"Solving a piece of the puzzle". Reconstruction of millennial-scale environmental and climatic change in the northern Andes during the last glacial cycle: An integration of biotic and abiotic proxy-information
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Chapter 4: North Andean environmental and climatic change at orbital to submillennial time-scales: vegetation, water levels and sedimentary regimes from Lake Fúquene 130-27 ka

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Chapter 4

North Andean environmental and climatic change at orbital to submillennial time-scales: vegetation, water levels and sedimentary regimes from Lake Fúquene 130 - 27 ka

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Abstract

We present a record of environmental and climatic change in the northern Andes during the last interglacial-glacial cycle based on integrated information from pollen and grain size distributions (GSD). The record reflects the 26.21-1.64 m interval of a new sediment core from Lake Fúquene (2540 m elevation; 5°N) in the Colombian Andes. The age model was developed by Groot et al. (2011) and shows this core interval reflects the period from 130-27 ka and the 1-cm sample increments yield an average resolution of 43 yr. We analysed in 2032 samples 66 pollen and spore taxa with optimal ecological constraints. We reconstructed upper forest line (UFL) positions between ~2200 and ~3400 m elevation. We found frequent temperature changes up to 2-3°C/100 yr. Regional vegetation change is mainly driven by obliquity (41 kyr), and eccentricity (100 kyr). Important short-lived upslope excursions of the UFL reflect millennial-scale climate variability superimposed on orbital-scale variability. These cycles reflect Greenland Dansgaard-Oeschger (DO) climate cycles in time and signature. DO cycles 8, 12, 14, 19, 20, 26, 27 and 28 are most prominently documented. Cycles vary from ~1.5 to 3 kyr with an average of 2.7 kyr.

Changes in species composition of montane forest are evident and trees with mostly pioneer qualities (Alnus, Myrica, Quercus and Weinmannia) migrate in the forefront. Other trees like Podocarpus, Miconia, and Hedyosmum mostly follow later. Although these first observations shed new light on the consistency of non-analog vegetation in long Pleistocene records of biome dynamics, more robust analysis of this data set is needed. Changes in regional vegetation distribution and forest composition, changes in local aquatic vegetation, and changes in GSD of sediments supplied to the lake allow to develop an integrated reconstruction of the biotic and abiotic environments in the drainage basin.

1. Introduction

One of the major achievements in the study of earth’s system history is the reconstruction of climate evolution over millions of years (Zachos et al., 2001; Walker and Lowe, 2007; Tripati et al., 2009). Marine sediment archives (Peterson et al., 2000; Hughen et al., 2004; Johnsen et al., 1997), and the composite stack records that were based on these data (Imbrie et al., 1984; Lisiecki and Raymo, 2005), and further archives from high latitude ice sheets (Grootes et al., 1993; Johnsen et al. 1997; NGRIP-members, 2004; Jouzel et al., 2007; Loulergue et al., 2008) and low latitude tropical glaciers (Thompson
et al., 1995, 1998, 2005) have provided a picture of the long-term Pleistocene climate variability with amazing detail. However, such studies on the long-term evolution and millennial-scale variability of terrestrial ecosystems are rare (e.g. Allen et al., 1999; Wijmstra, 1969; Heusser and Heusser, 1990; Reille and De Beaulieu, 1990; Guiot et al., 1989; Tzedakis et al., 1997, 2001, 2004, 2006), in particular for the tropics (e.g. Kershaw, 1986; Mayle et al., 2000; Torres et al., in review; González-Carranza et al., 2012). One of the reasons is that terrestrial environments are prone to discontinuities in sediment accumulation and erosion of the sediment archive. Notwithstanding these caveats, a better understanding of the dynamic part of terrestrial ecosystems is of high relevance for the people that live in these dynamic environments (Willis et al., 2007). In particular, the studies on the potential impact of anthropogenic climate change on the environment (IPCC, 2007; The Physical Science Basis) are in need of long-term multi-proxy records of past change with a better than centennial resolution. It could be claimed that most understanding of climate history finds its source in Earth systems from the uninhabited parts of the globe, while the impact of climate change on the environments of the inhabited parts of the globe is poorly understood (IPCC, 2007; Impacts, Adaptation and Vulnerability). The study of terrestrial pollen records has proven to provide valuable understanding of the dynamic histories of ecosystems (e.g. Mayle et al. 2000; González-
Developing an age model for long terrestrial sediment sequences reaching beyond radiocarbon time control is notoriously difficult. In the present study of the upper part of an almost 60 m long core we rely on cyclostratigraphical time constraints, a methodology developed in marine micropaleontology but hardly applied to long lacustrine pollen records (Groot et al., 2011). We used radiocarbon ages and biostratigraphic events in the uppermost part of the core. For the part beyond radiocarbon time control we identified that the obliquity cycle (41 kyr) is the main driver behind environmental change (Groot et al., 2011). As the arboreal pollen record reflects temperature change most closely we filtered the 41-kyr cycle from this time series and tuned it to the filtered 41-kyr cycle from the marine benthic standard LR04 δ¹⁸O record (Lisiecki and Raymo, 2005). The result is a robust tuned age model showing that the full core interval of 58.4 to 1.64 meter composite depth (mcd) reflects the period from 284,000 to 27,000 years before present (284-27 ka) (Groot et al., 2011). In Groot et al. (in review) we compared the method of cyclostratigraphy including tuning the arboreal pollen percentage (AP%) record to LR04 record, with traditionally used visual curve matching. Although cyclostratigraphy is a widely accepted method (Lourens et al., 1996; Joordens et al., 2011) to develop an age model, the suite of tie points produces a linear depth versus time graph. This is an inevitable part of the cyclostratigraphical method as the tuning procedure is carried out in a linear time domain. The quasi-linear sediment accumulation rate should be considered as an artifact of the method and downcore analysis of grain size distributions (GSDs) clearly shows frequent changes in the quality of supplied sediments and the energy levels of sediment transport (Vriend et al., 2012). Also a downcore X-ray fluorescence (XRF) based geochemical analysis of sediments showed a dynamic abiotic basin environment (Bogotá-A et al., 2011c) strongly suggesting non-linear sediment accumulation rates. The age model of the core is robust for long-term environmental change while it is a challenge to explore how GSDs and XRF-based geochemical data can be used to show changes in sediment accumulation in between tie points. Therefore, in comparisons with other cores the present record does not allow to evaluate leads or lags of millennial-scale cycles in the Greenland and Antarctic ice cores (NGRIP-members, 2004; Johnsen et al. 1997), known as Dansgaard-Oeschger (DO) cycles (Oeschger et al., 1984; Dansgaard et al., 1993). Calculated rates of change (RoC) with respect to temperature (e.g. Úrrego et al., 2009) or ecological change (e.g. González-Carranza et al., 2012; De Boer et al., in review) are tentative estimates. However, all proxy records from the present record can be compared without restrictions and show at an hitherto untouched level how the biotic and abiotic systems in the drainage basin are interrelated. The abrupt end of the present record at 27 ka most plausibly relates to erosion due to a sudden streamline displacement in the lake basin. This happened in a dynamic episode just before the last glacial maximum (LGM) and it coincided with the end of sediment accumulation in the adjacent Bogotá basin (Hooghiemstra, 1984; Torres et al., 2005). Sediment cores collected at the border of the lake basin reach up to latest
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Holocene time (Bogotá et al., 2011a) showing that the lake accumulated sediments up to the present-day and that our coring site is not representative in this aspect.

The objective of the present paper is to present the environmental history of the last interglacial-glacial cycle that is reflected in the upper part of the Fq-9C core (25.98 to 1.64 mcd interval). This interval contains 2032 pollen samples and has an average temporal resolution of 43 yr. The 284 to 130 ka interval of this record is published elsewhere (Bogotá-A et al., this volume). Changes of the aquatic vegetation in the lake are related to changes in sediment composition (Vriend et al., 2012) to form the basis for the reconstruction of changes in the water level and sedimentary environments. The average resolution of 43 yr in this upper part of the record allows for the first time to analyse rapid climate change at millennial to centennial time scales and variability is compared to Greenland DO cycles. We also analyse forest dynamics by assessing leading and late-successional species.

2. Setting of study area

2.1 Geography and climate

Lake Fúquene (5°27’N, 73°46’W) lies at 2540 m elevation in the Fúquene basin, which is located in the Eastern Cordillera of Colombia (Fig. 2). The basin is surrounded by mountains, which are mainly composed of Cretaceous and Tertiary rocks and reach up to 3500 m elevation. The lake came into existence during middle Pleistocene time when a colluvial dam blocked the Suarez River near the village of Saboyá (Sarmiento et al., 2008) and water stagnated behind the dam. Today, Lake Fúquene covers a small area of the southern part of the basin while the northern part of the basin is covered by marsh. Sediment accumulation in the northern basin apparently has continued through Pleistocene time and formed a sediment plug to keep water in the southern basin. The thickness of accumulated lacustrine sediments is unknown but minimally 60 m. Today, lacustrine sediments stretch over some 80 km in north-south direction and these sediments cover some 400 km². The present-day Lake Fúquene is a small remnant of a much larger Pleistocene lake that covered most of the intramontane high plain of Ubaté-Chiquinquirá (Sarmiento et al., 2008; Vriend et al., 2012). The lake reflects an open hydrological system. The Ubaté River in the south and some small water currents in the east form the inlets. Water leaves the lake in the northwest by the Suarez River. The present-day lake only receives water from the southern part of the basin which has a surface of ~900 km² (Montenegro-Paredes, 2004). The lake is proximal to the rock formations that form the main source areas of the sediments (Sarmiento et al., 2008; Bogotá-A et al., 2011c). During the last decades agricultural activities and land reclamation caused the water level lowered significantly. Around AD 1930 the lake had a surface of some 60 km² but today no more than some 25 km² is left (CAR, 2000). Water depth in the present lake varies from 2 to 6 m.

The modern precipitation regime in the study area is controlled by the annual migration of the Intertropical Convergence Zone (ITCZ). Two dry seasons from December to February, and from June to August alternate with two rainy seasons from March to May,
and from September to November. The region is relatively isothermic during most of the year. The mean annual temperature (MAT) is 13.5°C. The daily temperature range is large and during the dry seasons night frost may occur (van Geel and van der Hammen, 1973). Mean annual precipitation (MAP) varies from 770 mm in the south of the basin where a rain shadow effect occurs, to 1080 mm in the north. This explains why dry montane forest (500-1000 mm MAP), wet montane forest (1000-2000 mm MAP), and transitional forest types can be present simultaneously in this intramontane valley (van Geel and Van der Hammen, 1973).

2.2 Vegetation

The altitudinal distribution of the vegetation in the study area was presented by Cuatrecasas (1958), Van der Hammen and González (1960), Van der Hammen (1974), Cleef (1981), Cleef and Hooghiemstra (1984), Cortes and Rangel (2000), Rangel (2000), Hooghiemstra and Van der Hammen (2004), Cortés-Sánchez et al. (2008) and Van der Hammen (2008). Modern pollen rain samples from páramo vegetation were studied by Grabandt (1980, 1985) to analyse the composition of pollen spectra along an altitudinal gradient. However, these pollen spectra are biased because a large area below the potential upper forest line (UFL) was already deforested when samples were collected causing underrepresentation of arboreal pollen (AP). We follow the relationship be-
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tween AP% and position of the UFL elaborated by Hooghiemstra (1984) and Groot et al. (2011). The zonation of vegetation along the elevational gradient is largely determined by the MAT. The lowermost occurrence of Andean forest taxa coincides with the lowermost occurrence of significant night frost; the highest occurrence of closed Andean forest reflects the UFL and coincides with the MAT of 9.5°C. We used a temperature gradient of 0.6°C per 100 m vertical forest displacement. The modelling study in Groot et al. (2011) showed that changes in atmospheric pCO2 also have an undetermined but significant impact on the position of the UFL supporting earlier evidence for this conclusion by Boom et al. (2001).

Plant taxa each have their own ecological envelope but when suites of taxa do have similar altitudinal distribution, zonal vegetation belts can be recognised (Bach and Gradstein, 2011; Vásquez and Givnish, 1998). We follow the altitudinal vegetation zonation for the northern Andes put forward by Cuatrecasas (1958) and Van der Hammen (1974) and further elaborated in Hooghiemstra (1984), Van ‘t Veer and Hooghiemstra (2000) and Bogotá-A et al. (2011b). We recognised the following vegetation

Table 1. List of taxa reflecting the regional vegetation (top) and local vegetation (bottom) analysed in the composite Fúquene-9C record. All taxa not included in the pollen sum are marked by an asterisk (*) (adapted from Hooghiemstra, 1984 and Van ‘t Veer and Hooghiemstra, 2000). For the taxa of local importance, representing the azonal aquatic vegetation in the basin, a separate ‘local pollen sum’ is indicated by two asterisks (**).

<table>
<thead>
<tr>
<th>Lower Montane Forest</th>
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<tbody>
<tr>
<td>Acalypha, Alchornea, Cecropia, Urticaceae-Moraceae</td>
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<th>Upper Montane Forest</th>
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<tbody>
<tr>
<td>Alnus, Cleithra, Croton, Cyatheaceae, Daphnopsis, Drimys, Eugenia, Gaiadendron, Gunnera, Hedyosmum, Ilex, Juglans, Melastomataceae, Micona, Monnina, Myrica, Myrsine, Myrtaecae, Podocarpus, Proteaceae, Quercus, Sapindus, Styloceras, Symlocus, Thalictrum, Vallea, Weinmannia</td>
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<th>Subparamo</th>
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<tr>
<td>Asteraceae liguliflorae, Asteraceae tubuliflorae, Ericaceae, Hypericum, Polylepis-Acaena</td>
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<th>Grassparamo</th>
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<tbody>
<tr>
<td>Aragoa, Caryophyllaceae, Draba, Gentiana, Geranium, Lysipomia, Lycopodium foveolate, Plantago, Poaceae, Puya, Valeriana</td>
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<th>Drought indicators</th>
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<tr>
<td>Borrella, Chenopodiaceae, Dodonea</td>
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<th>Aquatics and marsh vegetation</th>
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<table>
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<tr>
<th>Algae</th>
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<tr>
<td>Debarya*, Spirogyra*, Zygnema*</td>
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<tr>
<th>Fungal spores</th>
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<tr>
<td>Sporormiella*</td>
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zonation for the northern Andes put forward by Cuatrecasas (1958) and Van der Hammen (1974) and further elaborated in Hooghiemstra (1984), Van ‘t Veer and Hooghiemstra (2000) and Bogotá-A et al. (2011b). We recognised the following vegetation
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belts: subandean forest (1000-2300 m), Andean forest (2300-3200 m), subpáramo vegetation (3200-3500 m), and grasspáramo vegetation (3500-4200 m) (Table. 1). Although taxa respond individually to climate change, many taxa respond in concert and, therefore, can be considered an altitudinally constrained plant association (‘vegetation belt’) (Shipley and Keddy, 1987). However, such altitudinally constrained vegetation belts reflect an abstraction as, for example, present-day trees with a main cover below 2300 m in the subandean vegetation belt may locally reach higher elevations and contribute to forest associations at significantly higher elevations. Cecropia may reach to ~2600 m as a pioneer along rivers, Acalypha may occur up to 2700 m (even up to 3000 m), Alchornea and Croton may reach up to 2800 m, Hieronyma and Cyathea tree ferns have been locally observed up to 3000 m, even up to 3200 m. Pilea may reach up to 3100 m (A.M. Cleef personal communication 2010). These examples make clear that the altitudinal range of the optimum plant cover, and consequently the highest pollen production, may vary at spatial and temporal scales. Therefore, modern plant associations are to some degree ephemeral and calibration of the pollen record to modern vegetation associations should be carried out with care (González-Carranza et al., 2012). Present-day altitudinal envelopes of the plant taxa which were selected to be analysed during pollen analysis, were actualized based on the literature and field observations by A.M. Cleef (Fig. 3).

The ecology of the modern aquatic and marsh vegetation in the Colombian Andes was studied by Cleef (1981), Rangel and Aguirre (1983, 1986), Cleef and Hooghiemstra (1984), and Chaparro (2003). Rangel (2003) described the actual hydroseries in the upper montane forest belt of the study area. We followed Van ‘t Veer and Hooghiemstra (2000), Torres et al., (2006) and Bogotá-A et al. (2011) and used the proportions of successional plant associations to estimate water depth (Fig. 4). We used Isoëtes and Potamogeton to infer deep water; Ludwigia, Myriophyllum, Hydrocotyle, Typha, Apiaceae, and Ranunculaceae to infer shallow water; Cyperaceae to infer swamp conditions; and Rumex and Polygonum to infer wet shore conditions. Torres et al. (2005) showed that Isoëtes indicates deep water conditions when lacustrine conditions prevail.

