass spectrometry analysis) at Woods Hole Oceanographic Institution (NOSAMS).

3. Results

The total core length of the 2009 core is 12.1 m, very similar to the 12.3 m long core raised in 1989. The two cores shared a major sedimentary transition at c. 7.4 m depth from clay-rich to organic rich sediments. The Llav09 stratigraphy of the core reflects a phase from 12.1 m to 7.35 m core depth that is composed of pale clays rich in glacial rock flour. Above 7.35 m core depth the sediments are gyttjas that are generally black or dark green in coloration. Between and 6.3 and 4.55 m core depth fine, pale, laminations are present. From 4.55 m to the top, the sediment was characterized by a brown organic gyttja. Nine ¹⁴C accelerator mass spectrometry (AMS) ages on bulk sediment (Table 1) were calibrated using Calib 7.10 (Stuiver et al., 2018) and plotted using Bchron (Parnell, 2014) (Fig. 2). The derived chronology provided a basal age of c. 16.28 k BP at 12.1 m.

3.1. Local pollen zones

Three pollen zones are recognized based on clusters apparent in the DCA results (Fig. 3). Samples in the basal group Llav-1 lie within the period 16.28–14.75 k cal BP, Llav-2 samples date to 14.75–13.1 k cal BP, and samples between 13.1 and 9 k cal BP fell within Llav-3. The segregation of these zones is remarkably clean, with very little overlap in this unconstrained ordination. BCP analysis was applied to the DCA Axis 1 and 2 scores to determine times of abrupt vegetation change. The BCP was also run on the *Sporormiella* percentage to identify the transition to abruptly lower levels of spores representing local megafaunal population collapse. A major shift observed in the posterior probability of the BCP occurs between 12.9 and 12.5 k cal BP (Fig. 7).

3.2. Pollen zone Llav-1 (12.1 m–7.4 m; c. 16.2–14.7 k cal BP)

This basal zone was characterized by sediments rich in mineralogenic elements such as Si, Rb, and Ti. Ca was also high and probably reflects limestone ground up by glacial activity (Fig. 4). Contrastingly, the proxy for organic content, the ratio of incoherent/coherent (inc/coh), which represents increased organic content, was low and matched observations based on loss-on-ignition (Fig. 4). Fossil pollen concentrations were low, beginning at c. 600 grains per cm³, but increased to 30,000 grains per cm³ at 14.87 k cal BP (Fig. 5). The pollen spectrum is dominated by Poaceae

Table 1

Llavivucu accelerator mass spectrometry ¹⁴C dates for the 2009 sediment core. ¹⁴C radiocarbon dates were calibrated using Calib 7.10 (Stuiver et al., 2018).

Lab ID	Depth (cm)	¹⁴ C yr BP	Error	¹⁴ C k cal BP	2-sigma	¹³ C
OS-77533	0	3760	47	4060	3908–4181	–26.87
OS-77596	221.2	7920	98	8724	8510–8998	–26.97
OS-77534	449.5	10,600	49	12534	12427–12651	–22.13
OS-77519	545	11,250	50	13077	12959–13205	–25.93
OS-77394	615.9	12,700	95	15022	14486–15347	–26.2
OS-77395	727.5	12,800	101	15198	14779–15588	–25.95
OS-77396	826.8	12,150	69	13963	13766–14143	–26.09
OS-77397	997	13,450	138	16123	15727–16557	–25.82
OS-78053	1021	13,200	124	15788	15343–16147	–24.18

