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Major altitudinal shifts in Andean vegetation on the Amazonian flank show temporary loss of biota in the Holocene

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Abstract

The Lateglacial and Holocene vegetation history from the Amazonian flank of the south Colombian Andes has been studied in a 12 m long sediment core from Lake La Cocha (2780 m altitude). 18 AMS ^{14}C ages and 550 pollen samples yielded a history of a ~25 yr resolution. Montane forest extended up to 2200 m during the Lateglacial and shifted during a 10,000 yr period with millennial-scale and centennial-scale variability superimposed, to its present-day limit at 3550 m. We hypothesise that Intertropical Convergence Zone (ITCZ)-modulated trans-Amazonian moisture flows are an important driver of forest dynamics but influence of ENSO (El Niño Southern Oscillation) variability after 7000 yr BP may also be reflected in the record. Quasi-forest stability lasted for maximally 200 to 600 years. Upslope forest shifts up to 300 m/100 yr, reflecting a 1.5°C temperature increase were common during the Holocene. During several intervals of fastest forest migration the subpáramo disappeared for short intervals of time, suggesting that upslope forest migration exceeded the migration capacity of the subpáramo biome. From Lateglacial time onwards a suite of arboreal taxa show successive upslope expansion events, suggesting internal forest dynamics during the shift of residence areas from their glacial to Holocene altitudinal intervals. Logging, preferentially *Podocarpus*, frequent fires, forest disturbance and changes of the diatom flora in the lake suggest strong human impact after 1405 cal. yr BP.

Keywords

charcoal, climate variability, diatom record, Holocene, Lateglacial, local extinction, migration capacity, pollen record, subpáramo biome, upper forest line

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Introduction

Postglacial montane forest dynamics in the tropics is poorly understood, causing problems for a critical assessment of the potential impacts of global change. Among the most precise records of climate change are ice core records. Greenland ice cores show Holocene climate as relatively stable but ice cores from tropical glaciers show that climate changed significantly during the Holocene (Thompson et al., 1998). From the area below the tropical glaciers high-resolution records of Holocene climate change are lacking. To improve our understanding of forest dynamics at millennial to centennial timescales new records with robust time control are needed. Such records, in particular from locations with high sensitivity to climate change, show how ecosystems are responding and such information may fuel the debate on how global change (Intergovernmental Panel on Climate Change (IPCC), 2007) can potentially affect these biomes.

Lake sediments, and the fossil pollen and diatoms in them, are well known for their potential to reconstruct past changes in vegetation, environments and climate (Birks and Birks, 1980; Faegri and Iversen, 1989; Moore et al., 1991; Stoermer and Smol, 1999). In the temperate latitudes hundreds of sites have produced informative records of the dynamic past, but for the tropical latitudes such information is still scarce. For Central and South America, Marchant et al. (2009) synthesized pollen-based records of climate change since the last glacial maximum (LGM) at 21,000 years ago. With focus on Colombia, Marchant et al. (2001) elaborated a synthesis of 40 pollen records reflecting the last 6000 years. In ten windows of time, regional-scale climate change was inferred. Remarkably enough, during several time slices opposite trends in temperature and moisture change were identified depending on altitude. This highlights a geographically complex mosaic pattern of past climatic conditions, as is the case today.

Here we present a continuous new sediment record from Lake La Cocha that spans over the last 14,000 yr and shows unprecedented detail. Our objectives are to reconstruct and to assess Holocene vegetation and climate change at near equatorial latitude. Using a methodology from previous studies we reconstruct water-level changes of Lake La Cocha on the basis of aquatic vegetation (Torres et al., 2005; Van ’t Veer and Hooghiemstra, 2000) and diatom records, resulting in better reconstructions of water-level change in the past (Vélez et al., 2005a, 2005b). To place results in a wider regional context the climate record of Lake La Cocha is compared with records from the savannas at the foot of the Andes and the Andean flank which are also under influence of moisture supply from the Amazon Basin.

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Environmental setting of the study area

Lake La Cocha is located in the Guamués Basin at 2780 m altitude in Eastern Cordillera of Colombia (01º06'N, 77º09W) (Figure 1). The lake is confined by mountains which reach elevations between 2800 and 3600 m. Lake La Cocha is among the largest lakes in the northern Andes and is surrounded by wetlands. The basin faces the Amazonian lowlands and precipitation mainly originates from the Atlantic Ocean through convective precipitation originated by orographic uplift of air masses along the western flank of the Andes. Water-level fluctuations mainly relate to changes in the intensity of trans-Amazonian moisture flows (Gan et al., 2004; van Boxel et al., forthcoming). The meteorological station near the lake, located at 2830 m, shows that the mean annual precipitation (MAP) varies geographically from 1300 to 2000 mm (Moreno Diaz, 2004) with most precipitation falling between April and August and lowest precipitation in December. In the adjacent dry inter-Andean high plains MAP varies from 700 to 1400 mm (Wetlands International, 2007). The upper forest line (UFL) lies at ~3550 m (Rangel-Ch and Ariza-N, 2000) where a mean annual temperature (MAT) is ~9.5°C (Groot et al., 2011). As climatic conditions on the Andean flank are very humid we use a lapse rate of 0.5°C/100 m vertical forest displacement (Javellas and Thouret, 1995). Although the calculated MAT at the altitude of the lake is ~13.3°C the observed MAT is 11.6°C (Moreno Diaz, 2004). The colder temperatures in the lake valley compared with other sites at similar elevations are ascribed to the permanent flow of moist air masses from the Amazonian lowlands (Baker et al., 2001; Fu et al., 2001; Marengo et al., 2004; Vizy and Cook, 2007).

For the altitudinal vegetation distribution we followed Van der Hammen (1974), Cleef and Hooghiemstra (1984), Van der Hammen and Cleef (1986), (AM Cleef, personal observations and unpublished data, 2006–2011). Subandean forest reach to ~2300 m and is mainly reflected in the pollen record by *Acalypha, Alchornea, Cecropia*, Palmae, *Hieronima, Ficus* and Malpighiaceae. Andean forest ranges from 2300-3500 m up to ~3550 m with *Weinmannia, Alnus, Myrica, Styloceras, Podocarpus, Clusia, Myrsine, Juglans, Ilex* and *Hedyosmum* as frequent elements in this zone. The distribution of *Quercus* reaches its southernmost position on the slopes of the Patía River valley at some 20 km distance from the lake (Hooghiemstra, 2006; Cleef, personal communication, 2011). *Quercus* pollen is hardly registered showing that the pollen spectra reflect a limited area around the lake basin. Subpáramo vegetation stretches from ~3550 m to ~3650 m and is mainly reflected in the pollen spectra by Asteraceae, Ericaceae, *Polylepis, Escallonia* and *Hypericum*. Grasspáramo occurs above ~3650 m and is dominated by graminaceous genera such as *Agrostis, Calamagrostis, Festuca, Muehlenbergia* and *Swallenochloa*, stem rosettes of *Espeletia*, and the herbaceous genera *Gentiana, Halenia, Valeriana* and *Aragoa*. Most land surface above 3600 m is located on the Cerro Patascoy (Figure 2).

Around the lake the montane forest below ~2850 m, which possibly resembled today's vegetation on La Corota island (Pantoja Chamorro, 1999), has been replaced by pasture lands, meadows, and agricultural fields. Remnants of the original forest are dominated by *Ocotea guianensis* and *Weinmannia pubescens*. In the shrub stratum, *Miconia harlineii, Miconia* sp. and the fern *Ascotrichyum arborium* are dominant. In the herbaceous stratum the ferns *Polypodium* sp., *Anthurium* sp. and *Cavendishia* sp. are the main taxa. Today *Ocotea* sp. and *Nectandra* sp. have lost much abundance and most of the stands of *Podocarpus oleifolius* have been cleared. Reed swamps of *Scirpus californicus* are abundant around the lake and *Juncus bogotensis* occurs in wet grasslands and bogs (Figure 2).