3. Methods

3.1 Sediment collection and core treatment

Two ~60 m long sediment cores, labelled Fq-9 and Fq-10, were retrieved 10 m apart using a floating platform. Consolidated sediments were first approached at ~6 m below the water surface. Sediments were retrieved in segments of 100 cm length with a diameter of 75 mm. Core samples at the two drilling sites were collected with 50 cm overlapping depth intervals to maximize sediment recovery (Groot et al., 2011). Undisturbed sediments in pvc-tubes were directly transported to The Netherlands for further treatment. The fresh sediment surface was photographed in a standardized photographic room. Bulk chemistry was measured along the full length of both cores with an Avaatech XRF core scanner. For more detailed methodology we refer to Groot et al. (2011) and Vriend et al. (2012). Over 5000 samples at 1 cm increments were collected
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Fig. 3. Altitudinal ranges of selected pollen and spore taxa used to reconstruct regional vegetation change. Taxa are arranged after ecological preference. (a) Main ecological groups; (b) Modern altitudinal range in the study area; dotted line = full range; solid line = interval of optimum cover; (c) Mean annual temperature (MAT) along the altitudinal gradient; (d) Estimated mean annual precipitation (MAP) along the altitudinal gradient (compiled from the modern vegetation studies mentioned in the text); (e) Main functional place of taxon in the vegetation succession (compiled from the modern vegetation studies mentioned in the text) (Pion: pioneer; Midd. Succ.: middle succession; Clim.: climax).
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for analysis of pollen, organic matter content, and GSDs. Cores Fq-9 and Fq-10 were used to build a composite record with a minimal number of gaps in the sedimentary sequence. We used changes in the lithology, and the records of Fe and Zr to fine-tune the correlation. For further details the reader is referred to Groot et al. (2011). Sediment record Fq-9C represents approximately 90% of the sediment infill of the uppermost 60 m of the basin; the remaining 10% reflect small coring gaps, inadequate sediment intervals, and not analysed parts due to organizational problems. GSD were measured

with a Fritsch Analysette 22 laser particle sizer, which provides 56 size classes in the range from 0.15 to 2000 µm. Prior to grain-size measurement, the samples were prepared according to the methods described by Konert and Van den Berghe (1997). The clearly defined mode of 81 µm reflects sandy sediment, the mode of 21 µm coarse silt sediment, the mode of 7 µm fine silt sediment, and the mode of 2 µm clayey sediment. The organic matter content of the sediments was measured by the loss-on-ignition (LOI). For further details the reader is referred to Vriend et al. (2012). Pollen samples of 1 cm³ were treated according with standard procedures. For calculation of pollen concentration a tablet with a known number of *Lycopodium* spores was added to each sample before acetolysis. For more details we refer to Bogotá-A et al. (2011a).

3.2 Pollen analysis and zonation

The pollen sum includes taxa reflecting subandean forest, Andean forest, subpáramo, and grasspáramo. Taxa reflecting dry vegetation were added as a fifth group. On the basis of a critical evaluation of the pollen records from the Fúquene basin (Bogotá-A et

![Fig. 4. Preferential ecological position of aquatics, ferns and algae analysed in the Fq-9C pollen record along an ecological dry-to-wet gradient (compiled from the modern vegetation studies mentioned in the text).](image-url)
al., 2011a) and the Bogotá basin (Hooghiemstra, 1984) we selected 66 taxa for pollen analysis. These taxa have the most informative ecological ranges (Fig. 2). We aimed at a pollen count of 350 to 400 grains exclusive of *Alnus*, but for calculating the pollen percentages *Alnus* was included in the pollen sum. We considered the first 20% representation of *Alnus* as reflecting background noise (Van der Hammen and González, 1960; Hooghiemstra, 1984; Van ’t Veer and Hooghiemstra, 2000). At all events that the UFL is passing the elevation of the lake a significant change in representation of *Alnus* is evident as *Alnus* does not occur above the UFL. From previous altitudinal pollen studies of the Colombian Andes it appeared that changes in AP% respond quasi-linearly to temperature-driven vertical shifts on the UFL between 3500 m (the highest mountains at close distance) and the LGM position at ~2000 m (Van der Hammen and González, 1960; Hooghiemstra; 1984; Van’t Veer and Hooghiemstra, 2000; Groot et al., 2011). An AP representation of 40% is indicative of an UFL located at the level of the lake. As a rule of thumb every additional 5% reflects an UFL positioned at ~100 m higher elevation (Hooghiemstra, 1984; Groot et al., 2011). This estimate was subsequently fine-tuned by assessing the contributions of plant associations reflecting various elevational intervals (Cleef and Hooghiemstra, 1984).

The pollen diagram showing changes of aquatic vegetation was calculated on the basis of a local pollen sum. This sum includes aquatics reflecting deep-water plants (*Isoëtes, Potamogeton*), shallow-water plants (*Ludwigia, Myriophyllum, Hydrocotyle, Typha, Apiaceae, Ranunculaceae*), swamp vegetation (*Cyperaceae*), and wet-shore vegetation (*Rumex, Polygonum*). Pollen sum values showed a mean of 190 grains with extremes varying from 10 to 2116 grains. Spores of selected algae were used to support the environmental interpretation. Reconstruction of past water levels was based on information from the aquatic vegetation, GSD and proportions of organic matter reflecting the abundance of peat.

Pollen zones are based on stratigraphical constrained cluster analysis using the total sum of squares (CONISS; Grimm, 1987; Gill et al., 1993). Further visual subdivision served the stratigraphic description. Pollen records were made with AutoCAD 2007 LT software. A developed script to convert the CONISS output file was used to construct a readable file for drawing the dendrogram in AutoCAD.

4. Results and environmental and climatic reconstructions

The pollen percentage diagrams show the core interval from 25.98 to 1.64 mcd and reflect the period from 130 to 27 ka (Groot et al., 2011). Based on CONISS cluster analysis we recognized 7 zones reflecting the local vegetation development (Fig. 5; Table 2). Evidence of GSD and organic matter content follows Vriend et al. (2012). The interpretation of the proxy data is provided below and a synthesis is provided in Table 4. We recognized 10 zones in the regional vegetation development (Fig. 6; Table 3). The interpretation of the proxy data is provided below and a synthesis is provided in Table 5.
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4.1 Reconstruction of the local environment in the lake basin

The following reconstruction of the environment in the lake basin is based on the record of aquatics, the records of algae and fungal spores, and the grain size distributions (Fig. 5, Table 2). Reconstructions follow the 7 main zones and the 36 subzones (parts) indicated in Fig. 5. This paper starts with period 12; the periods 1 to 11 belong to the lower part of the record presented by Bogotá-A et al. (submitted).

Table 2. Description of the local pollen zones.

<table>
<thead>
<tr>
<th>Zone; Core interval; Nr. of samples</th>
<th>Characterisation of pollen zones</th>
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<tbody>
<tr>
<td>Fq-9C-1L; 2598-2589 cm; 180</td>
<td>Pollen spectra are dominated by the swamp indicator Cyperaceae. Shore vegetation and shallow water indicators, the latter mainly represented by Apiaceae, Hydrocotyle, Ludwigia and Myriophyllum, are present with low abundances.</td>
</tr>
<tr>
<td>Fq-9C-2L; 2388-2152 cm; 204</td>
<td>Cyperaceae are still dominant. Proportion of the shore indicator Polygonum increases with peaks up to 80%. Shallow water indicator Hydrocotyle shows a sharp maximum in the upper part of the zone. Low values of the algae Zygnema occur throughout the zone.</td>
</tr>
<tr>
<td>Fq-9C-3L; 2119-1550 cm; 475</td>
<td>Swamp indicator Cyperaceae shows lower values. Shore indicator taxa Polygonum and Rumex are present in this zone; Rumex shows an increase in the middle part of the zone with peaks up to 90%. Shallow water taxa, mainly represented by Apiaceae, Hydrocotyle (increased values in the middle part of the zone), Myriophyllum and Ranunculaceae show higher values in this zone. Deep water indicator Isoetes shows increased values with peaks up to 35%. The algae Spirogyra shows increased values with three distinct maxima; respectively in the lower-, in the middle- and in the upper part of the zone.</td>
</tr>
<tr>
<td>Fq-9C-4L; 1548-1183 cm; 326</td>
<td>Representation of Cyperaceae decreases slightly. Shore indicator taxa show low values in the lower part of the zone and increase in abundance, mainly by increased values of Rumex, in the upper part of the zone. Shallow water taxa, mainly represented by Apiaceae, Hydrocotyle and Myriophyllum (high values in the lower part of the zone up to 90% and decreasing towards top of the zone) show higher values in the lower part of the zone with a decreasing trend towards the upper part of the zone. Isoetes is absent in lowermost part of the zone (1550-1450 cm) and shows a peak up to 60% between 1450 and 1400 cm. The algae Debarya appears in the middle part of the zone and decreases again in the upper part of the zone.</td>
</tr>
<tr>
<td>Fq-9C-5L; 1182-815 cm; 320</td>
<td>Cyperaceae percentages show a continuous decrease. Shore indicator taxa are present. Shallow water taxa, mainly represented by Apiaceae (increased values up to 100%), Hydrocotyle, Myriophyllum (decreasing towards upper part of the zone) and Ranunculaceae (increased values in the upper part of the zone) show higher values of ca. 25%. Isoetes shows higher values of ca. 30% (with peaks up to 70%). Sporormiella spores are present in the lower and middle part of the zone.</td>
</tr>
<tr>
<td>Fq-9C-6L; 799-617 cm; 164</td>
<td>Cyperaceae show a decrease to values of ca. 40%. Shore indicator Rumex shows higher proportions in the lower and upper part of the zone. Shallow water taxa, mainly represented by Apiaceae (decreasing in the upper part of the zone), Hydrocotyle and Myriophyllum (higher abundances in this zone) show higher values up to 75%. Deep water taxa, Isoetes (increasing towards the top of the zone) and Potamogeton (high values in lower and middle part of the zone) show increasing values towards the upper part of the zone up to 50%.</td>
</tr>
<tr>
<td>Fq-9C-7L; 616-164 cm; 360</td>
<td>Cyperaceae reach values of around 60% in the middle part of the zone and decrease to values of around 30% in the upper part of the zone. Shore indicator taxa are present. Shallow water taxa, mainly represented by Apiaceae (increased values in the uppermost part of the zone), Hydrocotyle, Myriophyllum and Typha (higher values in the upper part of the zone) show slightly higher values in the upper part of the zone. Deep water taxa are continuously present in this zone with values up to 65%. The algae Spirogyra appears in the upper part of the zone.</td>
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</table>
Fig. 5. Pollen percentage diagram of the 2-26 m interval of composite core Fuquene-9C showing downcore cl diagram, diagram showing the contribution of clay (low energy environment), silt (medium energy environment), taxa of pollen, spores and algae, the hierarchical cluster division, and the CONISS cluster dendrogram are...
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Changes of the local vegetation. From left to right: estimated age (ka), depth scale (m), main local pollen nment), and sand (high energy environment) (after Vriend et al., 2012), pollen zones, records of the individu- are shown. Stars mark intervals with values >100%.
Fig. 6. Pollen diagram of the 2-26 m interval of composite core Fuquene-9C showing downcore changes of the scale (m), records of the individual pollen and spore taxa, the hierarchical cluster division, and the CONISS c
of the regional vegetation. From left to right estimated age (ka), pollen zones, main pollen diagram, depth
ISS cluster dendrogram are shown. Shadows show a 20% exaggeration of curves with low representation.
Period 12 (133.1-123.8 ka); zone Fq-9C-12L

During part 1 shows 10-35% clay, some 70% fine silt, and 5-10% organic matter pointing to a low energy depositional environment and a distal sediment source. Cyperaceous swamp vegetation is dominant with presence of *Hydrocotyle*, *Ludwigia* and *Apiaceae* in shallow water. Low lake level conditions prevailed. Absence of any supply of course sediment fraction points to a distal sediment source for the lake as a whole and/or that the water current draining the lake basin had a course at significant distance to the drilling site.

During part 2, clay is absent, coarse silt shows some 30% and the sand fraction around 15% while the proportions of organic matter is minimally 8% and peaking up to 35%. Supply of coarse sediment is collected in the peaty areas in the lake basin. Presence of *Polygonum* and *Rumex* point to wet shore vegetation, but cyperaceous reed swamp vegetation is fully dominant. As shallow water taxa are rare, peat seems to cover a significant part of the lake pointing to a very low lake level. Occasional heavy rains may explain occasional supply of moderate quantities of coarse sediments by the surrounding slopes.

During part 3 high proportions of fine silt (60-90%) admixed with 5-7% organic matter point to a low energy depositional environment. The aquatic vegetation is as poor in taxa as during the previous period: cyperaceous reed swamp fully dominated in the lake basin. During part 4 high proportions of clay (from 30% to 10% at the end of this period) and fine silt (60-80%) and ~5% presence of organic matter points to a very low energetic depositional environment. Cyperaceous reed swamp still dominated in the lake basin but presence of *Myriophyllum, Ludwigia, Hydrocotyle* and *Apiaceae* shows higher proportions of shallow water vegetation, while *Rumex* and *Polygonum* indicate that wet shore vegetation was present. Lake levels continued to be low. Absence of supply of course sediment fraction points to a distal sediment source for the lake as a whole and/or that the water current draining the lake basin had a course at significant distance to the drilling site.

During part 5 supplies of coarse silt (40-50%) and sand (10-25%) indicates sediments arrived in the lake basin at higher energy levels. The proportion of organic matter (~4%) probably reflects peat, which is an adequate medium to fix the coarse sediment fraction. Fine silt is still represented with some 40% and the abundant cyperaceous reed swamp vegetation is the place where fine silt is deposited. Some shore vegetation of *Polygonum* and *Rumex* was present. Open shallow water vegetation must have been rare as plants indicative of such environments (mainly *Hydrocotyle* and *Apiaceae*) hardly occurred. During this period lake levels continued to be low.

Period 13 (122.8-114 ka); zone Fq-9C-13L

During part 1 high proportions of clay (30-40%) and fine silt (~50%) points to a very low energetic depositional environment. Cyperaceous reed swamp still dominated in the lake basin but wet shore vegetation of *Polygonum* in particular had increased significantly. Vegetation of open shallow water showed a limited presence, mainly *Hydrocotyle, Ludwigia* and *Myriophyllum*. Low to very low lake levels prevailed in the basin.
Chapter 4

During part 2 input of coarser sediments increased: there is 20-50% coarse silt and occasionally spikes of sand reach 5-15%. However, clay still shows 15-30% representation while the proportion of fine silt is low. Depositional environments were apparently more diverse, varying from low energetic to higher energetic perhaps reflecting the main courses of water currents changed patterns in this part of the lake basin. High proportions of Polygonum and Rumex point to abundant presence of wet shore vegetation. Shallow water became more frequent as Hydrocotyle, Ludwigia and Myriophyllum reached significant values. Also the first presence of algae (Zygnema) supports that open shallow water became more abundant. Lake levels probably increased slightly.

During part 3 periodic supply of sand (proportions of 10% up to 60%) and coarse silt (proportions between 30% and 60%) indicate the sedimentary environment reached higher energetic levels. Proportions of organic material are still low (~5%) indicating that up to this moment the record has not shown evidence of relevant peat growth. At the end of this interval peat formation became rapidly important. Compared to part 2 the vegetation changed hardly: cyperaceous reed swamp continued to be the dominant and wet shore vegetation was frequent. The lake level may have been similar to part 2 or slightly higher.

During part 4 the most salient change is the dramatic increase of organic material (proportions from 35% to 60%) pointing to extensive peat growth in the lake. Cyperaceous reed swamp continued to be dominant and wet shore vegetation as well as shallow-water vegetation became less common. Peat offers a good matrix to conserve sand during the first part of this interval. The change to clay during the latter part of this interval suggests that the main water current in this part of the basin gradually were at larger distance to the coring site and depositional environments at the coring site were very quiet. A rapid increase of Hydrocotyle and algae of Spirogyra is supporting this interpretation.

Period 14 (112.6-87.4 ka); zone Fq9C-14L

During part 1 proportions of organic material continued with very high values of 50% to peak values of 80% and the sedimentary environment reconstructed for the last interval of the previous period continued. Lower proportions of clay and more frequent presence of sand point to a higher energetic level. Sediment source areas may have been more proximal and/or main water currents may have been located at closer distance to the coring site. In shallow water Hydrocotyle was common and algae (Spirogyra and Zygnema) were for the first time in the record abundant. After the extension of peat had reached its maximum the decrease of peat progressed rapidly in the last part of this interval. Cyperaceous reed swamp reduced and aquatic vegetation of shallow water, Apiaceae and Myriophyllum in particular, became more common.

During part 2 coarse silt (45-70%) and occasional peaks of sand (7-30%) are most conspicuous. Fine silt shows proportions of 10-40% and the contributions of clay and organic matter both are low. Cyperaceous swamp vegetation was dominant. On wet shores Polygonum in particular was frequent. Higher representation of the shallow water taxa Apiaceae, Hydrocotyle and Myriophyllum in combination with presence of algae (Spirogyra in particular) indicates that much peatland drowned and made place for
## Table 3. Description of the regional pollen zones.

