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The Last Glacial Maximum: stability and change in a western Amazonian cloud forest

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ABSTRACT: The climatic and vegetation history of a western Amazonian cloud forest is documented in a continuous pollen record spanning the full last glacial period between 43.5 and 22k cal. yr BP. The chronology for this record is based on eight radiocarbon dates yielding a low-resolution pollen analysis for the region. A bioclimatic envelope model was generated on the basis of modern altitudinal distributions and the pollen data, which produced a glacial palaeotemperature estimate of ca. −5 °C relative to present. Palaeoecological evidence of continuous moist cloud forest cover in the basin indicates that western Amazonian forests were not fragmented during the LGM. This evidence supports wet conditions in western Amazonia at the LGM and further refutes hypotheses of Amazonian aridity during the last ca. 44k cal. yr BP. Copyright © 2005 John Wiley & Sons, Ltd.

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KEYWORDS: Lake Consuelo; western Amazonian cloud forests; Last Glacial Maximum; species migrations; forest constancy.

Introduction

Glacial climate fluctuations caused significant changes to the structure and distribution of natural communities worldwide. It is widely accepted that species responded to past climatic changes by adjusting their geographical ranges as occupied areas became unfavourable (Prentice *et al.*, 1991; Davis and Shaw, 2001). In the Neotropics however, the magnitude and mode of these changes during the Last Glacial Maximum (LGM) are fairly unknown due to the lack of Palaeoecological records. Relatively few records exist from the Andes (Hooghiemstra, 1984, Hansen *et al.*, 1984, Rull, 1998; Heusser *et al.*, 1999, van der Hammen and Hooghiemstra, 2003, Mourguiart and Ledru, 2003) or the Amazon lowlands (Absy and van der Hammen, 1976; Bush *et al.*, 1990; Absy *et al.*, 1991; van der Hammen *et al.*, 1992; Colinvaux *et al.*, 1996; Salgado-Labouriau *et al.*, 1997; Mayle *et al.*, 2000; Burbridge *et al.*, 2004), while most glacial records show sedimentary hiatuses around the LGM, severely limiting the available information on glacial climate and vegetation change in Neotropical regions (Ledru *et al.*, 1998). As a consequence, the magnitude of glacial temperature decline and moisture balance in the tropics still remain controversial. Estimates of temperature depression for tropical regions during the LGM range from −2 to −9 °C relative to modern (Ballantyne *et al.*, 2005). Glacial temperature depression of ca. −2 °C have been estimated on the basis of marine records (e.g. Rühlemann *et al.*, 1999; Lea *et al.*, 2003) while estimates of ca. −9 °C are based on terrestrial records (e.g. Porter, 2001; Paduano *et al.*, 2003; Ballantyne *et al.*, 2005). At a regional scale, consistent views also exist. For instance, in the Central Andes and western Amazonia estimates of the magnitude of glacial cooling based on a range of Palaeoecological and climatic proxies consistently range between 5 and 9 °C (Wright *et al.*, 1989; Klein *et al.*, 1998; Porter, 2001; Mourguiart and Ledru, 2003; Paduano *et al.*, 2003; Bush *et al.*, 2004).

Vegetation response to past climate changes has also led to opposing views among palaeoecologists during the past few decades. One of the first postulated premises concerning vegetation changes during glacial periods in the tropical regions is the refugia hypothesis (Haffer, 1969). This hypothesis stated that the Amazon Basin was dry during the LGM and that this aridity resulted in extensive forest fragmentation, promoting speciation within geographically isolated forests, so-called forest refugia (Haffer, 1969). Forest fragmentation in Amazonia has been supported on the basis of increased dominance of grass pollen in multiple records from the region (e.g. Absy *et al.*, 1991; van der Hammen and Absy, 1994; Mourguiart and Ledru, 2003). However, re-assessments of such records have suggested alternative interpretations and questioned basic assumptions of the refugia hypothesis (Nelson *et al.*, 1990; Colinvaux *et al.*, 2001; Baker *et al.*, 2004). The evidence shows constant forest cover with dynamic community composition in Amazonia during the Pleistocene and is supported both in lacustrine (Colinvaux *et al.*, 1996; Bush *et al.*, 2002; Burbridge *et al.*, 2004) and deep-sea Amazon fan sediments (Haberle, 1997; Kastner and Goñi, 2003). The linkage between reduced moisture and forest fragmentation is also controversial, as

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slightly drier conditions would not necessarily result in forest fragmentation (Bush and Silman, 2004). Accordingly, polarised views prevail regarding moisture conditions and vegetation response as well as the causation of forest fragmentation by reduced moisture in Amazonia during the LGM.

