A long history of cloud and forest migration from Lake Consuelo, Peru

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ABSTRACT

The complete paleoecological history from Lake Consuelo forest yields a record of ground-level cloud formation and changes in its lower altitudinal limit over the last 46,300 cal yr BP. The timing of early lake level fluctuations prior to 37,000 cal yr BP appears sensitive to North Atlantic temperature oscillations, corresponding to Dansgaard–Oeschger interstadials 11, 10 and 8 recorded in GISP2. After the LGM, the first hint of warming is recorded in Lake Consuelo at 22,000 cal yr BP and agrees with other estimates for the region. The mid-Holocene (7400–5000 cal yr BP) was the period of highest rates of change and most significant reorganizations in the Consuelo forest. These community changes resulted from a regionally widespread dry period. Results from Lake Consuelo indicate that moisture availability, mediated through cloud cover, played the most significant role in ecological change in this system. Rates of past climate fluctuations never exceeded the forest capacity to accommodate change. Unfortunately, this might not be the case under predicted scenarios for the end of the current century.

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Introduction

Tropical cloud forest ecosystems are highly sensitive to climate change as they mostly depend on regular cloud immersion. Their biological responses to current climate change are widely recognized and documented (Foster, 2001; Pounds et al., 1999; Still et al., 1999). These include amphibian extinctions and upslope migrations of avian populations (Pounds et al., 1999, 2006) resulting from the lifting of cloud base and reduced cloud immersion due to current global warming. Hence, our modern picture of tropical cloud forests can be summarized as a sensitive ecosystem threatened by global climate change. However, to realize how these systems will respond to future climate change, we need to investigate their past history. We believe that long-term perspectives provide invaluable information on the ecological history of ecosystems and have a great potential to enlighten conservation policy (Willis and Birks, 2006).

Given the importance of cloud immersion to montane forests, past precipitation and temperature regimes would have controlled both their location and species composition. Tropical precipitation patterns responded to precessional forcing during the past (Baker et al., 2001a; Bush et al., 2004a; Clement et al., 2004; Cruz et al., 2005; van der Hammen and Hooghiemstra, 2003; Wang et al., 2004). Consequently, it might be expected that the boundaries of cloud forests have a long history of instability. Here we present the most detailed and complete record to span >45,000 calibrated years BP (cal yr BP) from a modern tropical cloud forest. Situated near the lower limit of modern ground-level cloud formation, Lake Consuelo provides an excellent setting to investigate the effect of past climate change and fluctuating cloud immersion on the biotic communities of western Amazonia. We also address the timing of deglaciation in the region, Late-Pleistocene changes in moisture availability, Holocene climatic fluctuations and the rate of past ecological changes.

Regional setting

Lake Consuelo (13°57.1′S, 68°59.45′W) is immersed in ground-level clouds on most days and its at 1360 m above sea level (asl), 2500 m down slope from the Bolivian Altiplano and Lake Titicaca (Fig. 1). The lake is located within a small, closed basin with moderately steep slopes that result in thin soils with duff layers thickening above 1400 m asl. We found 37 different species with ≥10 cm diameter at breast height just within a 0.1 ha plot in the largely undisturbed forest around Lake Consuelo. This vegetation can be described as a montane cloud forest with high abundance of mosses and epiphytes (e.g. Bromeliaceae) and a mixture of lower and upper montane elements (e.g. *Maquira coriaceae* and *Myrsine* sp.). Roughly 25% of the species composition of this forest is dominated by *Wettinia* cf. *augusta* and a species of treefern (*Cyathea* sp.). Other common species found in the Consuelo forest are *Dictyocaryum lamarckianum*, *Iriartea deltoidea*, *Euterpe precatoria*, *Simira* sp., *Podocarpus* sp. and *Symplocos* sp. (Urrego et al., 2005). Lake Consuelo is located within one of the humid regions, and very close to the Manu super-humid region, identified by Killeen et al., (2007) as biodiversity hotspots.

Instrumental data for temperature or precipitation are not available for the site, however interpolated average monthly values from nearby weather stations (Hijmans et al., 2005) provide estimates

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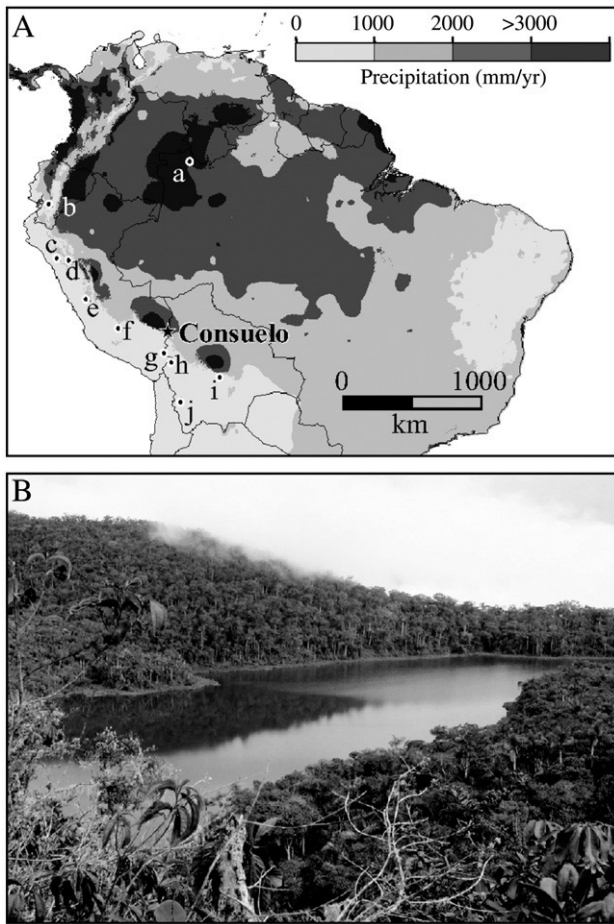E-mail address: durrego@fit.edu (D.H. Urrego).

Figure 1. (A) Location map for Lake Consuelo and other paleoenvironmental study sites discussed in the text: (a) Pata; (b) Chorreras; (c) Compuerta; (d) Chochos; (e) Junín; (f) Pacucha; (g) Titicaca; (h) Huinamarka; (i) Siberia; (j) Salar de Uyuni. (B) Photograph of Lake Consuelo and surrounding cloud forest.

of c. 22.2°C and c. 2400 mm per annum, respectively. Precipitation varies from c. 260 mm during the dry season (June-August) to c. 2140 mm during the wet season (September-May). Both intrannual and interannual precipitation variability are associated with El Niño Southern Oscillation (ENSO). In general, warm-ENSO phases are manifested as lagged negative precipitation anomalies over the Amazon basin and cold phases, or La Niña, as positive anomalies (Malhi and Wright, 2004; Marengo et al., 2008b; Poveda and Salazar, 2004). Intrannual precipitation variability in the region is also associated with the South American Low Level Jet (SALLJ, Wang and Fu, 2004) and the South American Summer Monsoon (SASM, Zhou and Lau, 1998). Daily temperatures range from an annual minimum mean of 17°C to an annual maximum mean of 27°C (Hijmans et al., 2005). Minimum daily temperature during the dry season can be further reduced as much as 3.5°C by southern hemisphere cold fronts, also known as *friagems* (Marengo and Rogers, 2001).

Methods

Two sediment cores were collected using a Colinvaux–Vohnout piston corer (Colinvaux et al., 1999). Coring sites were selected based on a preliminary bathymetric assessment of the lake. Core Consuelo 1 (CON1) was raised from the deepest point (c. 10.5 m of water) and yielded an 8.8-m sediment column. Core Consuelo 2 (CON2) was collected from the shallows beneath c. 2 m of water and yielded 1.37 m of sediment. The starting coring point was set half a meter above the water depth to ensure capturing the mud-water interface. Sediment

cores were transported unopened to the laboratory and stored in a dark cold room at 4°C. Sedimentary descriptions were made using Munsell color charts (Munsell, 1994). The chronology was derived from 22 (CON1) and 4 (CON2) ^{14}C AMS dates from bulk gyttja and macrofossils (Table 1, Fig. 2). Calibrations of ^{14}C dates for the record of Lake Consuelo in previous publications (Bush et al., 2004b; Urrego et al., 2005; Urrego and Bush, in press) were calibrated using the CALIB 5.0 computer program (Stuiver and Reimer, 1993) and the dataset of Stuiver and Reimer (2005) for ages between modern and 20,000 ^{14}C yr BP. Calpal-2004 (Weninger et al., 2004) was used to calibrate ages >20,000 ^{14}C yr BP for previous Lake Consuelo publications. For the present paper the radiocarbon calibration was revised based on the newly available calibration curve Fairbanks0107 (Chiu et al., 2007; Fairbanks et al., 2005). The Fairbanks0107 was chosen over CALIB (Stuiver and Reimer, 2005) and the updated Calpal-2007$_{Hulu}$ (Weninger and Jöris, 2008) curves because it produces more stable calibrations and reduced calendar year uncertainties. Calibrated sample ages were based on means. Ages were linearly interpolated between dates for both cores, and in CON2 extrapolated for the youngest sediments assuming a modern top age (Fig. 2).

