

A 24,700-yr paleolimnological history from the Peruvian Andes

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Abstract

A new paleolimnological dataset from Lake Pacucha (13 °S, 3095 m elevation) in the Peruvian Andes provides evidence of changes in lake level over the past 24,700 yr. A late-glacial highstand in lake level gave way to an early-Holocene lowstand. This transition appears to have paralleled precessional changes that would have reduced insolation during the wet-season. The occurrence of benthic/salt-tolerant diatoms and CaCO₃ deposition suggest that the lake had lost much of its volume by c. 10,000 cal yr BP. Pronounced Holocene oscillations in lake level included a second phase of low lake level and heightened volatility lasting from c. 8300 to 5000 cal yr BP. While a polymictic lake formed at c. 5000 cal yr BP. These relatively wet conditions were interrupted by a series of drier events, the most pronounced of which occurred at c. 750 cal yr BP. Paleolimnological changes in the Holocene were more rapid than those of either the last glacial maximum or the deglacial period.

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Introduction

A few decades ago, a debate was initiated by the radical suggestion that tropical South America was arid during glacials and only wet during interglacial times (Haffer, 1969). A rather general statement that cooler oceans would reduce precipitation and therefore beget aridity was the underpinning of the argument. This view of Neotropical aridity was widely accepted (Whitmore and Prance, 1987), but has not stood the test of time (Colinvaux et al., 2001). A different view is now well established that precessional rhythms are more important controllers of tropical precipitation than simple glacial–interglacial oscillations (Baker et al., 2001a; Bush et al., 2002; Clement et al., 2001; Colinvaux et al., 2001).

Past lake levels may have been influenced both by temperature and precipitation. A last glacial maximum (LGM) cooling in Amazonia of c. 3–5°C (Bush et al., 2001; Liu and Colinvaux, 1985), and in the high Andes of c. 5–8°C (Bush et

al., 2007b; Hooghiemstra, 1984; Van der Hammen, 1974), may have helped maintain high lake levels. Some paleoclimatic models have projected that even during periods of lower precipitation, drought deficit was mitigated by a relatively cool climate (Cowling et al., 2004; Cowling et al., 2001). This same argument has also been used to suggest that evaporation from Andean lakes may have been substantially reduced, allowing wet conditions to persist even in the absence of strong inputs of moisture from Amazonia (Mourguiart and Ledru, 2003). There is little doubt that the flow of moisture from the lowlands to the Andes was an important component of Andean paleoclimates. Similarly, that glacial cooling would have reduced evaporation from the lake surface seems probable. However, as Baker et al. (2003) observe, the moisture supply from the Amazon lowlands at the LGM does not seem to have been ecologically limiting, suggesting the persistence of moist conditions in Amazonia. Indeed, the case for significant decreases in basinwide Amazonian moisture at the LGM has yet to be made. The LGM lowlands are documented in a scatter of records (e.g. Absy et al., 1991; Behling, 2002; Bush et al., 2004a; Colinvaux et al., 1996), but contra expectations for widespread aridity,

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dated lake lowstands are both time-transgressive and relatively brief, suggesting rather rapid shifts in precipitation:evaporation balance (Bush et al., 2007a).

We now recognize that it is not possible to talk about all of the South American tropics as being synchronously influenced by climate change, any more than this can be done for northern latitudes (Bush and Silman, 2004; Marengo, 2007; Marengo and Nobre, 2001). Rather, evidence points to climates responding to centennial to millennial-scale forcing, some of which may be local or relatively remote solar forcing, e.g. El Niño Southern Oscillation influences from the Pacific or the bipolar seesaw of the tropical Atlantic (Baker, 2002). Increasingly, evidence has emerged supporting synchronous, but oppositely signed events in the northern and southern hemispheres (e.g. EPICA Project Members, 2006). However, whether the millennial-scale phenomena linked to variations in the meridional overturning circulation are apparent in the tropical Andes has yet to be resolved. Even the detection of the strongest of all those cycles, the Younger Dryas event, has been keenly debated (Hansen, 1995; Heine, 1993; Paduano, 2001; Van 't Veer et al., 2000; Van der Hammen and Hooghiemstra, 1995).

Currently, most of the discussion of Andean climates tacitly accepts a 5–8°C temperature depression at the LGM, a relatively early deglaciation (between 22,000 and 19,000 cal yr BP), and focuses on trying to resolve causes of precipitation change at a centennial to millennial scale (Aalto et al., 2003; Maslin and Burns, 2000; Mayle et al., 2000; Moy et al., 2002; Rodbell et al., 1999; Smith et al., 2005; Urrego et al., 2005). The principle hypotheses that need to be tested are: 1) that the LGM on the Altiplano was a time of lake lowstands probably coupled to Amazonian aridity (Mourguiart and Ledru, 2003). 2) That the LGM was a time of lake highstands on the Altiplano in response to a precessionally strengthened South American Summer Monsoon (SASM) (Baker et al., 2001a; Fritz et al., 2004; Fritz et al., 2007). 3) That the Younger Dryas event was not

manifested in the Central Andes (Hansen, 1995; Heine, 1993), and 4) that El Niño Southern Oscillation (ENSO) within the Holocene has had a major effect on lake level in the Central Andes (e.g. Moy et al., 2002; Riedinger et al., 2002; Sandweiss et al., 2001). Here we present a 24,700-yr paleolimnological record from Lake Pacucha, Peru, that adds new information to all of these debates.

The site

Lake Pacucha lies at 13°36'26" S, 73°29'42" W at 3095 m elevation. The lake occupies c. 7.5 km² and has a maximum depth of c. 30 m (Fig. 1). Though presently lying in a deforested basin, the vegetation in the absence of human disturbance would, at this elevation, probably have been Andean cloud forest. Tree line in this section of the Andes has been extensively lowered by millennia of occupation (Ellenberg, 1958), and would otherwise probably lie at c. 3500 m.

The origin of the lake is not known, but we infer it to be a solution basin. The basin clearly lies below local glacial influence (moraines terminate at c. 3700–3400 m in nearby valleys). The original basin may have been deepened by a landslide that partially blocked an outflowing stream, but the antiquity of that event is not known. A small stream drains into the eastern end of the lake with a corresponding outflow over a sill on the northern shore. However, relative to lake volume, these streams are rather small. The lake is a site of known archaeological importance with pre-Incan settlements, representing the Chanka civilization around its shores (B. Bauer pers. comm.).

Some moisture arrives year-round to the site, although November to April is considered to be the wet season. The SASM brings moisture to this location, resulting in an annual precipitation of c. 700 mm. Given the high proportion of Amazonian moisture input to Pacucha, this lake should be highly sensitive to Amazonian aridity or a weakening of SASM.

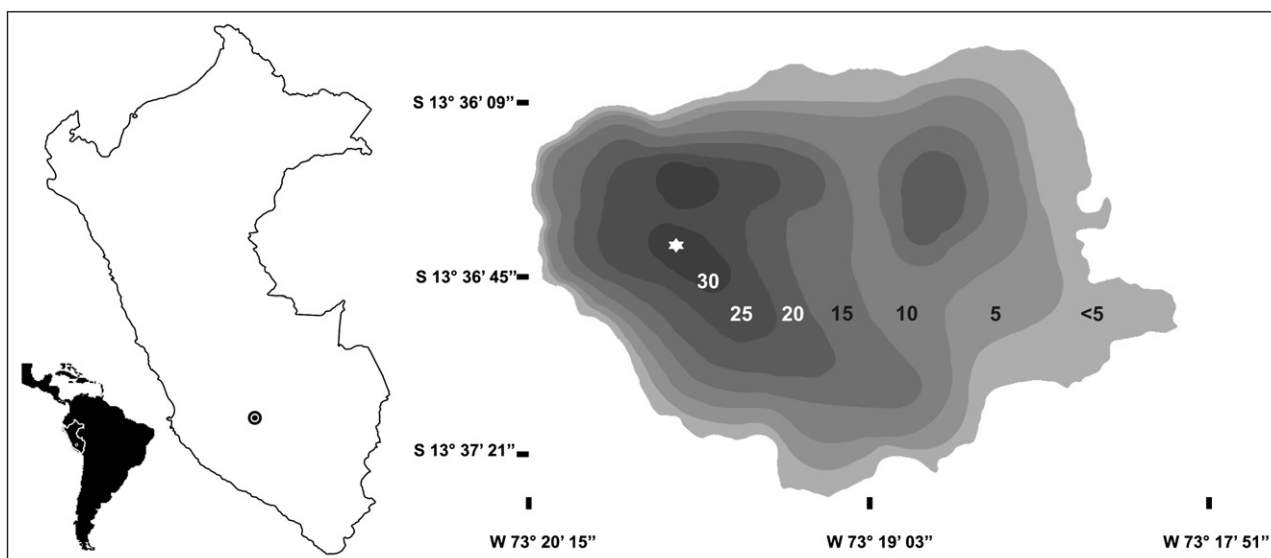


Figure 1. Sketchmap showing the location and bathymetry (depths in m) of Lake Pacucha, Peru. Star marks the position of coring operation.

