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Glacial-Interglacial changes in moisture balance and the impact on vegetation in the southern hemisphere tropical Andes (Bolivia/Peru)

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Abstract

A palynological investigation of the last glacial-interglacial cycle in the southern hemisphere tropical Andes reveals changes in the moisture balance as the main driver in vegetation change. Thirty accelerated mass spectrometry radiocarbon dates, biostratigraphy and tephra correlation reveal that a 119 metre sediment core recovered from the Huiñaimarca sub-basin of Lake Titicaca (16.0° to 17.5° S, 68.5° to 70° W; 3810 masl) contains sediments covering >151,000 years. Correlation of aridity indicators with precessional variations in insolation is used to fine tune the structure of the age-depth curve within this period.

Variations in *Isoëtes* concentration (above/below 10,000 grains/cm^3) identify the extent of shallow water environments. Examination of other palaeolimnological indicators (*Pediastrum*) and consideration of the bathymetry of the Huiñaimarca sub-basin allow the reconstruction of lake level fluctuations. These data indicate five wet/dry cycles between c. 151,000 and 14,200 cal yr BP. High stands are suggested during the transition into (c. 134,000 cal yr BP), and out of (c. 114,000, 92,000 cal yr BP), the last interglacial,and during full glacial conditions (c. 70,000 and 45,000 cal yr BP). These cycles are superimposed on a general trend of deepening lake levels through the glacial period.

This interpretation is supported by correlation with sediments from Salar de Uyuni (20°S, 68°W; 3653 masl). The youngest wet episode is concurrent with palaeolake Minchin (c. 45,000 cal yr BP), with further evidence for an additional wet period commencing c. 28,000 cal yr BP, concomitant with palaeolake Tauca. The timing of lake level fluctuations is also supported by palaeoshoreline reconstructions from the Uyuni-Poopó region. However, our data do not suggest a major peak in lake level in Huiñaimarca during the Ouki lake cycle (c. 120,000-98,000 cal yr BP) as

inferred from U-Th ages obtained from palaeoshorelines around Lago Poopó. The most extreme dry event occurs during the last interglacial period and resulted in a sedimentary hiatus tentatively dated to c. 121,000-129,000 cal yr BP.

The observed wet/dry cycles are shown to have a marked and rapid impact on the vegetation. The aridity of the last interglacial promoted a community dominated by Chenopodiaceae/Amaranthacae, with no modern Andean analogue. *Polylepis/Acaena* pollen is also shown to fluctuate markedly (0-20%), particularly during the transitions into, and out of, the last interglacial. It is probable that this pollen taxon is primarily representative of the high altitude arboreal genus *Polylepis*, which is a key component of highly biodiverse Andean woodlands today. Rapid fluctuations indicate the sensitivity of this ecosystem to natural environmental pressure and potential vulnerability to future human impact and climate change.

The 100,000 year (eccentricity) solar cycle is shown to be the major controlling factor in moisture balance and vegetation over the last glacial-interglacial cycle. However, significant fluctuations in moisture balance are also evident on timescales considerably shorter than the full glacial-interglacial cycle. We have linked these to precessional (21,000 year) forcing. Nevertheless, precise independent dating during the full glacial cycle is required to confirm the importance of this forcing mechanism.

Key words (up to 6)**:** Altiplano, Fossil pollen, Huiñaimarca, Minchin, Salar de Uyuni, Titicaca

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1. Introduction

The tropical Andes play a fundamental role in global climate systems today (Zhou and Lau, 1998; Lenters and Cook, 1999; Garreaud et al., 2003), yet the contribution of different mechanisms affecting these systems in the past remains controversial. Debate has focused primarily on the nature of the moisture balance in the Andes during the Last Glacial Maximum (LGM, c. 26,000-21,000 cal yr BP/22,000-18,000 ^{14}C yr BP). Geomorphological, sedimentological, biological and geochemical data have been presented from terrestrial and aquatic records in support of both wetter and drier conditions (e.g. Clapperton, 1993; Thompson et al., 1998; Heine, 2000; Smith et al., 2005a, b). In the southern hemisphere tropical Andes, records from: i) Lake Siberia (17[o] 50'S, 64[o] 43'W; Mourguiart and Ledru, 2003) and ii) Huiñaimarca (16[o] 20'S, 68[o] 57'W; Argollo and Mourguiart, 2000) have been interpreted as indicative of lowered LGM precipitation, although alternative mechanisms and interpretation have been postulated by Baker et al. (2003). Conversely, LGM sediments from the Lago Grande basin of Lake Titicaca (Baker et al., 2001b) and fluvial sediments from its southerly outflow, the Río Desaguadero (Rigsby et al., 2005), suggest deep fresh water. These data imply that there must have been a positive moisture balance at this time to allow the overtopping of Lake Titicaca, i.e. wet conditions persisted.

While controversy surrounds the interpretation of LGM records, little is known regarding longer-term fluctuations in moisture balance and its impact on the vegetation of the region. Radiocarbon and U-Th dating of palaeoshorelines in the Altiplano have suggested that six lake cycles occurred during the last glacial-interglacial cycle (Placzek et al. 2006a, b): the Ouki (120,000-98,000 cal yr BP), the Salinas (95,000-80,000 cal yr BP), the Inca Huasi (c. 46,000 cal yr BP), the Sajsi (c.

24,000-20,500 cal yr BP), the Tauca (18,100-14,100 cal yr BP) and the Coipasa (13,000-11,000 cal yr BP). Placzek et al. (2006b) suggest that the Ouki and the Tauca cycles created the deepest palaeolakes, reaching c. 80 m and c. 140 m, respectively. Cores recovered from the Salar de Uyuni (20°S, 68°W) provide the only published palaeoecological records from the southern hemisphere tropical Andes that cover the last glacial-interglacial cycle (Sylvestre et al., 1999; Baker et al., 2001a; Fritz et al., 2004; Chepstow-Lusty et al., 2005). However, the palynological record from Salar de Uyuni is not continuous because during arid phases the evaporitic deposits did not preserve micro-fossils. The intermittent presence of lake sediments beneath this modern salt pan indicates that the precipitation:evaporation (P:E) ratio was greater than today at various points during the last glacial-interglacial cycle (Baker et al., 2001a). Palynological data from the layers of lake sediment found beneath the Salar de Uyuni suggest that during these episodes of high P:E ratios the glacial landscape was dominated by grasses with elements of high Andean woodlands continually present (Chepstow-Lusty et al., 2005)

In this paper, we present a more continuous palynological record from the last glacial-interglacial cycle (c. 151,000-14,200 cal yr BP) obtained from a 119 metre sediment core from the Huiñaimarca sub-basin of Lake Titicaca. Data are used to assess moisture balance changes and their impact on the vegetation through this period. Comparison and correlation with other records from the Altiplano place these data within a regional context.

2. Study area

2.1 Climate and vegetation

The precipitation of the Altiplano is governed by the strength and duration of the South American Summer Monsoon (Vuille et al., 2000; Garreaud et al., 2003). Pronounced precipitation minima occur across the central Andes between June and August, although precipitation is possible throughout the year due to the orographic effect of the high cordillera (Johnson, 1976). Precipitation is concentrated between December and March when prevailing wind direction reverses and Amazonian moisture flows into the Altiplano (Vuille et al., 2000). Temperatures are governed primarily by altitude, which at the shoreline of Lake Titicaca (c. 3810 metres above sea level [masl]; Juliaca, Peru) currently average c. 8°C annually, with monthly minima of c. -8°C (July) and maxima of c. 19°C (November). At this location, precipitation varies from <10 mm/month (June-August) to >100mm/month (January-March).

The vegetation of the high Andes (>3200 masl) in Bolivia/Peru is currently dominated by shrub- and grasslands (Puna). Puna ecosystems comprise plants with specialist adaptations to the cold and dry climate, with common families including Asteraceae, Brassicaceae and Poaceae. Within the grasslands occur pockets of evergreen woodland, dominated by the tree genus *Polylepis* (Rosaceae). Twenty-eight species of *Polylepis* are known, all of which are found in the Andes and exhibit a variety of specialist adaptations to survive at high altitudes (Kessler, 2002; Schmidt-Lebuhn et al. 2006). The woodlands are centres of biodiversity for flora and fauna, including marked bird endemism, with more than 40 endemic bird species found in some *Polylepis* patches (Fjeldså, 2002). However, this highly fragmentary, geographically-restricted biodiversity is threatened by ever-increasing human activity, particularly burning, livestock grazing, and direct exploitation for charcoal and firewood (Renison et al., 2002, 2004, 2005; Teich et al., 2005). In addition, further

pressure is likely to be exerted as predicted future climate warming allows the upslope

migration of other taxa, and greater opportunities for human impact (Fjeldså and

Kessler, 1996).

2.2 Site description

Lake Titicaca (16.0° to 17.5° S, 68.5° to 70° W; Figs. 1 and 2) is today divided

into two sub-basins: i) Lago Grande (or Chucuito), with a maximum depth of 285 m

and, ii) Huiñaimarca (or Wiñaymarka or Lago Menor), with a maximum depth of 40

m. In total this lake covers c. 8,500 km^2 and is fed by a watershed of c. 57,000 km^2

from the surrounding Cordilleras Oriental and Occidental (D'Agostino et al., 2002),

with the present day lake-level of Titicaca at c. 3810 masl. The water trapped between

these two mountain chains flows southward, moving from Lago Grande into

Huiñaimarca, via the Straits of Tiquina. Water that escapes Huiñaimarca does so via

the Río Desaguadero and continues southward to Lake Poopó (3686 masl) and the

modern salt pans, Salar de Coipasa (3657 masl) and Salar de Uyuni (3653 masl).

The outflow from Lake Titicaca is controlled by two hydrologic sills. The

northerly sill (3788 masl) is the Straits of Tiquina , while the southerly one (3804

masl) restricts water flowing from Huiñaimarca into the Río Desaguadero (Fig. 2a).

The sills constrain the current linkage between the two sub-basins, and with the basins

further south. In fact, a relatively small fall in lake level (c. 22 m) is sufficient to

result in the separation of Lago Grande and Huiñaimarca. Such hydrological isolation

occurred as recently as the mid-Holocene when lake levels may have dropped by as

much as 90 m (D'Agostino et al., 2002). Indeed, the narrowness and shallowness of

the Straits of Tiquina have been shown to limit water exchange between the two

basins to the extent that there are significant differences in the isotopic composition of

the water (Grove et al., 2003). These data suggest that for sustained periods Huiñaimarca has been effectively a small closed basin.