Climatic regimes in Amazonia today are fairly complex, making the reconstruction of past climates especially difficult. Regional variations may explain divergent past climate reconstructions as a single pattern is unlikely to portray past climate for the vast Amazonian region. More recently emerged views describe a relatively complex moisture and temperature history that is both spatially and temporally heterogeneous across Amazonia (Bush and Silman, 2004). Temporal variations such as the strengthening of Amazonian convection during the LGM (Baker *et al.*, 2001b) provide an example for the intrinsic complexity of this system. Accordingly, plausible reconstructions of past climatic and ecological changes in Amazonia ought to involve local factors and temporal variations, establishing a consistent correlation between modern and past climate scenarios (Mix *et al.*, 2001).

Montane forests, and especially cloud forests, are particularly sensitive to climate change as cloud base and cloud immersion regime are determined by both atmospheric temperature and humidity (Still *et al.*, 1999). Such effects of temperature and humidity on the cloud base position are both direct and indirect. Temperature increases cause the cloud base to rise, while increased air moisture resulting from increased evapotranspiration can cause the cloud base to decrease. Accordingly, as the cloud base depends on the relative magnitudes of both temperature and moisture, predictions about changes in cloud base are not straightforward.

In the western Amazonia, the modern-day balance of temperature and humidity are unlikely to have remained static in the face of past climate changes. Cloud formation processes were probably altered during periods of considerable climatic variation such as the LGM. Such changes likely influenced altitudinal distributions of cloud forest species and the structure of these forests *per se*, emphasising the significance of their vegetation history in reconstructing past climate.

In this paper, we present the vegetation and climatic history of an Andean cloud forest through the peak of the last ice age. Our analysis is based on the palynological analysis of a continuous sediment record spanning 43 500 to 22 000 cal. yr BP (43.5 to 22 cal. kyr BP, hereafter). The original record spans the period from 43.5 cal. kyr BP to modern. The selection of a cut-off point for this analysis is based on the previously identified onset of warming associated with regional deglaciation at the site (Bush *et al.*, 2004). The altitudinal location of this lake in the tropical Andes allows us to investigate such issues as: the altitudinal migration of species in response to temperature decline during the LGM and the degree of forest vegetation stability in a glacial-age cloud forest.

Study site and modern ecological and climatic setting

Lake Consuelo (13° 57.097° S, 68° 59.452° W) is located in southeastern Peru adjacent to the Bolivian border (Fig. 1). The lake lies at 1360 m above sea level (m a.s.l.), just above the modern cloud base. Lake Consuelo measures approximately 200 m wide by 700 m long and is situated in the middle of a closed basin of approximately 500 ha. This catchment basin has moderately steep slopes, ranging from 5° to 30°. We infer that tectonic activity is the most likely cause for the lake's formation, based on field observations and satellite imagery. Lake Consuelo is located on a mountain top and probably formed as a blocked drainage along a fault that finally sealed itself and held water.

In the forest around Lake Consuelo, soils are thin and superficial with high organic matter contents. Water depth ranges between 7 and 10.5 m in the centre of the lake, pH averages 5.7, and Secchi depth is reached at 1.1 m. Instrumental data for air temperature is not available for the site; however, combining known mean annual temperatures at lower elevations in the area with the known lapse rate gives an estimate of ca. 19 °C. Precipitation varies from ca. 700 mm in July and August to ca. 2000 mm in December, January and February (Vuille *et al.*, 2000).

Lake Consuelo is surrounded by cloud forest, characterised by the abundance and diversity of epiphytes and mosses, and terrestrial peat accumulation. We installed a 0.1 ha plot in which we measured all individuals ≥ 2.5 cm diameter at breast height. Just four families, Arecaceae, Moraceae, Rubiaceae and Cyatheaceae (tree ferns) made up 50% of the individuals. The most abundant species in the plot was the palm *Wettinia* cf. *agusta*, followed by *Cyathea* PN30594 (Cyatheaceae), *Maquira coriaceae* (Moraceae), *Simira* PN30595 (Rubiaceae), *Dictyocaryum lamarckianum* (Arecaceae), *Geonoma* PN30562 (Arecaceae), and *Euterpe precatoria* (Arecaceae). Taken together, these seven species account for 50% of the individuals in the plot.

The forest is composed of species that are typical of lower montane forest, with representatives near the upper end of their elevational range, e.g. *Euterpe precatoria* and *Iriartea deltoidea* (Arecaceae), and others near the lower limit of theirs, e.g. *Podocarpus* sp. (Podocarpaceae), *Symplocos* sp. (Symplocaceae), *Myrsine* sp. (Myrsinaceae) and assorted Lauraceae. One palm of note is *Dictyocaryum lamarckianum*. This species is found on wet hilltops and slopes in the lower montane Andes. At present, *D. lamarckianum* replaces the western Amazonian dominant palm *I. deltoidea* (Pitman *et al.*, 2001) just upslope of a narrow (100 m wide) zone of overlap (Silman, pers. obs.). Further downslope, we observed fairly homogeneous stands of bamboo (*Guadua sp.*). The lake shoreline is characterised by several species of Cyperaceae and *Sagittaria* (Pontederiaceae).