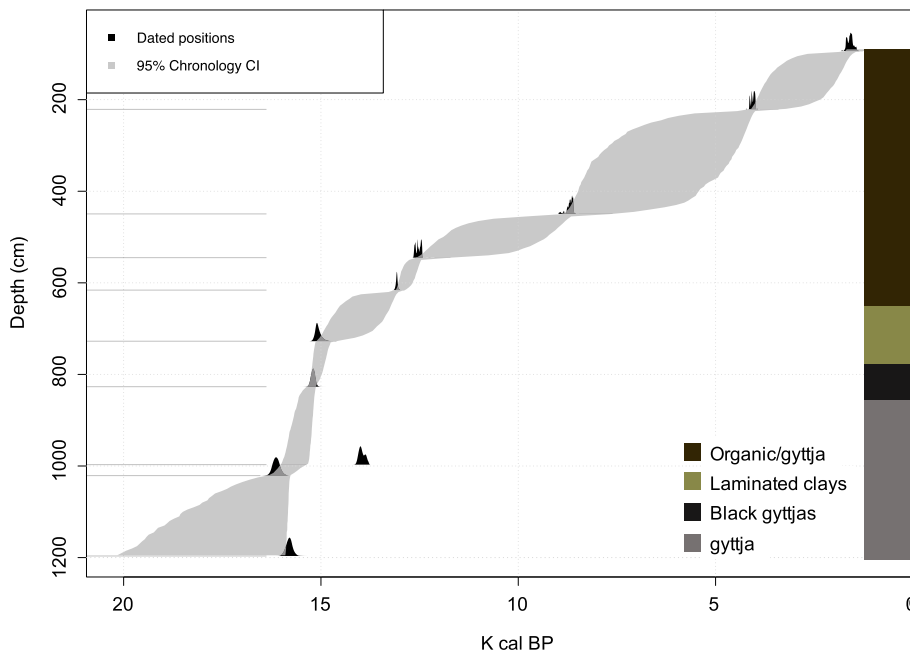


Fig. 2. Bayesian age model output from Bchron for the Lake Llavucu sediments, based on the probability density function for each calibrated radiocarbon age. A basal age of 16.28 k BP at 12.1 m depth was adopted for subsequent analyses.

and Asteraceae, which combine for 40–90% of the pollen sum. In the most basal samples, *Alnus*, *Hedysmum*, *Urticaceae* and *Polylepis*, account for about 50% of the pollen sum. In the uppermost samples of this zone, *Polylepis* rises in significance to c. 20% of the pollen sum. *Isöetes* is abundant (reaching 110% at 12.89 k cal BP), while *Sporormiella* is scarce (<1%) during this zone, and its concentrations is very low at < 235 spores per cm³. Charcoal was also rare in these samples (Fig. 5).

3.3. *Llav-2* (7.4 m– 6.1 m; c. 14.7–13.1 k cal BP)

This zone is characterized by reduced variance and much lower values of elements indicating minerogenic inputs compared with the previous zone. A single spike of Rb/Sr (Fig. 4) is apparent at 14.45 k cal BP and coincides with very high values of Si. The fossil pollen concentrations in this zone increase at 14.75 k cal BP to c. 50,000 grains per cm³ (Fig. 5). This change in concentration is not matched by a striking difference in the percentile pollen data.

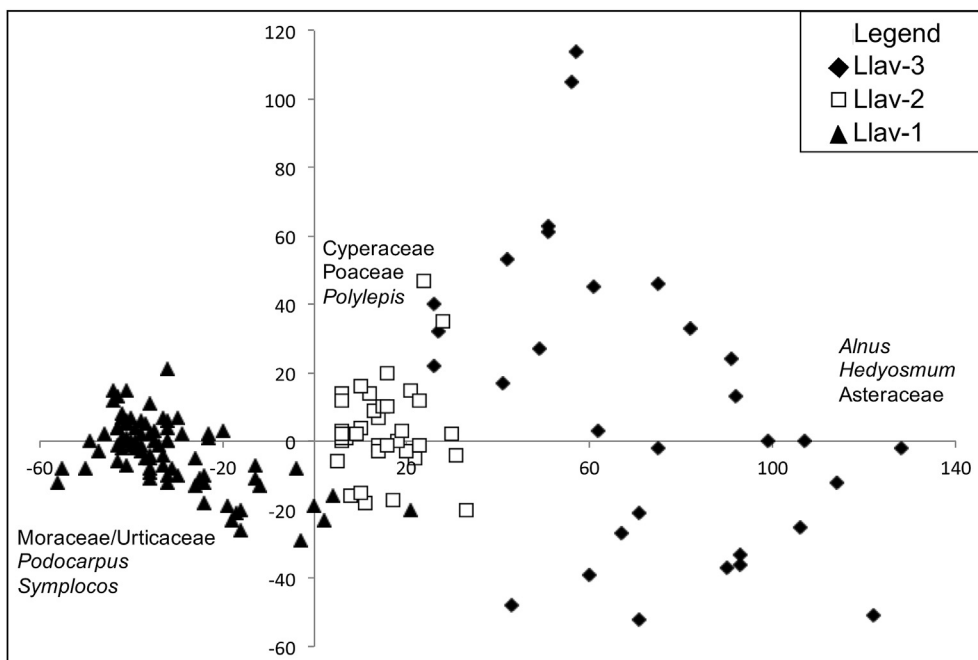


Fig. 3. Detrended correspondence analysis (DCA) results of the fossil pollen data of Lake Llavucu. Triangles represent pollen zone Llav-1 (16.2–14.75 k cal BP), open squares represent the pollen zone Llav-2 (14.75–13.1 k cal BP), and black diamonds represent the pollen zone Llav-3 (13.1–9 k cal BP).