Temperatures at this elevation average c. 13–15°C and occasional dry season frost would occur.

Modern limnological data from the lake are based on a single sampling carried out in July 2005. Using a YSI 85 multimeter, dissolved oxygen was measured to be 5.54 mg/L (100% saturation for this elevation and temperature based on Mortimer, 1956), specific conductance was 345 µS/cm, and no thermal stratification was evident in the upper 15 m of the water column. An Oakton pH meter documented a pH of 8.46.

Methods

A series of cores were raised between 2003 and 2005 from the deepest portion of the lake. A modified Colinvaux–Vohnout piston corer (Colinvaux et al., 1999) deployed from a floating platform, raised 5 cm diameter and 3 cm diameter cores that were sealed in the field. Ultimately, the limitation on core retrieval was flexibility in the lightweight coring device. With 30 m of casing and a total drillstring length of 45 m, the coring rig was functioning close to its limit. We did not hit bedrock, and the lake sediment extends for an unknown depth beyond our coring limit.

Three cores (PAC-B 11 m-long; PAC-D 11 m-long; and PAC-E 14.5 m-long) were scanned for density at 0.5 cm centers (gamma attenuation) using a GEOTEK multi-sensor core logger prior to opening. Once opened and split longitudinally, the cores were scanned again to acquire high-resolution digital color images. The three cores were then aligned and cross-correlated using highly distinctive density and banding patterns. By overlapping the three sections a continuous 14.5 m-long record was obtained. Color was additionally described using Munsell color charts.

Eighteen samples were taken for ¹⁴C accelerator mass spectrometry (AMS) dating. Radiocarbon dates between 0 and 11,000 calibrated years before present (cal yr BP) were calibrated using CALIB 5.2 (Stuiver and Reimer, 1993; Stuiver et al., 2005). Dates >11,000 yr in age were calibrated using Fairbanks et al. (2005); hereafter all ages are given in cal yr BP.

The cores were subsampled for fossil diatoms, loss-on-ignition (LOI), and fossil pollen. Loss-on-ignition samples were

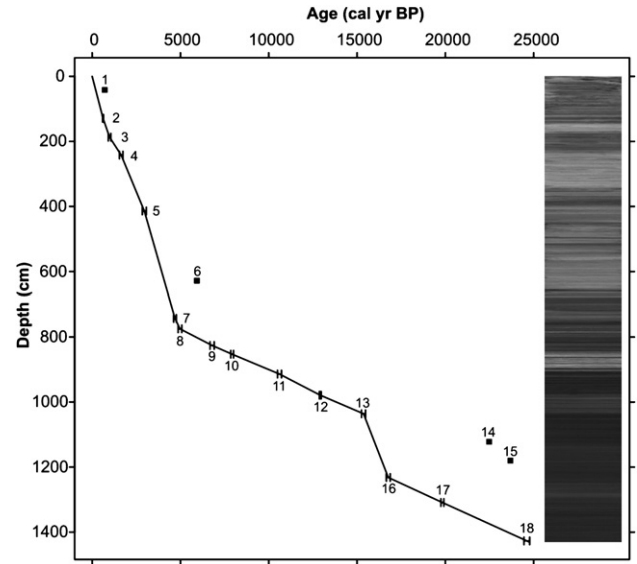


Figure 2. The stratigraphy and chronology of sediment cores raised from Lake Pacucha, Peru. Details of the ¹⁴C dates are given in Table 1. Radiocarbon dates treated as outliers are shown as open squares.

placed in weighed crucibles, and reweighed following 24 h at 105°C, 4 h at 550°C, and 2 h at 950°C (Heiri et al., 2001). Subsamples for diatom analysis were taken to provide a temporal resolution of c. 220 yr between samples. Diatoms were extracted by heating samples in H₂O₂, rinsing with H₂O, evaporating a subsample onto a coverslip and mounting in naphrax (Battarbee, 1986). Counting was carried out on a Zeiss Axioskop at 1000× magnification. Photographs of specimens were taken with an 8 megapixel Nikon camera. Complete transects were counted until, wherever possible, a total of 500 frustules was reached.

Where one or more entire slides were counted and the total number of frustules was below 500, this was taken to indicate probable dissolution of valves. Subtracting the number of valves counted from 500 provides a crude dissolution factor, such that high values indicate poor preservation.

Identifications were made using standard texts (e.g. Lange Bertalot, 1998; Lange Bertalot, 2000; Patrick and Reimer, 1966; Patrick and Reimer, 1975). Nomenclature follows the California Academy of Sciences <http://www.calacademy.org/research/diatoms>.

Data were entered into EXCEL spreadsheets, plotted using C2 (Steve Juggins, Newcastle University), with multivariate analyses conducted in PC-ORD4 (McCune and Mefford, 1999). Detrended Correspondence Analysis (DCA) was run on a log-normally transformed matrix of the 42 taxa that occurred at 3% or more within the fossil record (after Birks and Birks, 1998).

Results

Stratigraphy

The 14.5 m-long core showed distinct depositional phases. Much of the core was faintly laminated (Table 1), but in the

Table 1
Stratigraphic summary for the sediments of core PAC-E, Lake Pacucha, Peru

| Interval (cm) | Laminations per cm | Color | Sediment type |
|---------------|--------------------|--------------------------------|---|
| 0–160 | 3–8 | Very dark grayish brown | Clay |
| 160–185 | 3–7 | Brown | Clay |
| 185–250 | 6–18 | Very dark grayish brown | Clay |
| 250–355 | 4–8 | Brown | Clay |
| 355–410 | 0–5 | Very dark grayish brown | Clay |
| 410–660 | 5–20 | Brown | Clay with occasional organic-rich bands |
| 660–1040 | 10–50 | Black/dark gray/ dark olive | Organic-rich gyttja |
| 1040–1430 | not evident | Dark greenish gray | Silt |

Table 2
Calibrated ages derived from radiocarbon dates for samples from Lake Pacucha, Peru

| Sample number | Depth (cm) | ¹⁴ C age | Mean calibrated age (bold) and (min. – max. ages), cal yr BP | Sigma range (σ) | CAMS-OS (laboratory code) |
|---------------|------------|---------------------|--|-----------------|---------------------------|
| 1 | 43 | 875±25 | 729 (683–775) * | 2 | OS-64477 |
| 2 | 129 | 635±25 | 615.5 (590–641) | 2 | OS-64479 |
| 3 | 187 | 1110±40 | 987 (915–1059) | 2 | OS-64476 |
| 4 | 242 | 1800±40 | 1642 (1543–1741) | 2 | CAMS-110133 |
| 5 | 414 | 2875±40 | 2953.5 (2841–3066) | 2 | CAMS-110134 |
| 6 | 630 | 5190±45 | 5894.5 (5837–5952) * | 2 | CAMS-110135 |
| 7 | 743 | 4265±35 | 4690 (4614–4766) | 2 | CAMS-110136 |
| 8 | 775 | 4480±40 | 4972 (4866–5078) | 2 | CAMS-123761 |
| 9 | 826 | 6025±40 | 6793.5 (6675–6912) | 2 | CAMS-110137 |
| 10 | 853 | 7160±35 | 7926 (7847–8005) | 2 | CAMS-123762 |
| 11 | 914 | 9430±40 | 10606.5 (10493–10720) | 2 | CAMS-123837 |
| 12 | 979 | 11050±45 | 12916 (12868–12964) | 1 | OS-64478 |
| 13 | 1036 | 13195±50 | 15366 (15249–15483) | 1 | CAMS-110138 |
| 14 | 1124 | 18670±70 | 22282 (22196–22368) * | 1 | CAMS-123763 |
| 15 | 1182 | 19650±110 | 23477 (23310–23644) * | 1 | OS-64510 |
| 16 | 1232 | 14275±45 | 16766 (16656–16876) | 1 | CAMS-123764 |
| 17 | 1309 | 16700±50 | 19830 (19746–19914) | 1 | CAMS-123765 |
| 18 | 1427 | 20660±90 | 24612 (24451–24773) | 1 | CAMS-123766 |

¹⁴C-AMS dates were converted to calibrated years BP using Calib 5.0.2 (Stuiver et al., 2005; numbers 1–11) and Fairbanks et al. (2005; numbers 12–18). Values in bold represent mean values and were used for creating the age model.