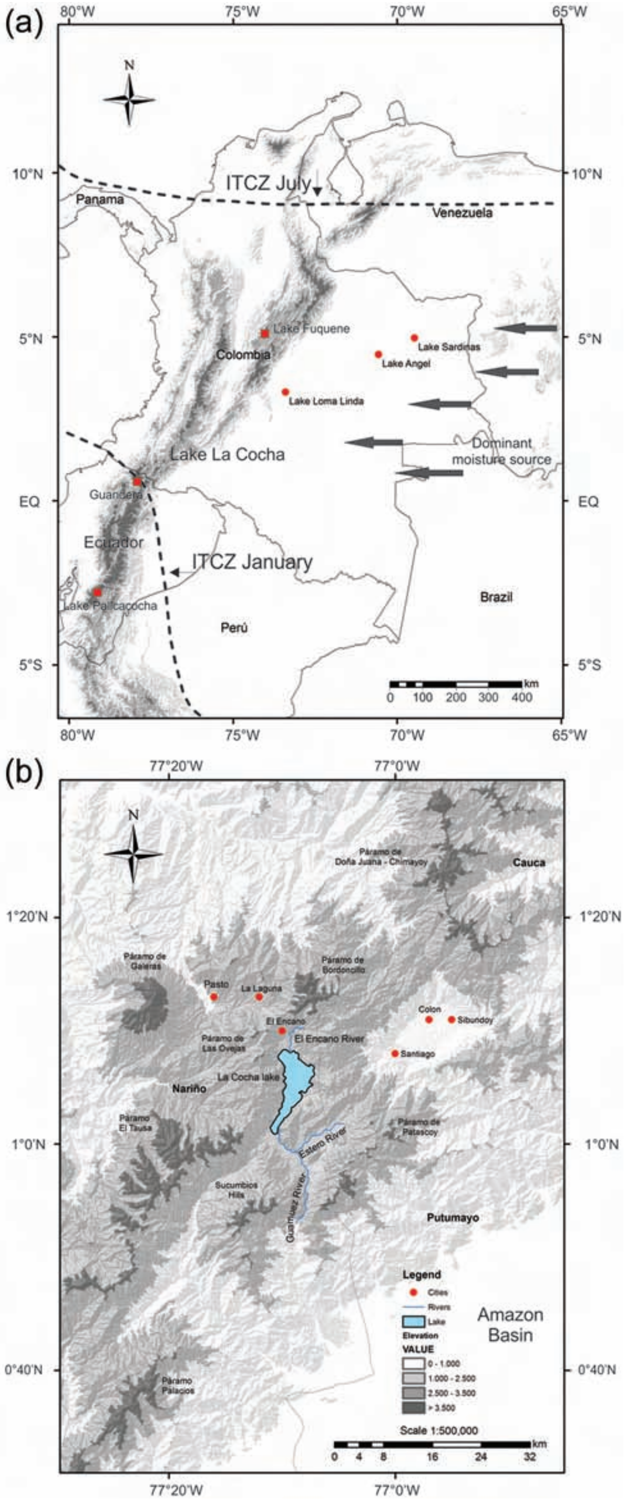


Figure 1. (a) Location of the study area, the pollen sites mentioned in the text, the seasonal positions of the Intertropical Convergence Zone (ITCZ), and main moisture supply to the eastern Andean flank (arrows). (b) Lake La Cocha (2780 m altitude) and surroundings. The present-day distribution of páramo coincides with the contour of >3500 m.

Methods

A 1200 cm long core La Cocha-1 (CH1) was retrieved from the wetlands on the northern side of lake (Figure 2). The uppermost 100 cm of sediments contained superfluous water and could not be collected; it is expected these sediments are of sub-recent age. The core was obtained with a Russian Corer of 50 cm length and

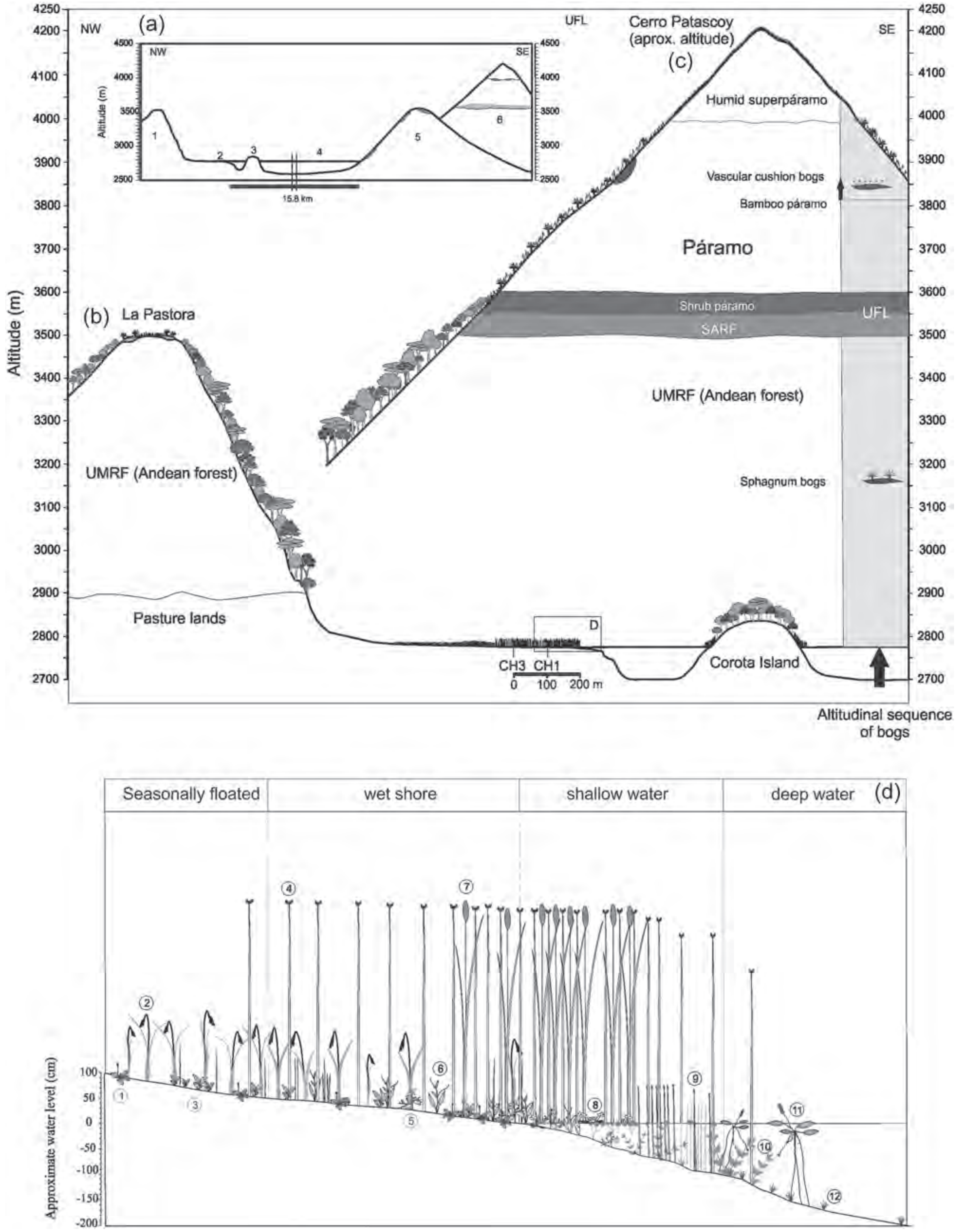


Figure 2. (a) Schematic idealized transect through the northwestern part of the Guamués Basin including Lake La Cocha, southern Colombia. (b) Vegetation profile showing La Pastora mountain, the wetlands at the border of the lake with the site of core CH1, and the Corota Island in the lake. (c) Schematic cross-section showing the altitudinal vegetation distribution up to 4200 m on the Cerro Patascoy southeast of Lake La Cocha. (d) Schematic cross-section through the border of the lake showing the main aquatic plant taxa: 1: *Plantago*; 2: Cyperaceae (*Schoenoplectus californicus*); 3: *Rumex*; 4: *Juncus*; 5: *Ludwigia*; 6: *Polygonum*; 7: *Typha*; 8: *Hydrocotyle* and *Ranunculus*; 9: Cyperaceae spp.; 10: *Myriophyllum*; 11: *Potamogeton*; 12: *Isöetes*.

75 mm diameter. Core segments were extracted and wrapped in plastic foil and protected by PVC guttering. Cores were transported to Amsterdam and stored in a dark room at 4°C. For pollen analysis samples of 1 cm^3 were taken at 2 cm increments along the core. Samples were treated with standard procedures for pollen preparation including sodium pyrophosphate, acetolysis, and

heavy liquid separation by bromoform (Faegri and Iversen, 1989). Pollen samples were mounted in a glycerin-gelatin medium. Prior to processing, one tablet of exotic *Lycopodium* spores was added to each sample for calculation of the pollen concentration and pollen influx values. For identification of pollen and spores we used the pollen morphological studies by Heusser (1971), Hooghiemstra (1984), Roubik and Moreno (1991), Colinvaux et al. (1999), Herrera and Urrego (1996), Velásquez (1999), Bogotá-Angel (2002), the pollen reference collection of the University of Amsterdam, and the online neotropical pollen key (http://research.fit.edu/bushlab/ pollen_db.htm).