2.3 Previous palaeoenvironmental work

Six sediment cores reflecting periods of varying duration have been obtained from Lake Titicaca: three from Lago Grande - i) >370,000 years (J.A. Hanselman, unpublished data; S.C. Fritz, unpublished data), ii) c. 29,000 years (Rowe et al., 2003) and, iii) c. 27,000 years (Baker et al., 2001b; Paduano et al., 2003; Tapia et al., 2003), and three from Huiñaimarca - i) >151,000 years (this paper), ii) >27,000 years (Ybert, 1992; Wirrmann, 1994; Wirrmann and Mourguiart, 1995; Argollo and Mourguiart, 2000; Mourguiart and Ledru, 2003) and, iii) c. 3,500 years (Abbott et al., 1997).

Argollo and Mourguiart (2000) worked on the 27,000 yr-long record that was raised from 19 metre water depth in the western depression of the Huiñaimarca sub-basin (Fig. 2b). They interpreted the sedimentary, palynological and ostracod data to indicate lower lake levels between c. 25,000-18,000 cal yr BP, with a cooling of -6°C relative to modern between c. 20,000 and 19,000 cal yr BP. A sedimentary hiatus is identified at c. 15,000-14,000 cal yr BP, followed by a period of warming accompanied by lake level rise until c. 10,500 cal yr BP. Subsequently, a dry early Holocene is recognised (c. 8,000 cal yr BP) prior to the onset of modern conditions. The palynological evidence from this core shows marked fluctuations in the terrestrial and aquatic elements, including the green algal genus *Pediastrum* (Ybert, 1992; Argollo and Mourguiart, 2000). The late Holocene records from this sub-basin have been interpreted as indicative of rapid (centennial) fluctuations in lake level; +5 to -10 metres (Abbott et al., 1997).

2.4 Cores examined

In 2001, core LT01-3B was raised by the NSF/ICDP GLAD800 drilling rig from the deepest part of Huiñaimarca (Fig 2); an area known as Chua where water depth is currently c. 40 m. The Chua area of the lake is a narrow depression (c. 5% of Huiñaimarca's present surface area) located in the northern portion of the basin close to the inflow from Lago Grande via the Straits of Tiquina. The majority of Huiñaimarca is significantly shallower than Chua, with c. 45% of Huiñaimarca's surface area having water depths of 10-20 m water, and c. 50% having less than 10 m depth (Fig 2b). The palynological data from the 119 m long LT01-3B core are considered in this paper. A regional context is achieved through reference to a 135 m core obtained during the same expedition from Lago Grande (LT01-2B) and a 220.6 m core retrieved from Salar de Uyuni in 1999 (Baker et al., 2001a; Fritz et al., 2004; Chepstow-Lusty et al., 2005).

3. Methods

3.1 Chronology

The Huiñaimarca chronology was established by two methods. Firstly, the age-depth curve between 40 and 0 metres below lake floor (mblf) was constructed from 6 AMS ^{14}C dates from core LT01-3B (Table 1) and 24 ^{14}C AMS dates from the sister core LT01-3A (Table 2). Cross correlation of dates between these two cores was justified as they were recovered only 50 metres apart and have near identical stratigraphic and magnetic susceptibility profiles (Fig. 3a and b); the consistency in sedimentation patterns was supported by the horizontal nature of the bedding in the centre of the basin shown on seismic profiles (D'Agostino et al., 2002).

Calibration of ^{14}C dates was carried out using CALIB 5.0.2 with southern hemisphere correction for ages between 0-11,000 cal yr BP (Stuiver and Reimer, 1993; McCormac et al., 2004). For older dates back to 50,000 cal yr BP, the calibration curve by Fairbanks et al. (2005) was used, as no southern hemisphere correction is yet available. Where reference is made to previously published radiocarbon dates the appropriate calibrations have been carried out to allow direct comparison, with the original ^{14}C dates provided.

Secondly, sediments between 119 and 40 mblf were found to be beyond the limit of ^{14}C dating. Therefore, a chronology was established by tying a distinctive tephra layer found at 93.77 mblf (LT01-3B) with its equivalent in the Lago Grande core (LT01-2B) that has been independently dated to 151,000 cal yr BP. The chronology was validated by biostratigraphic comparison with fossil pollen from LT01-2B (Hanselman, unpublished data) and orbitally tuned to the precessional cycle (Table 3).

The calculations used to generate the full age depth profile (Fig. 3d) are detailed in Table 4.

3.2 Laboratory methods

Standard palynological methods were followed (Stockmarr, 1972; Faegri and Iversen, 1989). As with other palynological studies from Lake Titicaca (Paduano et al., 2003; Hanselman et al., 2005) sodium metatungstate (specific gravity 2.09) was used for density separation to concentrate pollen in clay-rich samples. Samples were mounted in glycerol and counted using a Zeiss Axioskop photomicroscope at x400 and x1000 magnification. A total of 300 fossil terrestrial pollen grains were identified in each sample (i.e. excluding unidentifiable damaged grains) or, in low concentration

samples, 2000 exotic *Lycopodium* spores were counted. Percentage values for aquatic taxa, fern spores and the green algal genus *Pediastrum* were calculated relative to the terrestrial pollen sum and their own abundance.

Overall 147 pollen taxa were identified and 85 unknown pollen types designated. Taxa shown in Fig. 4a are those reaching >5% abundance of terrestrial pollen in at least one sample. Identifications were based primarily upon the modern reference collection held at Florida Institute of Technology (>3200 South American pollen types), digital images from the "Neotropical Pollen Database" (http://research.fit.edu/bushlab/pollen_db.htm, Bush and Weng, 2006), and pollen atlases (Markgraf and D'Antoni, 1978; Hooghiemstra, 1984; Faegri and Iversen, 1989).

Pollen percentages, concentrations per taxon and total concentrations were calculated and graphed using C2 software (Juggins, 2003).

3.3 Zonation

Zonation of the pollen diagram was achieved solely on the basis of *Isoëtes* micro-spore concentration (Fig. 4b) because: i) it is independent of the arid indicator proxies used to fine tune the chronology, and ii) *Isoëtes* has very specific habitat requirements, i.e. it is found in water depths of up to 4 metres in mountain environments (>3200 masl) (Hutchinson, 1975, p. 72; Ybert, 1992; Torres et al., 2005), and is therefore sensitive to moisture balance changes. Zonation was achieved by assigning all samples with *Isoëtes* >10,000 spores/cm^3 in two concurrent samples, into relatively "*Isoëtes* rich" zones (i.e. there is an extended area of water depth 0-4 metres), and those with lower concentrations into "*Isoëtes* poor" zones. The interpretation of *Isoëtes* micro-spores abundance must take into account the

possibility that fluctuations in lake area, and consequent changes in the proximity of source plants to the core site, may affect the signal (Figs. 2b and 5). The bathymetry of the basin is discussed below while algal and diatom abundances are used to help interpret lake depth fluctuations.

The zones provide a framework for understanding the changes in the moisture balance record and should not be taken as rigid in terms of timing, because transitional and marginal phases are clearly evident.

4. Results

4.1 Chronology

Prior to 151,000 cal yr BP (>93.77 mblf) no age vs. depth correlation has been attempted because of the absence of radiometric dating and the lack of obvious tie points (Fig. 4).

Between 151,000 and 40,000 cal yr BP (93.77-40 mblf) the chronology has been established by the correlation of a tephra layer at 151,000 cal yr BP with the equivalent layer in Lago Grande. Through this period the age vs. depth curve has been fine tuned by linking aridity indicators with lows in insolation (Table 3). The resultant age vs. depth curve suggests slow sedimentation at the onset and termination of Marine Isotope Stage (MIS) 5 and a fairly constant sedimentation rate through the rest of the core. A hiatus, tentatively assigned to the period c. 121,000-129,000 cal yr BP, coinciding with the peak of sub-stage 5.5 (Martinson et al., 1987). The hiatus has been correlated with an extended period of elevated Chenopodiaceae/Amaranthaceae (hereafter Cheno/Ams) type pollen in the Lago Grande core (Hanselman et al., 2005).

The chronology between 40,000 and 0 cal yr BP (40-0 mblf) is well constrained through radiocarbon dating (Tables 1 and 2),with a flattening of the age vs. depth

curve c. 14,200 cal yr BP (c. 4.5 mblf) indicating very slow sedimentation rates or possibly a hiatus (Fig. 3d). During the glacial isotope stages 4, 3, and 2 (c. 72,000-12,000 cal yr BP, c. 63-4 mblf) sedimentation gradually decreased.

4.2 Pollen analysis

High variability in concentrations of both the terrestrial pollen (147 to 58,954 grains/cm^3) and aquatic taxa (38 to 41,068 grains/cm^3) characterize the Huiñaimarca record (Fig. 4). Despite little compositional variability, the relative proportions of taxa represented in the record alter markedly through time (Fig. 4a). Ten zones have been identified and are described with reference to compositional changes in the pollen assemblages.

119.7-93.77 mblf (>c. 151,000 cal yr BP), 39 samples

The lower section of the core is characterised by rapid fluctuations in the magnetic susceptibility (Fig. 3b), concentration values (c. 750-32,000 terrestrial pollen grains/cm^3) and assemblage composition, e.g. Asteraceae, Cheno/Ams, *Podocarpus* (Fig 4a) and Cyperaceae, *Isoëtes*, *Myriophyllum* (Fig. 4b). No clear equivalent biostratigraphic zone is evident in the Lago Grande core (Hanselman, unpublished data).

93.77-92.5 mblf (c. 151,000-134,000 cal yr BP), 4 samples

This period of elevated aquatic concentrations (*Isoëtes* >10,000 grains/cm^3) is, like much of the sequence, dominated by *Isoëtes* spores (46-84%). This zone also contains a high abundance of the green algal genus *Pediastrum* (71-93%) throughout. The link between *Pediastrum* and *Isoëtes* is maintained through much of the core.

There is a rise in terrestrial pollen concentrations through this zone. This is driven by increases in Asteraceae (6-12%) and Cheno/Ams (1-3%) and a peak in *Polylepis/Acaena* type (3-19%) pollen. Poaceae remains stable through this period and is the most prolific taxa comprising >45% of the pollen in all samples.