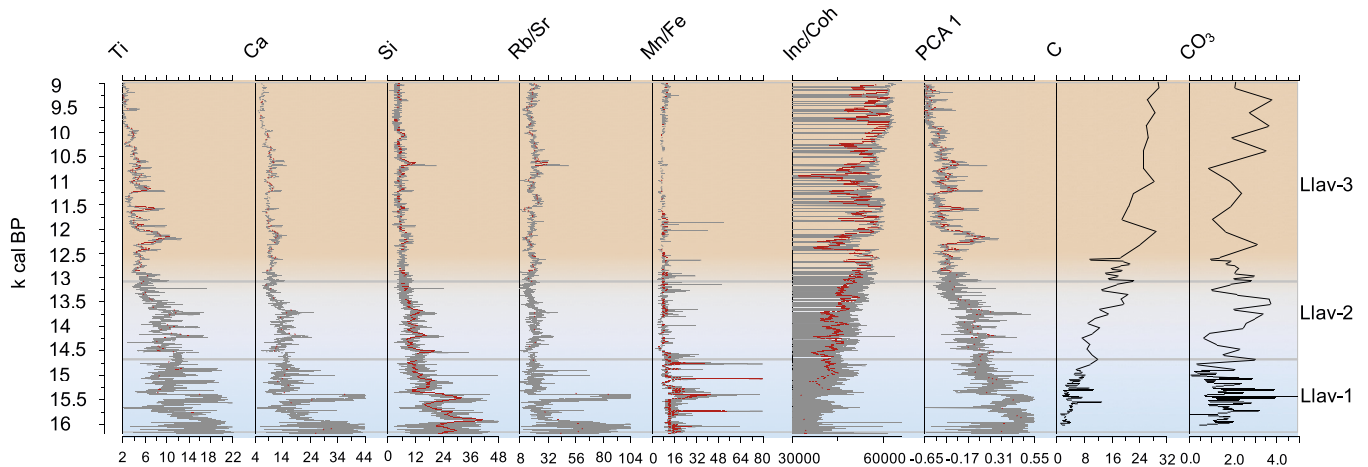


Fig. 4. XRF and loss on ignition (C and CO₂) data from Llaviucu sedimentary core. The red lines show the 50-year running mean for selected chemical elements and ratios. PC1 accounted for 34.6%, while PCA2 accounted for 12.6% of the variance. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Overall this zone shows strong percentages of Poaceae, establishment of Cyperaceae, reduced percentages of Asteraceae, and increasing representation of woody taxa such as *Acalypha*, *Symplocos*, and *Vallea*. Charcoal increases in frequency and abundance during this zone, as does *Sporormiella*, which varies between highs of c. 10% to lows of c. 1.5%. The concentration data for *Sporormiella* go through a similar scale of variability from 21 to 582 spores per cm³. *Isöetes* percentages fall as low as 5%.

3.4. Llav-3 (6.1 m–4.57 m; c. 13–9 k cal BP)

Increasing carbon content and low minerogenic inputs characterize this zone. Between 12.5 and 11.9 kcal BP there is a reduction in the inc/coh ratio (Fig. 4) suggesting reduced organic content in the sediment. Pollen concentrations are steady and relatively high as Poaceae reaches a peak abundance at c. 12.9 k cal BP of c. 65%. Thereafter, Poaceae abundances decline to c. 30% as woody taxa such as *Polylepis*, *Urticaceae*, *Hedyosmum*, *Podocarpus*, *Acalypha*, *Symplocos* and *Vallea* increase in abundance. *Isöetes* shows a sharp recovery to c. 45% in the basal samples of this zone, but following a peak at 12.9 k cal BP, its abundance drops rapidly so that it is at c. 5% of the pollen sum by 11.9 k cal BP. *Sporormiella* shows a peak to c. 3% (282 spores per cm³) at c. 12.7 k cal BP, after which its abundance remains steady for the remainder of the early Holocene at c. 3–1.5%. Charcoal increases in abundance at 12.7 k cal BP and it becomes a consistent and abundant component of the sediments thereafter. Between c. 12.25 and 12 k cal BP there is a marked increase in T, Ca, Si, and in PCA axis 1 scores.

4. Discussion

4.1. Palaeoecological and palaeoclimatic overview

The lowest moraine in the Llaviucu Valley lies at c. 2850 m elevation. Whether this moraine was from the LGM or from a previous ice advance is not known. The Lake Llaviucu sediment core provides evidence that the final deglaciation of the Llaviucu Valley above 3150 m elevation began at c. 16.28 k cal BP. This age is within error of estimates by Bromley et al. (2016) for a short-lived ice advance that produced the last glacial maxima in Peru. As ice retreated, a lake formed that was impounded by the terminal moraine.

Initially, the sediments were composed of rapidly deposited (Fig. 2) minerogenic material that was low in organic content. High values of Ti, Ca, and Si are all indicative of fine sediment inputs that were dominated by glacial rock flour (Fig. 4). By c. 15.3 k cal BP the strongest of these inputs were subsiding. The very low fossil pollen concentrations and a disproportionate input of wind-dispersed Andean forest taxa point to so little local productivity that even a few Andean forest individuals could have a significant impact. The fossil pollen data indicate that the landscape around the lake was a glacial foreland inhabited by páramo grassland species. Although Andean forest species are important on a percentile basis (Fig. 5), they are very unlikely to have been growing on site as a forest. One interpretation of these data is that there was long-distance transport of the pollen of *Alnus*, *Hedyosmum*, *Myrsine*, *Urticaceae*, *Polylepis* and *Podocarpus* to the site. An alternative interpretation, supported by a growing body of evidence for the importance of microrefugia (Correa-Metrio et al., 2013; Rull, 2009), is that a few individuals of these taxa could have survived close to the ice-front in a super-páramo setting.