<table>
<thead>
<tr>
<th>Zone; Core interval; Nr. of samples</th>
<th>Characterisation of pollen zones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fq-9C-1R; 2598-2226 cm; 311</td>
<td>Pollen spectra are dominated by Andean forest taxa (75-90%) of which <em>Alnus, Hedysmus, Micronia, Myrica, Myrsine, Podocarpus, Quercus</em> and <em>Weinmannia</em> are most conspicuous. Subandean taxa are present (1-4%). Subparamo taxa, mainly represented by Asteraceae, Ericaceae and <em>Hypericum</em> show low values in the lower part of the zone and higher values (10-20%) in the upper part. Grassparamo taxa, mainly represented by Caryophyllaceae, <em>Geranium</em>, Poaceae and <em>Valeriana</em> show low values in the lower part of the zone and higher values (up to 7%) in the upper part. <em>Dodonaea</em> is the main indicator of dryness.</td>
</tr>
<tr>
<td>Fq-9C-2R; 2225-2101 cm; 92</td>
<td>Andean forest taxa are still dominant (ca. 85%) with two peaks up to 95%, one peak halfway the zone mainly represented by <em>Alnus</em> and one peak in the upper part represented by <em>Alnus, Juglans, Myrica, Myrsine and Weinmannia</em>. Subandean taxa, mainly represented by <em>Acalypha</em> and <em>Urticaceae/Moraceae</em> are present in the lower part of the zone (up to 10%). Subparamo and grassparamo taxa show a sharp maximum in the upper part of the zone, mainly represented by Asteraceae and Poaceae. Dryness indicators are present; in the lower part of the zone mainly represented by <em>Dodonaea</em> and in the upper part by <em>Borreria</em>.</td>
</tr>
<tr>
<td>Fq-9C-3R; 2100-1936 cm; 134</td>
<td>The proportion of Andean forest taxa decrease to 70%, mainly represented by <em>Alnus, Hedysmus, Illx</em> (with a sudden increase in this zone up to 8%); <em>Micronia, Myrica, Podocarpus, Quercus</em> and <em>Weinmannia</em>. Subandean forest taxa show very low values. Subparamo taxa show higher values (up to 10%), mainly represented by Asteraceae, Ericaceae and <em>Hypericum</em>. Grassparamo taxa, mainly represented by <em>Geranium, Lycopodium foveolate</em>, Poaceae and <em>Valeriana</em> show low values in the lower part of the zone and higher values (up to 10%) in the middle part. <em>Borreria</em> is the main dryness indicator in this zone with increased values up to 5%.</td>
</tr>
<tr>
<td>Fq-9C-4R; 1935-1441 cm; 398</td>
<td>Andean forest taxa, mainly represented by <em>Alnus, Hedysmus, Illx</em> (decreasing in the upper part of the zone); <em>Micronia, Myrica, Myrsine</em> increase in the lower part of the zone, decrease in the middle part of the zone to ca. 50% and increase again in the upper part of the zone to ca. 70%. Subandean forest taxa show an increase in the upper part of the zone up to ca. 10%. Subparamo taxa, represented by Asteraceae, Ericaceae, <em>Hypericum</em> and <em>Polylepis</em> show a decrease in the upper part of the zone from 25% to ca. 5%. Grassparamo taxa, mainly represented by Caryophyllaceae, <em>Geranium, Lycopodium foveolate, Plantago, Poaceae</em> and <em>Valeriana</em> show higher proportions up to 20%. <em>Borreria</em> is the main dryness indicator in the lower and middle part of the zone and <em>Dodonaea</em> in the uppermost part of the zone.</td>
</tr>
<tr>
<td>Fq-9C-5R; 1440-1339 cm; 97</td>
<td>Andean forest taxa, mainly represented by <em>Alnus and Myrica</em> are dominant again with values up to 75%. Subandean forest taxa are almost absent. Subparamo taxa, mainly represented by Asteraceae and Ericaceae show higher values up to 10%. Grassparamo taxa, mainly represented by Caryophyllaceae, <em>Geranium</em> (present continuously), Poaceae and <em>Valeriana</em> are present (15-20%). Dryness indicators are almost absent in the zone.</td>
</tr>
<tr>
<td>Fq-9C-6R; 1338-1106 cm; 229</td>
<td>Andean forest taxa, mainly represented by <em>Alnus, Eugenia, Hedysmus, Micronia, Melastomataceae, Myrica, Myrsine, Podocarpus, Quercus</em> and <em>Weinmannia</em> show a decreasing trend towards the upper part of the zone (from 75% to 45%). Subandean forest taxa show higher proportions in the upper part of the zone. Subparamo taxa, represented by Asteraceae, Ericaceae, <em>Hypericum</em> and <em>Polylepis</em> are present (10-20%). Grassparamo taxa, mainly represented by <em>Geranium, Lycopodium foveolate, Poaceae</em> and <em>Valeriana</em> show an increase in the upper part of the zone up to 15%. Dryness indicators are present in only small amounts and <em>Borreria</em> shows a slight increase in the upper part of the zone.</td>
</tr>
</tbody>
</table>
| Fq-9C-7R; 1105-415 cm; 246           | Andean forest taxa, mainly represented by *Alnus, Hedysmus, Micronia* (in the lower part of the zone), *Myrica* and *Podocarpus* shows lower proportions of ca. 25%. Subandean forest taxa are almost absent in this zone. Subparamo taxa show higher values up to 30%. Grassparamo taxa, mainly represented by *Aragoas* (increased values lower part of the zone), Caryophyllaceae, *Geranium*,
### Chapter 4

**Table 3. Description of the regional pollen zones; continued**

| Fq-9C-8R; 799-736 cm; 64 | Lycopodium foveolatum, Poaceae and Valeriana show higher values up to 60%. Dryness indicators, mainly represented by *Borreria* are present in the lower part of the zone. Andean forest taxa, mainly represented by *Alnus, Clethra, Hedyosmum, Miconia, Melastomataceae (other), Myrica, Myrsine, Podocarpus, Quercus, Vallea and Weimannia* show higher values up to ca. 70%. Subandean forest taxa are present (ca. 5%). Subparamo taxa show decreased values (ca. 20%). Grassparamo taxa, mainly represented by *Lycopodium foveolatum* and Poaceae show a decrease in the lower part of the zone to ca. 20% and a slight increase in the upper part to 25%. Dryness indicators, mainly represented by *Dodonaea* are present (1-2%). |
| Fq-9C-9R; 735-406 cm; 268 | Andean forest taxa, mainly represented by *Alnus* (decreasing in the upper part of the zone), *Hedyosmum* (increasing in the upper part of the zone), *Miconia, Myrsine, Podocarpus, Quercus, Thalictrum, Vallea and Weimannia* show lower values of 35%. Subandean forest taxa show increasing proportions in the upper part of the zone up to 15%. Subparamo taxa, mainly represented by *Asteraceae and Polyplepis* (increased values up to 50%) show higher values up to 30%. Grassparamo taxa show higher values of ca. 30% of which Caryophyllaceae, *Lycopodium foveolatum, Plantago, Poaceae* and *Valeriana* are most prominent. Dryness indicators, mainly represented by *Dodonaea* show increasing values in the upper part of the zone. |
| Fq-9C-10R; 405-164 cm; 193 | Proportions of Andean forest taxa, mainly represented by *Alnus, Hedyosmum, Miconia, Melastomataceae, Myrica, Myrsine, Podocarpus, Quercus, Thalictrum* (increased values in lower part of zone) and *Weimannia* show increasing values in the lower part of the zone to ca. 50% and decreasing proportions in the upper part of the zone to ca. 35%. Subandean forest taxa are continuously present (5-10%). Subparamo taxa show values between 10% and 20%, mainly represented by *Asteraceae and Polyplepis* (lower proportions of ca. 25%). Proportions of grassparamo taxa, mainly represented by Caryophyllaceae, *Lycopodium foveolatum, Plantago, Poaceae* (increasing values towards the upper part of the zone) and *Valeriana* (decreasing values towards the upper part of the zone) show increasing values throughout the zone from 35% in the lower part to 45% in the upper part of the zone. Dryness indicators are almost absent. |
### Table 4. Main characteristics of the local zone/subzones in core Fq-9C, based on local pollen and grain size distributions

<table>
<thead>
<tr>
<th>Zone</th>
<th>Subzone</th>
<th>Depth (cm)</th>
<th>Age (ka)</th>
<th>Time</th>
<th>EM dominant</th>
<th>Predomitant Vegetation</th>
<th>Energy level</th>
<th>Source distance</th>
<th>Def lake Size</th>
<th>Lake level</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
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<td>2598-2548</td>
<td>135.1-130.97</td>
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<td>distal</td>
<td>small</td>
<td>low</td>
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<tr>
<td>12</td>
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<td>2547-2495</td>
<td>130.95-126.89</td>
<td>2.23</td>
<td>c.silt, sand, org. matter</td>
<td>swamp, shore</td>
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<td>occas high</td>
<td>distal</td>
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<tr>
<td>12</td>
<td>3</td>
<td>2494-2443</td>
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shallow-water environments, suggesting the lake levels increased. This is supported by higher proportions of deep-water vegetation (*Isoëtes*).

During most of part 3 significant proportions of sand are supplied (10-30% with peaks up to 50% and 70%). In combination with high proportions of sandy silt (25% to 70%) a high energetic depositional environment is suggested in which cyperaceous swamp vegetation, wet shore vegetation and shallow water bodies are all common. The aquatic vegetation shows clearly that swamp vegetation further drowned and shallow water extended in area: in particular *Hydrocotyle* and the algae *Spirogyra* and *Zygnema* support this interpretation. The lake level increased gradually.

During part 4 there was no supply of sand but the proportion of coarse silt remained with 50-60% high. Compared to the previous interval, energetic levels in the sedimentary environment lowered to around moderate. Bodies of shallow water with wide variety of aquatic vegetation, including Apiaceae, *Hydrocotyle*, *Ludwigia*, *Myriophyllum* and Ranunculaceae allowed sediment transport. Vegetation of wet shores showed a low representation supporting the view that the lake level had increased again compared to the previous interval.

During part 5 sediment composition changed fully to the fine grained fractions: 20-50% clay and 60-95% clay+fine silt. This suggests depositional environments were extremely quiet and at low energetic levels. The aquatic vegetation consisted of cyperaceous reed swamp, the highest proportions of *Rumex* of the whole record, and substantial presence of *Hydrocotyle* and Ranunculaceae. Such aquatic environment is consistent with a low energetic depositional environment.

During part 6 the lake received sandy sediments again, first proportions up to 10%, later up to 60% and 70%, and coarse silt contributed with 40% to 60%. Fractions of clay and organic material are present, but in low values. Depositional environments were of moderate to high energetic level and sediment source and main river currents must have been located proximal to the coring site. The vegetation of the lake reflects this depositional setting: cyperaceous reed swamp is dominant, a suite of shallow-water plants *Hydrocotyle* and *Myriophyllum* in particular, are common, and abundant *Rumex* points to wet shore vegetation. The proportion of deep-water plants is low pointing to a water depth of a few meters, indicating lake levels were low up to this moment of the current record.

During part 7 depositional environments returned to low energetic levels as shown by the high proportions of clay (20-95%) and the high proportions of fine silt (50-70%). Cyperaceous reed swamp showed its maximal extension in the lake basin monitored by the record. Shallow water vegetation was represented by Apiaceae, *Hydrocotyle* and *Myriophyllum*, and deep-water vegetation virtually absent. Compared to the previous interval water levels lowered.

During part 8 fine-grained sediments (clay and fine silt) lowered proportions but still contributed with 45% to 65%. Coarse silt contributed with 30-50% pointing to low energetic sedimentary environments. The vegetation supports this interpretation by showing extensive cyperaceous reed swamp, only little wet shore vegetation and also little shallow water vegetation. Compared to the previous interval lake levels had lowered slightly.
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Period 15 (87.3-71.3 ka); zone Fq-9C-15L

During part 1 high proportions of sand (~30%) occurred together with high proportions of organic matter 10-20% most of the time with peaks up to 35% and 40%. This suggests that the matrix of cyperaceous reed swamp collected sand that was almost continuously supplied to the lake at significant energy levels. Wet shore vegetation (3-6%) was rare. Shallow water environments were abundant but only a few plants mainly *Myriophyllum* and little *Hydrocotyle* (15-60%) produced vegetation pointing to abundant shallow open water. This allowed the course sediment fractions to be transported to the coring site. Lake level stands are comparable to the previous interval.

During part 2 high proportions of sand (30-50% with peaks up to 90%) occurred together with low proportions of organic matter (2-6% most of the time), while supply of coarse silt (40-50%) and fine silt (15-20% most of the time) was comparable to the previous zone. The aquatic vegetation differs with the previous zone essentially in higher proportions of deep-water vegetation (*Isoëtes* 10%, peaking up to 50%) suggesting a rise of the water levels and concomitant higher available energy levels to transport sediments from the surrounding slopes into the lake basin. Also in comparison to the previous interval, apart from *Myriophyllum* here also *Hydrocotyle* and Apiaceae contributed to the shallow water vegetation. Cyperaceous reed swamp (40-70%) was abundant. The algae *Spirogyra*, *Zygnema* and *Debarya* were present during most of the time while at the end of this interval *Debarya* became for the first time in the current record abundant.

During part 3 fine-grained sediments reached high proportions again (clay 5-30% and clay + fine silt together up to 60-80%) while sand was absent. This points to a low energy level sedimentary environment. Indeed, dominance of cyperaceous swamp vegetation (30-50%) and *Myriophyllum*-dominated shallow water vegetation (20% up to 60%) supports this interpretation. Among algae only *Debarya* was abundant. Lake levels were lower than in the previous interval and there was much open shallow water with low energetic depositional environments.

During part 4 supply of clay and fine silt (20% most of the time, peaking several times to 60%) alternated with intervals when coarse silt (20%, peaking to 70%) and sand (10-30%) occurred, pointing to intermediate energetic levels for sediment transport. Peaks of sand coincide with peaks of deep water *Isoëtes* and these events may reflect short periods of high precipitation and increased lake levels releasing much energy to supply coarse sediments to the lake basin. Lake levels were low during most of the time explaining cyperaceous reed swamp was most dominant (60-80%). A high proportion of wet shore vegetation of Rumex and Polygonum (10-30%) corresponds with high proportions of organic material and peat (5-12%). Algae were continuously present.

Period 16 (71.2-55.3 ka); zone Fq-9C-16L

During part 1 clay as well as sand is almost absent. Fine silt shows 20-50%, coarse silt (40-55%) and organic matter 12-20% pointing to intermediate energy levels supplying fine- and coarse-grained silts. Cyperaceous reed vegetation was dominant (40-70%) and presence of peat offered a matrix to collect periodically sand. The proportions of shallow water vegetation (~20%) mainly *Hydrocotyle* and *Myriophyllum*, and deep-water
vegetation (*Isoëtes* reached for the first time in the record proportions up to 25%) are indicative of high lake levels and distal source area of the sediments. During part 2 the proportion of fine-grained sediments increased up to 20-35% for clay and up to ~45% for fine silt indicative of quiet and low energy depositional environments. Indeed aquatic vegetation shows abundant shallow water (*Apiaceae, Hydrocotyle* and *Myriophyllum*) and deep-water environment (*Isoëtes* shows highest proportions of the current record). Lake levels are estimated as high; possibly some 5 to 10 m above present-day level; and some 5 to 10 m below the highest maximum (i.e., ~20 m above present-day). Cyperaceous swamp vegetation was able to collect some sand, and presence of wet shore vegetation (2-20% representation) supports the ~5% organic matter in the sediments.

During part 3 the proportion of coarse silt increased to 60-70% and mainly clay disappeared from the fine sediment fractions pointing to sediment supply to the lake at higher energy levels. Shallow water vegetation increased while the share of deep-water vegetation lowered suggesting lake levels lowered. The proportion of wet shore vegetation did not change but cyperaceous reed swamp vegetation (40-70%) became more abundant. During part 4 the share of fine silt increased from ~20% to ~65% while presence of clay remained at levels between 18-25%. Sediment sources are more distal and depositional environments have lower levels of energy. This change is supported by more wet shore vegetation (5-10%, peaking up to 25% and 50%), more cyperaceous reed swamp (~50% representation), and less deep-water vegetation. Lake levels lowered.

During part 5 much sand was deposited in the lake basin (first ~70%, later lowering to 35% and 20%) pointing to a proximal sediment source and high energetic depositional environments. Deep-water vegetation reached high proportions (between 30% and 40%) suggesting high precipitation levels, sediment transport at high energetic levels, and higher lake levels than during the previous interval. Cyperaceous reed swamp (~60% representation) was abundant. During the last part of this interval when supply of sand diminished, Ranunculaceae and algae became most abundant suggesting more transparent waters than before.

During part 6 high proportions of clay (10-20%) and fine silt (30% to 60%) and absence of sand is indicative of a distal sediment source, and low energetic depositional environments. Deep-water vegetation is almost absent, shallow water vegetation shows a low representation, suggesting low water levels. Indeed, cyperaceous reed swamp (~80%) is very abundant and waters in between seem mainly devoid of aquatic vegetation. Wet shore vegetation is almost absent.