92.5-84.0 mblf (c. 134,000-112,300 cal yr BP), 12 samples

Isoëtes concentrations are low, <2,000 grains/cm^3 in all but two samples, through this zone, with *Pediastrum* extremely rare or absent. A peak in *Isoëtes* concentrations occurs at 86.67 mblf (c. 26,400 grains/cm^3; 80%), which is 4.8 m above the projected sedimentary hiatus in the core c. 121,000-129,000 cal yr BP. The hiatus probably correlates with the >90,000 cal yr BP erosion event identified in seismic profiles (D'Agostino et al., 2002).

Terrestrial pollen in the lower portion of this zone are dominated by Cheno/Ams (22-50%), which continue after the sedimentary hiatus (91.47 mblf) until being replaced by Asteraceae (21-43%), with Poaceae between 13 and 26%. Subsequently, Poaceae pollen dominate reaching 61%, while Cheno/Ams and Asteraceae pollen decline to 1 and 10%, respectively. In addition, a concomitant rapid rise in *Polylepis/Acaena* pollen (0-24%) occurs.

84.0-72.5 mblf (c. 112,300-88,200 cal yr BP), 20 samples

This zone is the most sustained period of elevated concentrations of *Isoëtes* in the core (53-90%); *Pediastrum* levels (7-87%), however, are more variable.

The pollen assemblage through this zone is dominated by Poaceae (41-67%), while the second most abundant taxon is Asteraceae (7-27%). Cheno/Ams pollen

return to background levels (<4%), while *Polylepis/Acaena* pollen initially decline from 26 to 0% and then recover slightly towards the end of the zone reaching 6%.

72.5-57.5 mblf (c. 88,200-65,300 cal yr BP), 23 samples

The reduction in *Isoëtes* concentration at the start of this zone is mirrored by a drop in terrestrial pollen concentration, with both declining slightly through the zone. The absence of any change in sedimentation (S.C. Fritz, unpublished data), as observed in the magnetic susceptibility data (Fig. 4b), suggests that this is therefore a product of biotic change. There is a peak in the aquatics at 70.47 mblf (c. 21,600 grains/cm^3). *Isoëtes* spores are notably lower (43-86%) in the middle of the zone, with *Pediastrum* almost absent except at the very beginning and end.

Poaceae (24-74%) and Asteraceae (3-22%) continue to be the dominant pollen taxa, while *Polylepis/Acaena* pollen disappear. Conversely, Brassicaceae and Moraceae/Urticaceae pollen increase in abundance steadily through this zone, both reaching 14% at the end.

57.5-51.5 mblf (c. 65,300-58,000 cal yr BP), 5 samples

The increase in *Isoëtes* concentration through this zone is mirrored by an increase in *Pediastrum* abundance, but not by a rise in terrestrial pollen concentration. Asteraceae pollen abundance is elevated throughout (14-27%), with Poaceae dominating the pollen spectrum and peaking at 52%, though showing lower representation at the beginning (30%) and end (33%) of the zone. *Polylepis/Acaena* pollen reappear at low levels (1%), and Cheno/Ams (0-7%), Apiaceae (0-4%) and *Podocarpus* (1-8%) pollen all increase in abundance.

51.5-27.5 mblf (c. 58,000-40,700 cal yr BP), 20 samples

The concentration of *Isoëtes* fluctuates markedly through this zone with peaks of 11,100 and 10,500 grains/cm^3 at 32.62 and 37.39 mblf, respectively. Elevated *Pediastrum* and *Isoëtes* spore abundance may indicate that this period is relatively wetter, particularly in the upper part of the zone.

Pollen counts and concentrations are extremely low (mean 1,155 grains/cm^3), which means that the statistical errors on the pollen percentages are large. There are a high proportion of damaged grains through this zone (6-28%). The major pollen types remain Poaceae (mean 53%) and Asteraceae (11%), while Brassicaceae (3%), Apiaceae (2%) and Caryophyllaceae (1%) are present through most of the zone and there are elevated proportions of *Podocarpus* (4%) and Moraceae/Urticaceae (3%).

27.5-23.5 mblf (c. 40,700-39,200 cal yr BP), 3 samples

This peak in *Isoëtes* concentrations occurs in the centre of a period of generally high, but fluctuating, *Pediastrum* abundance (6-73%) from 37-15 mblf (c. 43,500-35,100 cal yr BP). The change in aquatic concentrations that delimits this zone is less marked than previous transitions. As in the previous zone of elevated aquatic concentrations, *Polylepis/Acaena* (mean 1%) and higher Moraceae/Urticaceae (9%) pollen reappear in this zone, while the levels of *Podocarpus* (4%) and Apiaceae (1%) pollen remain constant.

23.5-7.0 mblf (c. 39,200-28,000 cal yr BP), 14 samples

Concentrations of *Isoëtes* fluctuate through this zone, while pollen concentrations are consistently low (mean 1,324 grains/cm^3), resulting in low counts and large error bars. Hence, detailed interpretation of the pollen assemblage is not

possible. Nevertheless, Poaceae pollen dominates the assemblage and there is a high proportion of damaged grains (0-32%), especially in the latter half of the zone.

< 7.0 mblf (< c. 28,000 cal yr BP), 6 samples

The low sedimentation rate centred at c. 4.5 mblf (Fig. 3d) makes it impossible to define when the high *Isoëtes* concentration in this zone terminated. Between 7 and 4.5 mblf (c. 28,000-14,200 cal yr BP), *Isoëtes* concentrations >10,000 grains/cm^3 suggest that the basin contained water, though *Pediastrum* is absent. After 14,200 cal yr BP aquatic concentrations rapidly decline; this is accompanied by a reduction in sedimentation and poor pollen preservation.

5. Environmental reconstruction

The major palynological changes in the Huiñaimarca record, both compositionally and in terms of abundance, occur on the 100,000 year glacial-interglacial (eccentricity) time scale. Interglacial sediments are dominated by Cheno/Am pollen while the majority of the glacial is dominated by Poaceae (Fig. 6a). The dominance of salt tolerant Cheno/Ams and a c. 8,000 year sedimentary hiatus during the last interglacial are interpreted as indicative of a P:E lower than present, i.e. evaporation exceeded precipitation and the basin was dry and possibly subject to erosion. This interglacial vegetation association is unlike any seen in the Andes today.

The presence of lake sediments throughout the glacial period indicates that it was relatively wetter than the majority of the last interglacial. The glacial flora is largely dominated by Poaceae but fluctuations in the moisture balance of varying magnitudes result in compositional and productivity changes in the pollen signal at sub-100,000 year time scales.

5.1 Bathymetry and the palaeoenvironmental record

To interpret the palaeoenvironmental record in detail the form of the Huiñaimarca sub-basin must be considered relative to the location of the core site. The asymmetric bathymetric profile of Huiñiamarca (Figs. 2b and 5) complicates interpretation of the palynological record. Two proxies are used to shed light on past lake depth: i) aquatic pollen/spores concentrations, principally *Isoëtes*, and ii) abundance of the green algal genus *Pediastrum*.

High concentrations of *Isoëtes* are likely to occur at the core site when either: i) a shallow water body (modern equivalent lake depth c. 0-4 m) means aquatic taxa are growing very close to the core site (Fig. 5a), ii) when there is an increased expanse of shallow water habitat, i.e. expansion of the lake out of the Chua depression (modern equivalent lake depth c. 20 m; Fig. 5b) or, iii) there is expansion of the lake onto the large adjacent flat area (modern equivalent lake depth >30 m; Fig. 5c).

Algal blooms are probably linked to increased nutrient supply, which is most likely either: i) a result of the lowering of lake level to the point where it is not permanently stratified or, ii) from in-washed nutrients as a result of increased erosion (though too much suspended material could reduce light availability and thereby limit productivity). Consistent with these projections the modern sediments from Huiñaimarca show low to moderate abundances of *Pediastrum.* Hence, the modern lake high stand in which the lake level is 6 metres above the sill, allowing flow down the Río Desaguadero, does not result in *Pediastrum* blooms.

5.2 Huiñaimarca lake level fluctuations

The absence of radiometric dates and a lack of sedimentological and palynological structure beyond 151,000 cal yr BP indicate that this section of the core is fragmentary, or has a very slow sedimentation rate, possibly spanning a number of glacial-interglacial cycles.

Between 151,000 and 28,000 cal yr BP the data suggest five wet-dry cycles that we link to precessional forcing (see Chronology section). Shifts in the moisture balance occur at a higher frequency than the full (100,000 year) glacial-interglacial cycle, with relatively wet and dry episodes evident within and between both states (Fig. 6). High lake levels in Huiñaimarca are revealed to occur during the transition into, and out of, the last interglacial period (c. 134,000, 114,000 and 92,000 cal yr BP), and during full glacial conditions (c. 70,000 and 45,000 cal yr BP) (Fig. 6a). Additionally, this sequence suggests that the LGM (21,000 cal yr BP) would have been a relatively wet time. However, the extreme cold of the glacial maximum may have inhibited biological productivity and hence there is not a typical "wet" signal associated with this time.

Comparison with the Salar de Uyuni record (Fig. 7) shows some agreement in the timing of wet episodes, particularly in the better dated upper portion of the Huiñaimarca core. The comparison of events and their timing in both records allows an assessment of episode magnitude. The accumulation of lake sediment preserving pollen in Salar de Uyuni indicates lakes were periodically present at this location and demonstrates that the P:E ratio was greater than that of today.

Three of the peaks in Huiñaimarca lake level (114,000, 92,000 and 70,000 cal yr BP) occur during a period of 'low' lake levels in Salar de Uyuni (119,000-54,800 cal yr BP) (Chepstow-Lusty et al., 2005). Lake sediments are preserved in Salar de Uyuni through this period although, for much of this time, it appears to have been either a

shallow lake or salt pan incapable of preserving pollen (Fritz et al., 2004; Fig. 7).

These differences emphasise the importance of local variations and suggests that

although relatively wetter at these times, the lake level at Huiñaimarca was not high

enough to sustain a hydrological connection with Salar de Uyuni.

The absence of substantial lake sediments from the Salar de Uyuni location and

inferred lower lake levels in Huiñaimarca are at odds with the large palaeolake surface

areas predicted for the Ouki lake cycle (120,000-98,000 cal yr BP) by Placzek et al.