Methods

Sediment cores were collected using a Colinvaux–Vohnout piston corer (Colinvaux *et al.*, 1999) from the deepest part of the lake (ca. 10.5 m). The coring rig was operated from a wooden platform attached to two anchored inflatable rafts. Two parallel cores were recovered from the bottom of the lake with a 0.5-m vertical offset to ensure retrieval of adjoining points between drives. The longest sediment column (8.8-m) was analysed as missing parts were not detected. For the purposes of this paper only the glacial segment of the core (i.e. from 4.6- to 8.8-m depths) was analysed, along with a sample from the very top of the core. This top sample allows comparisons between Holocene and glacial pollen assemblages.

The sediment core was transported to the laboratory in aluminium tubes and then stored in a dark cold room at 4 °C. Sediment density measures were performed on the intact core at 1-cm intervals in the Florida Institute of Paleoenvironmental Research (University of Florida) using a Geotek Multi-Sensor Core Logger. Once the tubes were opened, a stratigraphic description was concluded using Munsell soil colour charts.

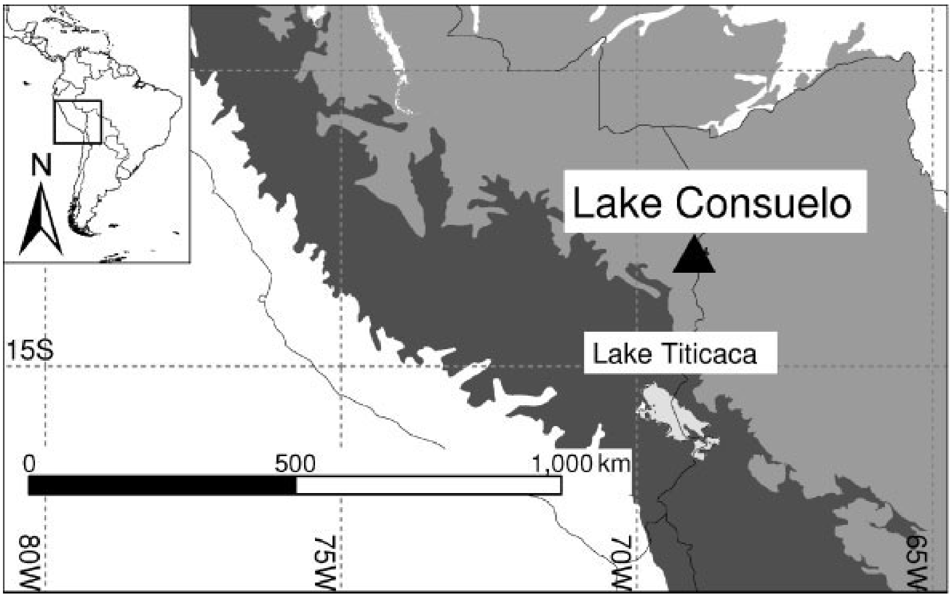

Figure 1 Map showing the location of Lake Consuelo relative to Lake Titicaca. Dark grey represents the Andes above 2000 m a.s.l. and light grey represents lower montane forests. Modified from Olson *et al.* (2001)

A preliminary low-resolution version of the pollen record from Lake Consuelo has been previously published (Bush *et al.*, 2004). For this paper, we have doubled the sampling frequency and have acquired new radiocarbon dates which provide a more detailed dataset and an improved depth–age model. The chronology of the entire core is based upon 21 ^{14}C AMS dates, with eight of those dates lying within the full glacial period. Seven out of these eight radiocarbon dates were used to construct the time control for the glacial period in Lake Consuelo. The one age rejected dates considerably younger than other neighboring ^{14}C ages in the core. This unusually young age is thought to have resulted from contamination with younger bulk sediment during laboratory handling. The calibrated timescale was completed by using recently expanded calibration curves (Weninger *et al.*, 2004). Sample ages were linearly interpolated between radiocarbon dates.

Subsamples (0.5 cm^3) were collected at 5- and 10-cm intervals for pollen analysis. Similarly sized subsamples were taken for loss-on-ignition (LOI) at 5-cm and 2.5-cm intervals depending on the sedimentation rate within different segments of the core. Standard pollen preparation techniques (Faegri and Iversen, 1989) were performed and a known number of exotic *Lycopodium* spores (Stockmarr, 1972) was added to each sample to calculate concentration and influx values. A minimum of 300 terrestrial pollen grains were counted for each sample under a Zeiss Axioskop photomicroscope at 400 × and 1000 × magnification. Aquatic and marsh pollen grains, and spores were also counted and, although excluded from the pollen sum, their percentages were calculated based on the total pollen sum of terrestrial elements. Identifications of pollen grains and spores were based on the Florida Institute of Technology reference collection and previously published pollen keys and descriptions (Hooghiemstra, 1984; Roubik and Moreno, 1991; Herrera and Urrego, 1996; Colinvaux *et al.*, 1999). Water, organic carbon and carbonate contents were determined by LOI at 105 °C, 550 °C and 1000 °C, respectively.