Local productivity increased quite quickly, transitioning from a glacial foreland akin to super-páramo to páramo within this zone (Fig. 5). This change is reflected in increased carbon content in the sediment (Fig. 4). The reduced proportion of Andean taxa suggested that there was no immediate population increase of arboreal elements.

Isöetes is an important proxy for two different facets of paleoecology at Lake Llaviucu, temperature and flow. *Isöetes* can be used to approximate temperature during zones Llav-1 and Llav-2. *Isöetes* is a common element of shallow waters and very sensitive to severe freezing (Bush et al., 2005; Ybert, 1988). As mean annual temperatures fall below 5 °C, i.e. above c. 4400 m in Ecuador, *Isöetes* becomes rare. At the lower end of its distribution it does not survive in lakes below 3400 m elevation (c. 10 °C), and has peak occurrences between c. 3800 and 4000 m (c. 6–7 °C) (Terneus, 2001). The basal sample in the Lake Llaviucu core has very low abundances of *Isöetes* suggesting that conditions were close to the cold thermal limit for this genus, i.e., mean annual temperature of c. 5 °C or about 6–7 °C cooler-than-modern (Fig. 6). The peak abundance of *Isöetes* at c. 14.89 k cal BP and its abundant presence until 13 k cal BP, suggest that it was well-suited to prevailing conditions and this may reflect the climatic optimum for the genus, i.e. about a 4–5 °C cooling relative to modern.