During part 7 fine silt was mainly replaced by coarse silt and supply of sand (values up to 40%) which points to higher energy levels in the lake basin. Indeed, deep-water vegetation became abundant (20%, peaking to 40%) showing much high lake levels and suggesting high precipitation. Absence of wet shore vegetation, shallow water plants and algae are in support of a highly dynamic and energetic environment.

Period 17 (54.6-46.7 ka); zone Fq-9C-17L

During part 1 supply of fine-grained sediments (20-25% clay and 5-40% fine silt) was relatively low. Most of the time coarse silt (50-65%) was most abundant. In combination with a substantial peak of sand (~30%) during the middle of this interval it is concluded
that sediment source areas were proximal and depositional environments had a substantial energetic level. Indeed, 10-25% deep-water taxa, for the first time in the current record consisting of much *Potamogeton*, and 40-60% shallow water taxa point to relatively high lake levels. Cyperaceous reed swamp was common but not dominant while in shallow waters Apiaceae, *Hydrocotyle* and *Myriophyllum* were abundant. A substantial proportion of organic material and peat (12-20%) supports the substantial presence of wet shore vegetation (15-30%) in which *Rumex* was most common. During part 2 supply of fine-grained sediments increased (8-30%), supply of coarse silt decreased (30-40%) but sand was supplied during most of the time. Depositional environments had increased in energy levels and sediment sources were proximal. Deep water vegetation consisting of *Isoëtes* and *Potamogeton* was common (10-30% most of the time) pointing to high lake levels. During this interval the record of *Polygonum*, most characteristic of wet shores, became unimportant suggesting that during the remaining part of this record, lake levels were much higher than before. Lower proportions of organic matter and peat (7-14%) correspond to lower presence of wet shore vegetation (8-15% most of the time). During part 3 supply of fine grained sediments was higher (up to 20% clay and up to 50% clay + fine silt) while sand was absent suggesting a distal sediment source, mainly deep water and quiet depositional environments in the lake. Also the deep-water plant *Potamogeton* was absent; the upper 30 m of the record suggests a positive relation between high energetic depositional environments and presence of *Potamogeton*. Shallow water vegetation had diminished (20% representation). This interval is the first showing high lake levels and very quiet low energetic lake environments. This interval may reflect conditions that lacustrine sediments were deposited at highest elevation in the lake basin (maximally up to ~20 m above the present-day lake level).

**Period 18 (46.6-26.97 ka); zone Fq-9C-18L**

During part 1, clay was rare and proportions of fine silt had lowered to 40% and 20% most of the time. Sand was continuously supplied to the lake basin suggesting sediment transport at high energetic levels in the lake basin. High precipitation and much erosion as a consequence, is inferred. A maximum abundance of deep water vegetation consisting of almost pure stands of *Potamogeton* (starting in this interval with the highest percentages (80%) measured by the record) suggests lake levels reached highest stands of the last glacial cycle, viz. some 20 m above the present-day levels. Indeed, wet shore vegetation and cyperaceous reed swamp was rare at the start of this interval and increased only slightly afterwards. During part 2 fine-grained sediments with a high share of clay prevailed (total values varying between 20% and 50% most of the time) pointing to a substantial lake surface with deep water and quiet low energetic depositional environments. This interpretation is supported by continuous and significant percentages of deep-water vegetation consisting of *Isoëtes* and *Potamogeton*. But frequent spikes of sand indicate that sediment sources may have been proximal and frequent extremes in precipitation gave rise to erosion and transport of sand into the lake basin. A high lake level, but lower compared to the previous interval, is inferred with frequent extremes in precipitation and erosion.
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Shallow waters showed vegetation dominated by just two aquatics: *Hydrocotyle* and *Myriophyllum.*

During part 3 most salient is the very low representation of fine-grained sediments (~12-30%) and the high proportions of sand (up to 15%), coarse silt (up to 50%) and organic matter (10% up to 30%). The high proportion of deep-water vegetation (20%, peaking up to 60%) to which *Potamogeton* contributed most abundantly points to high lake levels and high levels of precipitation are inferred. But deep water was apparently not in quiet conditions and this may relate to the maximum expansion of glaciers around this time (Van der Hammen, 1981; Van der Hammen et al., 1980/81). Wet shore vegetation was rare and in the large areas with shallow to deep waters *Myriophyllum* and *Potamogeton* were among the few important taxa.

During part 4 sediments consisted for ~40% of fine grained sediments of which clay formed the largest part (20-35%). Coarse silt was common (25-35%) and there was a frequent supply of substantial amounts of sand (varying from 10% to 40%) indicating the lake basin experienced regularly high levels of sediment transport under high precipitation regimes. This may relate to the maximal expansion of the glaciers on top of the surrounding mountains. High representation of deep water vegetation, consisting of *Isoëtes* and *Potamogeton,* and varying most of the time between 10% and 30% (with peaks up to 40% and 70%), supports the reconstruction of high lake levels and wet climatic conditions. Presence of cyperaceous reed swamp was limited and reed swamp diminished during this interval. Wet shore vegetation was rare and some peaks in the representation of *Typha* (for the first time in the record) suggests shores were damaged by the high energetic levels of sediment transport. It is plausible that during this interval the conditions developed for an important destabilization of the lake: water-levels were high, aquatic vegetation protecting to some degree the sediment infill of the lake was minimal, precipitation and erosion were high, and glaciers had reached as far down slope as ~2800 m (Van der Hammen et al., 1980/81) and had reached the lake surface at shortest distance.

Part 5 is the last short episode reflected by the pollen and sediment records. Sediments of younger age were not deposited or, have been eroded at a later moment and the sediment surface was set back in time. From other coring sites in the Fúquene Basin is known that sedimentation elsewhere in the basin continued up to recent times (Bogotá-A et al., 2011a). The present location reflects the deepest part of the modern lake, an area that potentially may reflect the ancient course of the main water currents. Such areas are prone to erosion and gaps in the sediment record as a consequence. However, considering the downcore grain size records and records of aquatic vegetation of the full 60 m of sediments, exceptional environmental conditions developed during this last part of period 18. The combination of high lake levels, high proportions of coarse sediments indicative of intensive erosion and high energy levels to transport sediments, combined with a low protection of the sediments because of the scarce presence of aquatic vegetation had not been seen before. These unprecedented conditions in the lake may explain that water currents with a high energetic erosive power, perhaps also related to the presence of glaciers at short distance, prevented further sediment accumulation. During part 5 coarse grained sediments prevailed (10% sand and 40-50% coarse silt) indicating that high energetic levels of sediment transport prevailed up to the end of the record. However, abundant cyperaceous reed swamp (40-50%) and shallow water vegetation in
which deep water indicating *Potamogeton* did not occur any more also offered very quiet depositional environments with distal sediment sources: this explains clay was represented by 20-30%. It may be plausible that after a period of some 30 kyr with high to very high lake levels, main water courses found new trajectories through the lake basin when the lake level dropped significantly within short time between 29 ka and 28 ka.

### 4.2 Reconstruction of regional vegetation change

The following reconstruction of vegetation change in the region around Lake Fúquene is based on the regional pollen record (Fig. 6, Table 3). Reconstructions follow the 10 main zones and the 53 subzones (parts) indicated in Fig. 6. This paper starts with period 11; the periods 1 to 10 belong to the lower part of the record presented by Bogotá-A et al.

**Period 11 (133.12-117.45 ka); zone Fq-9C-11R**

High proportions of montane forest taxa show the UFL had altitudinal positions around 3300 to 3400 m and this period clearly reflects warm interglacial conditions. High proportions of subandean forest indicate that the upper limit of the subandean forest belt was at close distance to the lake.

During part 1 AP of 80-85% indicates the UFL was around 3350-3400 m. High proportions of *Alnus* and *Myrica* show abundant presence of forest on wet soils, pointing to low lake levels. Low lake levels are confirmed by the aquatic pollen record. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Myrsine*, *Podocarpus*, *Quercus* and *Weinmannia*. Smaller contributions of *Eugenia*, *Ilex*, other Melastomataceae, *Symplocos* and *Thalictrum* show the diversity of the forest. During the second half of this interval *Podocarpus* in particular is losing cover. Significant proportions of *Acalypha*, *Alchornea* and Urticaceae/Moraceae show that subandean forest occurred up to elevations as high as 2300-2400 m and had reached the lake up to some 200 m vertical distance. *Quercus* has a large altitudinal range (Fig. 3) and the proportion of *Quercus* also reflects subandean forest. Presence of *Dodonaea* points to dry vegetation, possibly located in the rain shadow areas of the basin. The subpáramo is mainly represented by Asteraceae, Poaceae and *Hypericum* and this vegetation was limited to elevations between ~3400 and 3700 m, the latter being the highest parts of the surrounding mountains.

During part 2 AP percentages are most of the time >90% indicating the UFL had reached maximal elevations of ~3500 m. Indeed subandean forest had reached the lake at close distance as proportions of *Acalypha*, *Alchornea*, Urticaceae/Moraceae show high proportions. A spike of high representation of *Dodonaea* and Chenopodiaceae points to a dry excursion in climatic conditions pointing to damaged vegetation and erosion. At the same time a peak in *Cecropia* is indicative of forest turnover at lower elevations and also presence of *Croton* points to forest in which open patches are common. This climatic excursion is supported by the grain size record which shows increased proportions of coarse silt and sand also indicative of damaged vegetation cover and erosion. High proportions of *Alnus* and *Myrica* show abundant presence of...
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As in the previous interval subpáramo continued its presence above 3100 to 3300 within forest on wet soils, pointing to low lake levels. Low lake levels are supported by the record of aquatic vegetation. Andean forest consisted mainly of *Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Thalictrum* and *Weinmannia*. Smaller contributions of *Eugenia, Ilex, Juglans*, other Melastomataceae, and Proteaceae show the diversity of the forest. Subpáramo vegetation shows significantly lower percentages as in the previous interval indicating the UFL had made a discrete upslope shift of ~100-150 m and occurred from ~3500 m to the tops of the surrounding mountains at ~3700 m. Some grasspáramo vegetation with Poaceae, *Plantago*, and *Valeriana* may have occurred near the mountain tops at 3700 m.

During part 3 the AP percentages vary around 85% indicating the UFL shifted during this interval in some 4 oscillations around ~3400 m. The uppermost limit of subandean forest lowered to 2300-2400 m. High and stable proportions of *Alnus* and *Myrica* show abundant presence of forest on wet soils, pointing to low lake levels. Low lake levels are supported by the record of aquatic vegetation, which shows cyperaceous swamp vegetation was dominant in the lake. Andean forest consisted mainly of *Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Thalictrum*, and *Weinmannia*. Smaller contributions of *Eugenia, Ilex, Juglans*, other Melastomataceae, Proteaceae, *Symlocos*, and *Vallea* show the diversity of the forest. *Hedyosmum* is most responsive to the rapid UFL oscillations. Low values of Asteraceae, Ericaceae and *Hypericum* show that subpáramo (from 3400 m to the mountain tops at 3700 m) was poor in shrub and dominated by grasses and other páramo herbs such as *Plantago* and *Valeriana*.

During part 4 AP values are most of the time between 80% and 90% pointing to an UFL at 3300 m to 3500 m elevation. AP values show minimally 3 cycles of UFL shifts and the gap in the record in the middle part of this interval may obliterate another two cycles. A lower value of subandean forest indicates that this forest occurred now below ~2300 m which may point to more frequent night frost at the elevations above 2300 m. The UFL positions shows that average annual temperatures had not changed significantly compared to the previous interval. High proportions of *Alnus* and *Myrica* show abundant presence of forest on wet soils, pointing to low lake levels. Low lake levels are supported by the record of aquatic vegetation which shows, apart from abundant cyperaceous swamp vegetation, more wet shore vegetation in particular. Andean forest consisted mainly of *Hedyosmum, Podocarpus, Quercus* and *Weinmannia*. Smaller contributions of *Eugenia, Ilex, Miconia*, other Melastomataceae, *Myrsine, Proteaceae, Symlocos*, and *Thalictrum* show the diversity of the forest. As in the previous interval subpáramo continued its presence above 3300 to 3500 m up to the mountain tops and vegetation was dominated by herbs in particular Poaceae, Caryophyllaceae, *Geranium, Plantago* and *Valeriana*.

During part 5 AP values are most of the time between 70% and 80% pointing to an UFL at 3100 to 3300 m elevation. Peak values over 85% show a short excursion of the UFL to 3400 m. High proportions of *Alnus* and *Myrica* show abundant presence of forest on wet soils, pointing to low lake levels. Abundant presence of wet shore vegetation in the aquatic pollen record also points to very low lake levels. Andean forest consisted mainly of *Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus* and *Weinmannia*. Smaller contributions of *Drimys, Eugenia, Ilex, Juglans*, other Melastomataceae, *Myrsine, Symlocos, Thalictrum*, and *Vallea* show the diversity of the forest. As in the previous interval subpáramo continued its presence above 3100 to 3300 within
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A narrow altitudinal belt of some 150 m with low proportions of shrub. Above 3300-3500 m up to the mountain tops grasspáramo was dominated by herbs in particular Poaceae, Caryophyllaceae, Geranium, Plantago and Valeriana.

During part 6 AP values are between 72-78% pointing to an UFL at 3200-3250 m elevation. This short interval reflects a temperature minimum. High proportions of cool trees, such as Ilex, Vallea and Weinmannia show that the lake was located in the upper part of the Andean forest belt. Other important trees were Hedyosmum, Miconia, Podocarpus, and Quercus. Smaller contributions of Eugenia, Myrsine, and Symlocos show the diversity of the forest. High proportions of Alnus and Myrica show abundant presence of forest on wet soils, pointing to low lake levels. Low lake levels are supported by the record of aquatic vegetation which shows apart from abundant cyperaceous swamp vegetation abundant wet shore vegetation. Subpáramo vegetation occurred between 3200 and 3500 m and shrub of Ericaceae and Hypericum was more common than before. Grasspáramo occurred above 3500 m elevation and was comparable to the floristic composition during the previous interval. A peak in the representation of Borreria suggests presence of dry vegetation at locations located in the rain shadow.

During part 7 AP values vary between ~73-83% pointing to an UFL at 3200 to 3400 m elevation. High proportions of Alnus and Myrica show abundant presence of forest on wet soils, pointing to low lake levels. Abundant presence of wet shore vegetation in the aquatic pollen record also points to low lake levels. Andean forest consisted mainly of Hedyosmum, Miconia, Podocarpus, Quercus and Weinmannia. Smaller contributions of Drimys, Eugenia, Ilex, Juglans, other Melastomataceae, Myrsine, Symlocos, Thalictrum, and Vallea show the diversity of the forest. Subpáramo, present between ~3300 and ~3600 m, was poor in Ericaceae and Hypericum but asteraceous shrub was abundant. Above ~3600 m elevation grasspáramo was present with Poaceae, Caryophyllaceae, Geranium, Plantago and Valeriana as main components.

Period 12 (117.41-111.74 ka); zone Fq-9C-12R

This period is characterized by the highest positions of the UFL and reflects the warmest period of the record. In the Andean forest Quercus and Podocarpus reached highest proportions of the record. In the lake, peatland reached its maximum expansion pointing to very low lake levels.