(2006b) (Fig. 8). This prediction is based upon twelve U-Th dates obtained from five

sites within the watershed of Lago Poopó (see Table 2 and Fig. 1 in Placzek et al.,

2006b). The absence of lake sediments from Salar de Uyuni and the restriction of

raised shorelines of the Ouki lake cycle to the Poopó watershed could suggest that

either: i) there was no hydrological link between these basins at this time and

consequently the extent of this palaeolake was more limited or, ii) that the alternative

radiocarbon chronology presented by Placzek et al. (2006b) is correct. The age range

given by the calibratable ^{14}C dates obtained from the Ouki lake cycle are: 44,609 ±

927 to 33,422 ± 1937 cal yr BP (40,600 ± 1200 to 28,170 ± 290 ^{14}C yr; see Table 2 in

Placzek et al., 2006b). If these radiocarbon dates are correct then the Ouki lake cycle

fits well with the extended period of lake sediment ascribed to palaeolake Minchin in

Salar de Uyuni c. 48,000-36,000 cal yr BP (Fig. 8).

The generally higher lake level in Huiñaimarca after c. 60,000 cal yr BP (Fig.

6a) can be correlated with the sediments from palaeolake Minchin identified in Salar

de Uyuni: i) 48,000-36,000 cal yr BP (Fritz et al., 2004; Chepstow-Lusty et al., 2005)

and, ii) 30,000-73,000 cal yr BP (Fornari et al., 2001), and wet conditions identified

from cores drilled along the Río Desaguadero 50,000-38,000 cal yr BP (Rigsby et al.,

2005). It is important to note that at this point the peaks in *Isoëtes* in Huiñaimarca

switch from being indicative of increasing lake levels to decreasing lake levels, i.e. the maximum *Isoëtes* signal is at c. 20 m water depth (Fig. 5b). In the lower half of the core the lake level is increasing to reach this depth, whereas in the upper portion of the core the lake level has to drop down to this level (Fig. 6a). The generally higher lake levels from c. 65,300-28,000 cal yr BP are indicated by the consistent presence of *Pediastrum* and low magnetic susceptibility values (Fig. 6b).

High proportions of damaged grains c. 31,000-25,000 cal yr BP (up to 33%) probably indicate a reduction in vegetation cover, and hence pollen production, caused by intense cold. Elevated magnetic susceptibility values characterise sediments with high proportions of damaged grains and are consistent with increased rates of erosion. This setting is interpreted as being similar to a sparsely vegetated glacial foreland. The combination of low productivity and erosion increases the relative importance of reworked pollen entering the deposit.

The final episode of elevated *Isoëtes* concentrations identified in Huiñaimarca commences at c. 28,000 cal yr BP. This episode differs from the earlier *Isoëtes*-rich episodes as no rise in *Pedistrum* accompanies the increase in aquatic concentrations suggesting a large stratified lake with low nutrient availability. The timing correlates with palaeolake Tauca (26,000-14,900 cal yr BP) sediments from Salar de Uyuni (Baker et al., 2001a) and agrees with the assertion of Sylvestre et al. (1999) that the Tauca lacustrine transgression began prior to 18,840 ± 80 cal yr BP (15,430 ± 80 ^{14}C yr), as recorded in a different core from Salar de Uyuni. Wet conditions are therefore recorded in Huiñaimarca at least 2000 years earlier than Salar de Uyuni, probably reflecting the establishment time required for palaeolake Tauca. This ponding phase manifests itself in the Salar de Uyuni records as intercalated mud and gypsum, reflecting open water alternating with dry lake-bed conditions. This transitional phase

between salt-pan and deep lake lasted from c. 32,000 cal yr BP until 26,000 cal yr BP (Fritz et al., 2004). The establishment of a permanent deep water body supports the hypothesis that the LGM was wetter than present in the Andes c. 26,000-16,000 cal yr BP (Rigsby et al., 2005). Termination of this wet episode occurred in Huiñaimarca prior to c. 14,200 cal yr BP, as demonstrated by an increase in the percentage of damaged grains and a declining sedimentation rate, possibly indicating that the basin dried out at this time (Fig. 3d). A low lake level in Huiñaimarca c. 14,200 cal yr BP broadly agrees with estimates for the timing of the desiccation of palaeolake Tauca at c. 14,900 cal yr BP (Fritz et al., 2004), $13,992 \pm 72$ cal yr BP ($12,090 \pm 40$ [14]C yr BP) (Sylvestre et al., 1999) and c. 14,000-15,000 cal yr BP (Argollo and Mourguiart, 2000).

5.3 Impact on the vegetation

The fluctuation in moisture balance identified allows an insight into the response of key Andean taxa to climate change. Palynological data reveal fluctuations in the vegetation assemblage between 151,000 and 14,200 cal yr BP, with shifts in significant taxa between and within the glacial-interglacial cycle.

There are only three significant excursions from the dominance of Poaceae pollen through the Huiñaimarca core (Fig. 6a). The first excursion is during the last interglacial when drought tolerant Cheno/Ams and then Asteraceae replace Poaceae as the dominant taxa. The other two times occur at c. 65,000 and 58,000 cal yr BP when percentage abundances decline to 24 and 14%, respectively. Declines in Poaceae are coincident with peaks in Moraceae/Urticaceae and *Podocarpus* pollen, as well as exceptionally low pollen concentrations (394 and 148 grains/cm^3). These data suggest that the landscape around Huiñaimarca at this time was more or less barren

with very little local pollen production. As a result, taxa from outside the region that effectively disperse pollen over long distances, such as Moraceae/Urticaceae and *Podocarpus*, are consequently elevated in significance.

Fluctuations in moisture balance in the Andes clearly affect the vegetation composition. However, most taxa persisted throughout the last glacial-interglacial cycle even if at much reduced levels. This ability to survive in the landscape allows taxa to take advantage of shifts towards more favourable conditions. The rapid expansion of weedy Cheno/Ams (0-50%) could be anticipated during the transition to more the more arid conditions during the last interglacial. However, the rapid increases and decreases of *Polylepis/Acaena* (e.g. 2-24% between c. 113,000-112,000 cal yr BP) suggest a rapid change in the extent of woodland habitat which is, perhaps, more surprising.

Variability within interglacials in the Andes has been demonstrated by comparison of this and other pollen records from Lake Titicaca (Hanselman et al., 2005). In the Huiñaimarca record, drought and salt tolerant Cheno/Ams appear to dominate the early part of the interglacial flora. This assemblage has no known modern counterpart in the Andes with the closest modern pollen analogue coming from a halophytic salt marsh community in the Pampa grasslands of Argentina (Stutz and Prieto, 2003). Subsequently, a significant shift occurred during the interglacial, with Cheno/Ams being replaced by Asteraceae, shortly after the peak of the dry period. The peak in Asteraceae as observed in the Lago Grande core (LT01-2B) occurs while Cheno/Ams remain at elevated percentages (Hanselman et al., 2005). In Huiñaimarca, the rapid decline of Cheno/Am pollen is inferred to result from the refilling of the steep sided Chua depression, causing salt tolerant taxa that grew in the bed of the salt marsh (Fig. 5c) to be swamped as water levels rose (Fig. 5a, b). This

interpretation is consistent with the modern pollen study of Stutz and Prieto (2003) who found the highest Chenopodiaceae percentages (50-80%) limited to samples collected from within a salt marsh community.

There is also a clear response in the abundance of *Polylepis/Acaena* pollen to changes in the moisture balance. This pollen type is likely to represent *Polylepis* and suggests substantial range shifts of this tree and the associated woodland ecosystem. These woodlands were at their maximum extent during the warmer periods of increased moisture availability 116,000-106,000 and 97,000-86,000 cal yr BP (Fig. 6a). Fluctuations in woodland taxa coupled with pollen concentration values, (typically above full glacial lows of <1,000 grains cm^3, but below full interglacial highs of >10,000 grains cm^3), of 4,500-10,000 grains cm^3 (c. 118,000-106,000 cal yr BP) and 1,000-4,500 grains cm^3 (c. 106,000-70,000 cal yr BP) suggest relatively temperate conditions between c. 118,000 and 70,000 cal yr BP. The Andean flora varies through this transitional period and differs from the 'full' interglacial (MIS 5.5 equivalent) in the absence of Cheno/Ams (Hanselman et al., 2005) and 'full' glacial conditions (MIS 4-2 equivalent) in the proliferation of *Polylepis/Acaena* pollen. Leads and lags between pollen and marine isotope records have been identified from numerous regions of the globe, see Sirocko et al. (2007). However, the absence of independent dating, at this time, prevents us from commenting on leads and lags in this record. However, these data suggest a gradual and possibly stepwise transition between interglacial and glacial conditions. It is also intriguing to note that the most biodiverse Andean ecosystem seems to flourish during this transitional stage.

Only 157 m down slope, in the record from the Salar de Uyuni, *Polylepis/Acaena* pollen (most likely derived from the species *Polylepis tarapacana*; Chepstow-Lusty et al., 2005) persists through most of the glacial period with no clear

evidence of succession (c. 20-0%; Fig. 7). This continuity suggests that woodlands are present in the landscape even when there is no lake in this region to preserve the pollen produced. The peak abundance of *Polylepis/Acaena* pollen in Salar de Uyuni is coincident with the Minchin wet phase (maximum 26%; mean 10%) when insolation (January 15°S) is at a relative high (Fig. 7). The response of *Polylepis/Acaena* pollen during the Tauca wet phase is more muted (mean 6%) in Salar de Uyuni during low January insolation. However, increased isolation close to the termination of the Tauca wet phase in Salar de Uyuni seems to promote a rapid response in *Polylepis/Acaena* which rises to 21%. Such a significant and sudden response to slight fluctuations in moisture availability and temperature emphasises how close *Polylepis* and *Acaena* (and probably more specifically *P. tarapacana*) are living to the edge of their (its) ecological tolerance. This past sensitivity to environmental changes indicates a possible vulnerability of the genus *Polylepis*, and possibly *P. tarapacana* in particular, to human activity, future climate change and may hold the key to understanding the high biodiversity found in *Polylepis* woodlands today.

6. Conclusions

The pollen productivity of the vegetation in the southern hemisphere tropical Andes of Bolivia and Peru covaries with the eccentricity (100,000 year) glacial-interglacial cycle. We have linked shorter fluctuations in the moisture balance to variations in insolation on precessional (21,000 year) timescales. Links between lake level fluctuations and palaeolakes Tauca and Minchin, as identified by previous authors, remain tentative. Differences in the timing of events highlight the variation in the sensitivity of the records investigated and the proxies used, while emphasising the need for independent dating controls.