Sediment subsamples (0.5 cm^3) were collected at c. 400-yr intervals for pollen analysis. Samples were spiked with exotic *Lycopodium* spores (Stockmarr, 1972) to calculate concentration and influx. Pollen extraction followed the standard techniques of Faegri and Iversen (1989). A minimum of 300 terrestrial pollen grains was counted from each sample. Spores and aquatic pollen grains were also counted and, although excluded from the pollen sum, their percentages were calculated based on the total sum of terrestrial elements. The aquatic group included Cyperaceae, *Isoetes*, *Myriophyllum* and *Sagittaria*. Identifications of pollen grains and spores were based on the Florida Institute of Technology Neotropical pollen reference collection of >3000 types and the Neotropical Pollen Database (Bush and Weng, 2006), as well as other pollen keys and descriptions (Colinvaux et al., 1999; Herrera and Urrego, 1996; Hooghiemstra,

Table 1
AMS radiocarbon dates and calibrated ages determined using Fairbanks0107 (Chiu et al., 2007; Fairbanks et al., 2005) for cores CON1 and CON2 from Lake Consuelo, Perú.

Core	Depth (cm)	Lab no.	Description[a]	^{14}C age (^{14}C yr BP)	Cal range[b] (cal yr BP)[c]
CON1	10	OS-49603	Macrofossil	4670 ± 40	5334–5458
	30	OS-49602	Macrofossil	6520 ± 35	7409–7453
	45	OS-46848	Macrofossil	6980 ± 40	7759–7861
	60	OS-38421	Macrofossil	7230 ± 50	7980–8090
	60[d]	OS-48404	Bulk gyttja	2390 ± 35	2324–2450
	61.5	OS-46072	Macrofossil	7150 ± 45	7935–8001
	67	OS-46403	Macrofossil	7450 ± 55	8210–8350
	71	OS-45078	Bulk gyttja	7290 ± 50	8030–8170
	82	OS-45079	Macrofossil	7410 ± 50	8170–8290
	112	OS-45080	Bulk gyttja	8240 ± 45	9131–9293
	141	OS-38422	Bulk gyttja	9030 ± 50	10,170–10,240
	246	OS-38423	Macrofossil	11,900 ± 55	13,670–13,790
	322	OS-34712	Macrofossil	14,000 ± 55	16,200–16,460
	418	OS-38424	Bulk gyttja	16,950 ± 70	20,050–20,230
	465	OS-38527	Bulk gyttja	18,950 ± 85	22,410–22,630
	550	OS-38528	Bulk gyttja	22,100 ± 120	26,410–26,750
	625	OS-34713	Macrofossil	27,400 ± 130	32,520–32,940
	687.5	OS-47204	Macrofossil	31,600 ± 250	36,690–37,270
	694.5	OS-47205	Bulk gyttja	31,600 ± 250	36,690–37,270
	760	OS-38529	Bulk gyttja	35,100 ± 280	40,120–40,760
	790[d]	OS-34714	Macrofossil	26,000 ± 130	31,040–31,420
	875	OS-38530	Bulk gyttja	41,800 ± 570	45,760–46,840
CON2	8	OS-51329	Bulk gyttja	235 ± 30	211–333
	24	OS-51476	Macrofossil	1180 ± 30	1045–1133
	80	OS-54318	Macrofossil	3660 ± 30	3933–4029
	134	OS-54159	Bulk gyttja	9680 ± 65	11,000–11,220

[a] Macrofossil: terrestrial plant or wood remains.
[b] Mean age and $1\sigma = 68.3\%$ probability.
[c] Ages with standard error greater than 50 yr rounded to the nearest 10 yr.
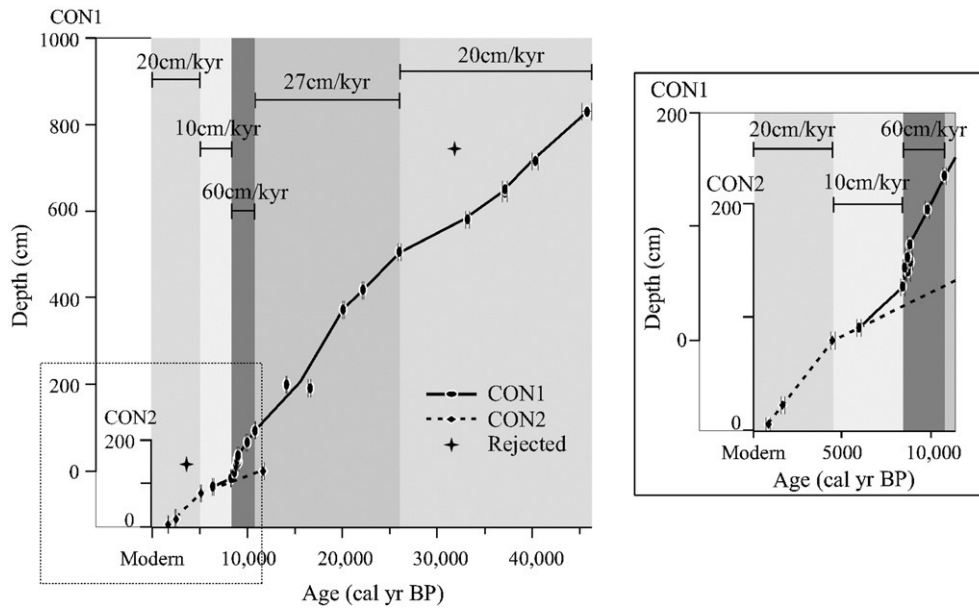[d] Rejected dates.

Figure 2. Age-depth curves for cores CON1 and CON2 from Lake Consuelo. Inset: close up of chronology for the last 10,000 yr. Gray bands highlight segments with constant sedimentation rate.

1984; Roubik and Moreno, 1991). Percentage and influx diagrams were constructed using the software C2 (Juggins, 2003). Diatom extractions were attempted but apparent rapid downcore dissolution prevented analysis. Additional subsamples were taken for loss-on-ignition (LOI) at 5-cm and 2.5-cm in CON1 and at 1-cm intervals in CON2, with the purpose to achieve a 100-yr resolution. Percentage weight by loss on ignition (LOI) at 550°C and 1000°C were determined to estimate organic carbon and carbonate contents, respectively (after Dean, 1974). Non-metric multidimensional scaling (NMDS) (Kruskal, 1964) was performed on untransformed percentage data using the R application GUI 1.21 (Urbanek and Lacus, 2007) and the Vegan package (Oksanen et al., 2007). NMDS was chosen over Detrended Correspondence Analysis because paleoecological data seldom meet the normality and linearity assumptions (McCune and Grace, 2002). The number of species used in the ordination was reduced by applying an abundance and persistence filter that efficiently preserved the main variability of pollen datasets, while eliminating the weight of rare taxa (after Birks and Birks, 1980). This filter retained terrestrial taxa with at least 1% (abundance) and occurring in at least 5 samples per record (persistence). Spores and aquatic elements were excluded from the ordination, as the goal was to explain fluctuations on the composition of the terrestrial vegetation. The Bray–Curtis dissimilarity distance (Faith et al., 1987) was used, and repeated runs for two dimensions were performed until a convergent solution was found. Principal components rotation and centering was then applied to the final solution (Minchin, 1987). The velocity of past ecological changes was evaluated by calculating rates of change (RoC) based on the Euclidean distances of adjacent time slices on the ordination space, and divided by the time elapsed between samples (Urrego et al., 2009). By calculating dissimilarities based on ordination scores, the weights of rare and common taxa were balanced. This approach ensured that important, but rare, indicator taxa were taken into account, while the effect of super-pollen-producer taxa was moderately reduced. Calculations of the RoC in Lake Consuelo record were possible because of robust age control (26 ages, Table 1) and because sedimentation rates were relatively linear (i.e. only 3 inflexion points, Fig. 2).