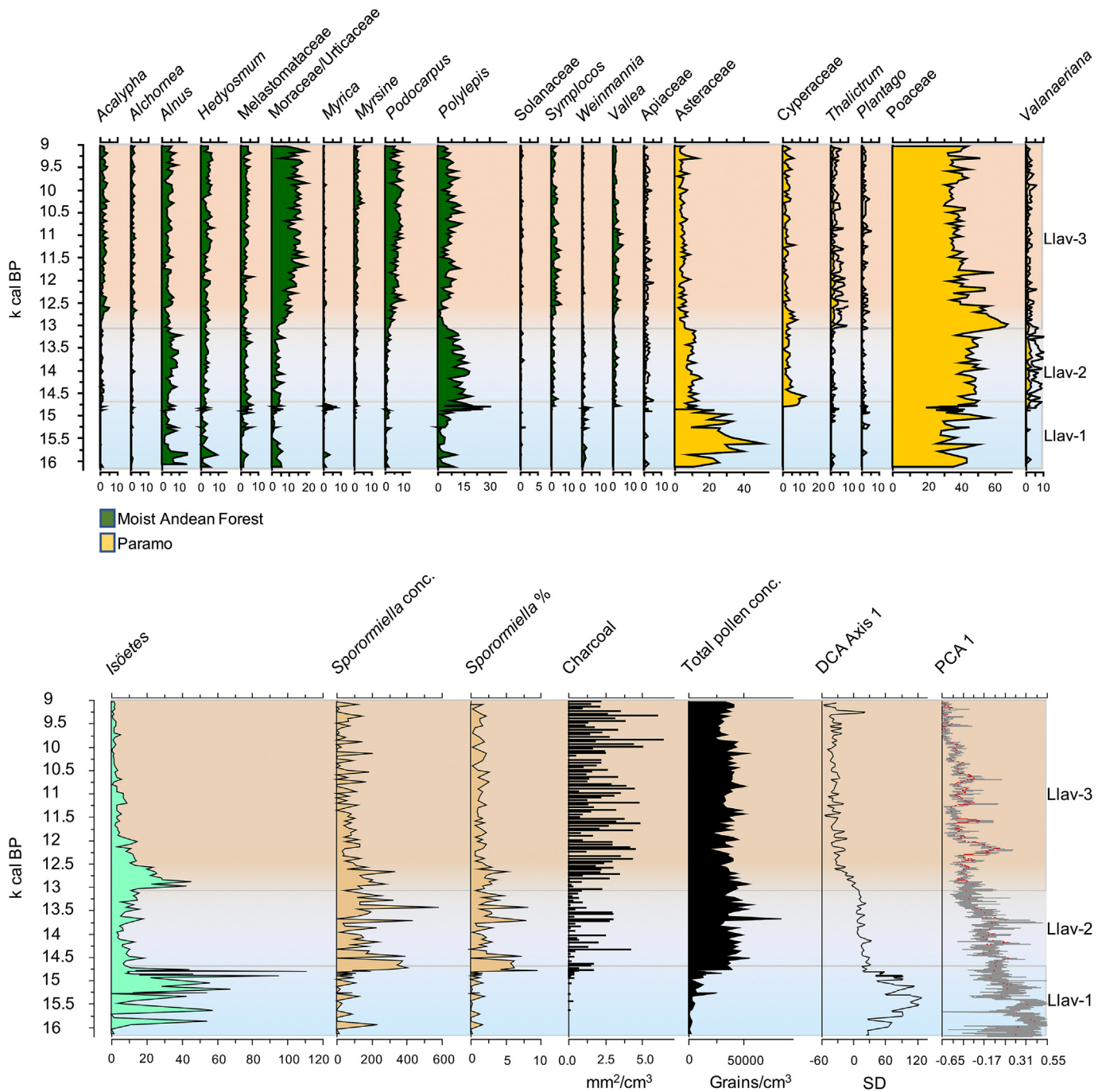


Fig. 5. Pollen diagram of the percentage data for selected pollen taxa recovered from the sediments of Lake Llavucu. A $5 \times$ exaggeration (open curve) is shown for values $< 2\%$. Green silhouettes indicate the Moist Andean taxa and yellow silhouettes indicates Páramo taxa (upper panel). *Isöetes* (light green) was not included in the pollen sum. Total pollen concentration is indicated as grains per cm^3 . Detrended correspondence analysis (DCA) Axis 1 sample scores was plotted against time in units of standard deviations of species turnover (Hill and Gauch, 1980). A 50-year running mean is shown overlying raw values for the PCA Axis 1 of the XRF data (bottom panel). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

A marked transition occurred at c. 14.7 k cal BP as the vegetation shifted to becoming more characteristic of a páramo grassland. A rise in pollen concentrations was indicative of denser vegetation as Asteraceae declined and Poaceae increased in abundance. The general lack of woody plants other than *Polylepis* was consistent with a wet páramo (Fig. 5). This transition at 14.7 k cal BP coincided with the onset of the Antarctic Cold reversal (ACR) (Fig. 6), which induced glacial re-advances in Peru and Bolivia (Jomelli et al., 2014). The first axis of the PCA of XRF data broadly replicated the Ti curve,

both of which show strong trends driven by a reduction in meltwater discharge and rock flour reaching the lake.

The cold event may have reduced the rate of melting and therefore of meltwater discharge from the upslope glacier. Evidence for reduced inflow to the lake comes from a decline in the abundance of *Isöetes* between 14.7 and 13 k cal BP (Fig. 6), the duration of the ACR. *Isöetes* is an aquatic quillwort that produces spores underwater. The transport of spores to the center of the lake can result from sediment focusing, but is enhanced by flowing