Following Van ‘t Veer and Hooghiemstra (2000), pollen grains and spores were classified into the following ecological groups: (1) subandean forest, (2) Andean forest, (3) subpáramo, (4) grasspáramo, (5) aquatic vegetation, (6) algae, (7) pteridophyte spores, and (8) fungal spores. The taxa of groups 1 to 4 constitute the pollen sum and mostly 350 pollen grains were included. Of less productive samples we counted two microscope slides and we rejected samples with a pollen sum lower than 50 grains. For relationships between the proportion of arboreal pollen (AP%) and the altitudinal position of the UFL we refer to Bakker et al. (2008), Hooghiemstra (1984), Van ‘t Veer and Hooghiemstra (2000), Groot et al. (2011) and Bogotá-Angel et al. (2011b). The AP%-based estimate of the altitudinal position of the UFL is always compared with the evidence provided by individual pollen taxa (Bogotá-Angel et al., 2011b; Groot et al., 2011). In general, we assume a vertical distribution of Andean forest of ~1200 m, for subpáramo 100–200 m, and for grasspáramo ~500 m unless proportions are indicative of different distributions. Reconstructed temperatures refer to the elevation of the lake (2780 m) and relate to the calculated MAT of 13°C.

We analysed diatom samples at 10 cm intervals along the core. For the extraction of the diatom valves each sample was immersed in 30 ml of H_2O_2 (30%) and left for 24 h at room temperature after which few drops of potassium permanganate and 10 ml of HCl were added. Finally, samples were washed three times with distilled water. Permanent slides were mounted in Naphrax. At least 400 valves were counted per sample. We used Patrick and Reimer (1966), Krammer and Lange-Bertalot (1986, 1991, 1997) and Lange-Bertalot (2000) for diatom identification. For the ecological interpretation we used Evans (1958), Patrick and Reimer (1966), Gasse (1980), Torgan and Biancamano (1991), Alles et al. (1991), Moro and Fürstenberger (1997), Gaiser and Johansen (2000), Sala et al. (2002) and Poulíčková and Hašler (2007). Raw counts of pollen and diatoms were transformed into percentages and we used TILIA and TILIAGRAPH (Grimm, 1987) to plot the diagrams. The zonation of the pollen record is based on CONISS cluster analysis using all taxa of the pollen sum with values >2% (Grimm, 1987). For the zonation of the diatom record, all taxa were included. The magnetic susceptibility was measured at 0.5 cm increments along the core using a Geotek Multi-Sensor Core Logger at the Vrije Universiteit Amsterdam.

The chronology of the sediments is based on accelerator mass spectroscopy (AMS) ^{14}C dating. In absence of plant macrofossils we dated 18 bulk samples of 1 cm^3. Samples were processed at the Centre for Isotope Research of Groningen University. The age–depth model and calibration of the radiocarbon dates were obtained through ‘Clam’. Ages of not-dated depth were obtained through the smooth-spline model (version 1.0; Blaauw, 2010). In this paper all ages are expressed as calibrated ages before present (cal. yr BP) noted in the following text as ‘BP’.

Results

The radiocarbon dates (Table 1) show a steadily increasing of age with depth except for the sample at 1153 cm core depth (Figure 3). The deposition of sand just above the sample indicates a dynamic high-energy environment and makes sedimentary irregularities plausible. Therefore, this date was excluded from the age model. The ages show that the core represents Lateglacial and Holocene times. Sediments have accumulated at a rate of ~0.8 mm/yr. The sediments are mainly composed of peat intercalated with few distinct sand and silt layers (Table 2, Figure 4). The measured magnetic susceptibility shows relatively low values along the core with an average of −1.7 SI indicative of organic-rich sediments. High values of 127 SI are correlated with the sand layers, evidencing minerogenic input in the lake basin.

We analysed 550 pollen samples for the past 14,085 BP yielding a resolution of ~25 years. We recognised 196 different pollen taxa and 14 taxa of pteridophyte spores (Supplementary Information Table S1, available online). In total 23 zones were recognised. The most important taxa making up the regional vegetation (Figure 5) show changes in altitudinal distribution and changes in vegetation composition. The records of aquatic taxa, ferns, and fungal spores (Figure 6) show changes of the water-level of the lake. Descriptions of the pollen zones of the regional and local pollen diagrams are provided in the Supplementary Information (Supplementary Information Tables S2 and S3, available online). Records of diatom species (Figure 7; Supplementary Information Table S4, available online) were grouped into four assemblages that were used as indicators of water-level changes (Supplementary Information Table S5, available online). The planktonic assemblage is composed mainly by *Aulacoseria ambigua*. This species indicates a permanent water body and high water-levels. The planktonic/littoral assemblage is mainly composed of *Eunotia praerupta, E. minor, E. bilunaris* and *E. flexuosa*. These taxa are indicative of permanent water and littoral conditions of low electrolyte content and low pH. The littoral assemblage is composed of *Aulacoseira cf. distans, Fragilaria brevistriata, F. pinnata, Diploneis elliptica, Synedra ulna, Gomphonema parvulum, Epithemia turgida* and *Tabellaria floculosa*. This assemblage is indicative of low water-levels and the extension of the littoral area. The aerophil assemblage is composed of mainly *Orthoseira roeseana* (morphotype spiralis in particular), *Melosira dickeii, Diadesmis contenta, Luticola mutica* (and varieties), and *Hantzschia amphioxys*. These taxa are indicative of very low water-levels and wet terrestrial conditions. We recognised eight diatom zones (Supplementary Information Table S6, available online).

Palaeoenvironmental reconstruction

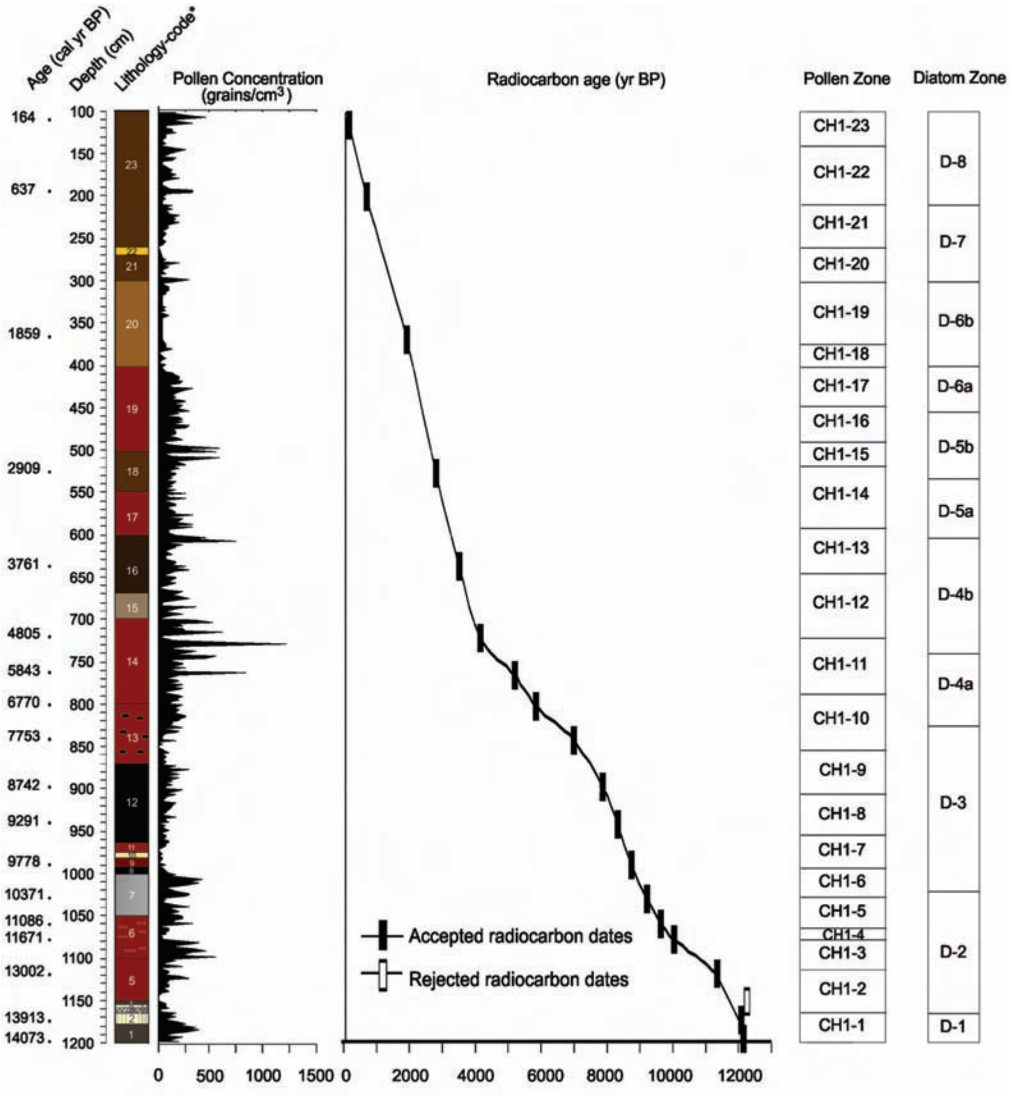
In the following section changes in the pollen record are interpreted as changes in the altitudinal position of the UFL, the composition of the vegetation, and the altitudinal extension of páramo in relation to the lake. Past climatic conditions such as temperatures and climatic moisture are inferred from changes in the vegetation (Supplementary Information Table S7, available online) and the limnological conditions as indicated by lithology, proportions of aquatic elements and diatoms. The sediments mainly consist of peat, indicating low-energy conditions allowing the accumulation of organic matter and the formation of peatland conditions that prevailed during the full period under consideration.