During part 1 AP values peak at 90% and later at 95% pointing to an UFL at ~3500 m elevation. Myrica shows stable proportions but values of Alnus lower in the second half of this interval. High proportions of wet shore and swamp vegetation in combination with high proportions of organic matter in the sediments point to abundant presence of peatland during the second half of this interval and lake levels must be very low. Subandean forest represented by Acalypha and Urticaceae-Moraceae in particular, show significant values indicating this forest occurred up to ~2400 m. Andean forest consisted mainly of Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Thalictrum, and Weinmannia. Smaller contributions of Drimys, Eugenia, Ilex, other Melastomataceae, Monnina, Proteaceae, Symlocos, and Vallea show the diversity of the forest. Subpáramo vegetation shows low values and must have been limited to a narrow altitudinal interval between ~3500-3600 m elevation. Above ~3600 m grasspáramo consistent
mainly of grasses and other paramo herbs were rare. Higher proportions of Dodonaea point to more dry and open vegetation in the rain shadow areas of the basin. During part 2 AP values peak at 97% due to a maximum representation of Alnus. Swamp forest on wet soils was dominated by Alnus and proportions of Myrica were remarkably low. The sediment record shows that peatland was abundantly present in the lake basin and Alnus carr might have expanded into the peatland areas. The UFL was at ~3400-3500 m elevation and montane forest shows a low diversity. Low values of subandean forest taxa point to a further down slope retreat to this forest (below 2400 m). Andean forest consisted mainly of Podocarpus and Quercus with an admixture of Hedysosmum, Miconia, Myrsine and Weinmannia and had a low taxonomic diversity. Subpáramo vegetation was dominated by shrub of Asteraceae and Hypericum. Grasspáramo was dominated by Poaceae and Plantago. During part 3 most of the record is lost due to a gap in sediment recovery. Low AP percentages at the start (68%) suggest the UFL migrated down slope as low as ~3100 m and this interval reflects a cooling phase in climatic conditions. It is plausible that most of the hiatus reflects an interval with increasing temperatures in order to meet the conditions at the start of the next interval. During part 4 AP values peak at 97% pointing to an UFL at ~3500 m elevation. Alnus and Myrica show abundant presence of forest on wet soils, pointing to low lake levels. The sediment record shows abundant presence of peatland and Alnus carr probably extended into these peatlands. The record of aquatic vegetation shows abundant presence of cyperaceous reed swamp also pointing to low lake levels. Abundant presence of swamp vegetation and during the first part of this interval abundant presence of peatland both support low lake level conditions. Peatland is diminishing during this interval. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilex, Miconia, Podocarpus, Quercus, and the highest proportions of Weinmannia seen in the record. Smaller contributions of other trees are limited to Clethra, Croton, Drimys, Monnina, Myrsine, and Symplcos show a floral composition different from the previous periods. High values of Borreria are indicative of climatologically drier conditions. In the subpáramo the proportion of ericaceous shrub increased significantly and this vegetation extended between 3100-3300 m and 3400-3600 m. Significant
values of Poaceae, Plantago, and Valeriana reflect the presence of grasspáramo in the highest areas above ~3500-3500 m. During part 2 AP values are ~70% most of the time indicating the UFL was around 3100 m. High proportions of Alnus and Myrica show abundant presence of swamp forest on wet soils, pointing to low lake levels. Abundant presence of swamp vegetation supports low lake level conditions. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilex, Miconia, Podocarpus, Quercus, Symlocos, and Weinmannia. Smaller contributions of Croton, Drimys, other Melastomataceae, Monnina, Myrsine, and Vallea show the diversity of the forest. High values of Borreria and presence of Dodonaea are indicative of climatologically drier conditions. The subpáramo extended from 3100 to 3400 m elevation and consisted of shrub of Asteraceae, Ericaceae and Hypericum. Significant values of Poaceae, Geranium, Lycopodium, Plantago, and Valeriana reflect the presence of grasspáramo in the areas above ~3400 m. During part 3 AP values reach a peak of ~75% indicating the UFL reached maximally 3200 m elevation. High proportions of Alnus and Myrica show abundant presence of swamp forest on wet soils, pointing to low lake levels. Abundant presence of swamp vegetation supports low lake level conditions. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilex, Miconia, Podocarpus, Quercus, Symlocos, and Weinmannia. Smaller contributions of Clethra, Daphnopsis, Drimys, other Melastomataceae, Monnina, Myrsine, and Vallea show the diversity of the forest. High values of Borreria and presence of Dodonaea are indicative of climatologically drier conditions. Stable values of 15-18% of subpáramo taxa including Asteraceae, Ericaceae, Hypericum and Polylepis indicate this vegetation had a wide altitudinal distribution between 3100 and 3400-3500 m elevation. The floristic composition of the grasspáramo was similar to the previous interval but low proportions indicate grasspáramo was restricted to the mountain tops only.

Period 14 (104.83-82.54 ka); zone Fq-9C-14R

During this period the UFL shifted down slope and the surroundings of the lake changed from Andean forest into paramo. During this process of climatic cooling, temperatures showed many rapid oscillations. During most of this period Quercus was rare while Polylepis and Symlocos were relatively abundant.

During part 1 AP values lower from ~65% to ~55% indicating the UFL lowered from ~3000 m to ~2800 m. High proportions of Alnus and significant values of Myrica show abundant presence of swamp forest on wet soils at the borders of the lake. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilex, Podocarpus, Quercus, Symlocos, and Weinmannia. Smaller contributions of Clethra, Drimys, Eugenia, Miconia, Monnina, and Myrsine show the diversity of the forest. High values of Borreria and presence of Dodonaea are indicative of climatologically drier conditions. Stable values of 15-20% of subpáramo taxa including Asteraceae, Ericaceae, Hypericum, and Polylepis indicate this vegetation had a wide altitudinal distribution between 3000-3300 m at the start to 2800-3100 m at the end of this interval. Polylepis was not present before and started in this interval an almost continuous record up to the top of this core. The grasspáramo extended from 3300 m at the start, to 3100 m at the end upslope. Apart from Poaceae,
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the grasspáramo included a suite of different herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago, and Valeriana.
During part 2 AP values lower to a minimum of ~50% indicating the UFL lowered to ~2700 m. High proportions of Alnus and significant values of Myrica show abundant presence of swamp forest on wet soils at the borders of the lake. Andean forest consisted mainly of Eugenia, Hedyosmus, Ilex, Podocarpus, Quercus, and Symlocos. Weinmannia was hardly present and it seems that the rapid expansion of Polylepis at the start of this period was in competition with Weinmannia; both trees are common near the UFL. Smaller contributions of Clethra, Drimys, Eugenia, Miconia, Monnina, Myrsine, Proteaceae, and Symlocos show the diversity of the forest. Proportions of Borreria decreased and climatic conditions turned more humid. Values of 15-20% of subpáramo taxa including mainly Asteraceae, Polylepis, and Ericaceae indicates this vegetation had at the end of this interval an altitudinal distribution between ~2700 and ~3000 m elevation. The grasspáramo extended from 3000 m upslope. Apart from Poaceae, the grasspáramo included a suite of different herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana.
During part 3 AP values reach a maximum of 60% and later of 65% indicating the UFL increased to ~2900 m and later to ~3000 elevation. High proportions of Alnus and significant values of Myrica show abundant presence of swamp forest on wet soils at the borders of the lake. Andean forest consisted mainly of Eugenia, Hedyosmus, Ilex, Podocarpus, Quercus, and Symplocos. Smaller contributions were only shown by Myrsine showing that the floristic diversity near the UFL was low. Low proportions of Borreria show that dry vegetation was limited in the basin. Values of 20-25% of subpáramo taxa including Asteraceae, Polylepis, Ericaceae and Hypericum indicate this vegetation belt extended to 3200-3300 m elevation. The grasspáramo extended from 3200-3300 m upslope. Apart from Poaceae, the grasspáramo included a suite of different herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana.
During part 4 AP values reach a minimum of ~42% indicating the UFL lowered to ~2600 m elevation. Alnus and Myrica showed significant values showing that swamp forest still occurred on wet soils at the borders of the lake. Andean forest consisted mainly of Eugenia, Hedyosmus, Ilex, Podocarpus, Quercus, Symlocos, and Weimannia. Smaller contributions were only shown by Myrsine showing that the floristic diversity near the UFL was low. Low proportions of Borreria show that dry vegetation was limited in the basin. Values of 25-30% of subpáramo taxa including Asteraceae, Polylepis, Ericaceae and Hypericum indicates this vegetation belt extended from ~2600 to ~2900 m elevation. The grasspáramo extended from 2900 m to ~3600 m and for the first time in the record superpáramo vegetation may have covered the mountain tops around the lake. Apart from Poaceae, the grasspáramo included a suite of different herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana.
During part 5 AP values reach three times a peak of ~70% and finally a peak of ~80% indicating the UFL reached three times ~3100 m and finally ~3300 m elevation. The successive peaks of AP consisted of different taxa: the first was mainly made up of Alnus, Myrica, Hedyosmus and Podocarpus; the second of Hedyosmus, Ilex, Miconia and Podocarpus; the third of Ilex; and the fourth of Alchornea, Alnus and Miconia. Proportions of Alnus are higher than in the previous interval indicating Alnus carr had
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expanded on wet soils at the borders of the lake. Andean forest consisted mainly of *Eugenia*, *Hedyosmum*, *Ilex*, *Miconia*, *Podocarpus*, *Quercus*, *Symplocos*, and *Weinmannia*. There were smaller contributions of a suite of taxa such as *Clethra*, *Croton*, *Daphnopsis*, *Drimys*, other Myrtaceae, *Gaiadendron*, other Melastomataceae, *Munnina*, *Myrsine*, Proteaceae, *Styloceras*, *Thalictrum*, and *Vallea* showing a very diverse montane forest. Representation of *Borreria* and also Chenopodiaceae and *Dodonaea* points to presence of dry vegetation in rain shadow areas. Values of 20-25% of subpáramo taxa including Asteraceae, *Polylepis*, Ericaceae and *Hypericum* indicates this vegetation belt extended to ~3400 m elevation. The grasspáramo occurred above 3400 m. Apart from Poaceae, the grasspáramo included a suite of different herbs such as *Aragoa*, Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Lysipomia*, *Plantago* and *Valeriana*.

During part 6 AP values vary around 55% indicating the UFL was located at ~2800 m elevation. High proportions of *Alnus* show that *Alnus* carr mixed up with *Myrica* had expanded on wet soils at the borders of the lake. Andean forest consisted mainly of *Eugenia*, *Hedyosmum*, *Ilex*, *Miconia*, *Podocarpus*, *Symplocos*, and *Weinmannia*. There were smaller contributions of a suite of taxa such as *Clethra*, *Croton*, *Daphnopsis*, *Drimys*, *Gaiadendron*, *Juglans*, other Melastomataceae, *Munnina*, *Myrsine*, and *Thalictrum* showing a diverse montane forest. Representation of *Borreria* points to presence of dry vegetation in rain shadow areas. Values of ~15% of subpáramo taxa including Asteraceae, *Polylepis*, Ericaceae and *Hypericum* indicates this vegetation belt extended between ~2800 m and ~3100 m elevation. The grasspáramo occurred above 3100 m. Apart from Poaceae, the grasspáramo was made up of Caryophyllaceae, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*.

During part 7 AP values show two peaks of ~70% indicating the UFL reached ~3100 m elevation. The first peak was mainly made up of *Alnus* and the second peak consisted of a suite of arboreal taxa of which *Podocarpus* and *Weinmannia* were the most important ones. Proportions of *Alnus* were high indicating *Alnus* carr was abundant on wet soils at the borders of the lake. The aquatic record shows much swamp vegetation and the sediment record a dominance of quiet sedimentary environments accumulating clay. Both conditions are in harmony with abundant *Alnus* carr. Andean forest consisted mainly of *Hedyosmum*, *Podocarpus*, *Symplocos*, and *Weinmannia*. There were smaller contributions of a suite of taxa such as *Miconia* and *Vallea* showing a diverse montane forest. Values of 10-20% of subpáramo taxa including Asteraceae, Ericaceae and *Hypericum* indicates this vegetation belt was relatively narrow and extended from ~3100-3300 m elevation. *Polylepis* was not present and *Weinmannia* formed the uppermost forests near the UFL. The grasspáramo occurred above ~3300 m. The grasspáramo was poor in herbs and Poaceae were very abundant. This complex of characteristics points to very dry climatic conditions. This conclusion is supported by abundant swamp vegetation indicating low lake levels and abundant *Alnus* carr also pointing to low lake levels.

During part 8 AP values show a minimum of ~50% indicating the UFL lowered to ~2700 m elevation. Proportions of *Alnus* were lower indicating *Alnus* carr had diminished. This is supported by the aquatic vegetation diagram, which is showing higher lake levels. Andean forest consisted mainly of *Eugenia*, *Hedyosmum*, *Ilex*, *Miconia*, *Podocarpus*, *Quercus*, *Symplocos*, and *Weinmannia*. There were smaller contributions of *Clethra*, *Croton*, *Drimys*, *Eugenia*, other Melastomataceae, *Munnina*, *Myrsine*, Pro-
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teaceae, Thalictrum, and Vallea showing a diverse montane forest. Representation of Borrella and Chenopodiaceae points to presence of dry vegetation in rain shadow areas. Values of 18-25% of subpáramo taxa including Asteraceae, Polylepis, Ericaceae, and Hypericum indicates this vegetation belt extended between ~2700 and ~3000 m elevation. The grasspáramo occurred above 3000 m. Apart from Poaceae, the grasspáramo included a suite of different herbs such as Aragoa, Caryophyllaceae, Draba, Gentiana, Geranium, Lycopodium, Lysipomia, Plantago and Valeriana. During part 9 AP show a peak of 69% indicating the UFL reached almost 3100 m elevation. Proportions of Alnus were higher than in the previous interval indicating Alnus carr had expanded on wet soils at the borders of the lake. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilx, Miconia, Podocarpus, Quercus, Symplocos, and Weinmannia. Taxa with small contributions were few showing a monotonous montane forest composition. Proportions of subpáramo taxa lowered from ~30% to ~10% indicating this belt with shrub became narrower: from ~3100-3400 m at the start to ~3100-3250 m at the end of this interval. Subpáramo vegetation mainly consisted of Asteraceae and Hypericum. The grasspáramo occurred above 3400-3250 m and was poor in species. Poaceae and Valeriana were the most important taxa. During part 10 AP values show three peaks of ~50% indicating the UFL reached three times ~2700 m and lowered to ~2600 m in between. The first peak was mainly made up of Alnus and Myrica; the second peak was made up by a suite of taxa such as Alnus, Hedyosmum, Quercus, Symplocos and Weinmannia; and the third peak consisted of Alnus, Clethra, Podocarpus Quercus and Weinmannia. Proportions of Alnus and Myrica were high indicating Alnus carr was abundant on wet soils at the borders of the lake and pointing to low lake levels. Low lake levels are supported by the aquatic record, which is showing abundant swamp vegetation. Andean forest consisted mainly of Eugenia, Hedyosmum, Ilx, Miconia, Podocarpus, Quercus, Symplocos, and Weinmannia. There were smaller contributions of a suite of taxa such as Clethra, Drimys, other Myrtaceae, Juglans, other Melastomataceae, Monnina, Myrsine, Proteaceae, Thalictrum, and Vallea showing a diverse montane forest. Forests near the UFL consisted of Polylepis, Weinmannia and Podocarpus and it is noteworthy that Vallea hardly contributed to these forests before 55 ka (start of period 18). Values of 30-35% of subpáramo taxa including Asteraceae, Polylepis, Ericaceae, and Hypericum indicates this vegetation belt occurred between ~2700 m and ~3000 m elevation. The grasspáramo occurred above ~3300 m. The grasspáramo consisted of a suite of herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago, and Valeriana. During part 11 AP values show three peaks of ~70% indicating the UFL reached three times ~3100 m and lowered to ~3000 m in between. The first peak was mainly made up of Hedyosmum and Quercus; the second peak is partly oblitered by a gap in the core but supposedly is mainly made up by subandeans forest taxa and Quercus; the third peak by Alnus, Myrica, subandeans forest taxa, and Quercus. A positive relationship between high proportions of Quercus and high proportions of subandeans forest taxa is apparent. Quercus has a large altitudinal interval (at present-day from 1100 m up to the UFL at 3200 m; Fig. 3) and the pollen record suggests that subandeans forest taxa were able to reach higher elevations using oak forest as a corridor. This is a good example of the variability of forest composition and shows that strict ecological envelopes do not occur. Alnus and Myrica show lower values and diminishing swamp forest is in harmony with
higher lake levels (see aquatic vegetation diagram). Peat land had expanded over former swamp forest and climatic conditions were much more humid than in the previous interval. Quercus and Hedyosmum may form wet forest, which supports wet climatic conditions. Andean forest consisted mainly of Clethra, Eugenia, Hedyosmum, Ilex, Miconia, Myrsine, Podocarpus, Quercus, and Weinmannia. There were smaller contributions of a suite of taxa such as Daphnopsis, Drimys, other Myrtaceae, Gunnera, Ilex, Juglans, other Melastomataceae, Myrsine, Proteaceae, Sapium, Styloceras, Symplocos, Thalictrum, and Vallea showing a diverse montane forest. Values of 5-10% of subpáramo taxa including Asteraceae, Polylepis, and few Ericaceae and Hypericum indicates subpáramo vegetation occurred as a narrow belt between ~3100 and 3200 m. The grasspáramo occurred above ~3200 m. The grasspáramo consisted of a suite of herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago, Puya, and Valeriana.

During part 12 AP values show a maximum of 80% indicating the UFL reached ~3300 m elevation. Proportions of Alnus and Myrica were higher than in the previous interval indicating Alnus carr and swamp forest had expanded on wet soils and peatlands (see sediment record) at the borders of the lake. Lake levels were lower than in the previous interval. Andean forest consisted mainly of Clethra, Eugenia, Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Thalictrum, and Weinmannia. There were smaller contributions of a suite of taxa such as Daphnopsis, Drimys, other Myrtaceae, Ilex, Juglans, other Melastomataceae, Proteaceae, Symplocos, and Vallea showing a diverse montane forest. Values of 10-15% of subpáramo taxa including Asteraceae, Polylepis, and few Ericaceae and Hypericum indicates this vegetation belt was narrow and occurred between ~3300 m and ~3500 m elevation. The grasspáramo occurred above ~3500 m. The grasspáramo consisted mainly of Poaceae, Caryophyllaceae, Plantago, and Valeriana.