A bioclimatic envelop model was generated based on modern distributional data from herbarium collections taken from the W^{3}TROPICOS database (http://mobot.mobot.org/W3T/Search/vast.html; www.salvias.com). The model is based on presence/absence of a taxon. A presence for this analysis is defined as a taxon exceeding 10% of its maximum representation (Bush *et al.*, 2004). The following taxa were selected on the basis of being reliably identified to the genus or species level: *Alchornea, Alnus, Alsophylla, Begonia, Bocconia, Celtis, Clethra, Cythea, Cystopteris, Dictyocaryum, Gaiadendron, Hedyosmum, Hyeronima, Ilex, Juglans, Myrica, Myrsine, Piper, Podocarpus, Polylepis, Symplocos, Trema, Vallea* and *Zanthoxylum*. This list contains both upland and lowland elements so that the model potentially predicts both warmer and cooler conditions.

The probability distribution of likely equivalent modern elevations for a given set of taxa encountered in a Palaeoecological sample was estimated using Bayes' theorem with a uniform prior (see Bush *et al.* (2004), supporting online materials for model details). The elevation output was then translated into a range of temperature estimates using the measured adiabatic lapse rate of moist air for the region (5.6 °C km^{-1}, Bush *et al.*, 2004). Then a palaeotemperature–age plot was constructed using the inferred palaeotemperature with the highest probability. Percentage and influx diagrams were constructed using the software C2 (Juggins, 2003).

Non-metric multidimensional scaling (NMDS) was used to summarise continuous changes in species composition into a reduced ordination space that characterises the main variability in species composition among samples found within the pollen dataset (McCune and Grace, 2002). In an ordination plot, similar samples are plotted close together whereas different samples are placed far apart. Only terrestrial taxa with percentages greater than 2% were used to avoid overweighting rare taxa. NMDS (Kruskal, 1964) was performed on the untransformed data using PC-ORD (Mather, 1976) and the Bray–Curtis dissimilarity distance. The proportion of the variance represented by the resulting two-axis NMDS solution was calculated based on the sum of squared distances between the distance in the ordination space and the distance in the original space (McCune and Mefford, 1999).

Results

Chronology and sediment description

The new radiocarbon calibration for Lake Consuelo indicates that the record spans the past 43.5 cal. kyr BP (Table 1). The

Table 1 Radiocarbon and calibrated ages for sediments from glacial deposits of Lake Consuelo, Peru. Calibration according to Calpal online (Weninger *et al.*, 2004)

	Laboratory number	Description	Depth (cm)	^{14}C yr BP ± age error	Cal. kyr BP ± σ	1σ age ranges[a]
1	OS-38527	Sediment	465.0	18 950 ± 85	22.34 ± 0.27	22.60–22.07
2	OS-38528	Sediment	550.0	22 100 ± 120	25.71 ± 0.37	26.08–25.34
3	OS-34713	Plant/wood	625.0	27 400 ± 130	30.69 ± 0.31	30.99–30.38
4	OS-47204	Plant/wood	687.5	31 600 ± 250	36.62 ± 0.32	36.94–36.30
5	OS-47205	Sediment	694.5	31 600 ± 250	36.62 ± 0.32	36.94–36.30
6	OS-38529	Sediment	760.0	35 100 ± 280	40.09 ± 0.68	40.77–39.41
7[b]	OS-34714	Plant/wood	790.0	26 000 ± 130	30.75 ± 0.21	30.54–30.96
8	OS-38530	Sediment	875.0	41 800 ± 570	43.43 ± 0.73	44.15–42.70

[a] 68% range in cal. kyr BP.
[b] Rejected date.

sedimentation rate shows little variation between 43.5 and 22 cal. kyr BP, displaying an inflection point at 40 cal. kyr BP (Fig. 2). Whether other departures from the basic rate of sedimentation are real or are the result of artefacts of dating uncertainties cannot be evaluated at this time. While most stratigraphic variations in the core are not well-defined, some sedimentary changes may be described. A sandy layer of ca. 2 cm thickness was recognised at the bottom of the core around 43.5 cal. kyr BP. Between 43.5 and 22 cal. kyr BP the sediments are massive gyttjas with alternating black and very dark grey portions of irregular breadth and indistinct limits (Figs 3 and 4). Darker gyttjas coincide with increases of organic carbon (LOI-550 °C) in the sediments (Fig. 3). Declines in sediment density are also evident at 26, 30.5 to 32, 37, 39.5 and 42 cal. kyr BP.

Pollen analysis

Pollen analyses were spaced to provide a ca. 400-yr temporal resolution to ensure the detection of the main millennial-scale vegetation and climatic changes in the region. Over 170 terrestrial pollen taxa were identified throughout the record from Lake Consuelo, along with four marsh and aquatic types, and 21 spore taxa. Only the most significant pollen and spore taxa are shown in Fig. 4. No zonation is offered for this data set as the pollen spectra are remarkably constant. Note that percentages of unknown taxa fluctuate around 1% (i.e., approximately three pollen grains per sample) throughout the core.