* Rejected ages.

middle and upper sections the banding was most pronounced (Fig. 2). In sections of very finely laminated core, where black and white band couplets were less than 1 mm in width, the pale bands reacted vigorously to HCl suggesting them to be rich in CaCO₃.

Chronology

Macrofossils were not evident in the core and so all ages are based on bulk sediment samples. To minimize hardwater error, laminae rich in carbonate were avoided and only the most organic-rich bands were dated. Samples were pre-treated to remove carbonate prior to dating.

Four dates (numbers 1, 6, 14 and 15; Table 2; Fig. 2) were rejected on the principle of parsimony, i.e. more than two dates would have to be rejected in each case to accept them. These outlier dates were clearly too old, and probably do represent samples with significant hardwater error.

The basal age for the longest core, PAC-E, appears to be about 24,700 cal yr BP. As we did not hit bedrock, the lake itself is of unknown age. The chronology suggests four sedimentary phases in which deposition ranged from 0.25 mm/yr in the late-glacial, to 1.4 mm/yr in the deglacial phase, before slowing to 0.27 mm/yr during the terminal Pleistocene and the early Holocene. After 5000 cal yr BP depositional rates accelerated to 1.54 mm/yr.

Loss-on-ignition

Sediments deposited between c. 24,700 and 16,000 cal yr BP are clays with 90% silica content and an organic content of <12% (Fig. 3). An abrupt doubling of the organic content of the sediment occurred at c. 16,000 cal yr BP. Thereafter,

organic content remained above 20% until c. 12,000 cal yr BP. The proportion of organic material fell as carbonate content increased from <5% to >30% between 11,300 cal yr BP and 7850 cal yr BP., with a peak of c. 60% at c. 11,000 cal yr BP. Carbonate and organic content vary inversely between 12,000 and 5000 cal yr BP, while silica content remains relatively constant at c. 50%. In the last 5000 yr, carbonate returns to its background level of <5% and organics and silica content vary inversely with c. 80% of the sediment comprised of silica.

The fossil diatom data described

Four local diatom zones were identified based on major changes in diatom assemblage and gross stratigraphy (Fig. 4).

Pac-1: 14.3–11.5 m depth (c. 24,700–16,000 cal yr BP)

Within this zone of clay-rich sediments, the diatom community was dominated by *Cyclotella stelligera* (20–96%), a diatom primarily of deep-water settings, and fluctuating abundances of the shallow water indicator *Staurisira pinnata*, generally 5–30% (Fig. 4). Between c. 19,700 and 19,300 cal yr BP, the proportion of *S. pinnata* peaked at c. 60%. After this peak, the abundance of *S. pinnata* dropped rapidly and remained low for the remainder of this zone. *Fragilaria* cf. *acutirostrata* and *Gyrosigma spencerii* occur consistently at low numbers throughout this zone.

Pac-2: 10.7–9.2 m depth (c. 16,000–11,000 cal yr BP)

This zone was marked by an increase of organic matter in the sediments and a contemporaneous transition from sediments dominated by *Cyclotella stelligera*, to one dominated by *Staurisira pinnata*, and other benthic or attached diatoms

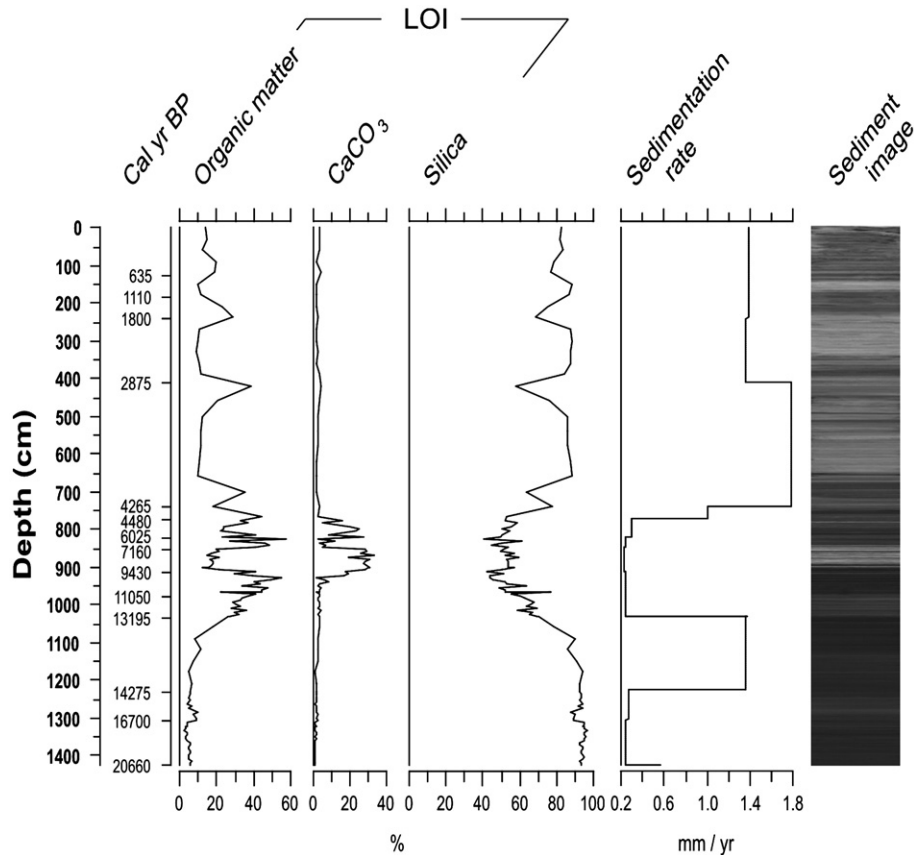


Figure 3. Loss on ignition data for sediments from Lake Pacucha, Peru.

Staurosirella leptostauron and *Fragilaria brevistriata*. The raphinid diatoms, *Navicula* cf. *mournei*, and *N. subrotundata* occurred as regular components at about 5% throughout this zone. *Achnanthis modestiforme* increased in abundance from a trace presence at the start of the zone to c. 40% at 11,500 cal yr BP. Although centric diatoms were generally rare in this zone, three distinct peaks of *C. stelligera* (c. 14,360 and 13,550 cal yr BP) and one of *Aulacoseira ambigua* (c. 12,940 cal yr BP) were evident.

Pac-3: 9.2–7.55 m depth (c. 11,000–5000 cal yr BP)

Sediments of this zone were lake muds intercalated with layers of CaCO_3 . This zone was dominated by raphinid diatoms and centrics were rare. However, two adjacent samples from within a 10-cm long layer of greenish gyttja, with inferred ages of c. 8730 and 8300 cal yr BP, contained up to 77% *Aulacoseira ambigua*. Samples from carbonate-layers flanking the peak of these centric-dominated samples had such low concentrations of diatoms that the counts were excluded from the analysis. Raphinid taxa generally associated with epilithic, epiphytic or moderately saline habitats with peak abundances in this zone were: *Achnanthes minutissima*, *A. exigua*, *A. cf. pusilla*, *Amphora veneta*, *Anomoneis* spp., *Cymbella cistula*, *Gomphonema parvulum*, *Navicula cryptotonella*, and *N. subrotundata*. *Hantzschia amphioxys*, an aerophilic taxon is recorded in

this zone. The araphinid diatoms *Staurosira construens*, and *Synedra* spp. increased in abundance, while *Staurosira pinnata* and *Staurosirella leptostauron* exhibit an overall decline. Toward the end of this zone, *Fragilaria brevistriata* started to increase in abundance at c. 7800 cal yr BP, fell in abundance between 7240 and 7000 cal yr BP, before rising to a more sustained peak at c. 6670 cal yr BP.