Period 15 (82.49-78.02 ka); zone Fq-9C-15R

This period reflects a short and warm interval at the end of MIS 5. Cold tolerant trees characteristic of the uppermost forests near the UFL such as Podocarpus, Quercus, Weinmannia, Vallea and Polylepis were rare. High lake levels during a warm climate point to very humid climatic conditions. High levels of superficially running water explain the abundant supply of coarse sediments (sand) into the lake. Myrica, and Alnus in particular, occurred abundantly as gallery forest on wet soils along rivers and therefore contributed substantially to the zonal vegetation in the area during this period.

During part 1 AP values vary between ~65% and ~75% indicating the UFL shifted between 3100 and 3300 m elevation. Alnus reached very high proportions while the aquatic pollen record indicates high lake level stands. Therefore, Alnus swamp forest occurred partly as narrow fringes around the lake and must have been abundant in particular on the slopes where Alnus formed a kind of gallery forest on wet soils. Andean forest consisted mainly of Hedyosmum, Podocarpus, Quercus, Thalictrum, and Weinmannia, but in addition of a high proportion of wet Alnus and Myrica dominated slope forest. There were smaller contributions of a suite of taxa such as Clethra, Drimys, Eugenia, Ilex, Juglans, Miconia, other Melastomataceae, Myrsine, Sapium, Symplocos,
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and Vallea showing a diverse montane forest. Values of 10-15% of subpáramo taxa including Asteraceae, Polylepis, and few Ericaceae and Hypericum indicates this vegetation belt was narrow and shifted between 3100-3300 m minimally and 3300-3500 m elevation maximally. The grasspáramo occurred above 3300-3500 m. The grasspáramo was dominated by Poaceae, Caryophyllaceae, Geranium, and Valeriana.

During part 2 AP values first show a minimum of 65% and subsequently two peaks of ~80% indicating the UFL started at ~3000 m and reached two times 3300 m elevation. During the first maximum wet Alnus forest continued as an important part of the zonal slope forests, as was the case in the previous interval. Humid climatic conditions continued to prevail. During the second high stand of the UFL also Hedyosmum and Podocarpus had a significant share in the Andean forest and precipitation levels, erosion, and high energetic sediment transport decreased (see sediment record). Andean forest was poor in species and consisted mainly of Alnus, Hedyosmum, Podocarpus, and Symlocos. There were smaller contributions of Drimys, Eugenia, other Myrtaceae, Ilex, Juglans, Monnina, Myrsine, Proteaceae, Stylloceras, Thalictrum, and Weinmannia showing a diverse montane forest. Subpáramo taxa reached values of ~10% most of the time pointing to a narrow belt dominated by Asteraceae and Ericaceae between ~3300 and 3400 m elevation. The grasspáramo occurred above ~3400 m. The grasspáramo consisted of few taxa belonging to the Poaceae, Caryophyllaceae, Geranium, Plantago, and Valeriana. Plantago shows in this interval relatively high abundance reflecting wet bog vegetation where water is stagnating. This supports wet climatic conditions.

Period 16 (77.98-68.04 ka); zone Fq-9C-16R

This period shows the transition from, mostly warm, MIS 5 conditions to cool and cold MIS 4 conditions. Climatic cooling occurred in three distinct cycles. The successive cool intervals had consistently lower temperatures. From this period onwards Polylepis and Miconia were more abundant. As a matter of fact, from this period onwards the páramo showed floristic changes in more detail.

During part 1 AP values showed a peak of 85% indicating the UFL reached ~3400 m elevation. Proportions of Alnus and Myrica were high indicating swamp forest was abundant on wet soils at the borders of the lake and pointing to low lake levels. Low lake levels are supported by the aquatic record, which is showing abundant swamp vegetation. Andean forest consisted mainly of Hedyosmum, Miconia, other Melastomataceae, Podocarpus, Quercus, and Weinmannia. There were smaller contributions of a suite of taxa such as Clethra, Eugenia, Ilex, Juglans, other Melastomataceae, Myrsine, Thalictrum, and Vallea showing a diverse montane forest. Forests near the UFL consisted of Polylepis, Quercus, Weinmannia, and Podocarpus. Subpáramo taxa reached less than 10% showing this vegetation had a limited altitudinal distribution between ~3400 and ~3550 m elevation. Asteraceae, and Polylepis were dominant and Ericaceae and Hypericum less common. The grasspáramo occurred above ~3550 m. Apart from Poaceae, the grasspáramo included Caryophyllaceae, Geranium, Plantago, and Valeriana.

During part 2 AP values show a peak of ~80% indicating the UFL reached ~3300 m elevation. Proportions of Alnus and Myrica were high indicating Alnus carr was abun-
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dant on wet soils at the borders of the lake and pointing to low lake levels. Low lake levels are supported by the aquatic record, which is showing abundant swamp and wet shore vegetation. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Podocarpus*, *Quercus*, and *Weinmannia*. Abundant presence of *Quercus* probably facilitated subandean forest taxa to reach higher elevations and to mix with the lowermost Andean forest. There were smaller contributions of a suite of taxa such as *Clethra*, *Drimys*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, *Monnina*, *Myrsine*, Proteaceae, *Sapium*, *Styloceras*, *Symlocos*, *Thalictrum*, and *Vallea* showing a diverse montane forest. Values of 10-16% of subpáramo taxa including *Polylepis*, and less Ericaceae and *Hypericum* indicates this vegetation belt expanded altitudinally and occurred between ~3300 m and ~3500 m elevation. The grasspáramo occurred above ~3500 m. Apart from Poaceae the grasspáramo consisted of a suite of herbs such as *Aragoa*, Caryophyllaceae, *Draba*, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. During part 3 AP values show a distinct peak of 85% indicating the UFL reached ~3400 m elevation. Proportions of *Alnus* and *Myrica* were high indicating swamp forest was abundant on wet soils at the borders of the lake and pointing to relatively low lake levels. Low lake levels are supported by the aquatic record, which is still showing abundant swamp vegetation. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Podocarpus*, *Quercus*, and *Weinmannia*. There were smaller contributions of a suite of taxa such as *Clethra*, *Daphnopsis*, *Drimys*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, *Myrsine*, Proteaceae, *Sapium*, *Styloceras*, *Symplocos*, *Thalictrum*, and *Vallea* showing a very diverse montane forest. Characteristic cool arboreal taxa (*Weinmannia*, *Vallea*, *Podocarpus*) and *Quercus* increased in proportion near the end of this interval documenting lowering temperatures on the basis of a changing floristic composition. Values of subpáramo taxa increased from ~10% to ~25% indicating this vegetation belt expanded. *Polylepis* and Ericaceae in particular increased in proportion. It extended from 3000-3200 m at the start to 2800-3100 m at the end of this interval. The grasspáramo occurred above 3100-3200 m. Poaceae and *Valeriana* increased in proportion but other páramo taxa such as *Aragoa*, Caryophyllaceae, *Geranium*, *Lycopodium*, and *Plantago* showed a consistent representation.
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During part 5 AP values show a distinct peak of 85% indicating the UFL reached ~3400 m elevation. Proportions of Alnus and Myrica were high indicating swamp forest was abundant on wet soils at the borders of the lake and pointing to relatively low lake levels. Low lake levels are supported by the aquatic record still showing abundant swamp vegetation. Andean forest consisted mainly of Hedyosmum, Miconia, Podocarpus, Quercus, and Weinmannia. There were smaller contributions of a suite of taxa such as Clethra, Daphnopsis, Drimys, Eugenia, other Myrtaceae, Ilex, Juglans, other Melastomataceae, Myrsine, Proteaceae, Styloceras, Symlocos, Thalictrum, and Vallea showing a diverse montane forest. Forests near the UFL consisted of Polylepis, Quercus, Podocarpus, and Weinmannia. Among subandean taxa Cecropia was relatively well represented indicating significant turnover of lower montane forest. Subpáramo taxa reached ~5% showing this vegetation had a very limited altitudinal distribution between ~3400 and ~3500 m elevation. Asteraceae and Polylepis were dominant and Ericaceae and Hypericum less common. The grasspáramo occurred above ~3500 m. Apart from Poaceae, the grasspáramo included Aragoa, Caryophyllaceae, Gentiana, Geranium, Lycopodium, Plantago, and Valeriana.

During part 6 AP values lower from ~55% to ~45% indicating the UFL lowered from ~2800 m to ~2600 m. For the second time in this record (the first time was period 14, part 10) the UFL had reached the lake to very short distance. This trend of cooling showed two rapid cycles mainly triggered by Quercus and Weinmannia. Proportions of Alnus and Myrica diminished indicating Alnus carr had retreated at the borders of the lake. This corresponds to the record of aquatic vegetation showing higher lake levels. Andean forest consisted mainly of Hedyosmum, Miconia, Podocarpus, Quercus, and Weinmannia. There were smaller contributions of a suite of taxa such as Clethra, Daphnopsis, Drimys, Eugenia, other Myrtaceae, Gaiadendron, Ilex, Juglans, other Melastomataceae, Monnina, Myrsine, Sapium, Styloceras, Symlocos, Thalictrum, and Vallea showing a very diverse montane forest. Values of subpáramo taxa increased from ~25% to ~30% indicating this vegetation belt expanded and extended at the end of this interval from 2600-2900 m elevation. Polylepis in particular increased in proportion. The grasspáramo occurred above 2900 m. Poaceae increased rapidly in proportion while other páramo taxa such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago, and Valeriana showed a consistent representation.

Period 17 (68-55.34 ka); zone Fq-9C-17R

During this period the UFL passed the elevation of Lake Fúquene for the first time in this record and the vegetation in the lake basin changed from forest into páramo. Decreasing temperatures coincided with increasing lake levels; less evaporation may (partly) explain this relationship. Trees making up the uppermost Andean forest are now best represented in the pollen record. Quercus did not belong to these trees and the absence of Quercus seems compensated by abundant presence of asteraceous dwarf trees and shrub. During this period, Podocarpus and Hedyosmum were the main trees in the uppermost forests.

During part 1 AP values decrease from ~38% to ~30% indicating the UFL lowered from ~2550 m to ~2400 m elevation. Myrica almost disappeared from the record but Alnus
kept ~25% representation indicating massive aeolian transport of Alnus pollen by upslope winds. Uppermost Andean forest consisted mainly of Hedyosmum, Miconia, Podocarpus, and Weinmannia. There were smaller contributions of Eugenia, Ilex, Myrsine, and Symplocos. Borreria reflects relatively dry environments with a high forest turnover. Values of 35-40% of subpáramo taxa dominated by Asteraceae and Polylepis indicate this vegetation belt occurred between 2400 m and 2700-2800 m elevation. The grasspáramo occurred above 2700-2800 m. The grasspáramo consisted of a suite of herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana. Lycopodium in particular is representative of the uppermost grasspáramo and the high proportions suggest the tops of the mountains were covered by superpáramo. During part 2 AP values started at 20% and increased to ~38% indicating the UFL had lowered to ~2200 m and shifted upslope to reach ~2550 m elevation at the end of this interval. At the UFL lowstand, Alnus showed still values of ~20% showing the general level of background pollen supply of this proliferous pollen producer (see also Hooghiemstra, 1984, p. 73). Uppermost Andean forest consisted mainly of Hedyosmum and Podocarpus and there was a low representation Eugenia, Ilex, Miconia, Myrsine, Symplocos, and Weinmannia. Borreria reflects relatively dry environments with a high forest turnover. Values of 35-45% of subpáramo taxa dominated by Asteraceae and Polylepis indicates this vegetation belt was wide and occurred at the start of the interval from ~2200-2600 m and at the end from ~2550-2900 m elevation. The grasspáramo was dominated by Poaceae, and included a suite of herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana. Lycopodium in particular is representative of the uppermost grasspáramo and the high proportions suggest the tops of the mountains were covered by superpáramo. During part 3 AP values reached a maximum of 40% indicating the UFL reached the level of Lake Fúquene. Alnus values reach ~35% indicating Alnus carr may have surrounded the lake for a short interval of time. At the same time lake levels lowered as the proportion of shallow water increased enabling Alnus carr to expand. Uppermost Andean forest consisted mainly of Hedyosmum, Miconia, and Podocarpus. There were smaller contributions of Clethra, Eugenia, Ilex, other Melastomataceae, Myrsine, Quercus, Symplocos, and Weinmannia. Borreria reflects relatively dry environments with a high forest turnover. Values of 30-40% of subpáramo taxa dominated by Asteraceae and Polylepis indicate this vegetation belt occurred between 2550 m and 2850 m elevation. The grasspáramo occurred above 2850 m. Apart from Poaceae, grasspáramo included a suite of herbs such as Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago and Valeriana. Lycopodium and Draba, in particular, are representatives of the uppermost grasspáramo and the high proportions suggest the tops of the mountains were covered by superpáramo. During part 4 AP values decrease from ~30% at the start to lowest values near the end of this interval. The second half of this interval shows a gap in the record. The UFL was at 2400 m at the start of this interval and lowered possibly to ~2200 m. Alnus is absent in the basin as Alnus does not occur above the UFL; its representation of ~20% shows the level of background noise. Uppermost Andean forest consisted mainly of Hedyosmum, Miconia, Myrsine, and Podocarpus. There were smaller contributions of Eugenia, Ilex, Symplocos, Thalictrum, and Weinmannia. The record of Borreria stopped during this interval suggesting the vegetation has reached a new stable altitudinal
distribution and vegetation turnover became low again. Values of 35-50% of subpáramo taxa dominated by Asteraceae and *Polylepis* indicate this vegetation belt had a wide altitudinal distribution and occurred between 2400 m and 2800 m elevation. The grasspáramo occurred above 2800 m. Apart from abundant Poaceae, the grasspáramo consisted of a suite of herbs such as *Aragoa*, Caryophyllaceae, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grasspáramo and the significant proportions suggest the mountains above ~3500 m were covered by superpáramo. During part 5 AP values fluctuate between ~20% and ~30% without showing distinct cycles. The UFL shifted around ~2300 m elevation. *Alnus* kept ~25% representation indicating massive aeolian transport of *Alnus* pollen by upslope winds. Uppermost Andean forest consisted mainly of *Hedyosmum* and *Podocarpus*. There were smaller contributions *Clethra*, *Croton*, *Drimys*, *Eugenia*, other Myrtaceae, *Ilex*, *Miconia*, *Myrsine*, Proteaceae, *Styloceras*, *Symplcos* and *Weinmannia*. Presence of *Croton* and *Borreria* suggest dry environments and open patches in the forest; this is congruent with low lake levels shown by high proportions of swamp vegetation in the aquatic pollen record. Values of 35-40% of subpáramo taxa dominated by Asteraceae and *Polylepis* indicate this vegetation belt occurred between ~2300 m and ~2700 m elevation. The grasspáramo occurred from 2700-3400 m. Apart from Poaceae, the grasspáramo consisted of a suite of herbs such as *Aragoa*, Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grasspáramo and significant proportions suggest the mountains above ~3400 m were covered by superpáramo. During part 6 AP values show a maximum of ~35% and lower again to ~26% indicating the UFL reached 2450-2500 m elevation and lowered to ~2300 m. Values of *Alnus* surpass the background level of 20% indeed, indicating *Alnus* swamp forest occurred for a short while around the lake at the start of this interval and proportions lower subsequently to background values indicating the UFL dropped below the level of the Lake Fúquene. Uppermost Andean forest consisted mainly of *Hedyosmum* and *Podocarpus*. There were smaller contributions of *Ilex*, *Miconia*, Proteaceae, *Symplcos*, *Vallea*, and *Weinmannia*. Values of 30-40% of subpáramo taxa dominated by Asteraceae and *Polylepis* indicate this vegetation belt occurred between 2450 m and ~2800 m at the start and from ~2300 m to ~2700 m at the end of this interval. The grasspáramo occurred above 2700-2800 m. Apart from Poaceae, the grasspáramo consisted of a suite of herbs such as *Aragoa*, Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grasspáramo and the high proportions suggest the mountains above ~3500 m were covered by superpáramo.

Period 18 (54.64-51.76 ka); zone Fq-9C-18R

This period reflects a significant warm climatic excursion and the forest belt was positioned around Lake Fúquene again. The floristic composition of the forest that returned during this period is remarkably similar to the forest that disappeared at the end of period 16. Minor differences are that *Miconia*, other Melastomataceae, *Myrsine*, and *Thalictrum* became a stable component of the Andean forest. Also *Quercus* and *Vallea*
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returned as more stable and dominant components than before.