The highest UFL position at ~3550 m in period 19 (later intervals show disturbed vegetation) equals ~60–70% AP. The lowest UFL position in periods 2 and 3 typically show a lake located in the upper parts of the grasspáramo, indicating the UFL lies at ~2300 m (Table S7, available online). This setting equals ~10% AP. Periods 16 and 17 show ~30% AP and pollen spectra typically from a lake surrounded by subpáramo vegetation that extended

Table 1. AMS radiocarbon-dated samples from core La Cocha-1 and sample specific data.

Sample code	Depth (cm)	Material dated	Radiocarbon age (1σ, ^{14}C yr BP)	Calendar age range (cal. yr BP)	Best date (cal. yr BP)	Sedimentation rate (yr/cm)
GrA-40671	110	bulk	165±45	14–293	164	2
GrA-35263	194	bulk	695± 35	556–691	637	6
GrA-39979	366	bulk	1915±25	1814–1922	1859	7
GrA-35266	525	bulk	2805± 35	2806–2996	2909	7
GrA-39981	637	bulk	3520±30	3683–3843	3761	8
GrA-35265	720	bulk	4165± 40	4700–4907	4805	13
GrA-39982	763	bulk	5200±30	6036–6135	6089	24
GrA-39972	801	bulk	5845±30	6706–6824	6770	24
GrA-39818	841	bulk	7005±30	7672–7825	7753	25
GrA-39819	898	bulk	7880±40	8645–8903	8742	17
GrA-39997	941	bulk	8325±40	9177–9390	9291	13
GrA-39998	989	bulk	8755±40	9658–9890	9778	10
GrA-40019	1029	bulk	9220±40	10,268–10,477	10,371	15
GrA-35267	1060	bulk	9650±50	10,957–11,210	11,086	23
GrA-40020	1079	bulk	10040±45	11,538–11,803	11,671	31
GrA-40158	1119	bulk	11350±50	12,913–13,090	13,002	33
GrA-40195	1174	bulk	12080±45	13,827–13,998	13,913	17
GrA-35469	1198	bulk	12150±60	13,934–14,198	14,073	7
GrA-40194	1153 (*)	bulk	12260±50	13,607–13,771	13,688	*

*Rejected date; a value for sediment accumulation rate is not appropriate.



* For lithology code see Table 2.

Figure 3. Left to right: calibrated ages, depth scale, lithological column (for explanation of the numbers see Table 2), pollen concentration record, depth versus age graph and the positions of the radiocarbon samples and their age intervals, and the pollen and diatom zones.

Table 2. Lithological intervals of core La Cocha-1.

Depth (cm)	Lithology	Lithology code
100–260	Dark-brown peat	23
260–270	Light-brown peat	22
270–300	Dark-brown peat	21
300–400	Dark-brown reddish peat	20
400–500	Brown reddish peat	19
500–550	Dark-brown peat	18
550–600	Dark-brown reddish organic mud	17
600–670	Dark-brown mud	16
670–700	Silt	15
700–800	Dark-brown reddish peat	14
800–870	Dark-brown reddish peat (with black organic segments)	13
870–962	Black peat (much decomposed)	12
962–974	Reddish peat	11
974–982.5	Silt with fine sand fraction	10
982.5–993	Reddish peat with some silt intercalations	9
993–1000	Black peat (very decomposed)	8
1000–1050	Dark-brown peat (much decomposed) + clay fraction	7
1050–1100	Dark-brown reddish peat (lighter at different segments)	6
1100–1150	Dark-brown reddish peat	5
1150–1155	Brown mud (much decomposed)	4
1155–1159	Fine sand with silt	3
1154–1165	Coarse sand	3
1165–1179	Dark-brown mud with silt alternations	2
1164–1200	Organic peat	1

from 2600 to 2900 m (Table S7, available online). Period 13 shows pollen spectra with an AP% of 40% typically of proportions near the UFL. These periods show the relationships between AP% and the position of the UFL and the quasilinear relationship is in agreement with the results from the Fúquene Basin (Groot et al., 2011). The characteristic information for each period is summarised in Table 3.

Discussion

The elevation of the lake at 2780 m is halfway between the lowest and highest altitudinal position of the UFL, and thus offers an excellent opportunity to investigate the effects of climate change on altitudinal vegetation distributions. The lowest position in the record of the UFL at ~2200 m was reached during the Lateglacial and the highest position at 3550 m during the Holocene. The UFL is first recorded at 2200 m (14,085–13,820 BP) and for the first time reached a stable position around 2400 m at 11,200 BP (period 5), around 2600 m at 8020 BP (period 10), around 2800 m at 3840 BP (period 13), around 3000 m at 2100 BP (period 18), and it reached present-day levels of 3550 m at 1910 BP (period 19). *Hedyosmum, Miconia*, Urticaceae-Moraceae, and *Myrsine* are best represented when the UFL was below 2600 m. The first three taxa have significant pioneer qualities (Bogotá-Angel, 2011b) and we take this as evidence that these taxa migrate upslope preferentially in the forefront of the expanding forest. In addition, these taxa, *Hedyosmum* in particular, disperse efficiently into the páramo (Moscol-Olivera et al., 2009). While the UFL shifted from 2600 to 2800 m the proportions of *Podocarpus* and *Alnus*, both with pioneer qualities, first increased, followed by the palm *Ceroxylon, Weinmannia, Miconia* and *Psychotria*. Indeed Moscol-Olivera et al. (2009) showed that pollen of *Weimannia* is poorly distributed into the páramo and thus its representation is indicative of local presence. After the UFL had surpassed the elevation of the lake, also asteraceous ecotone taxa and later on rosaceous taxa are registered. In conclusion, pioneer taxa are more abundant in the forefront of expanding forest and taxa from late successional stages follow later (Bogotá-Angel, 2011b).

There are differing opinions about the process of reorganisation of altitudinal vegetation distributions from glacial to interglacial time. Individualistic migration patterns leading to no-analogue forest associations are advocated by Urrego et al. (2009) among others. In contrast T Van der Hammen, AM Cleef, and H Hooghiemstra advocate a concerted migration of many taxa that form altitudinally organised plant associations (‘vegetation belts’). In general they consider plant associations as mainly temperature (altitude) dependent (Hooghiemstra and Van der Hammen, 2004, and references therein). Urrego et al. (2009) call this view ‘community-based species migrations’. Our present high-resolution pollen record sheds new light on this debate. During the transition from Lateglacial to Holocene conditions, arboreal species with pioneer qualities took the lead in the forefront of expanding forest. However, pollen records showing longer intervals of time show that once the montane forest had reached its Holocene elevations its floristic composition did not differ essentially from its composition when this forest resided at lower elevations during glacial times (e.g. Bogotá-Angel et al., 2011a, 2011b; Van ‘t Veer and Hooghiemstra, 2000; Groot et al., forthcoming).