Pac-4: 7.55–0 m depth (5000–0 cal yr BP)

This zone comprised lake muds with relatively high organic content. Most samples in this zone were dominated by *Aulacoseira ambigua*, but *Navicula subrotundata* and *Staurosirella leptostauron* were intermittently abundant. Most of the raphinid diatoms found in Pac-3 were less abundant or absent in this zone. In the last 2000 yr of this record *Gyrosigma spencerii* occurred consistently for the first time since Pac-1.

Multivariate analysis of fossil diatom data

The first two axes of the DCA of fossil diatom data reveal strong separation of the four local diatom zones. Pac-1 (c. 24,700–16,000 cal yr BP) samples dominated by the *Cyclotella stelligera* are clustered near the origin of Axis 1, while the other extreme of Axis 1 is characterized by the samples rich in *Aulacoseira ambigua* that form Pac-4 (c. 5000–0 cal yr BP). Axis 2 is characterized by samples rich in

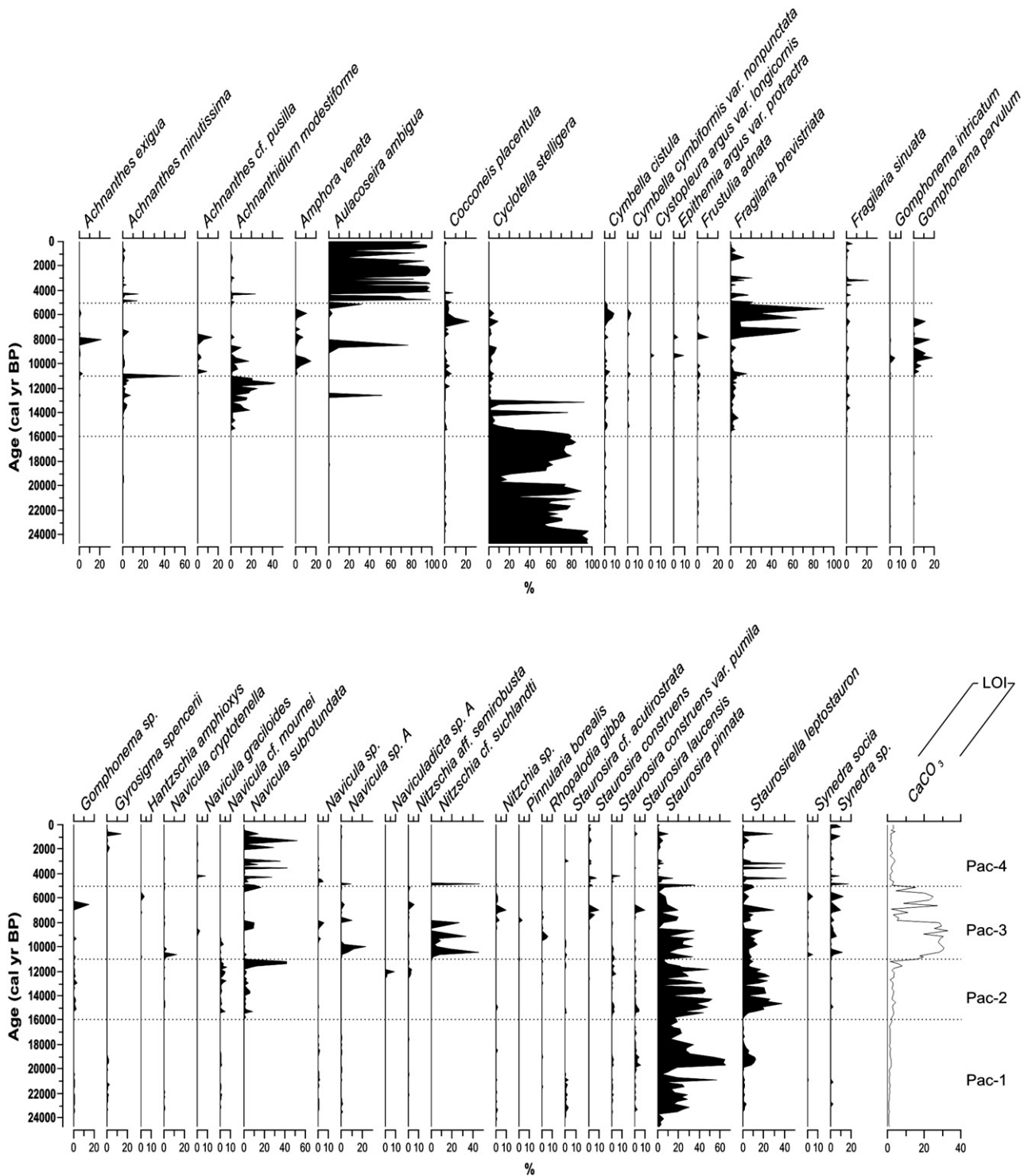


Figure 4. Percentage fossil diatom data for selected taxa (occurring at >3%) from the sediments of Lake Pacucha, Peru.

pennate diatoms, with samples rich in *Achnanthidium modestiforme*, *Navicula* cf. *mournei*, *Stauriosirella leptostauron* and *Stauriosira pinnata* that characterize Pac-2 (c. 16,000–11,000 cal yr BP), lying close to the origin. At the positive extreme of Axis 2 are the samples of Pac-3 (c. 11,000–5000 cal yr BP), which are rich in benthic, alkaliphilous species or shallow water-indicator species such as: *Amphora veneta*,

Rhopalodia gibba, *Anomoneis* spp., *Gomphonema parvulum*, and *Cocconeis placentula*.

The rate of change calculated from the Euclidean distance between samples on the first three axes of the DCA samples output suggests that the Holocene has been subject to much more rapid changes than any of those that took place during the terminal Pleistocene (Fig. 5B).

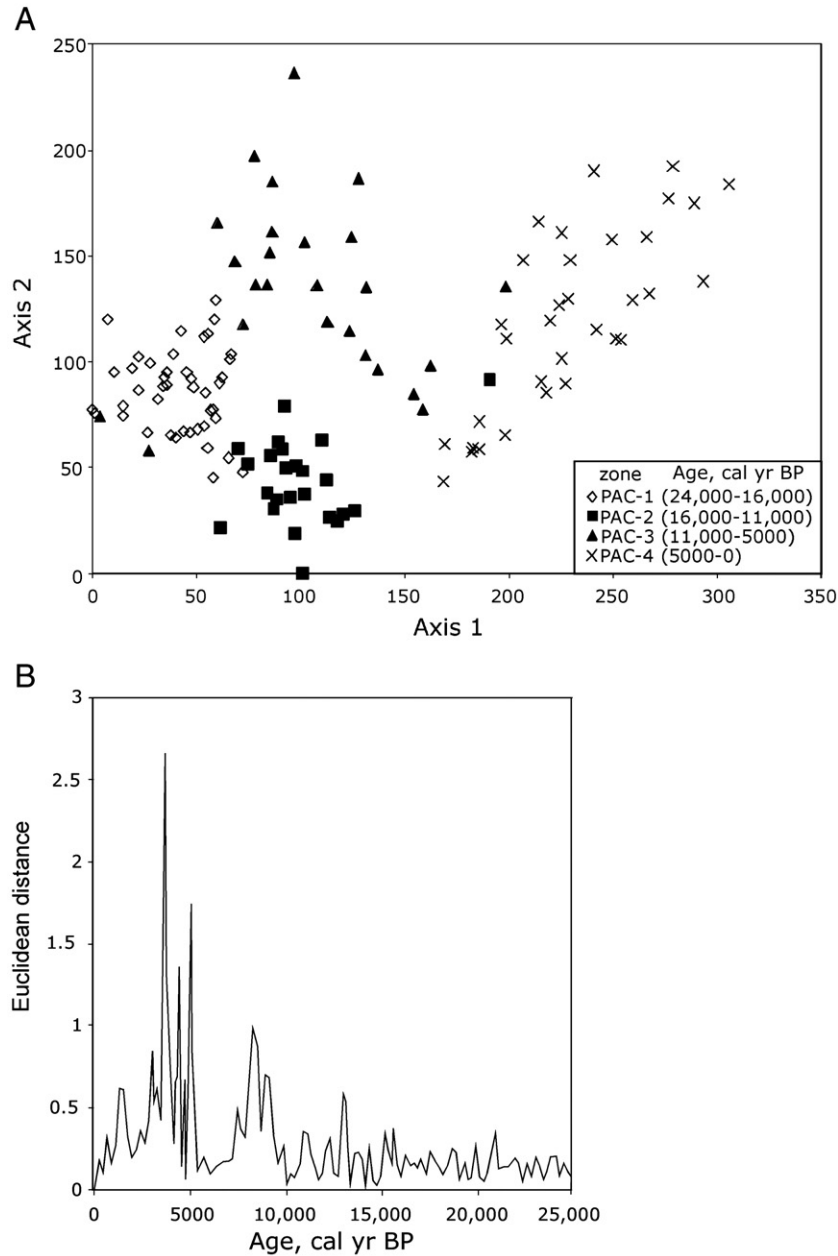


Figure 5. Results of the Detrended Correspondence Analysis of fossil diatoms data from Lake Pacucha. (A) Sample scores for Axes 1 and 2 showing locations of samples attributed to local diatom zones. (B) Rate of change (Euclidean distance between adjacent sample scores divided by inter-sample time) between samples plotted against time.