During this period AP values show two peaks of ~65% and later ~70% indicating the UFL reached ~3000 m and later increased up to ~3100 elevation. Proportions of *Alnus* and *Myrica* are higher indicating swamp forest was present on wet soils at the borders of the lake. As lake levels were high (see aquatic pollen record) the surface of *Alnus* forest was limited. Andean forest consisted mainly of *Clethra, Hedyosmum, Miconia*, other Melastomataceae, *Podocarpus, Myrsine, Podocarpus, Quercus, Vallea*, and *Weinmania*. There were smaller contributions of a suite of taxa such as *Clethra, Daphnopsis, Drimys, Eugenia*, other Myrtaceae, *Ilex, Juglans*, Proteaceae, *Styloceras, Symplocos*, and *Thalictrum* showing a diverse montane forest. *Dodonaea*, Chenopodiaceae and *Borreria* show significant values indicating dry environmental conditions and erosion in areas with a poor vegetation cover. Indeed the high turnover of vegetation within short intervals of time must have caused high levels of vegetation change. This short excursion reaching high interstadal temperatures must have caused also much dynamics at lower elevations and high values of *Cecropia* supports this view. Subandean forest taxa show high values and these trees probably used abundant presence of *Quercus* forest to reach higher elevations. Subpáramo taxa reached ~10-15% showing this vegetation had a limited altitudinal distribution between 3000-3100 m and 3200-3300 m elevation. *Polylepis* and Asteraceae were dominant and Ericaceae and *Hypericum* less common. The grasspáramo occurred above ~3100-3300 m. Apart from Poaceae, the grasspáramo included *Aragoa, Caryophyllaceae, Draba, Gentiana, Geranium, Lycopodium, Plantago* and *Valeriana*.

Period 19 (51.72-37.51 ka); zone Fq-9C-19R

During this period the UFL shifted further down slope and the lake was surrounded by cool subpáramo vegetation, during some intervals by even colder grasspáramo vegetation. Cold climatic conditions prevailed in combination with high lake levels suggesting low evaporation. For the first time in the record dwarf forest of *Polylepis* was very abundant around the UFL and the floral composition of these forests had changed significantly. Isolated patches of *Polylepis* forest may occur in the páramo up to some 800 m above the UFL. *Quercus* forest was abundant in the Andean forest belt. A high representation of selected subandean forest taxa at times strongly suggests that oak forest facilitated these species to reach higher elevations. These trees were able to extend their altitudinal range under specific conditions. *Daphnopsis* occurs today between 2400 and 2900 m elevation. Such conditions prevailed during the periods 13 and 14. However, *Daphnopsis* was not a significant element of the Andean forest during that time. During the periods 19 and 20, *Daphnopsis* was more common suggesting the uppermost Andean forests became richer in *Daphnopsis* during generally cold climatic conditions. Today the tree *Vallea* is characteristic of the uppermost Andean forest and the lower subpáramo. During periods 18 to 20 successive peaks of *Vallea* occurred when the UFL was at elevations between 2800 and 2400 m elevation, which perfectly supports the modern altitudinal range. In conclusion, the altitudinal range of individual trees may be similar as today, or differ substantiating the opinion that forest compositions are
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subject to change. However, the concept of existing main altitudinal forest belts is supported as changes in species composition and altitudinal range are limited.

During part 1 AP values show a minimum of 20% indicating the UFL lowered to ~2300 m elevation. Values of *Alnus* are below 20% and again show that 20% representation reflects a general background effect when *Alnus* forest is not present in the lake basin. Uppermost Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Myrsine*, *Podocarpus*, *Quercus*, *Thalictrum*, and *Weinmannia*. There were smaller contributions of *Clethra*, *Daphnopsis*, *Drimsys*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, *Miconia*, *Styloceras*, *Symplocos*, and *Vallea*. Values of 40-60% of subáramo taxa point to a wide subáramo belt between 2300 and 2700 m: the lake was located in the centre of the subáramo belt. *Polylepis* was more dominant than ever before in this record. Asteraceae shrub was co-dominant and *Hypericum* was more common than Ericaceae. The grassáramo occurred above 2700 m. Apart from Poaceae, the grassáramo consisted of a suite of herbs such as Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Lysipomia*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grassáramo and the high proportions suggest the mountains above ~3400 m were covered by superáramo.

During part 2 AP values show a maximum with values of 40-45% indicating the UFL reached 2550-2600 m elevation. At the start of this interval the UFL passed the elevation of the lake allowing *Alnus* to develop swamp forest around the lake. Indeed, the pollen record shows here a distinct and rapid increase from background values of below 20% to values indicating presence (~25%). Again, the record shows the sensitivity and reliability of *Alnus* to identify the moments the UFL is passing the 2550 m elevation level. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, other Melastomataceae, *Myrsine*, *Podocarpus*, and *Quercus*. There were smaller contributions of *Clethra*, *Daphnopsis*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, Proteaceae, *Thalictrum*, *Vallea*, and *Weinmannia*. Values of 20-30% of subáramo taxa dominated by *Polylepis* and Asteraceae, and less Ericaceae and *Hypericum*, indicates this vegetation belt occurred between 2550 m and ~2800 m elevation. The grassáramo occurred above 2800 m. Apart from Poaceae, the grassáramo consisted of a suite of herbs such as *Aragoa*, Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Lysipomia*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* are representatives of the uppermost grassáramo and the high proportions suggest the mountains above ~3500 m were covered by superáramo.

During part 3 AP values lower to a minimum of ~25% indicating the UFL lowered to 2300 m elevation. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Myrica*, *Podocarpus*, and *Quercus*. There were smaller contributions of *Clethra*, *Daphnopsis*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, *Monnina*, *Myrsine*, Proteaceae, *Styloceras*, *Symlocos*, *Thalictrum*, *Vallea*, and *Weinmannia*. Values of 25-35% of subáramo taxa dominated by Asteraceae and *Polylepis* indicate this vegetation belt occurred between ~2300 m and ~2600 m elevation. The grassáramo occurred above 2600 m. Apart from Poaceae, the grassáramo consisted of a suite of herbs such as Caryophyllaceae, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. *Lycopodium* is representative of the uppermost grassáramo and the high proportions suggest the mountains above ~3300 m were covered by superáramo.
During part 4 AP values show a maximum of 53% indicating the UFL reached 2700 m elevation. Proportions of *Alnus* and *Myrica* indicate swamp forest was present on wet soils at the borders of the lake. As lake levels were high (see aquatic pollen record) the surface of *Alnus* forest was limited. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, other Melastomataceae, *Myrsine*, *Podocarpus*, and *Quercus*. There were smaller contributions of *Clethra*, *Daphnopsis*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, other Melastomataceae, *Styloceras*, *Symplocos*, *Vallea*, and *Weinmannia*. Trees of subandean forest, *Cecropia* and *Acalypha* in particular, reached relatively high elevations. Presence of significant *Cecropia* and *Dodonaea* both point to a high turnover of forest, which is in harmony with the rapid shifts of forest along the mountain slopes during this short interval with higher temperatures. A value of ~25% of subpáramo taxa dominated by *Polylepis* and Asteraceae indicates this vegetation belt occurred between 2700 m and 3000 m elevation. The grasspáramo occurred above 3000 m. Apart from Poaceae, the grasspáramo consisted of a suite of herbs such as Caryophyllaceae, *Draba*, *Geranium*, *Lycopodium*, *Plantago*, and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grasspáramo and the high proportions suggest the mountains above ~3600 m were covered by superpáramo.

During part 5 AP values show a maximum of 45% indicating the UFL reached 2600 m elevation. A gap in the core obliterates mainly the first part of this interval. Potentially *Alnus* may form swamp forest but lake levels were very high allowing little space to develop swamp forest around the lake. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, other Melastomataceae, *Myrsine*, *Podocarpus*, *Quercus*, *Vallea*, and *Weinmannia*. There were smaller contributions of *Clethra*, *Daphnopsis*, *Eugenia*, other Myrtaceae, *Ilex*, *Juglans*, Proteaceae, *Styloceras*, *Symplocos*, and *Thalictrum*. Trees of subandean forest reached relatively high elevations assumedly using *Quercus* forest as a corridor. Values of ~25-40% of subpáramo taxa dominated by *Polylepis* and Asteraceae indicate that this vegetation belt occurred between 2600 m and ~2900 m elevation. The grasspáramo occurred above 2900 m. Apart from Poaceae, the grasspáramo consisted of a suite of herbs such as Caryophyllaceae, *Draba*, *Gentiana*, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. *Lycopodium* and *Draba* in particular are representatives of the uppermost grasspáramo and the high proportions suggest the mountains above ~3600 m were covered by superpáramo.

During part 6 AP values lower from ~40% at the start to ~30% at the end of this interval pointing to an UFL shifting down slope from the level of the lake (2550 m) to ~2400 m elevation. Andean forest consisted mainly of *Hedyosmum*, *Miconia*, *Myrsine*, *Podocarpus*, *Quercus*, *Vallea*, and *Weinmannia*. There were smaller contributions of *Clethra*, *Croton*, *Daphnopsis*, *Drimys*, *Eugenia*, other Myrtaceae, *Gaiaedendron*, *Ilex*, *Juglans*, other Melastomataceae, *Mannina*, Proteaceae, *Styloceras*, *Symplocos*, and *Thalictrum*. Trees of subandean forest reached relatively high elevations. Presence of *Dodonaea* and Chenopodiaceae are indicative of dry vegetation in the rain shadow areas of the basin. Values of 40-50% of subpáramo taxa dominated by *Polylepis* and Asteraceae, and lower proportions of Ericaceae and *Hypericum* indicates this vegetation belt was very wide and occurred between 2550-2900 m at the start and between 2400-2800 m at the end of this interval. The grasspáramo occurred above 2800-2900 m. Apart from Poaceae, the grasspáramo consisted of Caryophyllaceae, *Geranium*, *Lycopodium*, *Plantago* and *Valeriana*. 

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During part 7 three peaks of AP values of 45% show the UFL reached ~2600 m repeatedly. A gap in the core followed and at the end a 40% peak in AP shows the UFL reached the lake at 2550 m. Andean forest consisted mainly of *Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Vallea,* and *Weinmannia.* There were smaller contributions of *Clethra, Croton, Daphnopsis, Drimys, Eugenia,* other Myrtaceae, *Gaiadendron, Ilex, Juglans,* other Melastomataceae, *Monnina,* Proteaceae, *Styloceras, Symplocos,* and *Thalictrum.* Trees of subandean forest reached relatively high elevations. Presence of *Dodonaea* and Chenopodiaceae are indicative of dry vegetation in the rain shadow areas of the basin. Values of 30-40% of subpáramo taxa dominated by *Polylepis* and Asteraceae, and lower proportions of Ericaceae and *Hypericum* indicates this vegetation belt extended from 2600-2900 m. The grasspáramo occurred from 2900 to 3600 m elevation. Apart from Poaceae, the grasspáramo consisted of *Aragoa, Caryophyllaceae, Geranium, Lycopodium, Plantago* and *Valeriana.*

Period 20 (37.47-26.97 ka); zone Fq-9C-20R

During this period the UFL migrated to lower elevations and repeatedly the lake was surrounded by grasspáramo. Significant representation of subandean forest taxa and *Alnus* suggest that in contrast to shrubby subpáramo, open grasspáramo vegetation is more prone to supply of allochtonous pollen by upslpe winds. Higher proportions of Chenopodiaceae indicate climatic conditions were drier than before.

During part 1 AP values start at ~30% and show two peaks of ~45% indicating the UFL started at ~2400 m and reached ~2600 m elevation twice. Also the record of *Alnus* shows two peaks with values above background levels showing *Alnus* carr developed around the lake twice for a short while only. Andean forest consisted mainly of *Hedyosmum, Miconia, Myrsine, Podocarpus, Quercus, Vallea,* and *Weinmannia.* There were smaller contributions of *Clethra, Daphnopsis, Eugenia,* other Myrtaceae, *Ilex, Juglans,* other Melastomataceae, Proteaceae, *Styloceras, Symplocos,* and *Thalictrum.* Presence of *Dodonaea,* Chenopodiaceae, and *Borreria* shows there was significant dry vegetation in the rain shadow areas of the lake basin and *Dodonaea* also points to areas with superficial erosion. Values of 20-25% of subpáramo taxa dominated by *Polylepis* and Asteraceae, and lower proportions of Ericaceae and *Hypericum* indicates this vegetation belt extended at the start from ~2400-2700 m and during the peaks from ~2600-2900 m elevation. During the peaks the grasspáramo occurred from 2900 to 3700 m elevation and the mountain tops were covered by superpáramo vegetation. Apart from Poaceae, the grasspáramo consisted of *Caryophyllaceae, Geranium, Lycopodium, Plantago* and *Valeriana.*

During part 2 AP values show three peaks of ~60%, ~55, and ~50% indicating the UFL peaked at 2900 m, 2800 m, and 2700 m respectively. In between AP show 42-45% indicating the UFL was at 2550-2600 m elevation. The record of *Alnus* shows continuous presence of *Alnus* carr substantiating the interpretation that the UFL had not passed to elevations below the lake.
Andean forest consisted mainly of *Hedyosmum, Miconia,* other Melastomataceae, *Myrsine, Podocarpus, Quercus,* and *Weinmannia.* There were smaller contributions of *Clethra, Croton, Daphnopsis, Drimys, Eugenia,* other Myrtaceae, *Gaiadendron, Ilex,*
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_Juglans_, other Melastomataceae, _Monnina_, Proteaceae, _Styloceras_, _Symlocos_, _Thalictrum_, and _Vallea_. Presence of _Dodonaea_, Chenopodiaceae, and _Borreria_ shows there was significant dry vegetation in the rain shadow areas of the lake basin and _Dodonaea_ also points to areas with superficial erosion. Values of ~20% of subpáramo taxa dominated by _Polylepis_ and Asteraceae, and lower proportions of Ericaceae and _Hypericum_ indicates subpáramo vegetation extended over some 200 m altitudinally and reached during this interval elevations of 3000–3100 m maximally. The grasspáramo extended up to ~3800 m and covered the mountains around the lake up to the tops. Apart from Poaceae, the grasspáramo consisted of Caryophyllaceae, _Draba_, _Geranium_, _Lycopodium_, _Plantago_ and _Valeriana_. Subpáramo and grasspáramo were poor in shrub (low presence of Ericaceae, _Hypericum, Aragoa_) but herbs were present in a suite of taxa such as _Draba_, _Gentiana_, _Geranium_, _Lycopodium_, _Plantago_ and _Valeriana_. Presence of _Dodonaea_, Chenopodiaceae, and _Borreria_ shows there was significant dry vegetation in the rain shadow areas of the lake basin. Lake levels were high (see aquatic vegetation diagram) and the grain-size distributions show quiet sedimentary regimes. The slopes around the lake were covered by _Polylepis_ dwarf trees and asteraceous shrub and on wet soils around the lake shores _Plantago_ formed cushion bog vegetation. The abundant vegetation cover around the lake explains the high values of organic matter during this interval.

During part 3 AP values show 32–35% most of the time with a peak of 40% indicating the UFL was at 2450–2500 m most of the time with a short excursion in which the lake was reached closely. Andean forest consisted mainly of _Hedyosmum_, _Miconia_, _Myrsine_, _Podocarpus_, and _Quercus_. There were smaller contributions of _Clethra_, _Daphnopsis_, _Drimys_, _Eugenia_, other Myrtaceae, _Ilex_, _Juglans_, other Melastomataceae, _Monnina_, Proteaceae, _Styloceras_, _Symlocos_, _Thalictrum_, _Vallea_, and _Weinmannia_. Presence of _Dodonaea_, Chenopodiaceae, and _Borreria_ shows there was significant dry vegetation in the rain shadow areas of the lake basin. Values of ~15% of subpáramo taxa dominated by _Polylepis_ and Asteraceae, and lower proportions of Ericaceae and _Hypericum_ indicates subpáramo vegetation extended over a narrow altitudinal interval of some 100–200 m and reached elevations of 2600–2700 m maximally during this interval. The grasspáramo extended up to ~3400 m. Subpáramo and grasspáramo were poor in shrub (low presence of Ericaceae, _Hypericum, Aragoa_) but herbs were present in a suite of taxa such as Caryophyllaceae, _Draba_, _Gentiana_, _Geranium_, _Lycopodium_, _Plantago_, and _Valeriana_. Presence of _Dodonaea_, Chenopodiaceae, and _Borreria_ shows there was significant dry vegetation in the rain shadow areas of the lake basin.