In terms of presence/absence, the composition of the Andean flora is shown not to fluctuate markedly through the Huiñaimarca record (at the taxonomic resolution permitted by pollen analysis). However, marked shifts in the significance of taxa indicate that communities existed in the past that have no modern analogue in the Andes, i.e. the dominance of Cheno/Ams during the last interglacial. Changes in the flora have been shown to occur rapidly (1000's years), which are likely to have had a profound impact on the Andean landscape and the fauna associated. Peaks in *Polylepis/Acaena* pollen, probably indicative of expanded *Polylepis* woodlands, occur during periods of transition between glacial and interglacial states. These highly biodiverse woodlands seem to be at their most extensive during moist warmer periods in the transition from full interglacial to full glacial conditions (118,000-70,000 cal yr BP).

References

Abbott, M.B., Binford, M.W., Brenner, M., Kelts, K., 1997. A 3500 ^{14}C high-resolution record of water-level changes in Lake Titicaca, Bolivia/Peru. Quaternary Research 47, 169-180.

Argollo, J., Mourguiart, P., 2000. Late Quaternary climate history of the Bolivian Altiplano. Quaternary International 72, 37-51.

Baker, P.A., Bush, M.B., Fritz, S., Rigsby, C.A., Seltzer, G.O., Silman, M.R., 2003. Last Glacial Maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia): Comment and Reply. Geology on-line forum, e26-e27.

Baker, P.A., Rigsby, C.A., Seltzer, G.O., Fritz, S.C., Lowenstein, T.K., Bacher, N.P., Veliz, C., 2001a. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. Nature 409, 698-701.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., Broda, J.P., 2001b. The history of South American tropical precipitation for the past 25,000 years. Science 291, 640-643.

Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews 10(4), 297-317.

Bush, M. B., Weng, C. 2006. Introducing a new (freeware) tool for palynology. Journal of Biogeography on-line.

Chepstow-Lusty, A.J., Bush, M.B., Frogley, M.R., Baker, P.A., Fritz, S.C., Aronson, J., 2005. Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 yr ago. Quaternary Research 63, 90-98.

Clapperton, C.W., 1993. Quaternary geology and geomorphology of South America. Elsevier, Amsterdam.

D'Agostino, K., Seltzer, G.O., Baker, P.A., Fritz, S.C., Dunbar, R.B., 2002. Late-Quaternary lowstands of Lake Titicaca: Evidence from high-resolution seismic data. Palaeogeography Palaeoclimatology Palaeoecology 179(1), 97-111.

Faegri, K., Iversen, J., 1989. Textbook of pollen analysis. Wiley, Chichester.

Fairbanks, R.G., Mortlock, R.A., Chiu, T.-C., Cao, L., Kaplan, A., Guilderson, T.P., Fairbanks, T.W., Bloom, A.L., Grootes, P.M., Nadeau, M.-J., 2005. Radiocarbon calibration curve spanning 0 to 50,000 years BP based on paired 230Th/234U/238U and ^{14}C dates on pristine corals. Quaternary Science Reviews 24(16-17), 1781-1796.

Fjeldså, J., 2002. Polylepis forests - vestiges of a vanishing ecosystem in the Andes. Ecotropica 8(2), 111-123.

Fjeldså, J., Kessler, M., 1996. Conserving the biological diversity of Polylepis woodlands of the highlands of Peru and Bolivia: A contribution to sustainable natural resource management in the Andes. Nordic Foundation for Development and Ecology, Copenhagen.

Fornari, M., Risacher, F., Féraud, G., 2001. Dating of palaeolakes in the central Altiplano of Bolivia. Palaeogeography Palaeoclimatology Palaeoecology 172(3-4), 269-282.

Fritz, S.C., Baker, P.A., Lowenstein, T.K., Seltzer, G.O., Rigsby, C.A., Dwyer, G.S., Tapia, P.M., Arnold, K.K., Ku, T.L., Luo, S., 2004. Hydrological variation during the last 170,000 years in the southern hemisphere tropics of South America. Quaternary Research 61(1), 95-104.

Garreaud, R., Vuille, M., Clement, A.C., 2003. The climate of the Altiplano: Observed current conditions and mechanisms of past changes. Palaeogeography Palaeoclimatology Palaeoecology 194(1-3), 5-22.

Grove, M.J., Baker, P.A., Cross, S.L., Rigsby, C.A., Seltzer, G.O., 2003. Application of strontium isotopes to understanding the hydrology and paleohydrology of the Altiplano, Bolivia-Peru. Palaeogeography Palaeoclimatology Palaeoecology 194(1-3), 281-297.

Hanselman, J.A., Gosling, W.D., Ralph, G.M., Bush, M.B., 2005. Contrasting histories of MIS 5e and the Holocene from Lake Titicaca (Bolivia/Peru). Journal of Quaternary Science 20(7-8), 663-670.

Heine, K., 2000. Tropical South America during the Last Glacial Maximum: Evidence from glacial, periglacial and fluvial records. Quaternary International 72(1), 7-21.

Hooghiemstra, H., 1984. Vegetational and climatic history of the high plain of Bogotá, Colombia: A continuous record of the last 3.5 million years. Dissertation Botanicae 79. Gantner Verlag, Vaduz.

Hutchinson, G.E., 1975. A Treatise on Limnology: Volume III Limnological botany. John Wiley & Sons, New York.

Johnson, A.M., 1976. The climate of Peru, Bolivia and Ecuador. In: Schwerdtfegel, W. (Ed), World Survey of Climatology: Climate of Central and S. America. Elsevier Scientific Publishing Co., New York, pp. 147-215.

Juggins, S., 2003. C2 Program version 1.4. Department of Geography, University of Newcastle, Newcastle upon Tyne, UK. http://www.campus.ncl.ac.uk/staff/Stephen.Juggins/software/c2home.htm.

Kessler, M., 2002. The "Polylepis problem": Where do we stand? Ecotropica 8, 97-110.

Lenters, J.D., Cook, K.H., 1999. Summertime precipitation variability over South America: Role of the large-scale circulation. Monthly Weather Review 127(2-3), 409-431.

Markgraf, V., D'Antoni, H.L., 1978. Pollen flora of Argentina. The University of Arizona Press, Tucson, Arizona.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C., Jr., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages; development of a high-resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1-29.

McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F.G., Reimer, P.J., 2004. SHCal04 Southern Hemisphere calibration 0 - 11.0 cal kyr BP. Radiocarbon 46, 1087-1092.

Mourguiart, P., Ledru, M.-P., 2003. Last Glacial Maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia). Geology 31(3), 195-198.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Louks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51(11), 933-938.

Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C., Seltzer, G.O., 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. Palaeogeography Palaeoclimatology Palaeoecology 194(1-3), 259-279.

Placzek, C., Patchett, P.J., Quade, J., Wagner, J.D.M., 2006a. Strategies for successful U-Th dating of paleolake carbonates: An example from the Bolivian Altiplano. Geochemistry Geophysics Geosystems 7, electronic.

Placzek, C., Quade, J., Patchett, P.J., 2006b. Geochronology and stratigraphy of late
Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for
causes of tropical climate change. Bulletin of the Geological Society of
America 118, 515-532.

Renison, D., Cingolani, A.M., Suarez, R., 2002. Effects of fire on a *Polylepis
australis* (Rosaceae) woodland in the mountains of Córdoba, Argentina
[Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en
las montañas de Córdoba, Argentina]. Revista Chilena de Historia Natural
75(4), 719-727.

Renison, D., Cingolani, A.M., Suarez, R., Menoyo, E., Coutsiers, C., Sobral, A.,
Hensen, I., 2005. The restoration of degraded mountain woodlands: Effects of
seed provenance and microsite characteristics on *Polylepis australis* seedling
survival and growth in Central Argentina. Restoration Ecology 13(1), 129-
137.

Renison, D., Hensen, I., Cingolani, A.M., 2004. Anthropogenic soil degradation
affects seed viability in *Polylepis australis* mountain forests of central
Argentina. Forest Ecology and Management 196(2-3), 327-333.

Rigsby, C.A., Bradbury, J.P., Baker, P.A., Rollins, S.M., Warren, M.R., 2005. Late
Quaternary palaeolakes, rivers, and wetlands on the Bolivian Altiplano and
their palaeoclimatic implications. Journal of Quaternary Science 20(7-8), 671-
691.

Rowe, H.D., Guilderson, T.P., Dunbar, R.B., Southon, J.R., Seltzer, G.O.,
Mucciarone, D.A., Fritz, S.C., Baker, P.A., 2003. Late Quaternary lake-level
changes constrained by radiocarbon and stable isotope studies on sediment

cores from Lake Titicaca, South America. Global and Planetary Change 38, 273-290.

Schmidt-Lebuhn, A. N., Kumar, M., Kessler, M., 2006. An assessment of the genetic population structure of two species of *Polylepis* Ruiz & Pav. (Rosaceae) in the Chilean Andes. Flora 201, 317-325.

Sirocko, F., Claussen, M., Sanchez Goni, M. F., Litt, T. (Eds), 2007. The climate of past Interglacials. In: J.J.M. van der Meer (Series Ed), Developments in Quaternary Science. Elsevier, London, Vol. 7.

Smith, J.A., Seltzer, G.O, Farber, D.L., Rodbell, D., Finkel, R.C., 2005a. Early local last glacial maximum in the tropical Andes. Science 308, 687-681.

Smith, J.A., Seltzer, G.O., Rodbell, D.T., Klein, A.G., 2005b. Regional synthesis of last glacial maximum snowlines in the tropical Andes, South America. Quaternary International 138-139, 145-167.

Stockmarr, J., 1972. Tablets with spores used in absolute pollen analysis. Pollen et Spore XIII(4), 615-621.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. Radiocarbon 35(1), 215-230.

Stutz, S., Prieto, A. R., 2003. Modern pollen and vegetation relationships in Mar Chiquita coastal lagoon area, southeastern Pampa grasslands, Argentina. Review of Palaeobotany & Palynology 126, 183-195.

Sylvestre, F., Servant, M., Servant-Vildary, S., Causse, C., Fournier, M., Ybert, J.-P., 1999. Lake Level chronology on the southern Bolivian Altiplano (18-23°S) during Late-glacial time and the early Holocene. Quaternary Research 51, 54-66.

Tapia, P.M., Fritz, S.C., Baker, P.A., Seltzer, G.O., Dunbar, R.B., 2003. A Late Quaternary diatom record of tropical climatic history from Lake Titicaca (Peru and Bolivia). Palaeogeography Palaeoclimatology Palaeoecology 194(1-3), 139-164.