A few ‘misplaced’ samples cross into another zone. Most notably samples from Pac-2 or Pac-3, occur in Pac 1 or Pac 4. In each case, the sample differs from those of its stratigraphic neighbors by being rich in centric diatoms.

Discussion

The multivariate analysis separates samples from relatively deep-water habitats across Axis 1, while Axis 2 separates samples from relatively shallow water environments. The basal samples of this core that form Pac-1 represent full glacial conditions in the Peruvian Andes. The assemblage, dominated by *Cyclotella stelligera*, appears to represent a thermally stable,

deep-water environment favoring moderately eutrophic settings. This diatom is tolerant of a range of salinities, and can be found in both deep and shallow water, but is generally most abundant in relatively cool, deep settings (De Oliveira et al., 1986; Pienitz et al., 1995; Rühland et al., 2003; Steinitz-Kannan et al., 1986; Steinitz-Kannan et al., 1993). Within zone Pac-1, peaks of *Staurosira pinnata* and *Staurosirella leptostauron* indicate the presence of shallow-water habitats (Schmidt et al., 2004). Like *C. stelligera*, *S. pinnata* has a relatively high tolerance to dissolved inorganic carbon and is moderately alkaliphilic (Rühland et al., 2003). *S. leptostauron* is a colonial alga that lives in very shallow water, but is otherwise ecologically similar to *S. pinnata* (Steinitz-Kannan et al., 1986).

Based on the diatom assemblages, a slight reduction in lake level may be evident at 23,500 cal yr BP, with lake levels oscillating, but remaining generally high until c. 16,000 cal yr BP. Within this period, the peaks of these shallow water diatoms coincide with occurrence of *Gyrosigma spencerii*, an epipelagic, salt-tolerant diatom that is commonly found in water with high conductivity (Sylvestre et al., 2001). One possibility is that the oscillations in lake level correspond to a series of warm and cool events, with the strongest warming at c. 19,500 cal yr BP. Such an inferred warming is consistent with deglacial ages for other Andean locations beginning as early as 23,000 cal yr BP (Smith et al., 2005), with a more consistent warming trend after 16,000 cal yr BP. It is notable that this lake does not contain evidence of a strong meltwater inflow, as there is none of the rapidly deposited clastics that are often associated with such systems (Bush et al., 2005; Colinvaux et al., 1997; Seltzer et al., 2000).

The transition from Pac-1 to Pac-2 is marked by an abrupt drop in lake level at c. 16,000 cal yr BP as centric diatoms are replaced by shallow-water and benthic indicator species. Some wetter oscillations occur in the early part of Pac-2, marked by sharp peaks of *Cyclotella stelligera* and *Aulacoseira ambigua*. A limnological transition is evident at c. 13,500 cal yr BP, as *C. stelligera* is replaced by *A. ambigua*. After this date, every deep-water event is dominated by *A. ambigua*, which is an indicator of polymictic environments (Rühland et al., 2003), possibly indicating sufficient seasonality to induce an overturning circulation. Pac-2 is effectively a slow transition between Pac-1 and Pac-3 as lake level falls and shallow water indicators, e.g. *Achnanthes* spp. and *Navicula* spp. become progressively more abundant. During Pac-3 the lake contracted to a very shallow system. Benthic species, e.g. *Amphora veneta*, *Anomoneis* spp., *Gomphonema parvulum* and *Rhopalodia gibba* (Gasse et al., 1997; Jenny et al., 2002), occur in the dark band of finely laminated couplets in which the pale bands are CaCO₃-rich layers. At high alkalinities diatom preservation is often poor (Gasse et al., 1997) and this zone has the largest number of samples from which fewer than 500 diatom frustules could be counted. The most probable explanation of this apparent loss of diatom abundance is post-depositional dissolution.

A series of peaks of *Fragilaria brevistriata* occurs between c. 8000 and 5000 cal yr BP. *F. brevistriata* is a small colonial diatom that is benthic, but whose chains can become part of the plankton (Patrick and Reimer, 1966; Steinitz-Kannan et al., 1986). Notably, the peaks of *F. brevistriata* alternate with peaks of CaCO₃ concentration and diatoms characteristic of very eutrophic or soil habitats, e.g. *Cocconeis placentula*, *Synedra* spp., and *Hantzschia amphioxys* (Patrick and Reimer, 1966). The CaCO₃ bands are very fine within the black gyttja matrix. It would appear that water levels rose enough for gyttja to accumulate, but that frequent, brief dry events lowered lake levels to the point that carbonate was deposited.

Pac-4 begins at 5000 cal yr BP with a deepening of the lake. *Aulacoseira ambigua* dominates most assemblages within this zone, although some lowstands are suggested by higher proportions of benthic or attached diatoms. A sample with

relatively high carbonate content and very low diatom preservation suggests a low-water event occurred at c. 750 cal yr BP.

Paleolake levels in a broader context

Lake Pacucha and the lakes of the Altiplano receive their moisture from SASM, therefore it would be anticipated that they should exhibit coincident highstands. Some difference of opinion has emerged with regard to the timing of the highstands on the Altiplano (e.g. Fritz et al., 2004; Placzek et al., 2006; Wirmann and Mourgiart, 1995). The most recent of the large paleolakes to form in the Altiplano was termed Lake Tauca. The first determinations of the Lake Tauca period based on palynological data were from short cores raised in the Lake Huiñaymarka sub-basin of Lake Titicaca. Those records suggested that the late-glacial period was a low stand, and that the high lake level formed as a result of meltwater runoff and occurred from c. 16,000 to 12,000 cal yr BP (Wirmann and Mourgiart, 1995). This argument for LGM aridity in the Andes was linked to a lack of moisture emanating from the Amazon Basin. The same argument of Amazonian aridity restricting moisture supply was invoked to explain the replacement of modern cloud forest with Puna grassland during the LGM at Siberia, Bolivia (Mourgiart and Ledru, 2003). Studies of sediment cores raised from deep-water in Lake Titicaca and deep drill cores from the Salar de Uyuni provide strong evidence of deeper-than-modern water levels from c. 30,000 until c. 15,000 cal yr BP. In the light of these records, Baker et al. (2003) suggested that an alternative interpretation of the Siberia record could invoke cooling rather than aridity. The Lake Pacucha data unequivocally support high Andean lake levels and a strong flow of Amazonian moisture during the LGM. It is important to note that the base of the Pacucha record does not reflect basin formation, and that a deep lake was already in existence at 24,700 cal yr BP.

The moisture creating that LGM highstand flowed into and across the Amazon Basin in the South American Low Level Jet (SALLJ). At the LGM the southward displacement of the ITCZ and strengthened tradewind activity resulted in a strengthened SALLJ (Cruz et al., 2005). Thus, as understanding of paleoclimatic mechanisms has improved, the basic prediction for Amazonian climates at the LGM has now swung from a default expectation of aridity to one of wetness.

The warming associated with deglaciation at Pacucha began perhaps as early as 23,000 cal yr BP, with the next millennia exhibiting oscillations in lake level. The timing of the oscillations in the Lake Pacucha record strongly resemble those from Lake Consuelo (13°S, 1360 m elevation; 470 km from Pacucha). The two records are both strongly influenced by the combination of deglacial warming and export of Amazonian moisture, consequently they appear similar to one another (Bush et al., 2004b; Urrego et al., 2005). At c. 16,000 cal yr BP the tendency toward a continuous warming is evident in both records, and at Pacucha this coincides with the onset a gradual fall in lake level.