The pollen record of south Peruvian Lake Consuelo at 1360 m elevation documents vegetation dynamics from the western Andean flank (Urrego et al., 2009). In our experience, however, vegetation records from the northern Andes that come from altitudes between 1000 and 1400 m are little responsive to climate change (Wille et al., 2001). During interglacial and glacial conditions this altitudinal interval was continuously covered by subandean forest (Hooghiemstra and Van der Hammen, 2004; Wille et al., 2001). The present record is most valuable in showing the transitional phase. ‘Individualistic migration’ versus ‘concerted association-based migration’ seems to reflect different stages in the same process of migrating biomes. This supports that changes in the altitudinal distribution of plant associations can be used as a proxy for temperature. It also suggests that plant associations

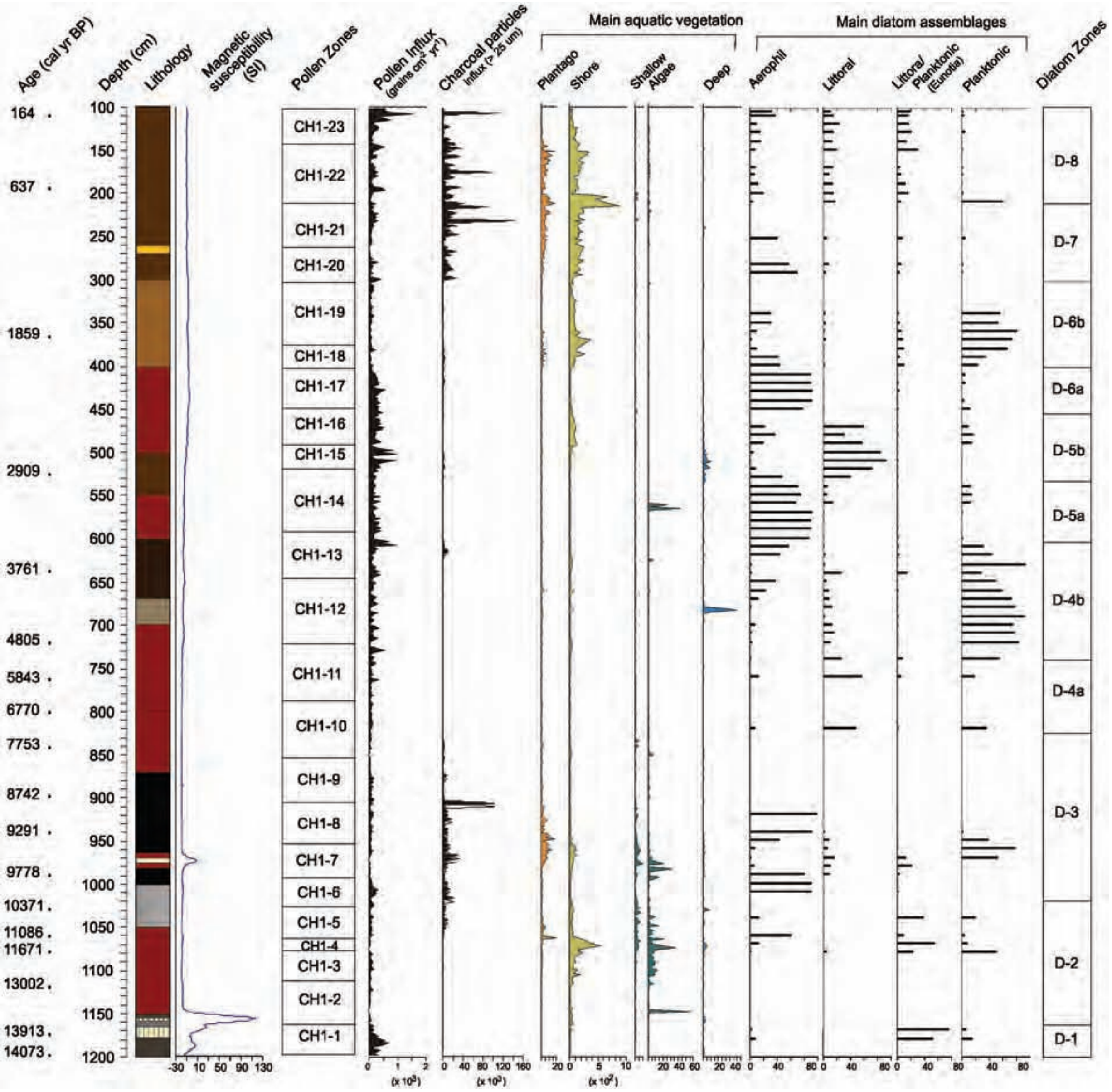


Figure 4. Left to right: calibrated ages, depth scale, lithological column, magnetic susceptibility record, pollen zones, pollen influx record, charcoal record, records of aquatic and wet shore vegetation, records of main diatom assemblages, and diatom zones. For explanation of the lithological column see Figure 3 and Table 2.

may temporarily change in composition but return to a relatively 'stable floristic composition' once the new residence interval has been reached. No-analogue forest compositions potentially may be of relatively short duration and further analysis is needed to clarify this debate in more detail (Urrego et al., 2009). We conclude that the pollen records of La Cocha (2780 m) and Consuelo (1380 m) both show clear evidence of expansion events of individual taxa, as well as concerted altitudinal migration of suites of taxa making up present-day lower montane forest, upper montane forest, and páramo. Both records show pioneers responding first to climate change. In this debate it is relevant to note that multiple field observations and vegetation analysis show that also today a number of taxa have altitudinal ranges deviating from the plant association in which they are categorised. Examples include *Acalypha*, *Cecropia*, *Ceroxylon*, *Croton*, *Hieronyma*, *Pilea*, and Cyatheaceae (Bogota-Angel et al., 2011b). For some taxa, such as *Podocarpus*, the proper ecological range is still poorly understood. Although frequently characterised as an exclusive 'montane' element, and therefore considered as indicative of cold conditions, a re-analysis of herbarium collections shows that *Podocarpus* has a wider altitudinal range (Cárdenas et al., 2011a, 2011b; Punyasena et al., 2011; see also Van der Hammen and Hooghiemstra, 2000) which indicates that making decisions whether or not we deal with no-analogue vegetation seems premature.

During several short intervals subpáramo vegetation is hardly present: during period 4, at the start of periods 7, 10 and 11, and to a lesser degree also during periods 15 and 18 (Figure 5). All these intervals coincide with a rapid upslope migration of montane forest. The pollen record suggests that montane forest has more pioneer qualities than the subpáramo and expands upslope faster. In these cases the narrow zone with subpáramo was replaced by forest with the consequent loss of subpáramo vegetation. There are few more examples of temporarily lost biomes, such as shown by the pollen record of Pedro Palo at 2000 m elevation (Hooghiemstra and Van der Hammen, 1993). This record suggests that during Lateglacial time the montane forest biome was regionally lost and dry vegetation from the Magadela Valley was transitional to dry páramo vegetation. We have not noticed before such clear examples of temporarily lost biomes and we