Results

Core CON1 from Lake Consuelo is 8.79-m long and spans the last glacial period (i.e. basal age 46,300 cal yr BP) through the mid-

Holocene, with 7 out of 22 samples pre-dating the full glacial (Table 1, Fig. 2). The youngest sample from 10 cm depth in CON1 dates to c. 5400 cal yr BP, indicating that the Late-Holocene sediments were lost during core recovery. Two radiocarbon dates were rejected on the principle of parsimony, i.e. including them would have led to a greater number of ages being rejected. The depth-age curve averaged c. 20 cm per millennium (henceforth cm/kyr) between 46,300 and 26,000 cal yr BP, but steepened sharply during the early Holocene to 60 cm/kyr (Fig. 2). An increased rate of deposition between c. 8200 and 7400 cal yr BP resulted in c. 60 cm of sediment accumulating (Fig. 2). Even in the center of this flat-bottom lake, the occurrence of slumping was indicated by dating reversals during this period (Table 1). A change in sedimentation was also evident in the CON2 record between 8200 and 7400 cal yr BP. Further dating of this interval might reveal similar age reversals. Sedimentation rates slowed down to c. 10 cm/kyr between 7400 and 5300 cal yr BP in both records. The entire pollen record from CON1 was joined with the last 5000 cal yr BP from CON2 to provide a complete paleoecological history of the site (Table 1, Fig. 2).

The large number of pollen and spore taxa found in the record from Lake Consuelo (i.e. over 260 taxa) reflects the high biodiversity that characterizes western Amazonia. The 38 most abundant terrestrial taxa plus the Aquatic group from cores CON1 and CON2 are plotted in Figure 3. The vast majority of those not plotted are woody species. Only c. 2% were unidentified grains. Concentration and influx curves co-vary and both show an increase around 22,000 cal yr BP (Fig. 3, only influx curve shown), probably associated with increased productivity after the last glacial maximum (LGM). We did not observe charcoal particles in the pollen slides, however a more rigorous assessment of the fire record from Lake Consuelo is still required. The discussion and interpretation of results are, for the sake of comparison with other sites, divided in two periods following the most accepted SPECMAP chronology (Imbrie et al., 1984) and the start of the Holocene (Hughen et al., 1996; Walker et al., 2008). However, it should be noted that species composition and stratigraphic changes in this record are continuous rather than discrete (Fig. 3).

The two-dimensional NMDS ordination for the records from Lake Consuelo produced a convergent solution after 1172 iterations with stress levels stabilizing at 16.4% (Fig. 4A). The most dissimilar pollen assemblages in both Axes 1 and 2 were those dating around 39,000 cal yr BP and mid-Holocene samples around 8600 cal yr BP (Fig. 4A, Supplemental material Table 1). MIS 3 samples had positive scores on Axis 1 whereas samples dating after 22,000 cal yr BP had negative
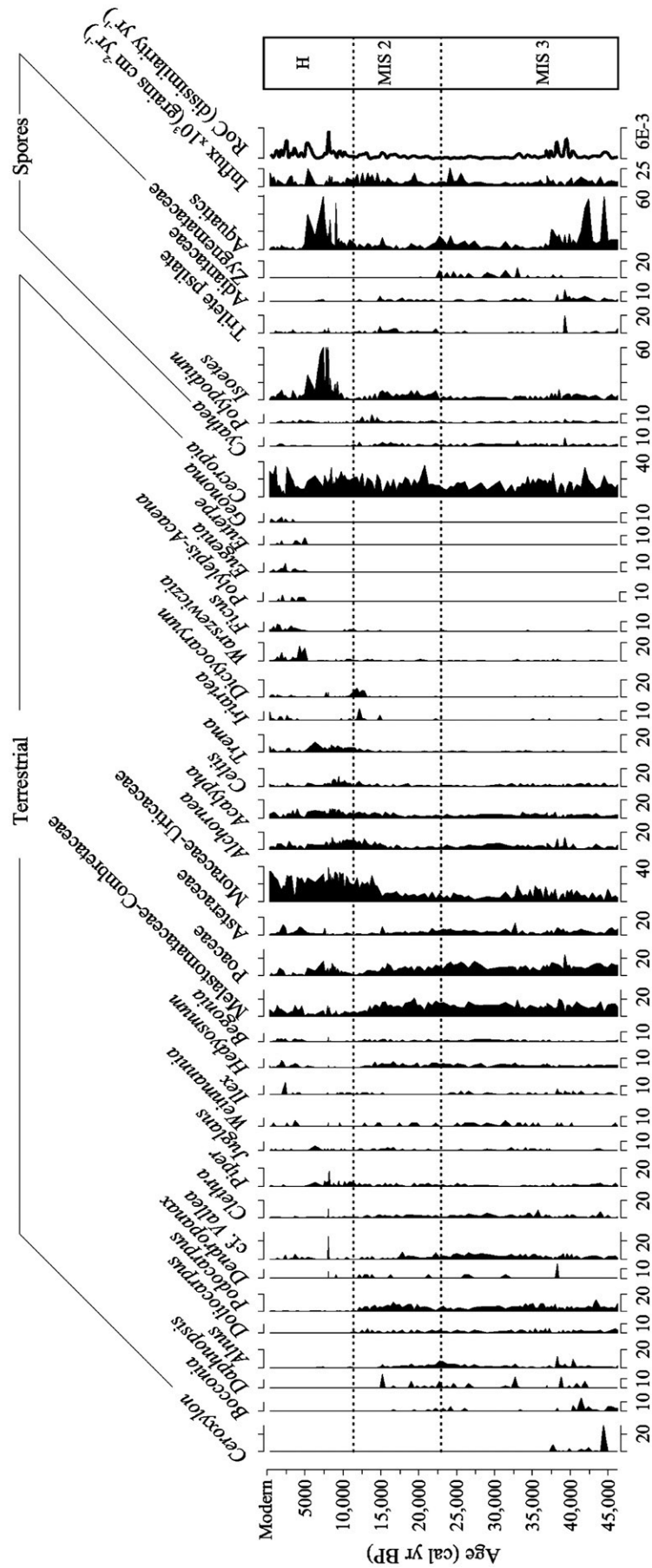
Figure 3. Simplified percentage pollen diagram, influx and rates of change (RoC) for cores CON1 and CON2 from Lake Consuelo. Terrestrial taxa are ordered according to their occurrence from past (left) to recent (right). Aquatic taxa include Cyperaceae, *Isoetes*, *Myriophyllum* and *Sagittaria*. MIS 3, MIS 2 = marine oxygen isotope stages 3 and 2, H = Holocene.
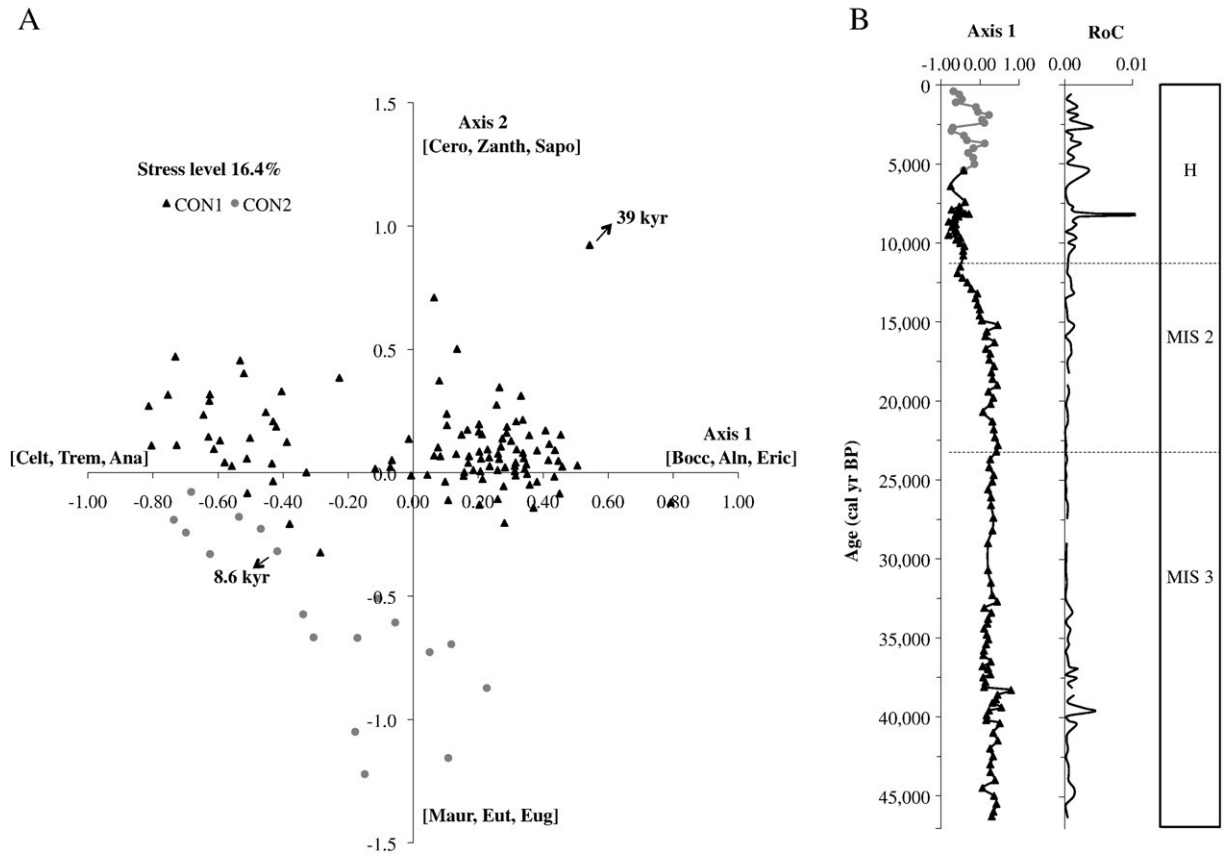
A