The period between c. 12,500 and 11,000 cal yr BP that encompasses the Younger Dryas event shows no marked change

in the diatom or sedimentary record. Pacucha is consistent with other Andean tropical southern Andean records, which apparently did not register this event, e.g. Lakes Chochos (Bush et al., 2005), Titicaca (Paduano et al., 2003) and Junin (Seltzer et al., 2000).

Considerable debate has surrounded the timing of Holocene high and low stands in Andean lakes and whether a single unifying precessional cycle underlies them. One observation is that the dry event appears to be time-transgressive, occurring as early as 9500–7300 cal yr BP at Lake Chochos, Peru (7°S) (Bush et al., 2005), versus c. 6000–2400 cal yr BP at Taypi Chaka Kkota, Bolivia (16°S) (Abbott et al., 2003). In a study of lakes on the Altiplano, Abbott et al. (2003) found about a 2000-year lag in the timing of the dry event, with more northerly lakes responding earlier. Abbott et al. (ibid) suggested that in a system where convection was so important to precipitation, a latitudinal drift in wet season insolation minima may have underlain the observed pattern. This rate of drift was close to 1° of latitude per millennium, and while perhaps explaining differences within the Altiplano, at larger scales inter-site variables may have been stronger than changes in insolation.

In most lakes investigated so far in the high Andes, the nadir of Holocene lake-level lagged the wet-season insolation minimum (e.g. Tapia et al., 2003). At Lake Pacucha, the relationship was a little more complex as the initial decline in lake level appeared to track changing insolation, but this is not a satisfying explanation of the entire lowstand history. The timing of onset of the marked lowstand at Pacucha is similar to that of Lake Junin (Seltzer et al., 2000) and the ice core from Huascaran (Thompson et al., 1995), both of which suggest strong insolation-related peaking around 9000–10,000 cal yr BP.

The lowstand that forms at Pacucha at c. 10,000 cal yr BP has the highest proportion of benthic and alkaliphilous diatoms in the core, and coincides with deposition of CaCO₃. Extremely fine laminations of black gyttja rich in salt-tolerant benthic species alternate with carbonate layers. Interspersed with these layers are some broader green-black gyttjas that contain *Synechra* species suggesting somewhat deeper water and relatively eutrophic conditions. It appears that wetter conditions were beginning to return to this record by c. 8700 cal yr BP. However, this band of *Aulacoseira*-rich sediment is only c. 10 cm in thickness, probably representing a period of about 600 yr. A summary diagram of diatom functional types relative to insolation and dissolution (Fig. 6) reveals an apparent conformity to the wet-season (September to March) precessional variation in insolation. As insolation falls, so convective activity lessens and precipitation is reduced: with clearer skies and less rainfall both the precipitation:evaporation ratio and lake level fall. The peak of this drought should have been at c. 10,000 cal yr BP, with rising lake levels thereafter.

After c. 8300 cal yr BP, there was some deepening of the lake, but the lake did not maintain a highstand and frequent dry events lowered lake levels markedly. This period of lake level volatility lasted until c. 5000 cal yr BP and coincided with the lowstand generally documented in Andean and Amazonian lake records (e.g. Abbott et al., 2003; Baker et al., 2001b; Paduano et al., 2003). A satisfactory explanation of the timing of this

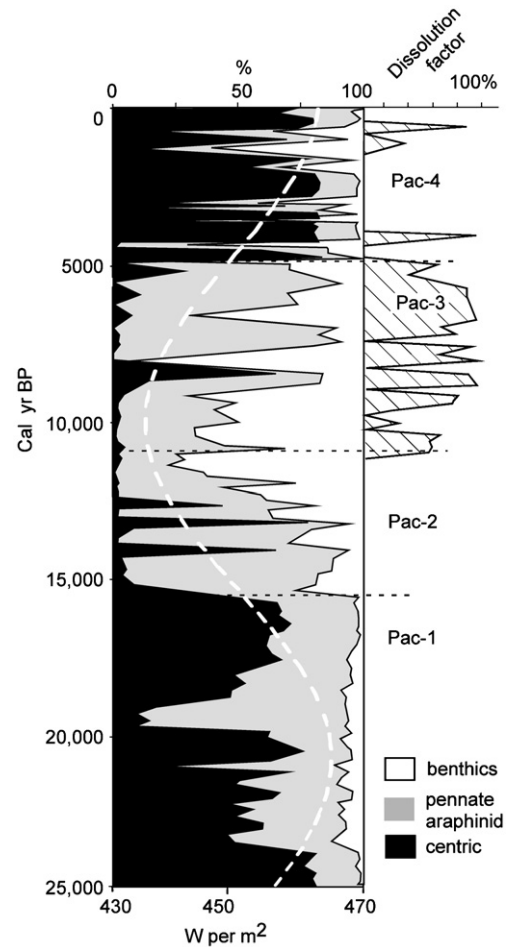


Figure 6. Summary diagram of fossil diatom data from Lake Pacucha, Peru. The “dissolution factor,” which is effectively 500 (our standard diatom count) minus the number actually counted on an entire slide, rises when diatom preservation is poor. Boundaries of the local diatom zones are shown by dotted lines. September to March (wet season) insolation for 13°S (Berger, 1992) is shown by the dashed pale line.

event is lacking, as it clearly lags precessional minima. One possibility is that the decline in El Niño activity between c. 8000 and 5000 cal yr BP establishes an ENSO neutral environment (Rein, 2007; Rodbell et al., 1999). It should be noted that El Niño did not die down completely during this period, but was overall just less active (Moy et al., 2002; Riedinger et al., 2002). When ENSO forcing is weak, it has been suggested that even small northward shifts of the ITCZ or establishment of a tropical North Atlantic warm pool can induce droughts in Amazonia (Baker, 2002; Marengo, 2004; Marengo, 2007; Vuille et al., 2000). Such a movement has been hypothesized as an explanation of the Amazonian megadrought of 2002–2005 (Marengo et al., 2008).

The additive effect of a weakened ENSO and slowly increasing wet season insolation may have thrown the region into a drought-prone state in which lake levels were generally higher than at the 10,000 cal yr BP nadir of insolation, but could quickly flip back to a lowstand state. Thus, insolation does play a role in the timing of the dry event in the Andes, but it may be that the role of insolation

changes from an essentially local forcing in the terminal Pleistocene and earliest Holocene, to a more indirect, but no less effective role in the mid-Holocene.

Within the generally highstand conditions of the last 5000 yr there were several instances when benthic diatoms increased in abundance, probably indicating brief lowering of lake level. The strongest of these events occurred at c. 750 cal yr BP and coincided with somewhat elevated sedimentary CaCO₃ concentrations. This lowstand is broadly coincident with one identified in the Quelccaya ice cap record (~700–800 cal yr BP) (Thompson et al., 2000).

One of the key observations that we make is that the most extreme climatic events of this record are not associated with climate change during the terminal ice age, but are within the Holocene. The rate of change between samples (Fig. 5B) shows increasing amplitudes through time. The highest rates of change that are coincident with the return of wetter conditions, possibly linked to enhanced El Niño activity, occur at c. 5000 cal yr BP. This period also corresponds to fossil pollen data for an intensification of human activity in the landscape (Valencia new data). With or without the influence of humans, rates of climate change appear to be faster within the Holocene than in full glacial or deglacial times. This observation also applies to lowland Amazonian pollen records (Absy et al., 1991; Bush et al., 2004a; Urrego et al., 2005), and is significant as we seek analogs for rates of anticipated climate change and their impacts on biodiversity.

Conclusions

A 24,700-yr sedimentary record from Lake Pacucha, Peru, yielded a fossil diatom record from the Central Andes. With regard to the four initial hypotheses raised: our data are consistent with a wet LGM not a dry LGM, there is no clear indication of a Younger Dryas event, and that ENSO may well significantly influence lake level in the Andes. Our data indicate a relatively early onset of deglaciation, and an insolation-driven history of lake level. The LGM highstand was consistent with other records from the Altiplano and the Amazon Basin and would be explained by a strengthened inflow of moisture from an ITCZ displaced to the south and intensification of the South American Low Level Jet (Bush, 2005). Deglaciation may have begun as early as 23,000 cal yr BP, marked by oscillations in lake level. At 16,000 cal yr BP lake level had dropped so that centric diatoms were replaced by benthic and shallow-water species. The pattern of lake level decline matched that of the precessional reduction in wet season (September–March) insolation. A lowstand formed c. 10,000 yr ago, at which point the lake was somewhat saline and precipitating CaCO₃. This dry phase was briefly interrupted at c. 8700 cal yr BP, but lake levels did not stabilize and the period from c. 8300 cal yr BP until c. 5000 cal yr BP was one of marked volatility of lake level. A mechanism is suggested in which, during a period of weak ENSO, the influence of the tropical Atlantic dipole was heightened, resulting in an overall wetter environment being interspersed with periods of drought in Amazonia.