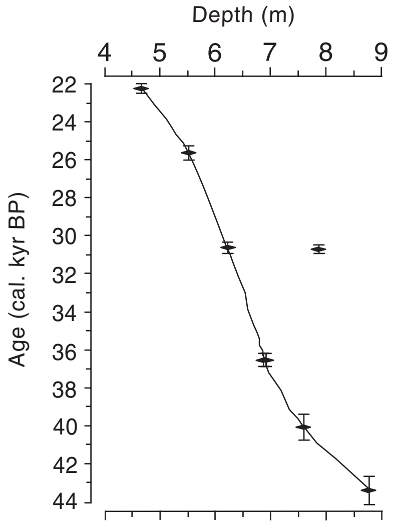

Figure 2 Age–depth model including 1σ error bars for radiocarbon dates from glacial deposits of Lake Consuelo, Peru

Despite the abundance changes of particular montane taxa in the record, the constancy of the forest vegetation is outstanding. Montane taxa such as *Alnus* (Betulaceae), *Daphnopsis* (Thymeleaceae), Solanaceae, *Hedyosmum* (Chloranthaceae), *Begonia* (Begoniaceae) and *Podocarpus* (Podocarpaceae) dominate the pollen spectrum between 43.5 and 22 cal. kyr BP. *Myrsine* (Myrsinaceae), Myrtaceae, Asteraceae, Poaceae and Melastomataceae/Combretaceae (probably Melastomataceae given their abundance at the site) are also consistently present during these glacial times. *Bocconia* appear to be dominant during early stages of the lake. An increase in the percentage of broken palynomorphs as well as a peak in *Cyathea* and *Polypodium* abundances indicate an unusual level of selective preservation around 39 cal. kyr BP. After 38 cal. kyr BP, Zygnemataceae (Chlorophyceae) progressively increase in abundance.

The Holocene pollen assemblage of Lake Consuelo is dominated by taxa characteristic of lower elevation montane forests. A distinctive set of taxa are unique to the forest of Lake Consuelo (not shown in Fig. 4). These taxa include assorted Rubiaceae and Leguminosae, *Iriartea* (Arecaceae), and *Dendropanax* (Araliaceae). *Lycopodium* (Lycopodiaceae) and *Polypodium* (Polypodiaceae) spores are also exclusive to the vegetation along with the aquatic *Sagittaria*.

Due to the steadiness of the sedimentation rates and the fairly robust chronology obtained for the record, both concentration and influx curves show highly correlated fluctuations. Therefore, only the total influx curve is shown in Fig. 4 where significant variations are evident between 43 and 40 cal. kyr BP, and between 26 and 23 cal. kyr BP.

Our bioclimatic envelope model for palaeotemperature yielded an estimate of 4.9 ± 0.7 °C cooling relative to present throughout the LGM (Fig. 4).

Ordination

NMDS analysis yielded a two-dimensional ordination after 59 iterations when the stress levels stabilised at 14.23. Axis 1 represents 70.8% of the variance while Axis 2 represents 20.8%.

The most dissimilar pollen assemblages were those dating 42.4, 39 and 38 cal. kyr BP. Despite small dissimilarities, the NMDS ordination plot showed no separation in the community composition throughout the glacial period. 96.4% of the samples were clustered around the origin of the ordination plot suggesting virtually no significant variation among samples in either of the two axes. In other words, the pollen assemblages from Lake Consuelo indicate that this cloud forest has been remarkably constant throughout the last glacial period, and much of the community change observed in the ordination is

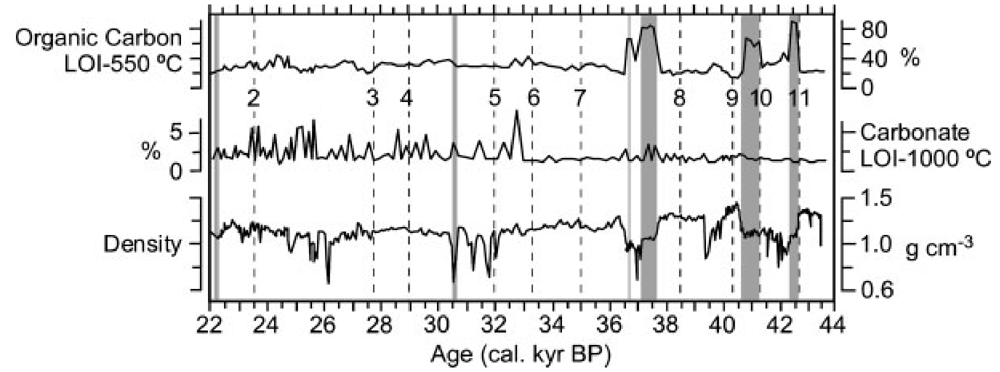

Figure 3 Sediment characteristics of the Lake Consuelo record, Peru. Percentage of organic carbon and carbonates as obtained from LOI and relative sediment density are plotted. Shaded bars represent the distribution of organic-rich gyttjas. Dotted lines represent the onset of Dansgaard–Oeschger events in GISP2 (Blunier and Brook, 2001)

likely due to local landslide dynamics, a ubiquitous feature of Andean forests (Silman, unpublished data).