B

Figure 4. (A) NMDS ordination plot for pollen record from Lake Consuelo (cores CON1 and CON2) and taxa with highest scores on each end of the Axes (see Supplemental material Table 2); Bocc = *Bocconia*; Aln = *Alnus*; Eric = Ericaceae; Celt = *Celtis*; Trem = *Trema*; Ana = Anacardiaceae; Cero = Ceroxylon; Zanth = *Zanthoxylum*; Sapo = Sapotaceae; Maur = *Mauritia*; Eut = *Euterpe*; Eug = *Eugenia*. (B) Axis 1 scores and rates of change (RoC) plotted against time. MIS 3, MIS 2 = marine oxygen isotope stages 3 and 2, H = Holocene.

scores (Fig. 4B, Supplemental material Table 1). Despite large dissimilarities between Late-Pleistocene and Holocene vegetation, there was not a sharp separation of their pollen assemblages. On the contrary, the ordination showed a gradual transition from MIS 3 to Holocene communities (Fig. 4B). Taxa driving the positive end of Axis 1 included *Bocconia*, *Alnus* and Ericaceae (Fig. 4A, Supplemental material Table 2).

Late MIS 3 (46,300–23,000 cal yr BP)

Despite its rather uniform appearance, some changes in the gross stratigraphy were observed in core CON1. Coring had terminated in a coarse-sediment layer of about 2-cm thickness at the bottom of core CON1 (i.e. 879 cm depth, ca. 46,300 cal yr BP). Between 877 and 465 cm (c. 46,300 and 22,520 cal yr BP) the sediments were massive gyttjas with alternating black and very dark brown portions of irregular breadth and indistinct transitions between the bands (Fig. 5). Darker gyttjas coincided with increases of LOI-550 in the sediments around 44,800, 42,000 and 37,000 cal yr BP (Fig. 5). The depth-age curve showed little variation during the MIS 3, displaying a slight inflection at 460 cm depth (c. 22,500 cal yr BP), when the sedimentation rate accelerated from 20 cm/kyr to 27 cm/kyr (Fig. 2).

During MIS 3, the forest differed markedly from that of the Holocene (Figs. 4 and 5). Taxa such as *Ceroxylon*, *Bocconia*, *Daphnopsis*, *Alnus*, *Doliocarpus*, *Podocarpus*, and *Dendropanax* were common during MIS 3 but virtually absent in the Holocene pollen spectra (Fig. 3). *Clethra*, cf. *Vallea*, *Piper* and *Juglans* had progressive population declines during MIS 2. The ferns *Cyathea* and *Polypodium* were most abundant during MIS 3 and 2, while algae of the Zygnemataceae were unique to MIS 3. Upper montane forest taxa, *Weinmannia*, *Ilex*, *Paullinia*, *Hedyosmum* and *Begonia* were represented in the pollen

record, but revealed considerable Pleistocene fluctuations in abundance. Melastomataceae–Combretaceae (probably Melastomataceae given their abundance in montane forests) and Poaceae displayed high percentages during MIS 3, followed by a gradual decline toward the Holocene (Fig. 3). Moraceae–Urticaceae, on the other hand, were less abundant between 46,300 and 23,000 cal yr BP than during the Holocene. Aquatic elements had peak abundances (up to 60%) between 46,000 and 37,000 cal yr BP and were less abundant (20%) during MIS 3. The RoC values were low between 46,000 and 40,000 cal yr BP but increased markedly between 40,000 and 37,000 cal yr BP (Fig. 4B).

MIS 2 (23,000–11,600 cal yr BP)

The sediments of CON1 after 22,000 cal yr BP were gyttjas with subtle variations in color from very dark brown to dark brown. A particularly dark section of gyttja was deposited between 333 and 321 cm depth (i.e. 22,000 to 21,000 cal yr BP, Fig. 5). LOI-550 in the sediments were relatively constant, with two minor peaks of C at c. 16,000 and 14,000 cal yr BP. Sedimentation rates were also constant over MIS 2, but increased toward the early Holocene (Fig. 2).

After 22,000 cal yr BP, upper montane forest taxa decreased significantly in abundance while lower-montane elements began to dominate the pollen spectra. Some upper montane taxa, e.g. *Bocconia*, *Daphnopsis*, *Doliocarpus* and *Dendropanax*, went locally extinct during this interval while abundances of *Alnus*, *Podocarpus* and cf. *Vallea* decreased to almost half of their MIS 3 percentages (Fig. 3). Abundance of some taxa that cannot be assigned with certainty to a particular ecosystem type, but which had been major forest components during MIS 3, e.g. Melastomataceae-Combretaceae, Poaceae and Asteraceae, also began to decline during MIS 2 (Fig. 3).
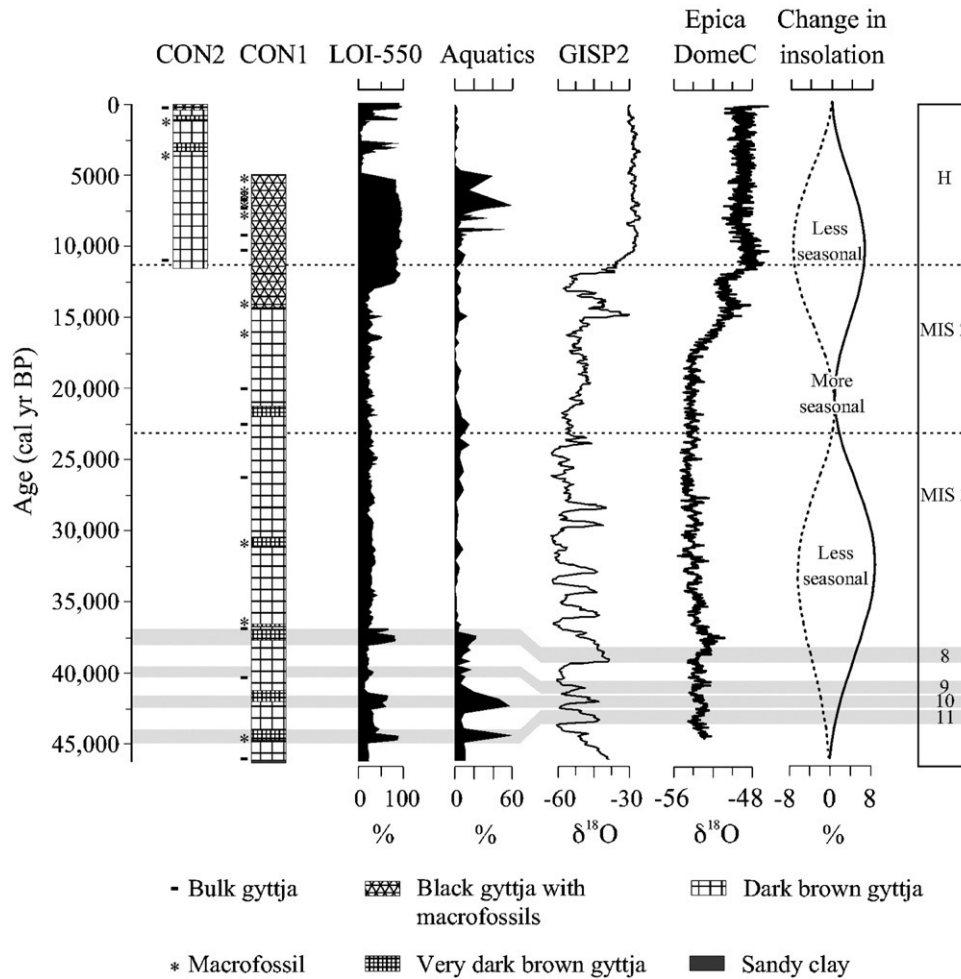
Figure 5. Sediment stratigraphy, location of radiocarbon samples and type, loss on ignition (LOI-550) results, and aquatic pollen percentage for cores CON1 and CON2 from Lake Consuelo. Temperature interpretation based on stable isotope analysis and ice accumulation data from GISP2 (Alley, 2004) and EPICA Dome C (Stenni, 2006). Gray bands represent Dansgaard-Oeschger interstadials 11-8. Change in insolation curves for wet (January, dotted line) and dry season (July, solid line) at 14°S over the past 46,300 cal yr BP. MIS 3, MIS 2 = marine oxygen isotope stages 3 and 2, H = Holocene.

