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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 Huiñaímarca 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/cm³) identify the extent of shallow water environments. Examination of other palaeolimnological indicators (Pediastrum) and consideration of the bathymetry of the Huiñaímarca 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 Huiñaímarca 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/Amaranthaceae, 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

**Words:** 488/500
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° 50’ S, 64° 43’ W; Mourguiart and Ledru, 2003) and ii) Huiñaimarca (16° 20’ S, 68° 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 Huinaimarca (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 Huinaimarca’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 Huinaimarca is significantly shallower than Chua, with c. 45% of Huinaimarca’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 Huinaimarca 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/cm³ 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/cm³; 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/cm³). 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.
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%).

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.

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/cm³ 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 *Pediastrum* 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 ¹⁴C 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 ± 72 cal yr BP (12,090 ± 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 \textit{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).

**Acknowledgements**

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**References**


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

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<td>40.00 - 70.51</td>
<td>(1206.4x - 4062.7)</td>
<td>1</td>
<td>44,193 - 81,001</td>
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<td>81,004 - 104,004</td>
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<td>(1164.4x - 14494)</td>
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<td>104,001 - 121,002</td>
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<tr>
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<td>(9565.2x - 745930)</td>
<td>1</td>
<td>128,999 - 150,999</td>
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</table>
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 Isotope 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) [Map of geographical features including Lago Grande, Huiñaimarca, Straits of Tiquina (3788 masl), and Rio Desaguadero outflow (3804 masl).]

b) [Map of Chua depression with LT01-3A/B标注.]
Figure 4b