Teich, I., Renison, D., Cingolani, A.M., Giorgis, M.A., Hensen, I., 2005. Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? Forest Ecology and Management 219(2-3), 229-241.

Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.-N., Mikhalenko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice cores. Science 282, 1858-1864.

Torres, V., Vandenberghe, J., Hooghiemstra, H., 2005. An environmental reconstruction of the sediment infill of the Bogota basin (Colombia) during the last 3 million years from abiotic and biotic proxies. Palaeogeography Palaeoclimatology Palaeoecology 226, 127-148.

Vuille, M., Bradley, R. S., Keimig, F., 2000. Interannual climate variability in the Central Andes and its relation to tropical Pacific and Atlantic forcing. Journal of Geophysical Research D: Atmospheres 105, 12447-12460.

Wirrmann, D., 1994. Lake Titicaca, Bolivia-Peru. In: Gierlowski-Kordesch, E., Kelts, K. (Eds), Global Geological Record of Lake Basins. Cambridge University Press, Cambridge, pp. 405-409.

Wirrmann, D., Mourguiart, P., 1995. Late Quaternary spatio-temporal limnological variations in the Altiplano of Bolivia and Peru. Quaternary Research 43(3), 344-354.

Wirrmann, D., Ybert, J.-P., Mourguiart, P., 1992. A 20,000 years paleohydrological record from Lake Titicaca. In: Dejoux, C., Iltis, A. (Eds), Lake Titicaca: A Synthesis of Limnological Knowledge. Kluwer Academic Pess, Boston, pp. 40-48.

Ybert, J.P., 1992. Ancient lake environments as deduced from pollen analysis. In: Deioux, C., Iltis, A. (Eds), Lake Titicaca: A Synthesis of Limnological Knowledge. Kluwer Academic Publishers, Boston, pp. 49-62.

Zhou, J., Lau, K.-M., 1998. Does a monsoon climate exist over South America? Journal of Climate 11(5), 1020-1040.

Table captions

Table 1: LT01-3B radiocarbon dates. Calibration method: C=CALIB 5.0.2 (Stuiver and Reimer, 1993; McCormac et al., 2004), F=Fairbanks0805 (Fairbanks et al., 2005), O=Outside calculation range of both calibration curves. For CALIB 5.0.2 ranges indicate the most probable age range at 1 sigma, for Fairbanks0805 ranges indicate one standard deviation.

Table 2: LT01-3A radiocarbon dates. Notation as Table 1.

Table 3: Tie points for >40,000 cal yr BP section of LT01-3B. Orbital tuning of aridity indicators to lows in insolation follows principles of Baker et al. (2001a).

Table 4: Calculation of Huiñaimarca age vs. depth curve (Fig. 3d). Below 93.77 mblf the absence of dates and lack of clear tie point prohibits the construction of an age vs. depth curve.

Table 1

Depth (mblf)	Lab code	^{14}C date	^{14}C +/-	Cal yr BP	Cal yr BP range	Calibration method
1.70	AA46954	3,400	40	3596	3554 - 3637	C
5.44	AA46955	23,700	260	28254	± 287	F
5.44	AA46955	23,340	300	27874	± 330	F
8.47	AA46956	21,850	210	26301	± 234	F
11.47	AA46957	27,360	320	32213	± 268	F
	AA46958	24,780	280	29607	± 548	F

Table 2

Depth (mblf)	Lab code	^{14}C date	^{14}C +/-	Cal yr BP	Cal yr BP range	Calibration method
1.16	AA48403	1,379	51	1248	1233 - 1297	C
2.01	AA48402	2,430	38	2420	2383 - 2459	C
2.87	AA48401	4,334	54	4850	4816 - 4891	C
3.42	AA48400	8,889	67	9909	9740 - 9946	C
3.83	AA48399	10,031	71	11545	11390 - 11653	C
3.84	AA46975	8,685	69	9612	9533 - 9671	C
4.38	AA48398	19010	150	22577	± 174	F
5.10	AA48397	22020	170	26481	± 190	F
5.47	AA48396	23840	200	28401	± 228	F
5.71	AA48395	20720	150	24778	± 267	F
6.95	AA46976	22510	160	26998	± 186	F
8.40	AA48394	24930	230	29891	± 510	F
9.94	AA46977	24760	200	29540	± 443	F
11.28	AA48393	28640	350	33392	± 536	F
14.38	AA48392	29940	420	35020	± 378	F
16.98	AA48391	31440	450	36408	± 465	F
19.62	AA48390	33160	550	38087	± 774	F
22.24	AA48389	32580	520	37479	± 686	F
25.24	AA48388	33170	590	38103	± 812	F
28.24	AA48387	38500	1100	42999	± 861	F
31.29	AA48386	34330	620	39584	± 924	F
33.61	AA48385	40300	1500	44382	± 1233	F
35.18	AA48383	37900	950	42544	± 681	F
37.29	AA48384	40700	1400	44687	± 1172	F
40.29	AA48382	43300	2100	-	-	O

42.28	AA48381	45100	2500	-	-	O
44.86	AA48380	44200	2100	-	-	O
46.28	AA48379	43000	1800	-	-	O
49.28	AA48378	42500	1800	-	-	O
52.29	AA48377	>43,600	-	-	-	O

Table 3

Depth (mblf)	Age (cal yr BP)	Reasoning
70.51	81,000	Middle of 'high' magnetic susceptibility zone (consistently >50 SI units) tied to low in insolation for January 15°S (Berger and Loutre, 1991).
76.87	104,000	Middle of 'high' magnetic susceptibility zone (consistently >50 SI units) tied to low in insolation for January 15°S (Berger and Loutre, 1991).
91.47	GAP 121,000- 129,000	Peak in Cheno/Am pollen tied to low in insolation for January 15°S (Berger and Loutre, 1991); duration of gap equivalent of dry zone indicated in Lago Grande during the peak of the interglacial by Cheno/Am pollen (Hanselman *et al.* 2005).
93.77	151,000	Ash band at 93.77 mblf matched with ash band in Lago Grande at 57.47 mblf (core section 21E-2). Projected age at this depth in Lago Grande c. 151,000 cal yr BP (S.C. Fritz pers. comm.).

Table 4

Model no.	Depth (mblf) [x]	Equation [$y =$]	R^2	Age (cal yr BP) [y]
1	0 - 3.90	$475.81e^{0.8256x}$	0.9811	476 - 11,907
2	3.90 - 4.43	$21961x - 73633$	0.9763	12,015 - 23,654
3	4.43 - 40.00	$9269.8\mathrm{Ln}(x) + 9997.1$	0.9567	23,794 - 44,192
4	40.00 - 70.51	$1206.4x - 4062.7$	1	44,193 - 81,001
5	70.51 - 76.87	$3616.4x - 173989$	1	81,004 - 104,004
6	76.87 - 91.47	$1164.4x - 14494$	1	104,001 - 121,002
7	91.47 - 93.77	$9565.2x - 745930$	1	128,999 - 150,999

Figure captions

Figure 1: Southern hemisphere tropical Andes. Huiñaimarca core site (LT01-3B) marked with white star, Salar de Uyuni core site marked with black star (Baker et al., 2001a; Chepstow-Lusty et al., 2005). Base map and ecoregions adapted from Olson et al. (2001).

Figure 2: a) Lake Titicaca (modified from D'Agostino et al., 2002), and b) Huiñaimarca sub-basin; numbers indicate current lake depth in metres (modified from Wirrmann et al., 1992). Core LT01-3A/B was obtained from the deeper area known as the Chua depression.

Figure 3: Huiñaimarca: a) magnetic susceptibility LT01-3A, b) magnetic susceptibility LT01-3B, c) pollen concentration (grains/cm^3) LT01-3B, d) dating profile (X indicates tie point, 1 = end of ^{14}C chronology (Table 1 and 2), 2 and 3 = peak in magnetic susceptibility (Table 3), 4 and 5 = gap in record (Table 3), 6 = tephra layer (Table 3)). For calculation of curve see Table 4, and e) correlation with Marine Istotpe Stages (MIS) chronology.

Figure 4: Huiñaimarca (LT01-3B) against depth (mblf). a) Total pollen concentration and percentage abundance of taxa (>5% in any one sample). b) Isoëte concentration (grey) and total aquatics concentration (dots), percentage abundance of aquatic taxa and percentage abundance of spores (calculated relative to the pollen sum). Exaggeration line (x10) shown for less abundant taxa. Dashed line indicates depth of break in core (91.47 m, Table 3).

Figure 5: Size and extent of shallow water habitat in Huiñaimarca relative to core site (Chua depression, marked X) for modern equivalent lake depths of: a) c. 10 m, b) c. 20 m and, c) c. 30 m. Note: the water level in Huiñaimarca relative to that in Lago Grande determines the direction of flow through the Straits of Tiquina. (Base map modified from Wirrmann et al., 1992).

Figure 6: Huiñaimarca (LT01-3B) total pollen concentration and selected taxa against age (thousands of years before present, kcal yr BP). a) Total pollen concentration and percentage abundance of taxa (>5% in any one sample). * Modern equivalent lake level estimates discussed and justified in "Environmental reconstruction" section. Vertical dotted line indicates Straits of Tiquina, vertical dashed line indicates Río Desaguadero. b) Total aquatics concentration, percentage abundance of aquatic taxa and percentage abundance of spores (calculated relative to the pollen sum) with insolation for January 15°S (Berger and Loutre, 1991) curves. Exaggeration line (x10) shown for less abundant taxa.

Figure 7: Salar de Uyuni against age (cal yr BP), redrawn from (Chepstow-Lusty et al., 2005). a) Total pollen concentration and percentage abundance of selected taxa. b) Percentage abundance of aquatics and percentage abundance of spores (calculated relative to pollen sum) with insolation for January 15°S (Berger and Loutre, 1991) curves. Age vs. depth curve generated using fourth order polynomial equation (y = -0.0000012x^{4} + 0.00049x^{3} - 0.044x^{2} + 2.40x) based on 12 radiocarbon and 14 U-series dates (see Fritz et al., 2004). Any gap greater than 1500 years between any two samples has been blanked out (±250 years either side of each sample).