Lowland or premontane taxa, e.g. Moraceae-Urticaceae, *Celtis*, *Alchornea*, *Acalypha*, *Trema*, *Iriartea*, and *Dictyocaryum*, increased in abundance before the beginning of the Holocene, replacing upper-montane taxa that went locally extinct. The forest palms *Iriartea* and *Dictyocaryum* were scarce during MIS 3, but increased three or four-fold at c. 12,000 cal yr BP. Among the ferns, *Cyathea* and *Polypodium* persisted during MIS 2, but their abundance declined as time progressed. The occurrence of *Isoetes* increased to c. 10% at c. 22,500 cal yr BP and dropped to c. 2% at c. 12,000 cal yr BP. The lowest percentages of aquatic elements were observed at this time. The RoC values were essentially constant between 22,000 and 11,600 cal yr BP (Fig. 4B).

Holocene (11,600 cal yr BP–modern)

The Holocene sediments in record CON1 were black gyttjas with high organic carbon contents from 198-cm depth to the top of the core (i.e. 12,000 to 5300 cal yr BP) (Fig. 5). The Holocene stratigraphy of core CON2 was more complex than that of core CON1, with dark brown gyttjas interrupted by very dark gyttjas rich in carbon (c. 3000 and 1000 cal yr BP) and a top 13-cm thick layer (c. 500 cal yr BP) of black gyttjas with high contents of organic carbon (LOI-550) and macrofossils (Fig. 5). In CON1, Holocene changes in sedimentation rates were more conspicuous than during MIS 3. Sedimentation rates essentially doubled from 27 cm/kyr during the early Holocene to 60 cm/kyr in the mid-Holocene (between 82 and 45 cm depth, c. 8200

and 7800 cal yr BP, respectively). This three-fold increase was followed by a decrease to 10 cm/kyr during the mid-Holocene (c. 7700 and 3900 cal yr BP), before returning to a rate of 20 cm/kyr after 3900 cal yr BP (Fig. 2).

The Holocene pollen assemblage of Lake Consuelo was typical of lower-elevation montane forests. Pollen of the tall palms *Dictyocaryum* and *Iriartea* was scarce, though both had small increases in abundance after 5000 cal yr BP. *Acalypha*, *Alchornea* and *Trema* were present throughout the record, but showed considerable increases in the Holocene (Fig. 3). *Warszewiczia*, *Ficus*, *Polylepis-Acaena*, *Eugenia*, *Euterpe* and *Geonoma* were among the taxa that colonized the site during the Holocene having been virtually absent during MIS 3 and 2. *Cecropia* was a common component of the forest (10–20% of the pollen sum) throughout the record with high abundances during the MIS 2. Within the Holocene *Cecropia* was slightly more abundant (20–25%) with peaks of c. 35% at c. 2500 and after c. 1000 cal yr BP (Fig. 3). *Cyathea* and *Polypodium* ferns virtually disappeared during the early Holocene but returned to the forest after 5000 cal yr BP. Aquatic taxa were most abundant between 9500 and 5000 cal yr BP and coincided with peaks in *Isoetes* (Fig. 3). All Holocene samples scored negative or close to zero on the NMDS Axis 1 (Supplemental material Table 2), which was mainly driven by *Celtis*, *Trema* and Anacardiaceae on the negative end (Fig. 4A). During the Holocene, the RoC increased steadily with a burst of species turnover (i.e. highest RoC) at c. 7500 cal yr BP (Fig. 4B). The late Holocene was also characterized by high RoC, comparable with those prior to 37,000 cal yr BP (Fig. 4B).

Discussion

Lake Consuelo recorded a remarkably continuous moist montane forest cover during the past 46,300 cal yr BP, despite major changes in species composition and periods of reduced moisture availability. These montane forests occupied the basin through periods of significant climate change such as the regional LGM (30,000–22,000 cal yr BP, Seltzer et al., 2002) when air temperatures were c. 5°C colder than today (Hostetler and Mix, 1999). However, the MIS 3 forest composition was significantly different from the composition of the Holocene forests (Figs. 4 and 5) evidencing changes in the altitudinal ranges and migrational patterns of species. In this section of western Amazonia, the short distance between lowlands and tree line (3500 m vertically and c. 30–50 km laterally) minimizes any temporal lags in migration due to spatial scale. While climate-driven range expansions across Europe and the eastern USA resulted in species migrating thousands of kilometers along a large ecological gradient (Davis and Shaw, 2001; Prentice et al., 1991; see McLachlan and Clark, 2004 for an alternative interpretation), the same ecological range can be spanned in 50 km in the Andes, providing an excellent test ground for migrational hypotheses. A sequential response of species was observed in Lake Consuelo, where individual taxa gradually immigrate and go locally extinct at different times and rates (Fig. 3). This observation is confirmed by the NMDS ordination analysis where, instead of clearly differentiated biomes characterizing the MIS 3 or the Holocene, we see pollen assemblages that smoothly transition from cool to warm periods (Fig. 4A). Gradual changes are also evident from the RoC, which show slow and steady changes during the regional LGM and MIS 2 (Fig. 4B), instead of the rapid changes expected under the vegetation-belt view (Hooghiemstra and van der Hammen, 2004) when one assemblage would be totally replaced by the other. Such trends support individualistic, as opposed to community-based species migrations during past climate changes. Holocene upslope migrations almost certainly led to a decrease in habitat availability for modern upper and mid-elevation species due to the essentially conical shape of mountains. Competition for space as temperature increased apparently led specialist species to migrate upslope reducing their habitat ranges, and generalist species to occupy newly vacated spaces and thereby expand their habitat ranges (see Urrego et al., 2005 for a more detailed discussion of the LGM conditions of Lake Consuelo).

Early regional deglaciation

The onset of warming conditions in the Lake Consuelo record indicated an early start of glacial retreat after the LGM. The beginning of deglaciation, defined here as the onset of warming conditions, was recorded in Lake Consuelo as a gradual shift from upper montane to lower montane forest starting at c. 22,000 cal yr BP (Fig. 3). The NMDS showed the first hint of warming at c. 22,000 cal yr BP when ordination scores shifted from the positive to the negative side of Axis 1 (Fig. 4B, Supplemental material Table 1) and the first local extinctions of upper montane species were witnessed in the pollen record (Fig. 3). This first wave of warming lasted until c. 20,000 cal yr BP (Fig. 4B). After a brief cooling, there was a slow but steady warming between 19,000 and 16,000 cal yr BP. The signature of increasing temperatures strengthened after c. 15,000 cal yr BP and modern warming was stabilized at c. 12,000 cal yr BP (Fig. 4B). Despite the magnitude of deglacial warming (c. 5°C), RoC remained low between 22,000 and 10,000 cal yr BP (Fig. 4B) suggesting that temperatures increased slowly and gradually and allowed species to cope with climate change by expanding their distributional ranges or tracking their bioclimatic envelops.

Age estimates for the onset of deglaciation from several proxies and sites in the Peruvian Andes yield a range between 22,000 and 12,000 cal yr BP. In northern Perú deglaciation timing is estimated to be later than in the south. For instance, the formation of Lagunas de Chochos and Chorreras from glacial retreat yields a deglaciation onset at c. 17,000 cal yr BP (Hansen et al., 2003). On the western flank of the Andes, steadily warming conditions are inferred from the Lake Compuerta record (roughly at the same latitude as Chorreras) beginning at c. 16,200 cal yr BP (Weng et al., 2006). On the eastern Andean flank, sedimentological, isotopic and palynological analyses of lakes and terminal moraines produce an age-estimate for deglaciation between 22,000 and 19,000 cal yr BP (Hanselman et al., 2005; Mark et al., 2002; Rodbell, 1993; Seltzer et al., 2002; Smith et al., 2005). Located on the eastern flank of the Andes and in the southern part of Peru, estimates of the onset of deglaciation from Lake Consuelo record are broadly consistent with these regional estimates, suggesting a start of significant regional warming c. 5000 yr earlier than in northern latitudes (e.g. Genty et al., 2006; Seltzer et al., 2002; Smith et al., 2005; Visser et al., 2003).