Discussion

Lake Consuelo provides a continuous glacial record from a montane cloud forest of western Amazonia which reveals the constancy of these communities during periods of major global climate change. Stable community composition is also supported by the NMDS ordination results. About 200 pollen and spore taxa identified in the record emphasise the characteristic high biodiversity of this forest. As neither cultivar taxa nor charcoal particles were registered in the record, we infer a lack of anthropogenic activities or land use in the basin. Field observations also support the lack of human activity around the lake.

The forest surrounding Lake Consuelo throughout the last glacial period was dominated by a mixture of both upper montane and lowland elements. Upper montane taxa include *Alnus, Vallea, Podocarpus, Myrsine* and *Symplocos*, which are virtually absent from the modern pollen assemblage (Fig. 4). Taxa characteristic of lowland vegetation such as *Acalypha, Alchornea, Piper, Celtis* and *Trema* are well represented in the Holocene forest (Fig. 4). Apart from fairly defined upper montane and lowland taxa, a significant abundance of pervasive elements such as *Cecropia*, Poaceae, Melastomataceae/Combretaceae and Moraceae/Urticaceae is recorded throughout the LGM as well as in the Holocene pollen assemblage. Such pollen taxa represent large groups of species and may be registered in a wide range of habitats, challenging the interpretation of their pollen signals and making their response to past climatic changes unreadable. Nevertheless, the abundance of lowland taxa during the LGM and the absence of montane elements from the Holocene pollen assemblage indicate significant dissimilarities between glacial and Holocene vegetation in Lake Consuelo (Bush *et al.*, 2004). Accordingly, such community compositional changes make the glacial community from Lake Consuelo typically different from that of the modern forest at 1360 m a.s.l (Bush *et al.*, 2004). This emphasises the importance of habitat availability necessary for species to cope with future climate changes.

Glacial age plant migrations and temperature change

The Andes must have represented a major physical barrier to both montane and lowland biota during past glacial ages. The simple geometry of mountains predicts that an elevational band high on a mountain occupies less surface area than an equivalently broad band lower on the mountainside. Thus, the area for montane species must have increased during the ice ages whereas it must have been reduced during the interglacials. This promoted downslope movement of the lower limit of montane species distributional ranges. Lake Consuelo record provides evidence for such a trend. Species characteristic of modern montane cloud forest dominate the basin during the LGM whereas lowland species present in the modern forest show relatively low abundances (Fig. 4). This trend supports the downslope expansion of montane-species distributional ranges during past glacial periods associated with temperature decline and shifting of the cloud-base.

Evidence of downslope migrations of montane taxa such as *Alnus, Hedyosmun, Juglans* and *Vallea* during the last glacial period is supported by the pollen record of Lake Consuelo. Taking *Alnus* as an example, the 75th percentile of its altitudinal distribution falls between 2400 and 3200 m a.s.l., whereas the 95th percentile falls between 1400 and 3800 m a.s.l. In Holocene lake records from Peru and Ecuador, *Alnus* pollen only achieves abundances of 15% or more between 2200 and 3700 m a.s.l. (Weng *et al.*, 2004a). Even in modern pollen rain studies based on moss-polsters, *Alnus* abundances only fall to <5% below 1800 m a.s.l. (Weng *et al.*, 2004b). The record of ca. 15% abundance of *Alnus* during the last glacial period in Lake Consuelo (1360 m a.s.l.) suggests its presence *in situ*, indicating downslope migrations equivalent to 1000 to 1700 vertical metres as a result of cooling. Comparable evidence of altitudinal-range expansion of montane species during cold intervals in the Andes has been provided from several palynological records (e.g. Hooghiemstra, 1984; van der Hammen and Hooghiemstra, 2003; Bush *et al.*, 2004). Downslope migrations of montane taxa have also been evidenced at Lake Siberia (Bolivian Amazon, 2800 m a.s.l.), the only available glacial record directly comparable with Lake Consuelo. In Lake Siberia, the transition between Andean forest and puna taxa, which was initially taken as a drought signal during the LGM (Mourguiart and Ledru, 2003), has recently been reinterpreted to be the result of altitudinal migration of the montane forest (Baker *et al.*, 2004).