The Holocene is seen to be a period of large limnological oscillations, which had profound ecological consequences on

this lake system. The changes were neither gradual nor linear, but rather consisted of rapid switching of conditions. From the archaeological record it is also evident that those climatic changes also induced cultural responses. As we search for analogs on which to base predictions of biodiversity loss in the face of coming climate change, it is important to realize that in the tropics rapid climate change has been a characteristic of the Holocene and climatic stability should not be assumed.

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References

- Aalto, R., Maurice-Bourgoin, L., Dunne, T., Montgomery, D. r., Nittouer, C.A., Guyot, J.-L., 2003. Episodic sediment accumulation on Amazonian flood plains influenced by El Niño/Southern Oscillation. *Nature* 425, 493–497.
- Abbott, M.B., Wolfe, B.B., Wolfe, A.P., Seltzer, G.O., Aravena, R., Mark, B.G., Polissar, P.J., Rodbell, D.T., Rowe, H.D., Vuille, M., 2003. Holocene paleohydrology and glacial history of the central Andes using multiproxy lake sediment studies. *Palaeogeography Palaeoclimatology Palaeoecology* 194, 123–138.
- Absy, M.L., Clief, A., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Silva, F. d., Soubiès, F., Suguio, K.T., van der Hammen, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de L'Amazonie au cours des 60,000 dernières années. Première comparaison avec d'autres régions tropicales. *Comptes Rendus Academie des Sciences Paris, Series II* 312, 673–678.
- Baker, P.A., 2002. Trans-Atlantic climate connections. *Science* 5565, 67–68.
- Baker, P.A., Bush, M.B., Fritz, S., Rigsby, C.A., Seltzer, G., Silman, M.R., 2003. Last glacial maximum in an Andean cloud forest environment (eastern Cordillera, Bolivia): Comment. *Geology* e26.
- 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.
- Battarbee, R.W., 1986. *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons, New York.
- Behling, H., 2002. Late Quaternary vegetation and climate dynamics in southeastern Amazonia inferred from Lagoa da Confusao in Tocantins State. *Northern Brazil Amazoniana* 17, 27–39.
- Berger, A., 1992. Astronomical theory of paleoclimates and the last glacial–interglacial cycle. *Quaternary Science Reviews* 11, 571–581.
- Birks, H.J.B., Birks, H.J.B., 1998. D.G. Frey and E.S. Deevey Review 1: Numerical tools in palaeolimnology—Progress, potentialities, and problems. *Journal of Paleolimnology* 20, 307–332.
- Bush, M.B., 2005. Of orogeny, precipitation, precession and parrots. *Journal of Biogeography* 32, 1301–1302.
- Bush, M.B., De Oliveira, P.E., Colinvaux, P.A., Miller, M.C., Moreno, E., 2004a. Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography Palaeoclimatology Palaeoecology* 214, 359–393.
- Bush, M.B., Gosling, W.D., Colinvaux, P.A., 2007a. Climate Change in the Lowlands of the Amazon Basin. In: Bush, M.B., Flenley, J.R. (Eds.), *Tropical Rainforest Responses to Climate Change*. Praxis Springer, Chichester, pp. 55–71.

- Bush, M.B., Hanselman, J.A., Hooghiemstra, H., 2007b. Andean montane forests and climate change. In: Bush, M.B., Flenley, J.R. (Eds.), *Tropical rainforest responses to climate change*. Praxis Springer, Chichester, pp. 33–48.
- Bush, M.B., Hansen, B.C.S., Rodbell, D., Seltzer, G.O., Young, K.R., León, B., Silman, M.R., Abbott, M.B., Gosling, W.D., 2005. A 17,000 year history of Andean climatic and vegetation change from Laguna de Chochos, Peru. *Journal of Quaternary Science* 20, 703–714.
- Bush, M.B., Miller, M.C., de Oliveira, P.E., Colinvaux, P.A., 2002. Orbital forcing signal in sediments of two Amazonian lakes. *Journal of Paleolimnology* 27, 341–352.
- Bush, M.B., Silman, M.R., 2004. Observations on Late Pleistocene cooling and precipitation in the lowland Neotropics. *Journal of Quaternary Science* 19, 677–684.
- Bush, M.B., Silman, M.R., Urrego, D.H., 2004b. 48,000 years of climate and forest change from a biodiversity hotspot. *Science* 303, 827–829.
- Bush, M.B., Stute, M., Ledru, M.-P., Behling, H., Colinvaux, P.A., De Oliveira, P.E., Grimm, E.C., Hooghiemstra, H., Haberle, S., Leyden, B.W., Salgado-Labouriau, M.-L., Webb, R., 2001. Paleotemperature estimates for the lowland Americas between 30°S and 30°N at the last glacial maximum. In: Markgraf, V. (Ed.), *Interhemispheric Climate Linkages: Present and Past Interhemispheric Climate Linkages in the Americas and their Societal Effects*. Academic Press, New York, pp. 293–306.
- Clement, A.C., Cane, M.A., Seager, R., 2001. An orbitally driven tropical source for abrupt climate change. *Journal of Climate* 14, 2369–2375.
- Colinvaux, P.A., Bush, M.B., Steinitz-Kannan, M., Miller, M.C., 1997. Glacial and postglacial pollen records from the Ecuadorian Andes and Amazon. *Quaternary Research* 48, 69–78.
- Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., 1999. *Amazon pollen manual and atlas*. Harwood Academic Press, New York.
- Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* 274, 85–88.
- Colinvaux, P.A., Irion, G., Räsänen, M.E., Bush, M.B., Nunes de Mello, J.A.S., 2001. A paradigm to be discarded: geological and paleoecological data falsify the Haffer and Prance refuge hypothesis of Amazonian speciation. *Amazoniana* 16, 609–646.
- Cowling, S.A., Betts, R.A., Cox, P.M., Ettwein, V.J., Jones, C.D., Maslin, M.A., Spall, S.A., 2004. Contrasting simulated past and future responses of the Amazonian forest to atmospheric change. *Philosophical Transactions of the Royal Society of London ser. b* 359, 539–547.
- Cowling, S.A., Maslin, M.A., Sykes, M.T., 2001. Paleovegetation simulations of lowland Amazonia and implications for neotropical allopatry and speciation. *Quaternary Research* 55, 140–149.
- Cruz, Jr., F.W., Burns, S.J., Karmann, I., Sharp, W.D., Vuille, M., Cardoso, A.O., Ferrari, J.A., Silva Dias, P.L., Vlana, Jr., O., 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. *Nature* 434, 63–66.
- De Oliveira, P.E., Steinitz-Kannan, M., Miller, M.C., Colinvaux, P.A., 1986. 1986 Las diatomeas del Ecuador III. Diatomeas fósiles de la laguna de Kumpaka Provincia de Morona Santiago. *Revista Geográfica, Instituto Geográfico Militar, Quito* 24, 41–60.
- Ellenberg, H., 1958. Wald oder steppe? Die natürliche pflanzendecke der Anden Perus. *Umschau* 1958, 645–681.
- EPICA PROJECT MEMBERS, 2006. One-to-one coupling of glacial climate variability in Greenland and Antarctica. *Nature* 444, 195–198.
- Fairbanks, R.G., Richard, A., Mortlock, R.A., Chiu, T.-C., Cao, L., Kaplan, A., Guilderson, T.P., Fairbanks, T.W., Bloom, A.L., 2005. Marine radiocarbon calibration curve spanning 0 to 50,000 years B.P. based on paired $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ and ^{14}C dates on pristine corals. *Quaternary Science Reviews* 24, 1781–1796.
- 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. Hydrologic variation during the last 170,000 years in the southern hemisphere tropics of South America. *Quaternary Research* 61, 95–104.
- Fritz, S.C., Baker, P.A., Seltzer, G.O., Ballantyne, A., Tapia, P.M., Cheng, H., Edwards, R.L., 2007. Quaternary glaciation and hydrologic variation in the South American tropics as reconstructed from the Lake Titicaca drilling project. *Quaternary Research* 68, 410–420.
- Gasse, F., Barker, P., Gell, P.A., Fritz, S.C., Chalief, F., 1997. Diatom-inferred salinity in paleolakes: an indirect tracer of climate change. *Quaternary Science Reviews* 16, 547–563.
- Hansen, B.C.S., 1995. A review of lateglacial pollen records from Ecuador and Peru with reference to the Younger Dryas Event. *Quaternary Science Reviews* 14, 853–865.
- Heine, J.T., 1993. A reevaluation of the evidence for a Younger Dryas climatic reversal in the tropical Andes. *Quaternary Science Reviews* 12, 769–779.
- Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25, 101–110.
- Hooghiemstra, H., 1984. *Vegetational and climatic history of the high plain of Bogota, Colombia*. *Dissertationes Botanicae*. J. Cramer, Vaduz, p. 79.
- Jenny, B., Valero-Garcés, B., Urrutia, R., Kelts, K., Veit, H., Appleby, P.G., Geyh, M., 2002. Moisture changes and fluctuations of the westerlies in Mediterranean Central Chile during the last 2000 years: The Laguna Aculeo record (33°59'S). *Quaternary International* 87, 3–18.
- Lange Bertalot, H. (1998). *Tropical diatoms of South America I. Iconographia diatomologica*. Koeltz Scientific Books.
- Lange Bertalot, H. (2000). *Diatoms of the Andes From Venezuela to Patagonia/Tierra del Fuego*. Koeltz Scientific Books.
- Liu, K.-b., Colinvaux, P.A., 1985. Forest changes in the Amazon basin during the last glacial maximum. *Nature* 318, 556–557.
- Marengo, J., 2004. Climatology of the LLJ east of the Andes as derived from NCEP reanalyses. *Journal of Climate* 17, 2261–2280.
- Marengo, J., 2007. Climate change and the hydrological modes of the wet tropics. In: Bush, M.B., Flenley, J.R. (Eds.), *Tropical Rainforest Responses to Climate Change*. Praxis, Chichester, pp. 237–268.
- Marengo, J.A., Nobre, C.A., Tomasella, J., Oyama, M.D., Sampaio de Oliveira, G., de Oliveira, R., Camargo, H., Alves, L.M., Brown, I.F., 2008. The Drought of Amazonia in 2005. *Journal of Climate* 21, 495–516.
- Marengo, J.A., Nobre, C.A., 2001. General characteristics and variability of climate in the Amazon Basin and its links to the global climate system. In: McClain, M.E., Victoria, R.L., Richey, J.E. (Eds.), *The Biogeochemistry of the Amazon Basin*. Oxford University Press, Oxford, pp. 17–41.
- Maslin, M., Burns, S.J., 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. *Science* 290, 2285–2287.
- Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. *Science* 290, 2291–2294.
- McCune, B., Mefford, M.J., 1999. *PC-ORD*. Multivariate analysis of ecological data. Software Design, Gleneden Beach, Oregon.
- Mortimer, C.H., 1956. The oxygen content of air-saturated fresh water, and aids in calculating percentage saturation. *Mitteilung Internationale Vereinigung für Limnologie* 6, 120.
- Mourguiart, P., Ledru, M.P., 2003. Last Glacial Maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia). *Geology* 31, 195–198.
- Moy, C.M., Seltzer, G.O., Rodbell, D.T., Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420, 162–164.
- Paduano, G. (2001). *Vegetation and fire history of two tropical Andean lakes, Titicaca (Peru/Bolivia), and Caserochocha (Peru) with special emphasis on the Younger Dryas chronozone*. Unpublished Ph.D. thesis, Florida Institute of Technology.
- 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, 259–279.
- Patrick, R., Reimer, C.W., 1966. *The diatoms of the United States: Volume 1*.
- Patrick, R., Reimer, C.W., 1975. *The diatoms of the United States: Volume 2*.
- Pienitz, R., Smol, J.P., Birks, H.J.B., 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology* 13, 21–49.
- Placzek, C., Quade, J., Patchett, P.J., 2006. Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for causes of tropical climate change. *Geol Soc Am Bull* 118, 515–532.
- Rein, B., 2007. How do the 1982/83 and 1997/98 El Niños rank in a geological record from Peru? *Quaternary International* 56–66.