Effects of cloud cover fluctuations

The continuous record of moist cloud forests from Lake Consuelo indicates humid conditions in the basin and the presence of semi-permanent to permanent cloud cover during MIS 3 (Urrego et al., 2005). This observation is consistent with evidence of wet conditions at the full glacial reported for several sites in the Peruvian and Bolivian Andes (Baker et al., 2001b; Fritz et al., 2004; Paduano et al., 2003). Early oscillations in lake levels at Consuelo are revealed by spikes in the abundance of aquatic taxa and distinct depositional episodes of organic rich gyttjas (Fig. 5). Increased abundance of aquatic elements indicate that shallow marshes were colonized by sedges (Cyperaceae) and *Myriophyllum* (Fig. 3), while high organic-content gyttjas are the result of productive wetland vegetation thriving along the shores of Lake Consuelo. Evidence for these fluctuations suggests multiple events of lake-level lowering each lasting c. 500–1000 yr. The timing of the events at 44,500, 42,500 and 38,000 cal yr BP, could correspond to Dansgaard-Oeschger (D/O) interstadials 11, 10 and 8 recorded in GISP2 (Blunier and Brook, 2001) within the Consuelo age errors (Fig. 5, Table 1). D/O 9 was a weaker event in many records but may still be represented in the data from Consuelo (Fig. 5).

EPICA Dome C isotope reconstructions (Stenni, 2006) showed an overall warming of air temperatures around 37,000 cal yr BP (Fig. 5). Relatively warm temperatures in Antarctica could result in reduced intensity of the cold-air polar incursions that reach Lake Consuelo during the dry season (austral winter). The significance of these polar outbreaks, or the lack thereof, in modulating daily minimum temperatures and particularly cloud formation in tropical South America during the austral winter has been previously discussed (Marengo and Rogers, 2001). With less Antarctic polar incursions, dry-season minimum daily temperatures in Consuelo probably increased and resulted in the altitude of ground-cloud formation moving upslope. Such a mechanism could suggest a Southern hemisphere influence of millennial-scale climate changes in Consuelo, but does not offer an explanation for lake-level changes prior to 37,000 cal yr BP, when a Northern hemisphere signal appears to dominate. Therefore, apart from the synchronous timing of low lake levels in Consuelo and increased temperatures in Antarctica around 37,000 cal yr BP, there appears to be no correlation between climatic changes in this part of western Amazonia and Southern-Hemisphere millennial-scale oscillations.

That none of the later D/O events of MIS 3 are recorded in Consuelo suggests that local climatic forcing, i.e. the climatic effects resulting from the development of regional ice caps, were stronger than the influences of distant oceans. The shift from a system apparently sensitive to changes in ocean circulation begs the question: how could this remote forcing cause a lowering of lake levels at Consuelo? Rather than speculate on the climatic linkage, the immediate cause of lowered lake level would have been reduced
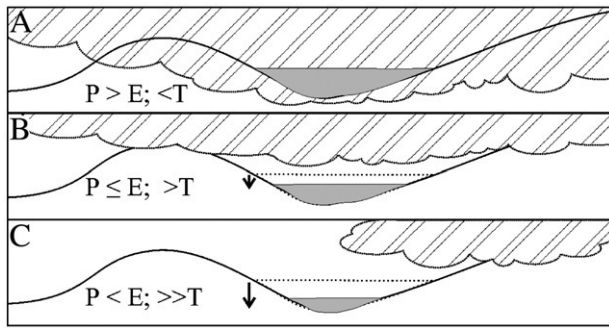
Figure 6. Schematic representation of the movement of ground-level cloud formation relative to moisture balances and temperature changes for Lake Consuelo; P = precipitation, E = evaporation; T = air temperature, <T = low temperatures, >T = warm temperatures, >>T = even warmer temperatures.

precipitation and/or a cloud base moving upslope (e.g. Fig. 6C). This could be explained by reduced organized convection over the Amazon basin (Bush and Silman, 2004) and perhaps even reduced evaporation in the equatorial Atlantic, the major moisture source for the Amazon basin. Precipitation, temperature and ground-level cloud formation could easily be related. Supporting this argument is that after 37,000 cal yr BP, the linkage is removed and the system appears to be an ever-wet cloud forest as precipitation may have increased but, more importantly, ground-level cloud formation moved downslope as temperatures fell during the LGM.

A profound drought caused lake levels at Titicaca to drop significantly between 33,000 and 28,000 cal yr BP (Baker et al., 2001a; Fritz et al., 2004). This interval was also the driest period recorded in Lake Pata in central Amazonia (Bush et al., 2004a) and its termination coincided with the onset of ice accumulation in the modern Sajama ice cap (Thompson, 2000). The timing of the dry event may have been precessionally driven as summer insolation maxima fell (Baker et al., 2001a; Fritz et al., 2004). However, the only MIS 3 dry events inferred from Lake Consuelo corresponded with D/O inter-stadials 11 to 8. Between 33,000 and 28,000 cal yr BP, the Consuelo forests were dominated by species currently associated with wet montane cloud forest and the aquatic vegetation had receded (Fig. 3). The RoC values were low and stable throughout this period and sediments had little change in their C content (LOI-550) (Figs. 4 and 5). Taken together, these factors suggested the regular occurrence of ground-level clouds and moist conditions at the site between 33,000 and 28,000 cal yr BP (Fig. 6A). It appears probable that the profound drought that lowered lake-level at Lake Titicaca c. 130 m just 170 Km to the southwest, had little or no effect on Lake Consuelo. Reconciling the apparently discrepant moisture histories of the Altiplano and Consuelo could be achieved again by recognizing the role of glacial temperature on cloud formation in this system. Reduced temperatures would have weakened the convection needed for SASM at the same time as the precessional influence may have weakened the SALLJ. The net effect of these factors would have been to reduce moisture delivery to the Altiplano. However, the same cooling would have placed the elevation of ground-level cloud cover right over Consuelo. As the precessional cycle caused increased wet-season insolation between c. 30,000 cal yr BP and 20,000 cal yr BP (Fig. 5), the SALLJ strengthened, and there was more convection to cause increased precipitation on the Altiplano. The cold temperatures and wet conditions ensured that Consuelo remained cloud-covered and lake levels high (Fig. 6A).

In contrast to the MIS 3 drought, the mid-Holocene drought that lowered lake level at Titicaca by 80 m was manifested at Lake Consuelo. Between 7400 and 5000 cal yr BP, a marked reduction in Consuelo's lake surface area and water depth is inferred, consistent with drought episodes reported for the region (Servant et al., 1981). Low sedimentation rates between 7400 and 5000 cal yr BP indicated low influxes of allochthonous material to the lake and corresponded

with a period of low rainfall. The inflexion point in the sedimentation rates could also indicate a hiatus in the record c. 5000 cal yr BP (Fig. 2), but whether there was a real stratigraphic gap or not, and whether it occurred before or after 5000 cal yr BP, cannot be established without analyzing and dating additional records from Lake Consuelo. Increased pollen influx and high abundances of aquatic elements indicated that Lake levels were lower than prior to 7400 cal yr BP. High abundance of aquatic elements indicated that the shoreline lay closer to the coring site than in periods when these elements were less abundant. The exposed lakebed supported a marsh, where sedges (Cyperaceae) colonized newly exposed margins and *Myriophyllum* and *Isoetes* occupied the shallows (Fig. 3). The terrestrial pollen record also revealed a change in the vegetation between c. 8200 and 3700 cal yr BP (Fig. 4B) with a sudden increase in *Begonia* abundance to 30% of the pollen sum, and *Clethra* reaching 10% (Fig. 3). In the modern forest, *Begonia* is an abundant component of secondary forests becoming particularly common after sudden disturbances such as landslides (Marchant et al., 2002). Additional evidence for increased disturbance in this forest comes from the absence of *Iriartea* and *Dictyocaryum* during the mid-Holocene and increased abundance of *Cecropia* and *Warszewiczia* after c. 6000 cal yr BP. The RoC and the ordination show that the forest composition changes during the mid-Holocene surpassed the speed of changes associated with the temperature fluctuations of MIS 3 or 2 (Figs. 4 and 5).