Figure 8: Regional lake level fluctuations in the southern hemisphere tropical Andes. Comparison of concentration data from Huiñaimarca and Salar de Uyuni with solar insolation (15°S January) and palaeolake reconstruction (Placzek et al., 2006b); alternative radiocarbon timing for Ouki lake cycle shown in grey.
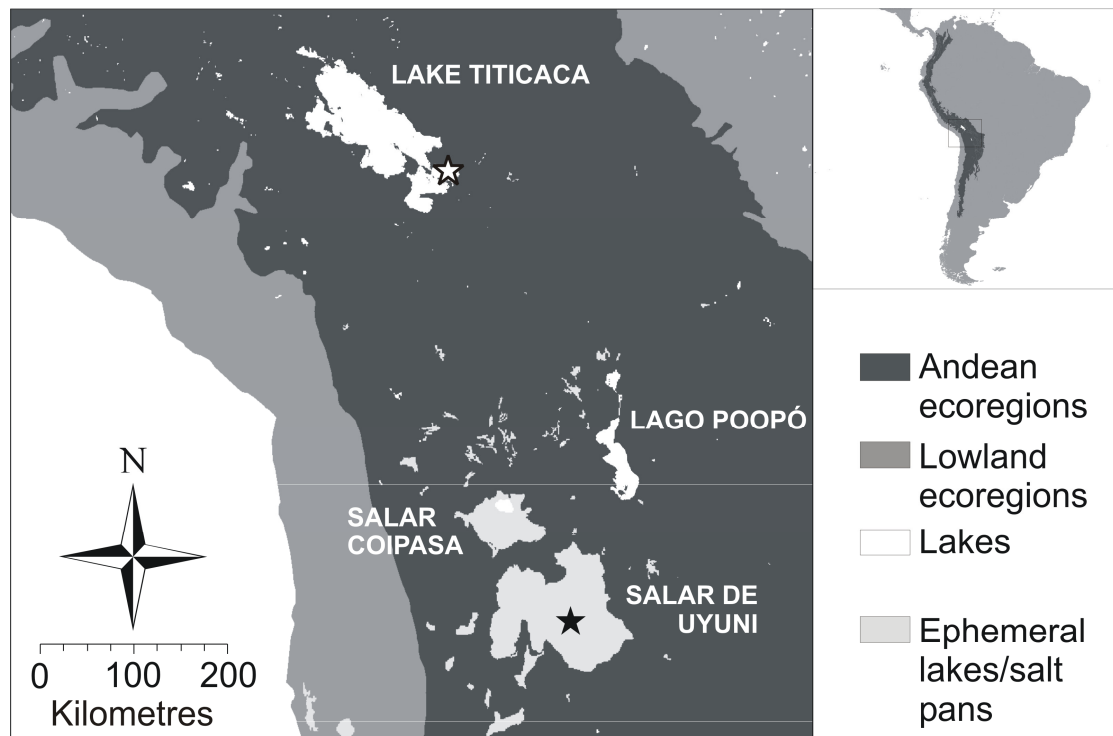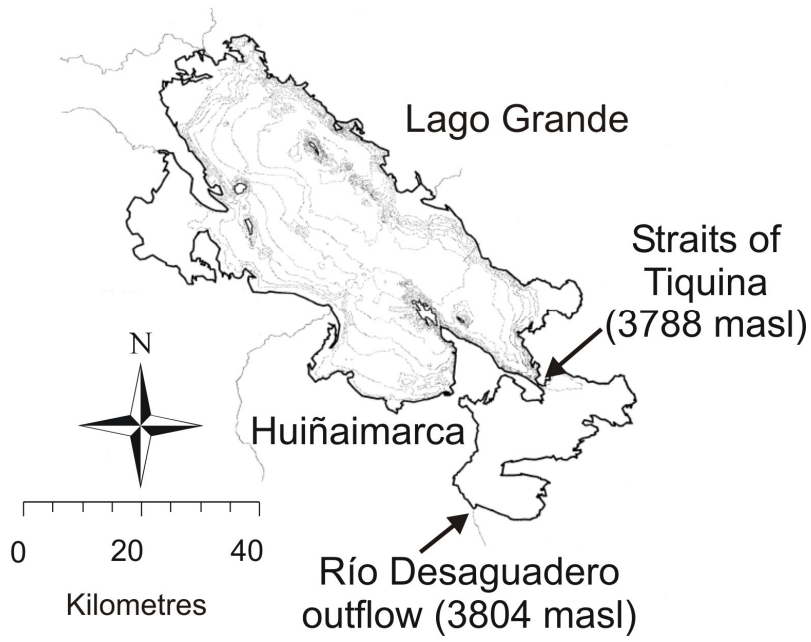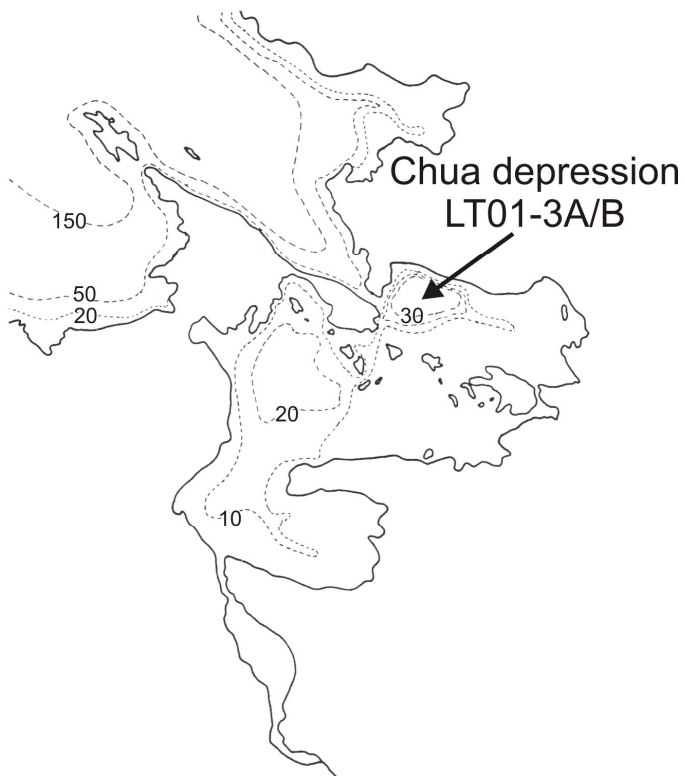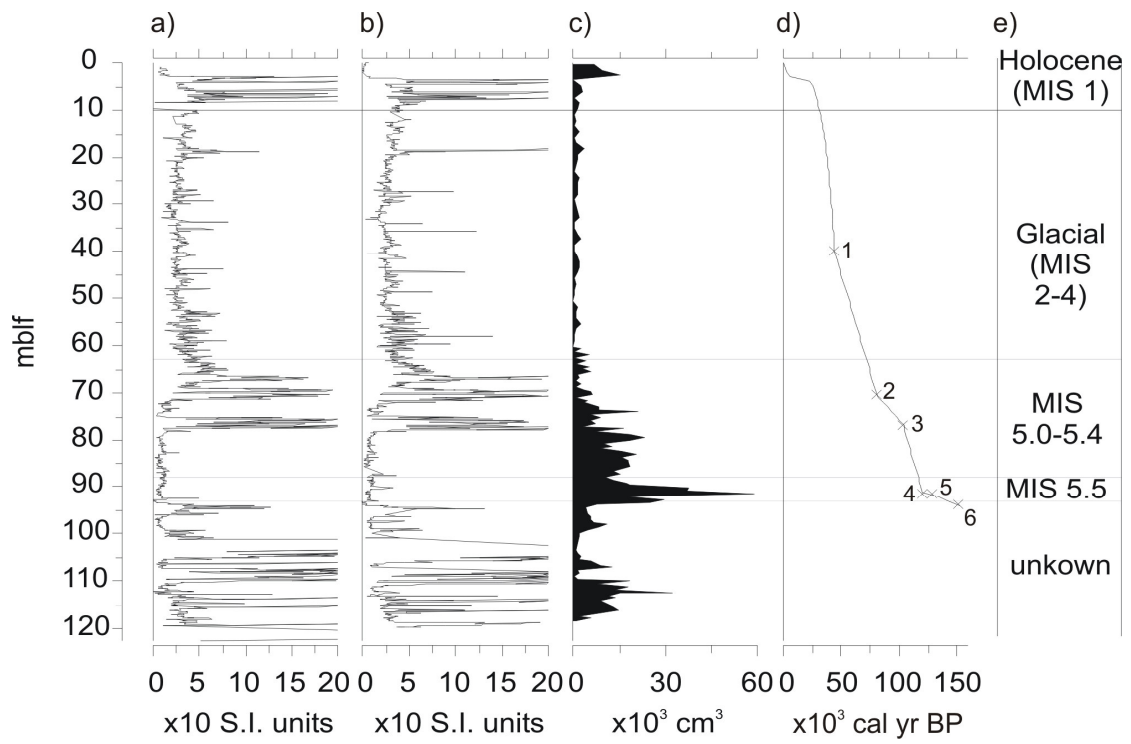
Figure 1

Figure 2

a)

b)

Figure 3

Figure 4a

Figure 4b

Figure 5

a)

b)   c. 20 m

c)