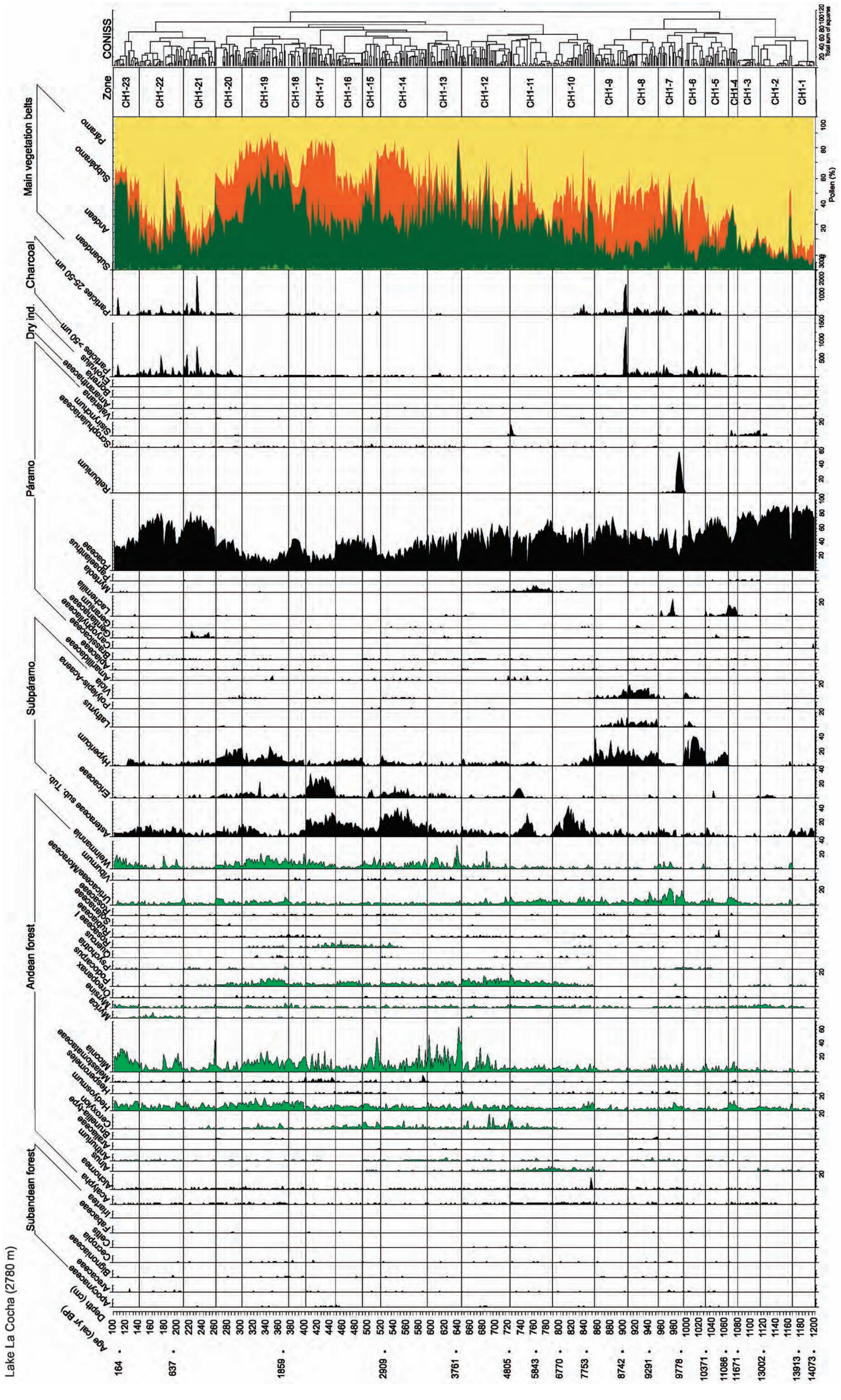


Figure 5. Pollen percentage diagram of core La Cocha-1 showing the records of the most important taxa arranged after ecological preferences. Left to right: calibrated ages, depth scale, records of the main individual taxa (taxa in green are related to distinct expansion events), record of charcoal fractions, main pollen diagram, pollen zones, and CONISS dendrogram.

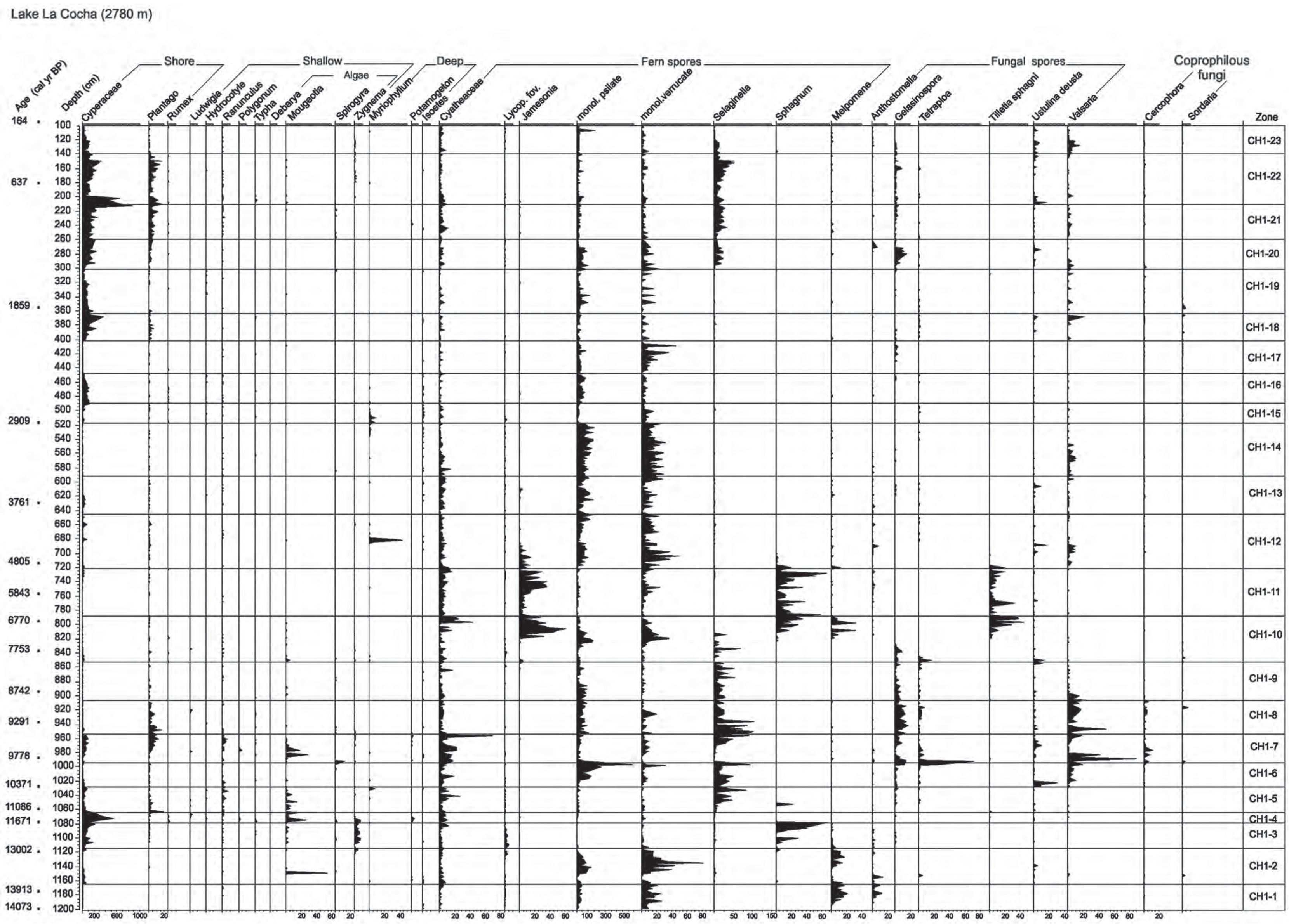


Figure 6. Pollen percentage diagram of core La Cocha-1. Left to right: calibrated ages, depth scale, records of taxa reflecting aquatic and wet shore vegetation, fern spores, fungal spores, coprophilous fungal spores, and pollen zones.