Contrasting glacial and interglacial droughts

Mid-Holocene dry conditions at Lake Consuelo are consistent with drought episodes reported for multiple sites in Amazonia and the Andes (Absy et al., 1991; Bush et al., 2007; Mayle et al., 2000; Servant et al., 1981). At Lake Pacucha, mid-Holocene dry conditions were manifested as a period of overall low lake level spanning several thousands of years, punctuated by wet phases (Hillyer et al., 2009; Valencia, 2006). Similarly, the lake levels at Titicaca were substantially lower than modern between c. 7200 and 5600 cal yr BP, with water levels as much as 90 m below present (Baker et al., 2001b; Hanselman et al., 2005; Theissen et al., 2008) and Lake Huiñaimarca experienced a dry period prior to 3500 cal yr BP (Abbott et al., 1997). Thus, the timing and intensity of mid-Holocene drought in Consuelo coincides with other records from the region, while MIS 3 periods of reduced moisture availability were not synchronous with those on the Altiplano. A critical difference between MIS 3 and the Holocene droughts was the c. 5–7°C difference in mean temperatures. Cool temperatures after 37,000 cal yr BP probably caused lowering of the cloudbank, immersing Consuelo in cloud (Fig. 6A). This immersion probably mitigated the effects of drought at Consuelo, but the Holocene warmth offered no such buffering. The Consuelo record did not provide direct evidence of warmer-than-modern tempera-tures during the mid-Holocene, but it indicated a lifting of ground-level cloud base. Because Lake Consuelo lies close to the modern elevation of ground-level cloud formation, either warmer or drier air, or a combination of both could cause relative humidity to fall, and for cloud to form at higher elevations (Fig. 6C). While changes in temperature and moisture availability could lower lake level, the added impact of increased evaporation from the lake surface may have been a relatively greater change in the hydrological balance of the basin during the Holocene (Fig. 6C). Thus, the lowest lake levels at Consuelo could reflect conditions leading to a peak of evaporative loss that may not correlate directly with lowest precipitation, but with an upslope movement of the lower limit of ground-level cloud.

Overall, the record from Lake Consuelo was consistent with mid-Holocene dry episodes recorded in the Andean Altiplano and portions of Amazonia (e.g. Absy et al., 1991; Baker et al., 2001b). However, the timing and duration of dry episodes across the continent indicate multiple events, rather than one time-transgressive episode and a common, and probably global, triggering mechanism. We hypothesize

that increased frequency of warm ENSO events during the mid-Holocene (Moy et al., 2002; Rodbell et al., 1999; Sandweiss et al., 1996) could account for recorded reduced lake levels due to decreased regional precipitation across South America. A clear analog for this effect could be the El Niño of 2005 (Marengo et al., 2008a). Further evidence and a better understanding of past, as well as present, climatic regimes controlling climate patterns over Amazonia and the eastern Andean flank would allow testing of this hypothesis.

Concluding remarks

The paleoecological record from Lake Consuelo indicated a constant forest cover during the past 46,300 cal yr BP withstanding considerable community turnover. These data add considerable detail to our image of regional climate change in western Amazonia and the eastern Andean flank. The altitudinal range fluctuations of montane taxa resulting from cooling during MIS 3 were typically individualistic. As a result, glacial vegetation at Lake Consuelo resembled the composition of montane forests growing today about 1000–1200 m upslope. Lake Consuelo was not moisture-limited during the LGM and supported a constantly present cloud forest for the last 46,300 yr. Then, the onset of deglacial warming began as early as 22,000 cal yr BP, in accord with other early estimates from southern Peru.

Results from Lake Consuelo indicate that moisture availability, possibly mediated through cloud cover, played the most significant role in rapid ecological change in this system. The period of most profound drought in the Peruvian-Bolivian Altiplano (33,000–28,000 cal yr BP) was not recorded in Lake Consuelo and was probably buffered by a continuous ground-level cloud cover. The mid-Holocene drought recorded in multiple records across the continent caused a reduction in lake levels, and perhaps drying of Lake Consuelo. As the lower limit of ground-level cloud formation lifted, it did not provide the same buffering effect as it did during the LGM.

Global climate models predict significant changes in seasonality of precipitation in the Neotropics to take place over the next 100 years (IPCC, 2007). It is evident from this study that cloud forests in western Amazonia are closely dependent on ground-level cloud formation and that climate change has caused the height of cloud formation to shift up and down slope during the past. Evidence from Lake Consuelo showed that past droughts caused rapid and abrupt ecological changes, as measured by RoC (Fig. 4B). However, such climatic fluctuations occurred at rates that did not exceed the capacity of the forest to accommodate change allowing it to persist over the last 46,300 cal yr BP. Cloud forests upslope of Lake Consuelo have experienced the buffering effect of semi-permanent cloud cover during the past as they sat above the fluctuating lower limit of ground cloud formation. The sensitivity of this limit to past temperature and moisture changes legitimizes the threat that future climate change poses on these ecosystems. A rate of change of 5°C increase in air temperatures in the next 100 years would exceed the speed of any climate change that these forests have experienced during the past 46,300 years, posing an unprecedented extinction risk to western Amazonian biodiversity. In addition, climate change is not the sole cause for current biodiversity loss in montane ecosystems, but as Pounds et al., (2006) have suggested, the synergism between new diseases and habitat stressors linked to climate change significantly increases the extinction risks.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yqres.2009.10.005.

References

Abbott, M.B., Seltzer, G.O., Kelts, K.R., Southon, J., 1997. Holocene paleohydrology of the tropical Andes from lake records. Quaternary Research 47, 70–80.

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.

Alley, R.B., 2004. GISP2 Ice Core Temperature and Accumulation Data. NOAA/NGDC Paleoclimatology Program, Boulder CO, USA., IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series #2004-013.

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.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. University Park Press, Baltimore.

Blunier, T., Brook, E.J., 2001. Timing of Millennial-scale climate change in Antarctica and Greenland during the last glacial period. Science 291, 109–112.

Bush, M.B., Silman, M.R., 2004. Observations on Late Pleistocene cooling and precipitation in the lowlands Neotropics. Journal of Quaternary Science 19, 677–684.

Bush, M.B., Weng, C., 2006. Introducing a new (freeware) tool for palynology. Journal of Biogeography 34, 377–380.

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., Silman, M.R., Urrego, D.H., 2004b. 48,000 years of climate and forest change in a biodiversity hot spot. Science 303, 827–829.

Bush, M.B., Silman, M.R., Listopad, C.M.C.S., 2007. Climate change and human occupation in Peruvian Amazonia: a paleoecological perspective. Journal of Biogeography 34, 1342–1356.

Chiu, T.C., Fairbanks, R.G., Cao, L., Mortlock, R.A., 2007. Analysis of the atmospheric ^{14}C record spanning the past 50,000 years derived from high-precision $^{230}Th/^{234}U/^{238}U$ and $^{231}Pa/^{235}U$ and ^{14}C dates on fossil corals. Quaternary Science Reviews 26, 18–36.

Clement, A.C., Hall, A., Broccoli, A.J., 2004. The importance of precessional signals in the tropical climate. Climate Dynamics 22, 327–341.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., 1999. Amazon Pollen Manual and Atlas. Harwood Academic Press, New York.

Cruz, F.W., Burns, S.J., Karmann, I., Sharp, W.D., Vuille, M., Cardoso, A.O., Ferrari, J.A., Silva Dias, P.L., Viana, O., 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. Nature 434, 63–66.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptative responses to quaternary climate Change. Science 292, 673–679.

Dean, W.E., 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Petrology 44, 242–248.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. Wiley, Chichester.

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

Faith, D.P., Michin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Foster, P., 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Science Reviews 55, 73–106.

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.

Genty, D., Blamart, D., Ghaleb, B., Plagnes, V., Causse, C., Bakalowicz, M., Zouari, K., Chkir, N., Hellstrom, J., Wainer, K., Bourges, F., 2006. Timing and dynamics of the last deglaciation from European and North African d13C stalagmite profiles—comparison with Chinese and South Hemisphere stalagmites. Quaternary Science Reviews 25, 2118–2142.

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

Hansen, B.C.S., Rodbell, D.T., Seltzer, G.O., León, B., Young, K.R., Abbott, M., 2003. Late-glacial and Holocene vegetational history from two sites in the western Cordillera of southwestern Ecuador. Palaeogeography, Palaeoclimatology, Palaeoecology 194, 79–108.

Herrera, L.F., Urrego, L.E., 1996. Atlas de polen de plantas útiles y cultivadas de la Amazonia colombiana. Tropenbos-Fundacion Erigaie, Bogotá, Colombia.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.

Hillyer, R., Bush, M., Valencia, B.G., Steinitz-Kannan, M., Silman, M.R., 2009. A 24,000-

year paleolimnological history from the Peruvian Andes. Quaternary Research 71, 71–82.

Hooghiemstra, H., 1984. Vegetational and climatic history of the high plain of Bogota, Colombia: A continuous record of the last 3.5 million Years. Gantner Verlag, Vaduz.

Hooghiemstra, H., van der Hammen, T., 2004. Quaternary ice-age in the Colombian Andes: developing an understanding of our legacy. Philosophical Transactions of the Royal Society of London 359, 173–181.