The palaeotemperature model developed for Lake Consuelo record deals with bioclimatic envelopes rather than communality. It is a taxon-based estimation that is independent of assumptions about communities and is not targeted on 'cold' or montane species but also includes the potential response of 'warm' or lowland species. Our bioclimatic envelope model estimates an average temperature depression of $4.9 \pm 0.7\,^{\circ}C$ during the LGM relative to modern (Fig. 4), based on the modern measured adiabatic lapse rate of $5.6\,^{\circ}C\,km^{-1}$ (Bush *et al.*,

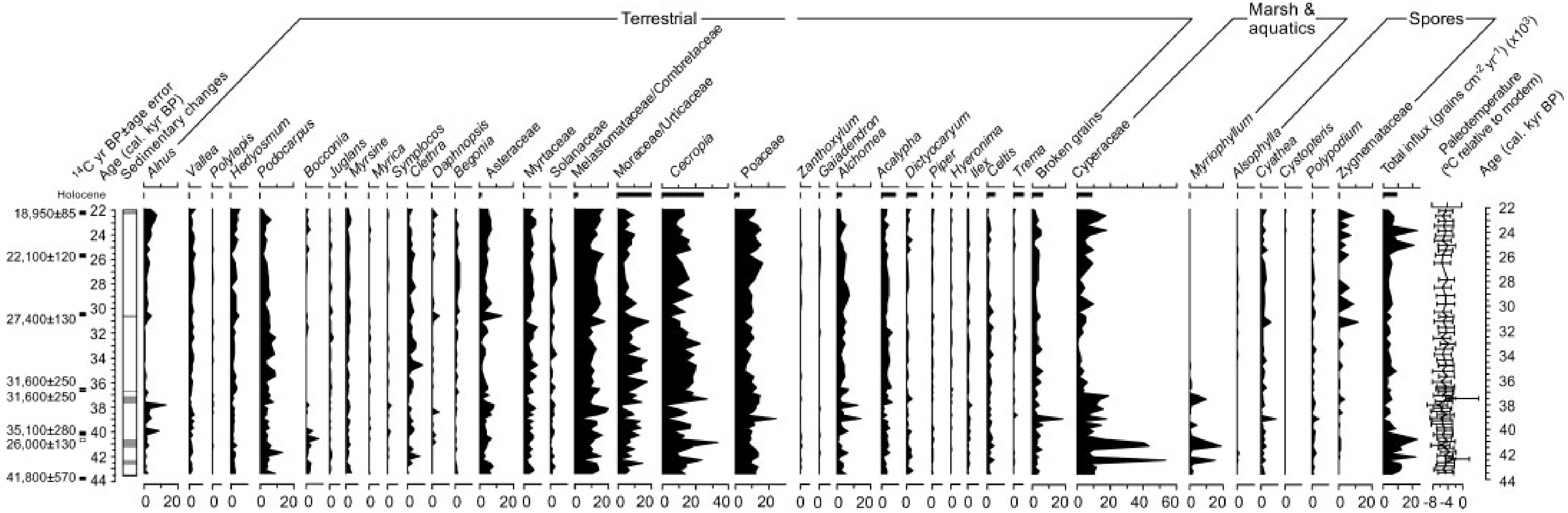

Figure 4 Percentage pollen diagram of selected taxa from Lake Consuelo, Peru. Curves represent pollen percentages in glacial deposits; top bars represent pollen percentages in Holocene sediments. From left to right: radiocarbon dates ± 1σ ranges, age scale, sedimentary changes, grey bands indicate the location of organic-rich gyttjas; terrestrial taxa organised on a montane to lowland gradient, taxa on the left are considered truly montane whereas taxa on the right are considered lowland indicators; marsh and aquatic and spore taxa; total influx; modelled palaeotemperature estimates ± 95% Bayesian credible intervals

2004). This estimate of glacial palaeotemperature is consistent with previous estimates of temperature decrease in the Andes and Amazonia (Klein *et al.*, 1998; Colinvaux *et al.*, 1999; Colinvaux and De Oliveira, 2000; Thompson *et al.*, 2000; Porter, 2001; Paduano *et al.*, 2003).

Moisture balance in western Amazonia during the LGM

Moisture availability changes in Lake Consuelo are indicated by water-level fluctuations, as recorded by marsh and aquatic taxa, and forest composition changes. Marsh and aquatic taxa (i.e. Cyperaceae and *Myriophyllum*) show their greatest abundances as well as the most prominent variations between 43.5 and 37 cal. kyr BP (Fig. 4). Increased marsh and aquatic taxa abundances may result from either extended shorelines due to increased water levels in fairly flat basins, or from shallower lake edges due to lowered water levels. The slopes on the hillsides of the Lake Consuelo are fairly steep (i.e. ca. 30 °), from which we infer that observed shoreline vegetation changes probably resulted from low lake stands. Colonisation of sedges (i.e. Cyperaceae) in newly uncovered margins and *Myriophyllum* in the resulting shallower lake borders correspond with lake-level declines. Cyperaceae and *Myriophyllum* drop from ca. 20% to less than 10% of the pollen sum shortly before ca. 37 cal. kyr BP (Fig. 4), which suggests the stabilisation of the shoreline vegetation.

A correlation between D–O (Dansgaard–Oeschger) cycles and lake-level oscillations in the early lake formation stages is apparent in the pollen record from Lake Consuelo between 43.5 and 37 cal. kyr BP (Fig. 3). The water-level variations probably reflect precipitation changes, although the response time of the lake is unknown and may be affected by groundwater. Rainfall fluctuations during the early lake formation mostly influenced the bordering vegetation while the core of the cloud forest remained unaffected. This suggests that precipitation changes between 43.5 and 37 cal. kyr BP were probably minor or short in duration as forest community composition was little changed. Low lake stands in Lake Consuelo are not evident after 37 cal. kyr BP and suggest a change in factors that determine local lake level.