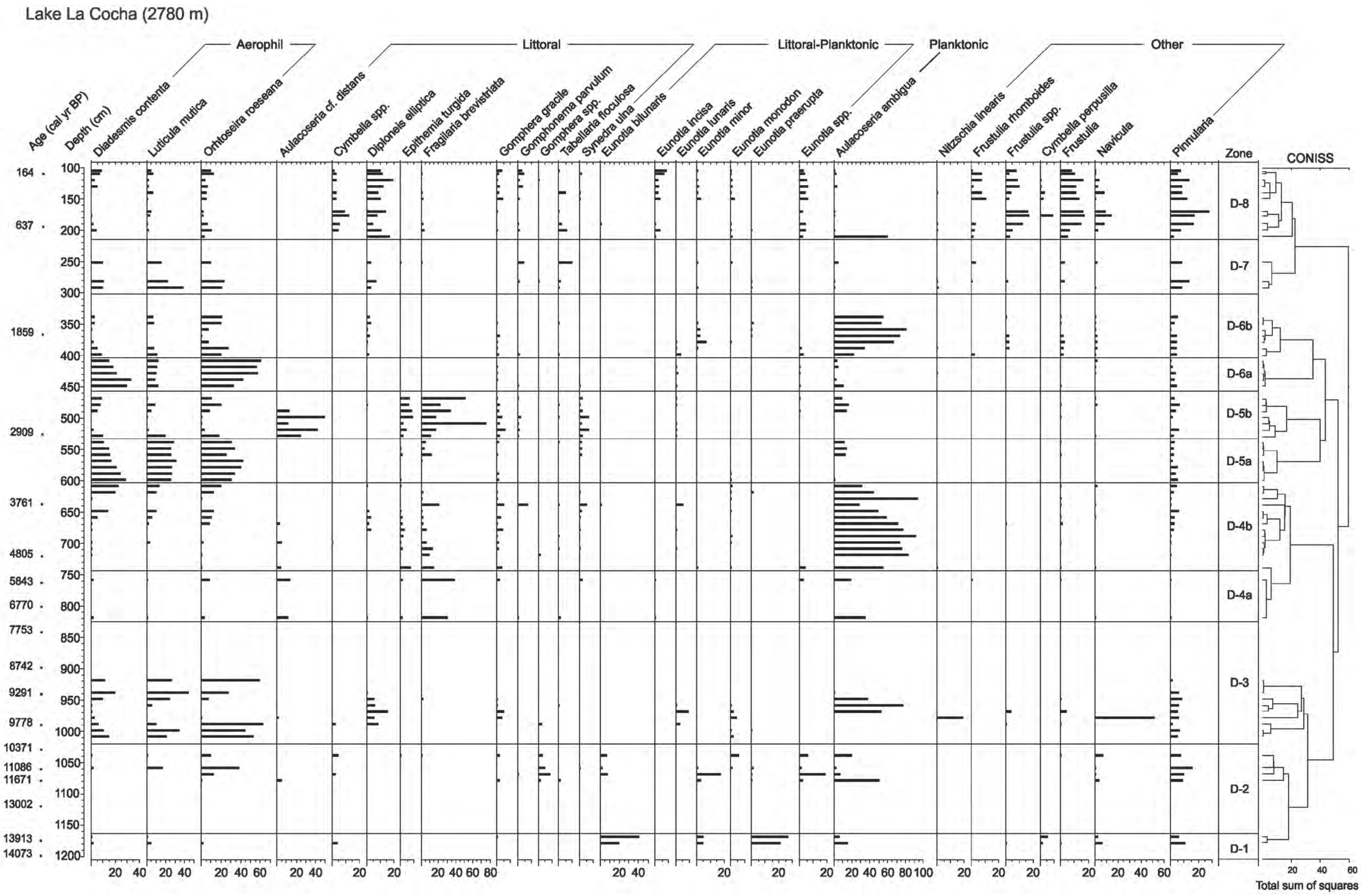


Figure 7. Diatom percentage diagram of core La Cocha-1. Taxa are grouped according to their mode of life. Left to right: calibrated ages, depth scale, records of individual diatom taxa, diatom zones, and the CONISS dendrogram.

Table 3. Characteristic information of the periods recognised in pollen record La Cocha-1, summarised from Table S7 (available online).

Period	Age (cal. yr BP)	Pollen zone	Diatom zone	UFL position (m)	MAT (°C)
1	14,085–13,820	CH1-1	D-1	~2200	−7.5
2	13,820–12,855	CH1-2	D-2	2300–2350	−6.5
3	12,855–11,640	CH1-3	D2	2350	−6
4	11,640–11,200	CH1-4	D-2	~2600	−4.5
5	11,200–10,350	CH1-5	D-2	~2400	−6
6	10,350–9840	CH1-6	D-3	~2350	−6
7	9840–9420	CH1-7	D-3	~2600	−4.5
8	9420–8855	CH1-8	D-3	~2450	−5.5
9	8855–8020	CH1-9	D-3	2350	−6
10	8020–6450	CH1-10	D3/D-4a	~2550–2650	−5/−4.5
11	6450–4850	CH1-11	D-4a/D-4b	~2600	−4.5
12	4850–3840	CH1-12	D-4b	~2600	−4.5
13	3840–3400	CH1-13	D-4b	~2800	−4
14	3400–2860	CH1-14	D-5a/D-5b	~2600	−4.5
15	2860–2670	CH1-15	D-5b	~2800	−4
16	2670–2400	CH1-16	D-5b	~2600	−4.5
17	2400–2100	CH1-17	D-6a	~2600	−4.5
18	2100–1910	CH1-18	D-6b	~3000	−3
19	1910–1405	CH1-19	D-6b	~3450–3600	Modern value (13–13.5)
20	1405–1100	CH1-20	D-7	Start of human impact	–
21	1100–745	CH1-21	D-7	Grasslands around lake	–
22	745–305	CH1-22	D-8	Forest expansion	–
23	305–127	CH1-23	D-8	Forest recovered from clearings	–

suggest that these phenomena are related to the vegetation dynamics discussed in the previous section.

The record shows increased variability in UFL positions after 7000 BP (period 10) reflecting moisture and temperature variation which coincides with increased variation in ENSO found in Lake Pallcacocha (Moy et al., 2002). At longer timescales, periods of ~2 millennia are superimposed on the ~10,000 yr long trend of the upslope-shifting UFL. We identified periods of relatively 'stable' environmental conditions and concluded that during Holocene times such periods vary from ~200 to ~600 years at most, showing high climate variability during Holocene times. Provisionally estimated rates of change (RoC) of altitudinal displacement of plant associations vary between 30 m (periods 7 and 9) and 60 m (periods 4 and 14), and in the most extreme events up to 300 m (period 18) altitudinal displacement of plant associations per century. More robust analysis of variability and RoC is in progress (González-Carranza et al., unpublished data, 2010).

The ecological significance of diatom categories and aquatic vegetation categories are mostly congruent. However, where different environmental conditions occurred as a mosaic, pollen and diatoms may reflect contrasting environments. However, trends in water depth are congruent, evidencing that the water-level reconstructions are robust. In general terms, low lake levels indicated by the diatom record occur simultaneously with the increase of páramo and subpáramo vegetation and high lake levels occur simultaneously with expansion of the forest.

During Lateglacial time the site was on a large shallow platform, probably exposed as a rocky surface. Sedimentation started when the water-table was about 12 m lower than today. The single and high peak in the magnetic susceptibility record in pollen zone 2 coincides with the rare event of minerogenic sediment input into the lake. The record shows that detrital sediments rapidly changed into organic-rich muds and peat, which explains that the remaining part of the magnetic susceptibility record provides a monotonous low signal. We assume that at the southern side of the lake a rocky threshold formed the outlet.

After cold grasspáramo conditions prevailed during Lateglacial times, the record shows a short but significant warming at 12,635 BP, followed by a cold period of some 800 years, and then followed by an even more significant temperature rise at 11,640 BP. This ~800 yr cool period compares in timing and sequence with the El Abra stadial (Van der Hammen and Hooghiemstra, 1995; Van 't Veer et al., 2000), the Colombian equivalent of the Younger Dryas chron. Our record shows a gradual rise of the UFL from Lateglacial time up to ~2000 BP. This is in contrast to the rapid upslope migration of the UFL at other places, such as Lake Fúquene (Van Geel and Van der Hammen, 1973) and Lake Pedro Palo (Hooghiemstra and Van der Hammen, 1993). We find it plausible that the records of Pedro Palo (2000 m altitude) and Fúquene (2540 m altitude) are mainly temperature and $p\mathrm{CO}_2$ driven (Groot et al., 2011). Also Huarascan (Peru) and Sajama (Bolivia) ice core records show rapid temperature increase at the start of the Holocene (Thompson et al., 1998) supporting the abrupt onset of a deglaciation. Most contrasting with these pollen sites is that Lake La Cocha is under massive influence of moisture supply by trans-Amazonian air flows (Fu et al., 2001; Vizy and Cook, 2007). The remarkably slow and gradual upslope migration during the Holocene of montane forest seems associated with an enhancement of orographic rainfall at the eastern slope of the Andes. The latter may be related to the coinciding southward migration of the ITCZ (Haug et al., 2001) and/or to an increasing sea surface temperature (SST) of the western Atlantic Ocean (Fu et al., 2001). The pollen record suggests that the modern altitudinal vegetation distribution on the Andean flanks facing Amazonia were not obtained until ~2000 BP (period19). A wetter mid Holocene is also supported by the relatively longer periods of permanent lake high levels observed at ~7000 to ~5000 BP and ~2100 to ~1700 BP as indicated by the diatom record. These ages are supported by pollen-based studies from the Llanos Orientales where savannas are under the influence of trans-Amazonian moisture transport also. A synthesis of pollen records (Berrio et al., 2002; Hooghiemstra and Berrio, 2007) show moist climate conditions during Lateglacial times (in our record periods 2–4), dry conditions from ~9000 to 6000 BP (in our record periods 5–11), increasing precipitation between ~6000 and 3500 BP (in our record periods 12–14), and modern (wettest) conditions during the last ~3500 BP (in our