Hostetler, S.W., Mix, A.C., 1999. Reassessment of ice-age cooling of the tropical ocean and atmosphere. Nature 399, 673–676.

Hughen, K.A., Overpeck, J.T., Peterson, L.C., Trumbore, S., 1996. Rapid climate changes in the tropical Atlantic region during the last deglaciation. Nature 380, 51–54.

Imbrie, J.D., Hays, J., Martinson, D.G., McIntyre, A., Mix, A., Morley, J.J., Pisias, N.G., Prell, W.L., Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine 18O record. In: Berger, A.L., Imbrie, J., Hays, J., Kukla, G., Saltzman, B. (Eds.), Milankovitch and Climate. Reidel, Dordrecht, Netherlands, pp. 269–305.

IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the IPCC. Cambridge Unversity Press, Cambridge, UK and New York, USA, p. 996.

Juggins, S., 2003. C2 data analysis. Version 1.4 Beta.

Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen, P.M., Mejia, J., 2007. Dry spots and wet spots in the Andean hotspot. Journal of Biogeography 34, 1357–1373.

Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 115–129.

Malhi, Y., Wright, J., 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 359, 311–329.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M.B., Cleef, A., Duivenoorden, J., Kapelle, M., De oliveira, P.d., Texeira de Oliveira-Filho, A., Lozano-Garcia, S., Hooghiemstra, H., Ledru, M.P., Ludlow_Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American pollen database. Review of Palynology and Paleobotany 121, 1–75.

Marengo, J.A., Rogers, J.C., 2001. Polar air outbreaks in the Americas: assessments and impacts during modern and past climates. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, San Diego, pp. 31–51.

Marengo, J.A., Nobre, C.A., Tomasella, J., Oyama, M.D., de Oliveira, G.S., de Oliveira, R., Camargo, H., Alves, L.M., Brown, I.F., 2008a. The drought of Amazonia in 2005. Journal of Climate 21, 495–516.

Marengo, J.A., Nobre, C.A., Tomasella, J., Cardoso, M.F., Oyama, M.D., 2008b. Hydro-climatic and ecological behavior of the drought of Amazonia in 2005. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 363, 1773–1778.

Mark, B.G., Seltzer, G.O., Rodbell, D.T., Goodman, A.Y., 2002. Rates of Deglaciation during the Last Glaciation and Holocene in the Cordillera Vilcanota-Quelccaya Ice Cap Region, Southeastern Peru. Quaternary Research 57, 287–298.

Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of Southern Amazonian rain forests. Science 290, 2291–2294.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM, Gleneden Beach, Oregon.

McLachlan, J.S., Clark, J.S., 2004. Reconstructing historical ranges with fossil data at continental scales. Forest Ecology and Management 197, 139–147.

Minchin, P.R., 1987. An evaluation of relative robustness of techniques for ecological ordinations. Vegetatio 71, 145–156.

Moy, C.M., Seltzer, G.O., Rodbell, D.T., Anderson, D.M., 2002. Variability of El Niño/ Southern Oscillation activity at millenial timescales during the Holocene epoch. Nature 420, 162–165.

Munsell, 1994. Munsell Soil Color Charts. Macbeth Divsiion Kollmorgen Instruments Corp., New Windsor, N.Y.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Steves, H.H., 2007. Vegan: community ecology package. R package version 1.8-8. http://cran.r-project.org/, http://r-forge.r-project.org/projects/vegan.

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.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398, 611–615.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azoofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctins from epidemic disease driven by global warming. Nature 439, 161–167.

Poveda, G., Salazar, L.F., 2004. Annual and interannual (ENSO) variability of spatial scaling properties of a vegetation index (NDVI) in Amazonia. Remote Sensing of Environment 93, 391–401.

Prentice, I.C., Bartlein, P.J., Webb III, T., 1991. Vegetation and climate change in eastern North America since the last glacial maximum. Ecology 72, 2038–2056.

Rodbell, D.T., 1993. The timing of the last deglaciation in Cordillera Oriental, Northern Peru based on glacial geology and lake sedimentology. Geological Society of America Bulletin 105, 923–934.

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.

Roubik, D.W., Moreno, E., 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden.

Sandweiss, D.H., Richardson, J.B.I., Reitz, E.J., Rollins, H.B., Maasch, K.A., 1996. Geoarchaeological evidence from Peru for a 5000 years B.P. onset of El Niño. Science 273, 1531–1533.

Seltzer, G.O., Rodbell, D.T., Baker, P.A., Fritz, S.C., Tapia, P.M., Rowe, H.D., Dunbar, R.B., 2002. Early warming of tropical South America at the last glacial-interglacial transition. Science 296, 1685–1686.

Servant, M., Fontes, J.C., Rieu, M., Saliège, X., 1981. Phases climatiques arides holocènes dans le sud-ouest de l'Amazonie (Bolivie). Comptes Rendus Academie Scientifique Paris, Series II 292, 1295–1297.

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.

Stenni, B., 2006. EPICA dome C stable isotope data to 44.8 kyr BP. IGBP PAGES/world data center for paleoclimatology. Data Contribution Series #2006-112. NOAA/NCDC Paleoclimatology Program, Boulder, Colorado USA.

Still, C.J., Foster, P.J., Schneider, S.H., 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature 398, 608–610.

Stockmarr, J., 1972. Tablets with spores used in absolute pollen analysis. Pollen et Spore XIII 615–621.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.

Stuiver, M., Reimer, P.J., 2005. CALIB Radiocarbon Calibration. 5.0.1html.

Theissen, K.M., Dunbar, R.B., Rowe, H.D., Mucciarone, D.A., 2008. Multidecadal- to century-scale arid episodes on the northern Altiplano during the middle Holocene. Palaeogeography, Palaeoclimatology, Palaeoecology 257, 361–376.

Thompson, L.G., 2000. Ice core evidence for climate change in the Tropics: implications for our future. Quaternary Science Reviews 19, 19–35.

Urbanek, S., Lacus, S.M., 2007. R: a language and environment for statistical computing.

Urrego, D.H., Silman, M.R., Bush, M.B., 2005. The Last Glacial Maximum: stability and change in a western Amazonian cloud forest. Journal of Quaternary Science 20, 693–701.

Urrego, D.H., Bush, M., Silman, M.R., Correa-Metrio, A., Ledru, M.P., Mayle, F.E., Valencia, B.G., 2009. Millennial-scale ecological changes in tropical South America since the last glacial maximum. In: Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), Past climate variability from the Last Glacial Maximum to the Holocene in South America and surrounding regions. Developments in Paleoenvironmental Research Series (DPER), Springer.

Urrego, D.H., Bush, M.B., (In press). Climate change and history of western Amazonian forests: A paleoecological analysis.

Valencia, B.G., 2006. Late Quaternary Vegetation and Climate Change in the Southern Andes of Peru. Florida Institute of Technology.

van der Hammen, T., Hooghiemstra, H., 2003. Interglacial-glacial Fuquene-3 pollen record from Colombia: an Eemian to Holocene climate record. Global and Planetary Change 36, 181–199.

Visser, K., Thunell, R., Stott, L., 2003. Magnitude and timing of temperature change in the Indo-Pacific warm pool during deglaciation. Nature 421, 152.

Walker, M., Johnsen, S., Rasmussen, S.O., Popp, T., Steffensen, J.P., Gibbard, P., Hoek, W., Lowe, J., Andrews, J., Björck, S., Cwynar, L.C., Hughen, K., Kershaw, P., Kromer, B., Litt, T., Lowe, D.J., Nakagawa, T., Newham, R., Schwander, J., 2008. Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using Greenland NGRIP ice core, and selected auxiliary records. Journal of Quaternary Science 24, 3–17.

Wang, H., Fu, R., 2004. Influence of cross-Andes flow on the South American low-level jet. Journal of Climate 17, 1247–1262.

Wang, X., Auler, A.S., Edwards, R.L., Cheng, H., Cristalli, P.S., Smart, P.L., Richards, D.A., Shen, C.C., 2004. Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. Nature 432, 740–743.

Weng, C., Bush, M.B., Curtis, J.H., Kolata, A.L., Dillehay, T.D., Binford, M.W., 2006. Deglaciation and Holocene climate change in the western Peruvian Andes. Quaternary Research 66, 87–96.

Weninger, B., Jöris, O., 2008. A 14C age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in Western Eurasia. Journal of Human Evolution. Journal of Human Evolution 55, 772–781.

Weninger, B., Jöris, O., Danzeglocke, U., 2004. Cologne Radiocarbon Calibration and Paleoclimate Research Package. Calpal beyond the gost.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in Biodiversity Conservation. Science 314, 1261–1265.

Zhou, J., Lau, K.M., 1998. Does a monsoon climate exist over South America. Journal of Climate 11, 1020–1040.