- Riedinger, M.A., Steinitz-Kannan, M., Last, W.M., Brenner, M., 2002. A 6100 14C yr record of El Niño activity from the Galapagos Islands. *Journal of Paleolimnology* 27, 1–7.
- Rodbell, D.T., Seltzer, G.O., Anderson, D.M., Abbott, M.B., Enfield, D.B., Newman, J.H., 1999. An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. *Science* 283, 516–520.
- Rühland, K.M., Smol, J.P., Pienitz, R., 2003. Ecology and spatial distributions of surface-sediment diatoms from 77 lakes in the subarctic Canadian treeline region. *Canadian Journal of Botany* 81, 57–73.
- Sandweiss, D.H., Maasch, K.A., Burger, R.L., Richardson III, J.B., Rollins, H.B., Clement, A., 2001. Variation in Holocene El Niño frequencies: Climate records and cultural consequences in ancient Peru. *Geology* 29, 603–606.
- Schmidt, R., Kamenik, C., Lange-Bertalot, H., Klee, R., 2004. *Fragilaria* and *Staurosira* (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for palaeoclimatology. *Journal of Limnology* 63, 171–189.
- Seltzer, G., Rodbell, D., Burns, S., 2000. Isotopic evidence for late Quaternary climatic change in tropical South America. *Geology* 28, 35–38.
- Smith, J.A., Seltzer, G.O., Farber, D.L., Rodbell, D.T., Finkel, R.C., 2005. Early local last glacial maximum in the tropical Andes. *Science* 308, 678–681.
- Steinitz-Kannan, M., De Oliveira, P.E., Miller, M.C., Colinvaux, P.A., 1986. Las diatomeas del Ecuador I. Diatomeas Fósiles de la Laguna de Cunro, Provincia de Imbabura. *Revista del Museo Ecuatoriano de Ciencias Naturales*, Quito.
- Steinitz-Kannan, M., Nienaber, M., Riedinger, M., Kannan, R., 1993. The fossil diatoms of lake Yambo, Ecuador. A Possible Record of El Niño Events. *Bulletin de l'Institut Français d'Études Andines* 22, 227–241.
- Stuiver, M., Reimer, P.J., 1993. Extended 14C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35, 215–230.
- Stuiver, M., Reimer, P. J., and Reimer, R. W. (2005). Calib 5.0 [WWW program and documentation].
- Sylvestre, F., Beck-Eichler, B., Duleba, W., Debenay, J.-P., 2001. Modern benthic diatom distribution in a hypersaline coastal lagoon: the Lagoa de Araruama (R.J.), Brazil. *Hydrobiologia* 443, 213–231.
- 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, 139–164.
- Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.-N., Henderson, K.A., Cole-Dai, J., Bolsan, J.F., Liu, K.G., 1995. Late glacial stage and Holocene tropical ice core records from Huascarán, Peru. *Science* 269, 46–50.
- Thompson, L.G., Mosley-Thompson, E., Henderson, K.A., 2000. Ice-core palaeoclimate records in tropical South America since the Last Glacial Maximum. *Journal of Quaternary Science* 15, 377–394.
- Urrego, D.H., Silman, M.R., Bush, M.B., 2005. The last glacial maximum: stability and change in an Andean cloud forest. *Journal of Quaternary Science*. *Journal of Quaternary Science* 20, 693–701.
- Van 't Veer, R., Islebe, G.A., Hooghiemstra, H., 2000. Climatic change during the younger Dryas Chron in northern south America: a test of the evidence. *Quaternary Science Reviews* 19, 1821–1835.
- Van der Hammen, T., 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* 1, 3–26.
- Van der Hammen, T., Hooghiemstra, H., 1995. The El Abra stadial, a Younger Dryas equivalent in Colombia. *Quaternary Science Reviews* 14, 841–851.
- 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* 105, 12447–12460.
- Whitmore, T.C., Prance, G.T., 1987. *Biogeography and Quaternary History in Tropical America*. Oxford Science Publications, Oxford.
- Wirmann, D., Mourgiart, P., 1995. Late Quaternary spatio-temporal limnological variations in the Altiplano of Bolivia and Peru. *Quaternary Research* 34, 344–354.