Around 40 cal. kyr BP, a range of both sedimentological and vegetation changes in the record lead us to infer wetter conditions probably correlated with the onset of maximum glacial conditions. These changes include increased sedimentation rate (Fig. 2), abundance changes in *Alnus, Bocconia, Myrica* and marsh and aquatic taxa along with decreased total pollen influx (Fig. 4). The increased abundance of *Alnus* and *Myrica* indicate both wetter and cooler conditions as these taxa are characteristic of wet upper Andean forests (Marchant *et al.*, 2002). Decreased in *Bocconia* abundance and marsh and aquatic vegetation suggest a joint dependence on the availability of shoreline area and rising water lake levels around 40 cal. kyr BP. *Bocconia*, presently restricted to altitudes between ca. 800 and 3500 m a.s.l., being most abundant between ca. 2800 and 3000 m a.s.l. (W^3TROPICOS database) and a characteristic disturbance taxon on landslides (Gentry, 1993), was probably abundant at the forest's edge of Lake Consuelo before 40 cal. kyr BP.

Moister conditions are also inferred from faster sedimentation rates and decreased total pollen influx after 40 cal. kyr BP. Greater sedimentation rates suggest an increased amount of material washed into the lake while decreased total influx indicates increased lake surface area and hence reduced pollen deposition in the coring site.

Lake Consuelo records a continuous moist cloud forest cover during the last glacial period. Despite periods of reduced lake levels, no evidence for forest fragmentation during the Late Pleistocene was found in the record, indicating that the LGM in the area was not dry. On the contrary, the constancy of cloud forest vegetation recorded in Lake Consuelo indicates moist conditions in the area, with cloud base equal to or lower than modern. Cloud forest vegetation characterised Lake Consuelo's basin during the past 43.5 cal. kyr BP evidencing the presence of at least a semi-permanent cloud cover throughout this period and provides evidence for sustained moist conditions during the Lateglacial period. Lake Consuelo also remained wet around 33 cal. kyr BP, a period of reduced lake levels in Salar de Uyuni in the Bolivian Altiplano (Baker *et al.*, 2001a).

Permanent moist conditions throughout the LGM in Lake Consuelo coincide with humid-forest reported for several sites in the Peruvian–Bolivian Altiplano. Moist conditions during the LGM have also been recorded in two pollen reconstructions from upslope and south of Lake Consuelo (Graf, 1989). Consistent evidence comes from Palaeolake Tauca which covered the Peruvian–Bolivian Altiplano between 25 and 16 cal. kyr BP, indicating wet glacial conditions (Baker *et al.*, 2001a; Fritz *et al.*, 2004). Wet conditions on the Altiplano during the LGM is also supported by vegetation and lake-level reconstructions from Lake Titicaca (Baker *et al.*, 2001b; Paduano *et al.*, 2003).

Downslope of Lake Consuelo, variation in lake level and subtle variations in the disposition of the dry forest and savanna at Lake Bella Vista and Chaplin (Mayle *et al.*, 2000; Burbridge *et al.*, 2004) are not paralleled in the Consuelo record. These observations suggest that the overall flux of moisture arriving in the Andean flank was not materially affected by ecotonal shifts in the Bolivian savannas.

Taken together, available Palaeoecological records for the last glacial period in western Amazonia and the Altiplano indicate prevalent wet conditions in the region during the last glacial period. Regional episodes of decreased moisture have also taken place during the Late Pleistocene in the Altiplano and western Amazonia. However, regional changes are not strictly synchronous, which emphasises the importance of understanding climate regimes at different spatial and temporal scales.

Conclusions

Palaeoecological data indicate the remarkable compositional stability of highly biodiverse montane forests in western Amazonia during the last glacial period. High-resolution pollen analyses of a complete record from a lake lying at 1360 m a.s.l. provide the vegetation and climate history for this part of western Amazonia through the last glacial period. Downslope migrations of individual species yielded palaeotemperature estimates of ca. $-5\,°$C corresponding with most estimations of air-temperature decline from tropical records.

Despite changes in species composition of the forest, no evidence of forest fragmentation or dry conditions in the area were found, based on sediment composition and the steadiness of moist cloud forests in the basin. Evidently, the rate of plant community changes in this part of western Amazonia has been consistent with the rates of climate change during the past.

Montane forests supported on the eastern flank of the Andes have been identified as conservation hotspots (Myers *et al.*, 2000) and contain an exceptionally diverse flora and fauna with high proportions of endemic species. Although we detected no human presence in the entire 43 500 yr history of this lake, the blasting of a new road at the foot of the slope upon which Consuelo sits likely heralds a larger environmental change than the oscillations of the Pleistocene.

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