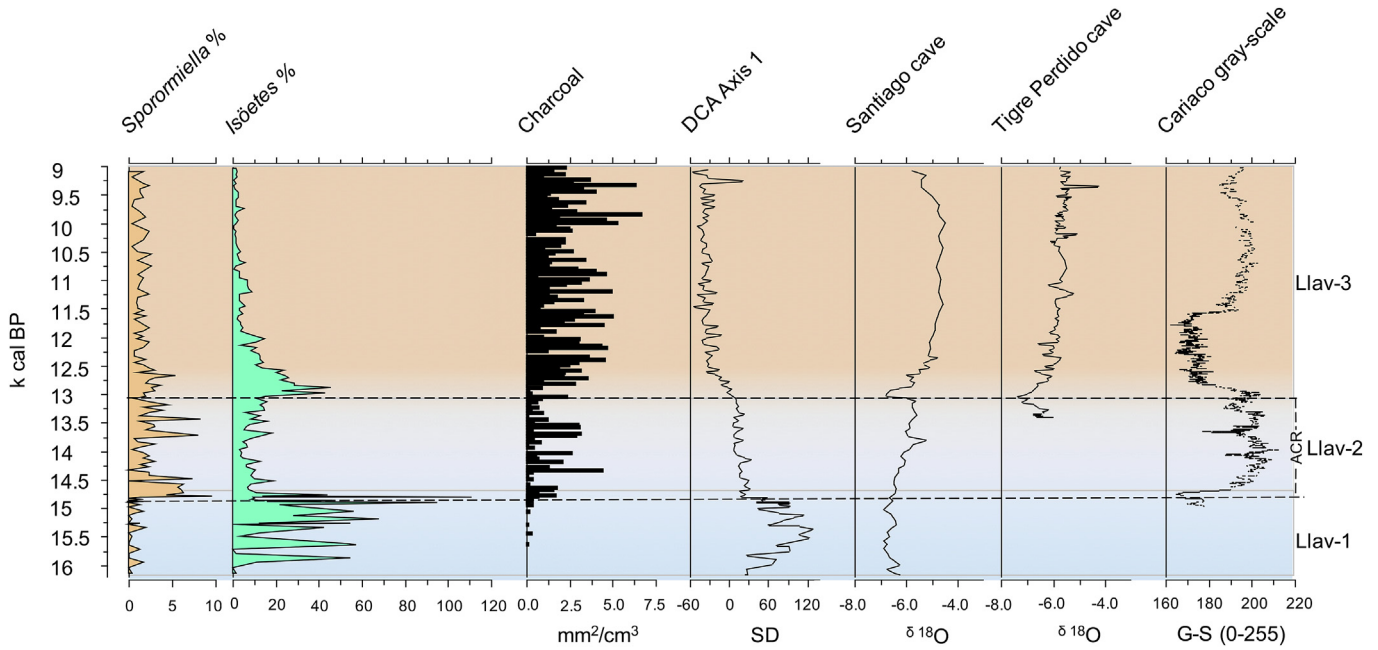


Fig. 6. Comparison between *Sporormiella*, *Isöetes*, charcoal, and DCA Axis 1 from Lake Llavucu with Santiago and Tigre Perdido Cave speleothem $\delta^{18}\text{O}$ records (Mosblech et al., 2012; van Breukelen et al., 2008) and gray-scale data from the Cariaco Basin. Dashed horizontal bar indicates the boundaries of the Atlantic cold reversal (ACR) episode.

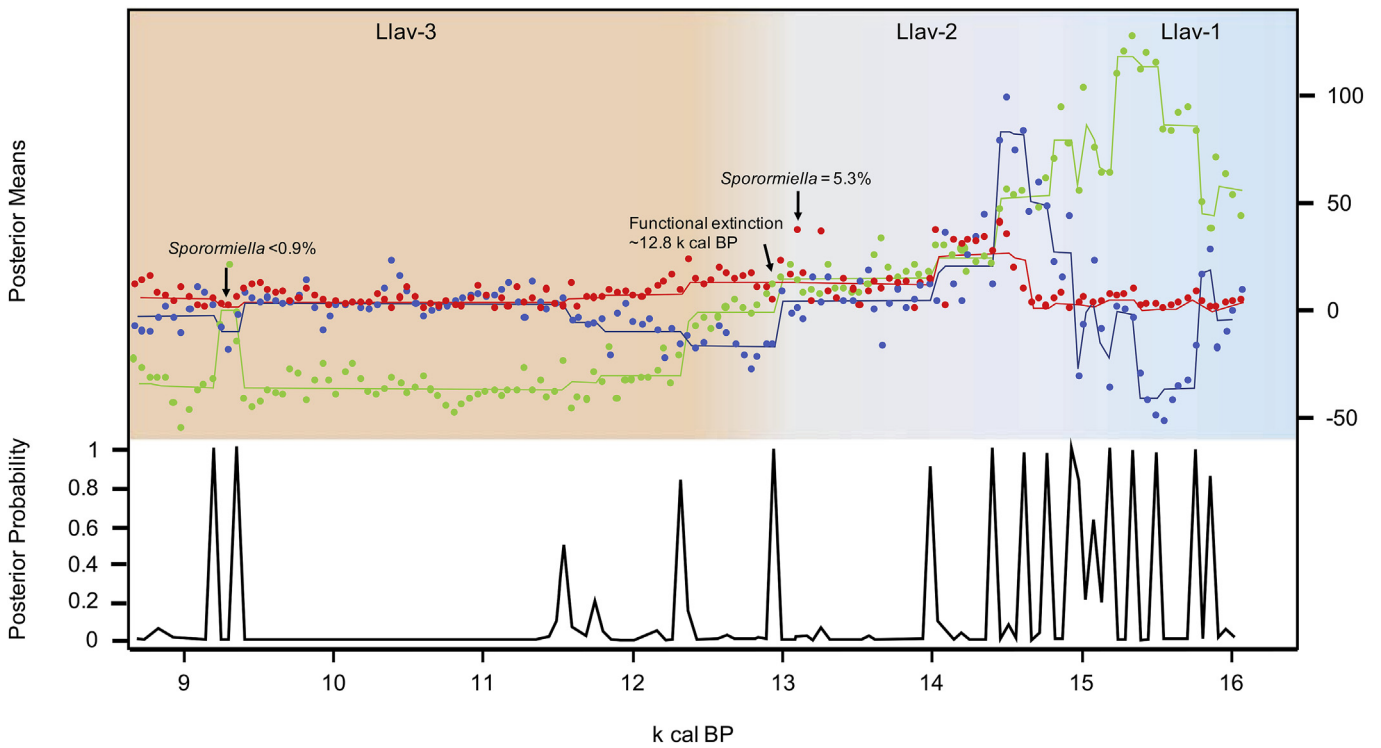


Fig. 7. Bayesian change point analysis (BCP) to detect rapid changes in the Lake Llavucu paleoecological record. Top panel: BCP on DCA Axis 1 (green) and 2 (blue), and on *Sporormiella* percentages (red). Bottom: Posterior probability of a significant change in vegetation associated with *Sporormiella* abundance. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

water suspending the spores (Hanselman et al., 2011). Taken together, the lack of minerogenic input and the lowered *Isöetes* abundance point to reduced inflow during a period of overall wet climatic conditions.