c. 34 m
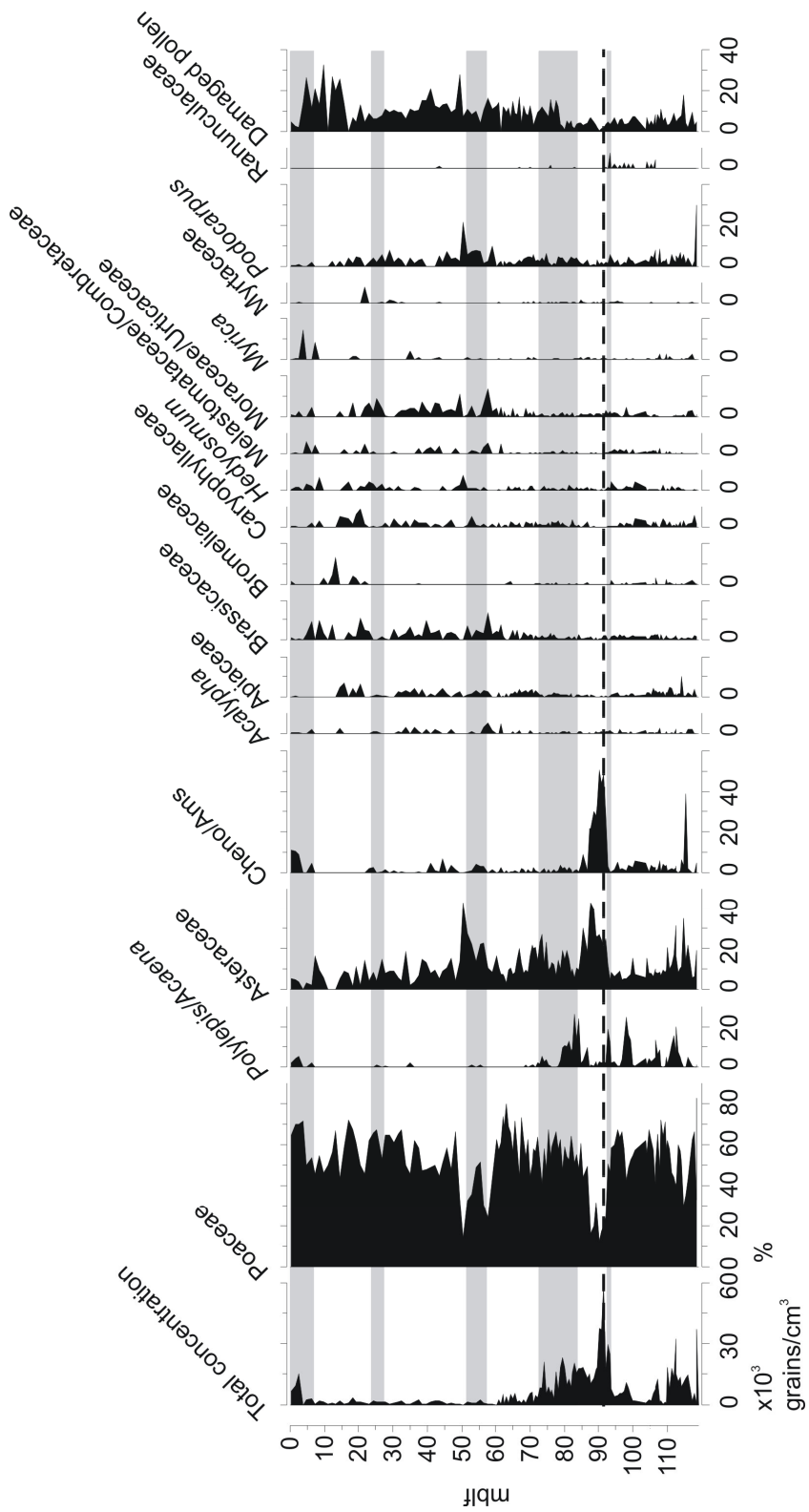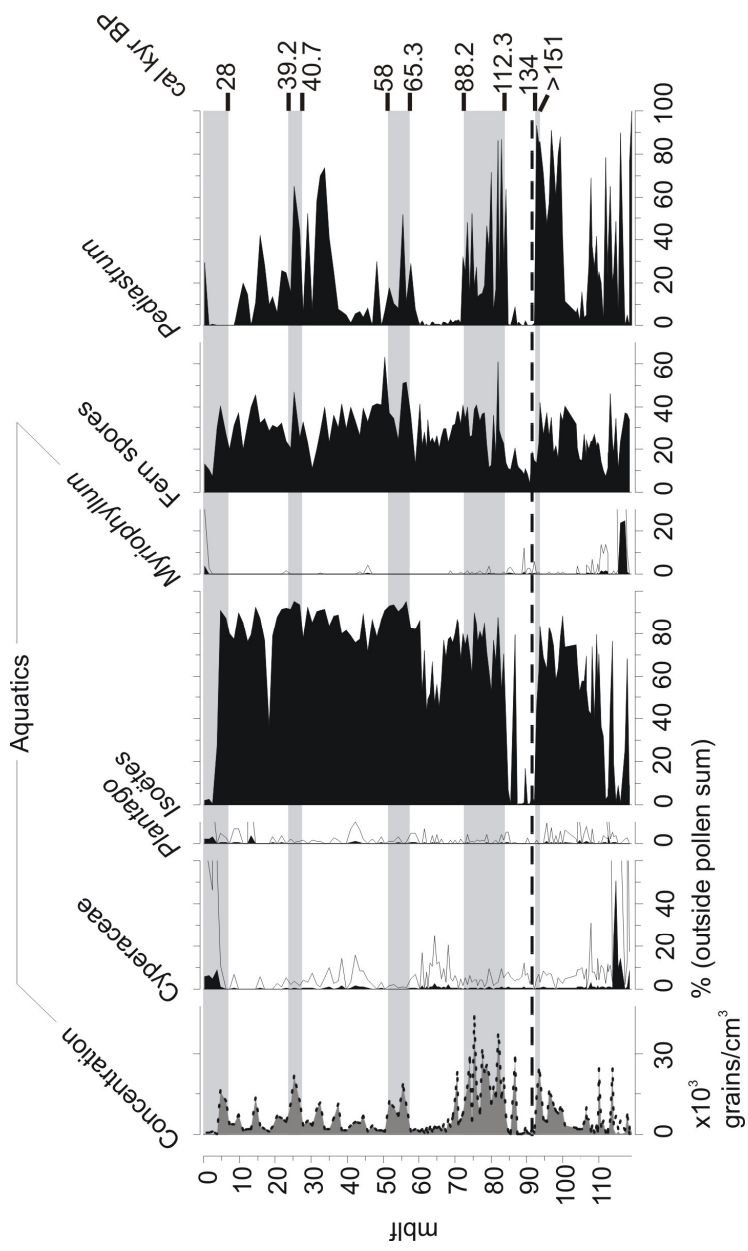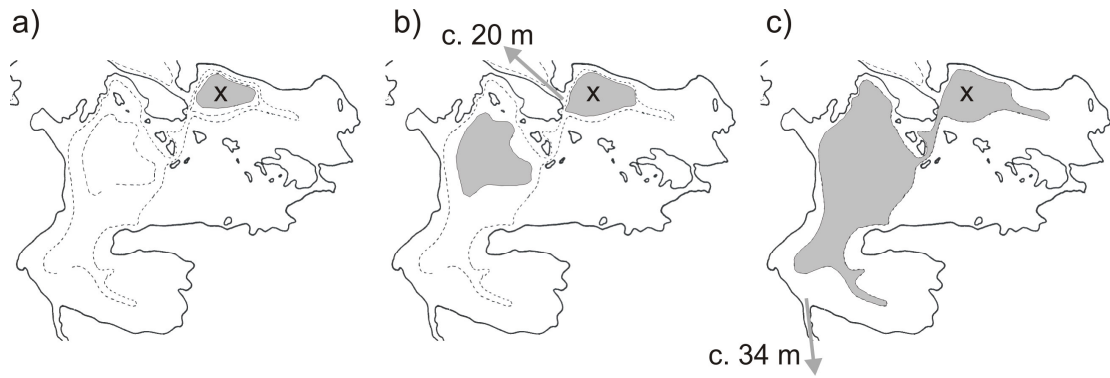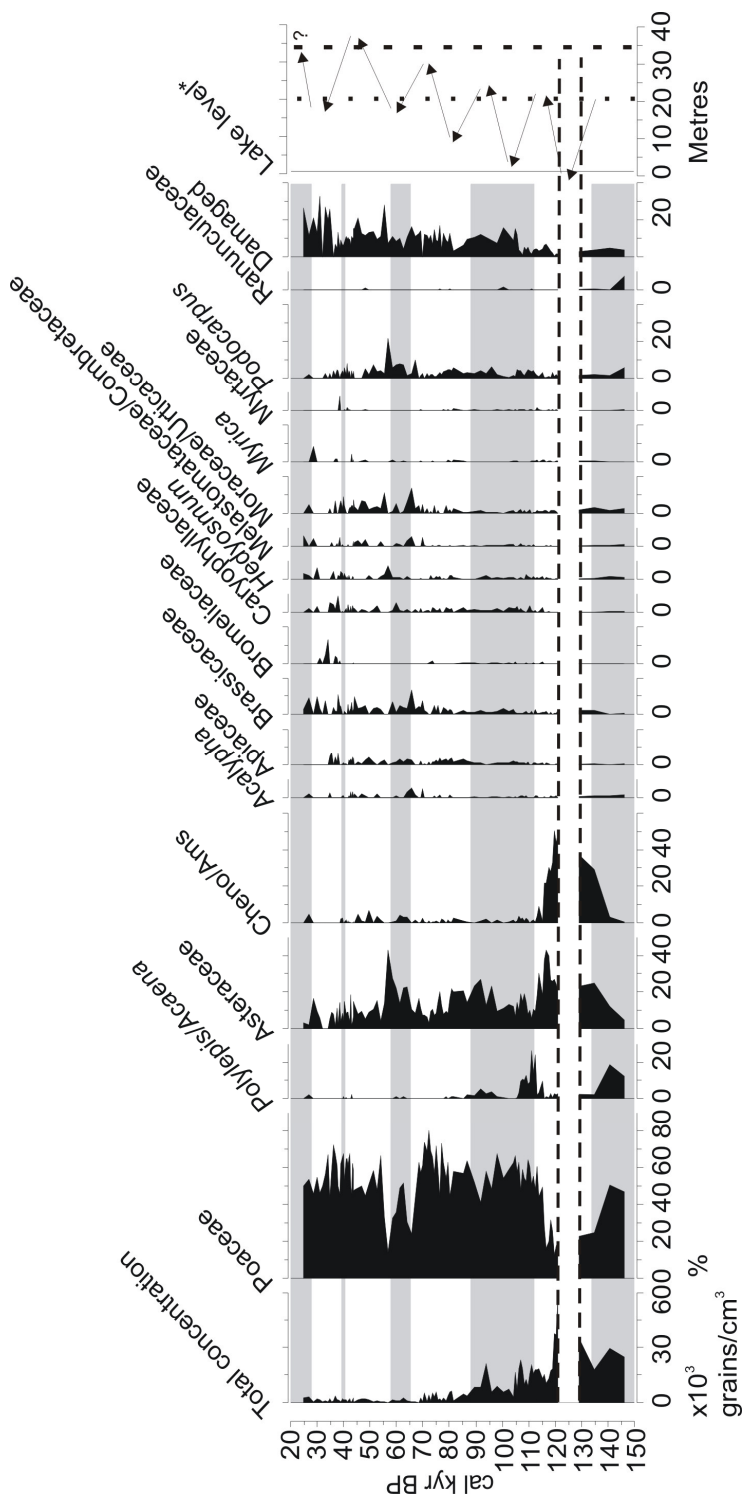
Figure 6b

Figure 7

Figure 8