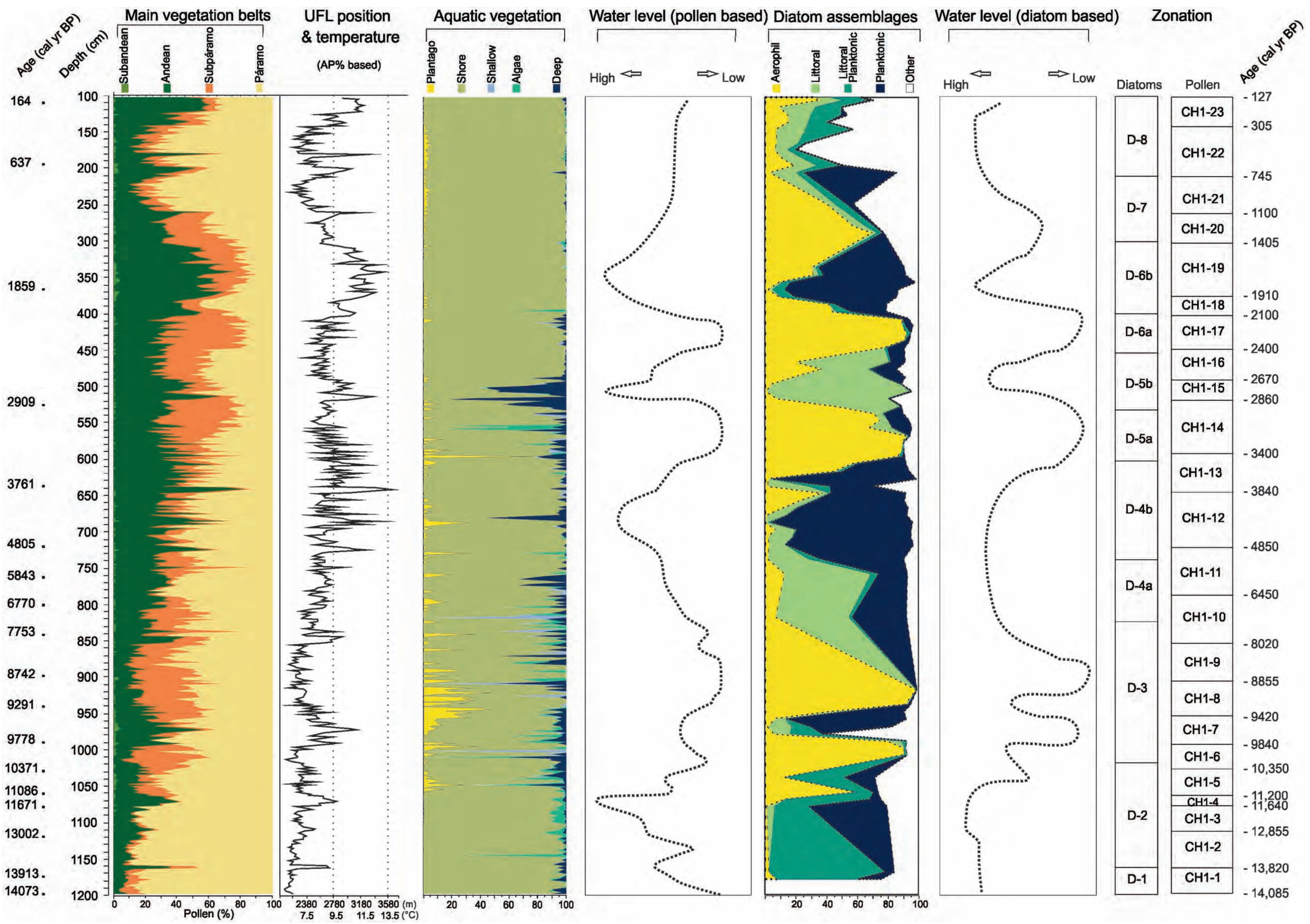


Figure 8. Summary of ecological and climatological changes identified after a multiproxy analysis of core La Cocha-1, 2780 m altitude, south Colombia Andes. Left to right: calibrated ages, depth scale, main pollen diagram showing downcore proportions of four categories reflecting the regional vegetation, UFL positions and temperature record, main diagram showing downcore proportions of five categories of aquatic vegetation, record of water-level changes (pollen based), main diagram showing five diatom assemblages, record of water-level changes (diatom based), diatom zones, pollen zones, and calibrated ages.

record periods 15–19). In Peru modern climate conditions were established at ~3.2 ka (Sandweiss et al., 2001). Similarly westernmost Amazonian lowlands may have reached modern conditions also only a few millennia ago (Behling et al., 1999).

The Ecuadorian pollen record of Guandera (Bakker et al., 2008) located ~80 km southwest of La Cocha shows that the UFL had its highest positions of 3600 to 3700 m from ~6000 to ~5000 BP. Subsequently the UFL lowered gradually and reached 3300 m elevation around 1000 BP. Thus, while the Guandera record shows an almost continuous downslope shift of the UFL from ~5000 to ~1000 BP, the record from La Cocha shows an upslope migration most of the time. We explain this difference by the impact of precipitation on the eastern Andean flank. During the last 5000 years opposite trends in climate change in the Colombian Andes were registered also by Marchant et al. (2001).

Charcoal is relatively abundant from 11,200 to 6450 BP (periods 5–10). Although people are locally present in the Andes (Bellwood, 2005; Grosjean et al., 1997) this charcoal signal more likely relates to fire in the grasspáramo. After 1405 BP (AD 545) abundant charcoal is clearly related to the use of fire during deforestation. Although in Peru there is evidence of maize cultivation as early as 4000 BP (Perry et al., 2006) we did not find such evidence in our record. It is known that the Andean region of Nariño was densely populated during pre-hispanic times, where agriculture was the economic base of the inhabitants (SINIC, 2008). Absence of cultivation in the relatively cold study area was probably compensated by productive Quillacingas territories at lower elevations (Banco de la República, 2008; Groot de Mahecha and Hooykaas, 1991; Rodríguez, 2005). For the inhabitants of the lake area, fishing and hunting might have been the main sources of food. The La Cocha record offers a new opportunity to further evaluate relationships between paleoecological and archaeological evidence.

Conclusions

In this paper we demonstrate the potential of high-resolution pollen analysis for reconstructing Holocene environmental and climate variability. On a shallow platform in the northern segment of Lake La Cocha a 11 m thick lacustrine and peaty sequence developed since 14,085 BP. 550 pollen samples yielded an average resolution of ~25 yr. Most significant is the long period of postglacial upslope migration of the UFL: starting at ~2200 m, the UFL reached ~2600 m around 8000 BP, ~2800 m around 3800 BP, ~3000 m around 2100 BP, and as recently as ~1900 BP the present-day elevation of 3550 m was reached. Postglacial temperature rise possibly had little influence on the altitudinal distribution of montane forest species on the Amazon-facing flank of the northern Andes. Trans-Amazonian moisture flows modulated by the ITCZ, and a possible impact of ENSO, both increasing during the Holocene, seem the main drivers of environmental and climate change. This is also supported by the longer periods of permanent high water-levels in thelake. Successively *Hedyosmum*, *Myrsine*, *Miconia*, Urticaceae-Moraceae, *Anthurium*, *Alnus*, *Podocarpus*, *Ceroxylon*, *Psychotria*, *Weinmannia*, Rosaceae, and *Myrica* show clear expansion events showing how the floristic composition of the uppermost montane forest developed during its upslope migration. After forest had reached the altitude of the lake, proportions of forest taxa varied without evidence of forest associations that principally differ from modern ones.

Intervals with quasi-stable environments lasted from 200 to 600 yr demonstrating a dynamic Holocene climate. Altitudinal forest displacements up to ~300 m per 100 yr (reflecting 1.5°C temperature change) are modest compared with RoC of up to 3.5°C in the Colombian record of Lake Fúquene (Groot et al., 2011). Here we document for the first time that the subpáramo biome was repeatedly 'lost' for a number of decades, showing that during events of fastest upslope forest shifts the migration capacity of the subpáramo was exceeded. In other words, the subpáramo biome does not adapt to rapidly changing conditions. Implications for the future are evident as projected scenarios for AD 2100 assume an increased temperature rise potentially exceeding natural migration capacities. The diatom record has proven a welcome addition to the aquatic pollen record when water-level changes have to be reconstructed. Anthropogenic deforestation started at 1405 BP (AD 545) and the relatively cold temperatures in the lake basin explain evidence of crop cultivation is lacking and economic activities were limited to timber production. The present record gives ecologists, climate modellers, and archaeologists another paleo-benchmark against which to test their hypothesis and models.

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