Another transition is evident at 13 k cal BP, as warmer and even

wetter conditions return (Figs. 4–6), but there is not a parallel rise in minerogenic inputs indicating that by this time the glacier had retreated far enough up valley to have a minimal impact on the sediments of Lake Llavucu. Both the Santiago and the Tigre Perdido cave isotope records exhibit an anomalously wet interval that

coincides with the peak of *Isöetes* at Lake Llaviucu (Fig. 6). The spread of Andean forest taxa between 13 k cal BP and 11.9 k cal BP suggests warming conditions. Between 13 and 12.5 k cal BP there is a substantial increase in Poaceae abundance that reaches its highest point (68%) in the record, suggesting open conditions. The decline of *Isöetes* to background levels at 11.9 k cal BP probably represents warming to within 2 °C of modern. As *Isöetes* is declining between c. 12.25 and 12 k cal BP, the chemical elements show a pattern that is similar to the more erosive phase of the deglacial. This surge of terrigenous minerals coincides with a decline in organic inputs and its proxy (inc/coh; Fig. 4). This erosive burst occurs shortly after an increase in charcoal inputs to the lake. While the erosion could be climate related, it is probable that slope destabilization by fire contributed to the signal. By 11.9 k cal BP the majority of this warming appears to have occurred as the pollen flora is basically indistinguishable from what would be expected at this elevation today (Mosblech, 2012).

4.2. Fire and megafauna

Macroscopic charcoal, which was a proxy for local fire occurrence, and *Sporormiella* spores, a proxy for herbivore presence, were both rare during the super-páramo phase prior to c. 14.7 k cal BP (Figs. 5 and 6). Fire would have been unlikely in this setting as the lack of fuel load has previously been shown to inhibit fire in glacial-aged Andean systems (Hanselman et al., 2011; Paduano et al., 2003). The relatively low abundance of *Sporormiella* (c. 1–3%) contrasts with the >20% found at Lake Pacucha in a drier, super-Puna, landscape (Rozas-Dávila et al., 2016). At Pacucha, Rozas-Dávila et al. (2016) suggested that megafaunal populations dropped precipitously during a wet event. Because Llaviucu was a wet páramo, a wetter habitat than puna, may have meant that this setting was never as suitable for megafauna as that of Pacucha.

Sporormiella abundance rose abruptly to c. 9.6% at c. 14.6 k cal BP co-occurring with a threefold increase in pollen concentrations (Fig. 5). The jump in pollen concentration suggests a more productive landscape, probably driven by marginally warmer conditions. Reduced meltwater discharge may also have made the valley bottom less marshy and made it more attractive as a grazing habitat. This peak in *Sporormiella* was its highest concentration and percentage recorded at Lake Llaviucu. It is worth noting that both *Sporormiella* and *Isöetes* are potentially transported to the deepest point in a lake by hyperpycnal flows (Hanselman et al., 2011; Raczka et al., 2016). Because *Isöetes* spores are transported to the center of the lake by very similar process to those moving *Sporormiella* spores, if they co-varied, transport and lake size would probably be driving both records. To find, as is the case at Lake Llaviucu, that the two records are largely independent of one another (Figs. 4–6) negates the probability that lake size and strength of in wash are more important than megafaunal density in determining the *Sporormiella* record.

Almost immediately after the inferred increase in megafaunal density, charcoal was found in the sediment (Fig. 6). For the next 2000 years, episodic fire events were evident and *Sporormiella* showed intermittent peaks as high as 8% of the pollen sum.

At Lake Pacucha, Peru, at lakes in SE Brazil, and in the North American midwest, the extinction of megafauna was estimated to have occurred when *Sporormiella* values fell below 2% of the pollen sum (Davis and Shafer, 2006; Gill et al., 2009; Raczka et al., 2018; Rozas-Dávila et al., 2016). The 2% threshold was adopted by Davis and Schafer (2006) to indicate when cattle were present in mid-western USA settings. Although widely adopted, this threshold has not been established in tropical forest settings, and while it is probably a good approximation, we adopted a different approach to define when our local threshold was exceeded.

At Lake Llaviucu, however, *Sporormiella* were found throughout the early Holocene between 0 and 2.3%. This level of *Sporormiella* may have reflected the local deer and camelids that survived the extinction event. We took these Holocene levels as being the background level for extant animals and looked for the last time when *Sporormiella* was above 2.3%. The last peak above this value was of 5% and occurred at c. 12.89 k cal BP, with the next sample, which showed lower abundance at c. 12.76 k cal BP. We inferred that c. 12.8 k cal BP was the time of functional extinction of the Pleistocene megafauna at Lake Llaviucu. The BCP analysis showed that significant changes occurred on the fossil record between 12.8 and 12.5 k cal BP (posterior probability >0.9; Fig. 7). This analysis reinforced our prediction that the functional extinction took place ~12.8 k cal BP. A posterior probability of >0.9% was also evident during early the Holocene, and this was due to the values of *Sporormiella* falling below 0.5% of the total pollen sum. This secondary loss of *Sporormiella* at 9.3 k cal BP may have been a real decline in surviving megafauna or, because values were so small, could have lain within stochastic variance.