During part 4 AP values reach ~45% but a significant gap in the record does not allow to conclude on the number of peaks during this interval. The UFL shifted around 2600 m. Andean forest consisted mainly of _Hedyosmum_, _Miconia_, _Myrsine_, _Podocarpus_, _Quercus_, and _Weinmannia_. There were smaller contributions of _Clethra_, _Daphnopsis_, _Drimys_, _Eugenia_, other Myrtaceae, _Juglans_, other Melastomataceae, Proteaceae, _Styloceras_, _Thalictrum_, and _Vallea_. Absence of _Dodonaea_, Chenopodiaceae, and _Borreria_ in this interval suggests wetter climatic conditions and this is supported by higher lake levels (see aquatic diagram). Values of ~15–20% of subpáramo taxa dominated by _Polylepis_ and Asteraceae, and lower proportions of Ericaceae and _Hypericum_ indicates subpáramo vegetation extended over some 300 m altitudinally and reached elevations of 2900 m maximally during this interval. The grasspáramo extended from 2900–3600 m.
Apart from Poaceae, the grasspáramo was poor in species and consisted of Caryophyllaceae, Lycopodium, Plantago and Valeriana. During part 5 AP values reach ~40% twice indicating the UFL reached the lake twice at very close distance. Andean forest consisted mainly of Hedyosmum, Miconia, other Melastomataceae, Myrsine, Podocarpus, Quercus, and Weinmannia. There were smaller contributions of a suite of trees such as Clethra, Croton, Daphnopsis, Drimys, Eugenia, other Myrtaceae, Gaiadendron, Ilex, Juglans, other Melastomataceae, Monnina, Proteaceae, Sapium, Styloceras, Thalictrum, and Vallea. Presence of Chenopodiaceae, Dodonaea, and Borreria shows there was dry vegetation in the rain shadow areas of the lake basin. Heliophyloous Croton points to open forest. Values of 10-15% of subpáramo taxa dominated by Polylepis and Asteraceae, and lower proportions of Ericaceae and Hypericum point to a narrow belt with subpáramo vegetation between 2550 m and 2700 m elevation. The grasspáramo extended up to ~3400 m. Apart from Poaceae, the grasspáramo consisted of Aragoa, Caryophyllaceae, Draba, Geranium, Lycopodium, Plantago and Valeriana.

5. Discussion

5.1 Age model uncertainties

Although the age model of the new Fq-9C record is robust at orbital time scales we assess here the uncertainties that are left at millennium time scales. The 9.07 m and 22.65 m peaks in the power spectra of the AP% time series were assigned to the obliquity and eccentricity components of astronomical forcing, respectively (Groot et al., 2011). The 41-kyr cycles were filtered from the AP% record and the standard marine benthic LR04 δ¹⁸O record (Lisiecki and Raymo, 2005) and both time series were subsequently tuned. Thus, the tuning procedure occurred in a linear time domain and therefore, the depth vs. age graph shows a linear relationship. It is beyond discussion that a linear depth vs. time relationship reflects an artefact of the cyclostratigraphy method to develop the age model (Blaauw, 2012). However, many sedimentary basins in the Colombian Andes have shown independent evidence that Pleistocene sediment infill was close to linear. We refer here to the upper 250 m of sediments in the Bogotá basin (Torres et al., 2005, Torres et al., in review) reflecting the last million years and the 12 m thick sediments of the La Cocha lake (González-Carranza et al., 2012) reflecting the last 14 cal ka. Downcore changes in the composition of GSDs (Vriend et al., 2012) in between the 13 tie points of the tuning procedure (Groot et al., 2011) make varying sediment accumulation rates plausible. This aspect needs further exploration and the time series of GSDs and geochemical elements (Bogotá-A et al., 2011) may provide interesting clues.

5.2 Forest dynamics and climate reconstruction

Our new record shows with unprecedented temporal resolution the dynamic history of montane forest. Nearly all taxa show records of significantly changing proportions. Among the Andean forest taxa, least expressive records are shown by Croton, Gaiadendron, Gunnera, Juglans, Monnina, Sapium, and Styloceras. Among the páramo taxa,
least expressive taxa are Asteraceae liguliflorae, Draba, Gentiana, Lysipomia and Puya. Although all these taxa do have a sufficiently characteristic ecological range (Fig. 2), which was the reason these taxa were selected to be analysed, their pollen syndromes are less suitable to reach records with sufficient representation. Such taxa should have a substantial indicator value to justify their incorporation in the selected suite of analysed pollen taxa. Indeed, Croton, Gunnera and Momina (heliophytes, indicative of open forest), and Draba (a common element of the superpáramo) have a high indicator value even when proportions are low. The remainder of taxa mentioned have insufficient representation and potentially can be neglected in a future study.

For the present study understanding of the ecological envelopes was optimized (Fig. 2) on the basis of literature and abundant personal observations reported by A.M. Cleef (2010). Potentially a next step in giving ecological ranges more accuracy is possible when the method shown by Punyasena et al. (2011) is followed. Using herbarium records and published physiological data taxa specific altitudinal and temperature distributions can be shown with even more accuracy and mean values can be calculated. In this way, potentially also relationships with the altitude of cloud forest (reflecting the zone of atmospheric condensation) and the altitudinal distribution of night frost (an important physiological factor constraining plant distributions) can be assessed. This method to quantitatively infer past temperatures opens a new approach which needs to be tested as potentially temperature reconstructions based on multiple individual taxa are more robust than estimates based on AP%.

The most striking feature during Pleniglacial time (MIS 3) is the expansion of Polylepis forest between ~51 ka and ~31 ka when cold and wet conditions prevailed. This period is found in all pollen records from Lake Fúquene (Bogotá-A et al., 2011a) and can be used on a regional scale as a biostratigraphical marker.

The interpretation of long pollen records in terms of environmental change and climate conditions is challenging as interpretations are based on the assumption that modern ecological envelopes of individual plant taxa are in balance with current environmental and climatic conditions and, therefore, are able to serve as a reference. Pollen-based plant associations that deviate from modern settings are considered as a non-analog (e.g. Urrego et al., 2009; Cárdenas et al., 2011). High-resolution pollen records, with a resolution better than the average life time of the trees making up the forest, are needed to address this important issue. For the northern Andes two high-resolution pollen records became available that shed new light on this discussion. The pollen record of lake La Cocha (1°N, 77°W, Eastern Cordillera, 2780 m elevation, 12 m core depth reflecting the last 14.085 cal ka, 550 pollen samples, 25 yr temporal resolution; González-Carranza et al., 2012) shows a trend of upslope migration of the UFL from ~11 to ~3 cal ka and concomitant species re-organisations before a quasi-stable forest composition is reached after ~3 cal ka. Events of rapid temperature increase are followed by very low representation, or even absence of subpáramo vegetation during some two centuries suggesting subpáramo shrub has potentially a lower migration speed than montane forest. Such a temporary loss of a biome may repeat under current conditions of rapid anthropogenic warming. The pollen record of the Llano Grande mire (6°N, 76°W,
Chapter 4

Western Cordillera, 3460 m elevation, 7.5 m core depth reflecting the last 17.3 ka, 136 pollen samples, 120 yr temporal resolution; Velásquez and Hooghiemstra, in review) shows at the Lateglacial-Holocene transition a rapid upslope shift of the UFL of ~ 700 m in ~200 years and plant assemblages show a continuous re-organisation during Holocene time, never reaching a quasi-stable forest composition. Both records show various tracks of forest encroachment after the last glacial: from a rapid upslope migration, mainly driven by MAT in the Western Cordillera, to a very slow upslope migration potentially driven by MAT and MAP on the Amazonian flank of the Eastern Cordillera. In addition, model experiments showed that changes in atmospheric pCO2 reflect also a relevant driver of temperature change (Groot et al., 2011).

Temporal changes in the organisation of plant communities is debated for a long time (Whittaker, (1962), Shipley and Keddy (1987) and references therein; Bach and Gradstein, 2011). Non-analog plant associations may occur for several reasons, such as effects of immigration and disappearance (extinction) of taxa in the study area (Hooghiemstra, 1984; Torres et al., in review). Here, we hypothesize that non-analog vegetation associations may reflect also transitional phases and that plant associations may reach after each period of environmental change finally a similar composition which is quasi stable at long Pleistocene time scales. Although this hypothesis needs robust testing the present level of data analysis shows that forest associations are relatively stable during late Pleistocene times. However, the new high-resolution pollen records La Cocha1 (González-Carranza et al., 2012), Llano Grande1 (Velásquez and Hooghiemstra, in review), and Fúquene-9C (Bogotá-A et al., this volume; and the present paper) suggest that that quasi-stable environmental conditions are lasting for half a millennium at the maximum (Table 5) hardly allowing montane forest to reach stable conditions. In addition, one may wonder if (undisturbed) present-day forest compositions reflect a quasi-stable association and it is plausible that modern forest compositions are not the adequate reference to assess the analog or non-analog status of past forest associations. In conclusion, we challenge discussions about the analog or non-analog status of pollen-based forest associations and we wonder how such plant associations of deviating species composition can meaningfully fuel the debate on the potential impact of global change. We expect that a more quantitative analysis of the present data set is needed to stimulate this discussion with more meaningful evidence.

5.4 Millennial-scale environmental variability

The analysis of biotic (pollen, LOI) and abiotic (GSDs) proxies allows to assess how climate-driven vegetation change in the Eastern Cordillera was registered in a sediment archive that itself is also the product of a changing abiotic environment (Fig. 7).

The main pollen diagram of the regional vegetation (Fig. 7a) shows a synthesis of the changing vegetation distribution along the altitudinal gradient. The record of *Alnus* is shown (Fig. 7b) because of its important role in the reconstruction with respect to its ecological envelope (potentially contributing to the regional and local vegetation), its climatic indicator value (shows the moments the UFL reached the elevation of the lake), and its pollen syndrome (the first 20% representation is background noise). Changes in
**Table 5. Main characteristics of the regional subzones pollen record Fq-9C for the period from 130 to 27 ka.**

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<th>Subzone</th>
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<th>Age period (ka)</th>
<th>Duration</th>
<th>Fq-9C Interval</th>
<th>Age period</th>
<th>Duration</th>
<th>Time C - W (kyr)</th>
<th>Time WW (kyr)</th>
<th>Time W - C (kyr)</th>
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**Table 5 continued...**
### Chapter 4

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Fig. 7. Summary of environmental change in the Fúquene Basin.
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the UFL position (Fig. 7c) and inferred temperature change (Fig. 7d) are shown. For the studied period the average duration of quasi stable environmental conditions is \( \sim 2.8 \text{ kyr} \), which is similar to the average duration of such period in the interval of 284-130 ka (Bogotá-A et al., 2011b, this volume).

Given the chronological uncertainties in between the tie points of the tuning procedure the present record shows an average temporal resolution of 43 yr. This allows to assess climate variability at millennial to centennial time scales. In terrestrial records millennial-scale climate variability is well known from the series of cool stadials and mild interstadials (e.g. Van der Hammen et al., 1971) and in Greenland ice core records millennial-scale climate variability is punctuated by Dansgaard-Oeschger (DO) events (Oeschger et al., 1984; Dansgaard et al., 1993). For the period from 120 to 10 ka 25 DO-cycles are recognized. In Greenland each cycle includes (1) a period of gradual cooling of \( \sim 5-10^\circ \text{C} \) lasting for \( \sim 600 \) to 2000 years, (2) a subsequent more rapid temperature decline of \( \sim 5 \) to \( 10^\circ \text{C} \) into peak stadial conditions, lasting another 300 to 700 years and, (3) a very abrupt warming of \( \sim 3 \) to \( 5^\circ \text{C} \) per century returning the cycle to interstadial conditions.

As the temperature amplitude over a full glacial-interglacial cycle in Greenland is over \( 30^\circ \text{C} \) and in the northern Andes around 8 to 9°C (Van ‘t Veer and Hooghiemstra, 2000) values of temperature change differ but the signature of climate change is comparable.

The Fq-9C record shows 18 millennial-scale cycles between 130 and 27 ka (Fig. 7; Table 5), which were related to Greenland DO-cycles (NGRIP Community Members, 2004; Groot et al., 2011). Poorly visible and missing cycles are plausibly related to the fact that the pollen record covers \( \sim 90\% \) of the sedimentary archive (Groot et al., 2011). DO cycles 4, 5, 15, 16, 17 and 22 are indistinctive and DO cycles 8, 12, 14, 19, 20, 26, 27 and 28 are most prominent. Most cycles lasted for 1 to 4 kyr with an average duration of 2.4 kyr. Cycles of longer duration (> 4 kyr) mostly show a long period of warming up extending over more than 2 kyr in cycles 18 and 8. Cycles 26, 24 and 14 include a hiatus and are disqualified to assess durations of time. The cooling part of the millennial-scale cycles had an average duration of \( \sim 700 \text{ yr} \). Some cycles show a long period of cooling: 3 kyr in cycle 26, 1.9 kyr in cycle 18, and 1.4 kyr in cycle 13. The cycles 28, 10, 8, and 6 show a fast cooling with a duration between 90 to 180 yr. Millenium-scale cycles have been associated with synchronic changes in strength and latitudinal migration of the ITCZ and the monsoon systems at low latitudes (Peterson et al., 2000; Wang et al., 2008).

The local vegetation (Fig. 7e) shows changing proportions of aquatic vegetation dependent on water depth. The changing proportions of GSDs (Fig. 7f) shows variations in the distance to the sediment source area (clay: distal; sand: proximal), the energy level of sediment transport (clay: low energetic level; sand: high energetic level), and water depth (clay: deep water environment; sand: shallow water environment / peat). The ratio between the proportions of shallow and deep water vegetation is an expression of water depth (Fig. 7g) and changing water levels are summarized in Fig. 7h. These relationships were explored in Vriend et al. (2012). The four sediment categories explain 70% of the observed variation in grain size classes allowing to infer specific depositional and environmental settings. Most of the unexplained variability in GSDs is located in the
coarse sediment fraction. The relative warm events of DO cycles (Fig. 7a) seem to coincide systematically with events of low water levels; we consider temperature-related changes in evaporation as the driving factor of these lake level variations. On its turn, many low water level events coincide (Figs. 7e, 7f) with abundant presence of peat (cycles 27, 26, 21, 14, 13, 9, 8, 7, and 6) or coarse sediments including sands and coarse silts (cycles 28, 24, 21, 20, 19, 18, 14, 13, 11, 10, 8, 7, and 6). Warm excursions are most clearly registered in the pollen record as warm vegetation has the highest degree of pollen identification. However, the coinciding larger coarse sediment fraction is less explained. Although cold excursions in the pollen record are less precisely registered as the representative vegetation is to a significant degree identified to the family level only (Poaceae, Asteraceae, Ericaceae), the coinciding fine sediment fractions are best explained in terms of environmental settings. Only in DO-cycle 9 the warm excursion coincides with fine grained sediments. Additional data analysis is needed to further explore relationships quantitatively.

Lowest water levels and smallest lake surface are observed during the last interglacial (MIS 5) allowing abundant sediment accumulation in a swampy environment in the northern part of the basin, as is the case today. Thus, during interglacial times the sediment plug in the northern part of the basin is gaining elevation over an area as large as swamps occur, apparently keeping the plug robust enough to keep water in the basin.

6. Conclusions

Among the most important results of this new pollen record is the improved understanding of forest dynamics. Montane forest seems in a delicate balance with climate allowing rapid changes in altitudinal distributions and species composition. Trees with pioneer qualities migrate in the forefront when montane forest moves upslope. So far, the important question is unanswered if montane forest again reaches the quasi-stable species composition it had before the period of rapid transition. Evidence from new high-resolution Holocene pollen records is contradictory. Analysing this type of forest dynamics requires more advanced quantitative data analysis and such aims form a challenge for new research.

This multi-proxy record shows a hitherto unknown level of dynamics in the biotic and abiotic compartments of the lake basin during the last interglacial (MIS 5)-glacial (MIS 4-2) cycle. Tropical montane forest appears to be in a sensitive balance with climatic conditions allowing for rapid changes in the altitudinal distribution and species composition. This conclusion has important implications for current and future anthropogenic driven climate change. At longer time-scales vegetation change is mainly driven by astronomical forcing. Regional vegetation change is driven by obliquity (41 kyr cycle) and eccentricity (100 kyr cycle). Aquatic vegetation is mainly driven by obliquity and precession (21 kyr cycle). This difference hints to regional mechanisms more related to temperature and $pCO_2$, and local mechanisms more related to precipitation and temperature-driven evaporation. Millennial-scale temperature oscillations in the northern Andes show the signature of millennial-scale climate variability in Greenland ice-cores. In our new record DO cycles 28, 27, 26, 20, 19, 14, 12 and 8 are most prominently reflected. Cycles have a duration varying from ~1.5 to 3 kyr with an average of 2.7 kyr.
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Combined information from distinct categories of GSDs and aquatic vegetation improves the robustness of water level reconstructions. In the pollen record, periods with high temperatures (and relatively low water values) are most accurately reflected, but these periods coincide in the GSD record with highest abundance of course grained sediments including the highest proportion of unexplained variability. We found that temperature shifts up to 2 to 3°C per 100 years occurred frequently. Rapid environmental change allows trees with pioneer qualities to migrate faster than late-successional species explaining changes in plant associations. Although this aspect is yet insufficiently analysed it seems that non-analog vegetation may reflect such temporary stages in a dynamic forest history. Events of rapid temperature increase are followed by very low representation, or even absence of subpáramo vegetation during some two centuries suggesting subpáramo shrub has potentially a lower migration speed than montane forest. Such a temporary loss of a biome may repeat under current conditions of rapid anthropogenic warming. The present record gives ecologists, paleo-ecologists, and climate modellers another paleo-benchmark against which to test their hypothesis and models. In the present study the high relevance of fine-resolution pollen analysis contrasts much with the little developed methodology to produce the data. The fast methodologies developed in the analyses of GSDs, XRF-based geochemical analysis, and stable isotope analysis should encourage palynologists to improve their methods dramatically.

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