The timing of this functional extinction was later than the 15.8 k cal BP suggested for Pacucha, but was similar to the loss of all *Sporormiella* from that record at c. 13 k cal BP. At both sites, the collapse of megafauna coincided with the arrival of fire.

Whether fire is natural in páramo is contentious. In dry puna settings around Lake Titicaca, fire is documented in the last interglacial 120,000 years ago (Hanselman et al., 2011). But the Altiplano is and was a much drier system than the páramo. Llaviucu is not only wet, but it lies in a valley where lightning strike is unlikely. Luteyn (2005) notes that while lightning strikes have been observed in the páramo, lightning induced fires have not. Similarly, natural fire is virtually unknown in moist Andean forest (Mueller-Dombois, 1981). White (2013) reviews the discussion of natural versus anthropic fire and concludes that the regular occurrence of fire in Andean palaeoecological páramo records is closely associated with human activity. White (2013) argues that the increase in fire at c. 15.8 k cal BP at Pacucha could be an early signal of human presence, contrasting the idea that the megafaunal population collapse was induced by climate upheaval (Rozas-Dávila et al., 2016). The first regular occurrence of charcoal at Lake Llaviucu occurs when the inflowing stream has been curtailed by the ACR. The charcoal that we quantified were fragments >180 µm, which are generally taken to be locally generated as such large particles disperse poorly, especially when stream flow is reduced. We observe that natural fire is so improbable at Llaviucu that it adds more weight to the hypothesis that humans were active in the Andes at least 1800 years before the earliest archaeological datum.

If it seems odd that in studying two Andean lakes we should have found exceptionally early human activity at both Lake Pacucha and Lake Llaviucu, the finding may have less to do with luck than geography. Both Pacucha (3000 m asl) and Llaviucu (3150 masl) are the lowest lying, easily accessible, lakes in the Andean highlands. By being low-lying they would be warmer and more protected than lakes further upslope and, as anyone working in the Andes can attest, the effects of hypoxia become much more marked just a few hundred meters upslope. Both lakes lie in natural corridors that people would pass through if they were following major valley systems to access the interior from the coast (Rademaker et al., 2012). Thus, these lakes may have been natural foci of early human entry into the central tropical Andes.

In summary, megafauna were probably always rare in this wet páramo. Their numbers increased when there was increased productivity at c. 14.8 k cal BP, but did not appear to benefit from any further palaeoclimatic changes or palaeoecological change. The decline of the megafauna at 12.8 k cal BP took place within a warm, wet episode as has been reported elsewhere (Cooper et al., 2015;

Rozas-Davila et al., 2016; Metcalf et al., 2016). Megafaunal populations did not rebound during the dry cool event of the ACR, possibly because they were already under hunting pressure from human activity. If the initial increase in fire frequency is attributable to humans, they lived alongside megafauna for about 2 k years, before landscape use intensified, and megafauna suffered local extinction.

5. Conclusions

A high-resolution multi-proxy palaeoecological and palaeoenvironmental record from Lake Llaviucu, Ecuador, provides insights into ecological changes through the last 16.2 k cal BP. The landscape transitions from a super-páramo as much as 7 °C cooler than modern, through a páramo to a forested setting. Modern forest conditions appear to have been established c. 11.9 k cal BP. The record offers insights into local responses to hemispheric climate events such as the ACR, which abated glacial retreat for about 1700 years. The record also provides evidence of a rise in fire frequency at c. 14.6 k cal BP, which is interpreted to be a signal of early human activity in this landscape. The local extinction of megafauna at c. 12.8 k cal BP, is indicated by the permanent decline of *Sporormiella* to levels seen throughout the early Holocene. Megafauna were probably never very abundant in this setting as *Sporormiella* concentrations and percentages are lower than those documented in other Andean and cerrado habitats. Whether all species survived initial contact with humans cannot be determined, but it appears probable that there was co-existence of humans and megafauna for about 1.8 k years in this setting; a finding that is consistent with other regional records, if frequent charcoal occurrence is taken to be the onset of human activity (Metcalf et al., 2016; Rozas-Dávila et al., 2016). The final demise of megafauna coincides temporally with the known presence of humans in the Andes, and with increased fire frequency in the Llaviucu record. Therefore, we conclude that humans were probably the driver of the final extinction of megafauna in the Llaviucu valley c. 12.8 k cal BP.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2018.12.005>.

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