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LATE GLACIAL AND HOLOCENE ENVIRONMENTAL CHANGE INFERRED FROM THE PÁRAMO OF CAJANUMA IN THE PODOCARPUS NATIONAL PARK, SOUTHERN ECUADOR

Cambios ambientales durante el Último Glacial y Holoceno inferidos del páramo de Cajanuma en el Parque Nacional Podocarpus, sur del Ecuador

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ABSTRACT

To reconstruct the environmental history including vegetation, fire and climate dynamics, from the Cajanuma valley area (3285 m elevation) in the Podocarpus National Park, southern Ecuador, we address the following major research question: (1) How did the mountain vegetation developed during the late Glacial and Holocene? (2) Did fire played an important control on the vegetation change and was it natural or of anthropogenic origin?. Palaeoenvironmental changes were investigated using multiple proxies such as pollen, spores, charcoal analyses and radiocarbon dating. Pollen data indicated that during the late Glacial and transition to the early Holocene (ca. 16 000–10 500 cal yr BP) herb páramo was the main vegetation type around the study area, while subpáramo and mountain rainforest were scarcely represented. The early and mid-Holocene (ca. 10 500 to 5600 cal yr BP) is marked by high abundance of páramo during the early Holocene followed by a slight expansion of mountain forest during the mid-Holocene. During the mid- to late Holocene (ca. 5600–1200 cal yr BP) there is a significant presence of páramo and subpáramo while Lower Mountain Forest decreased substantially, although, Upper Mountain Forest remained relatively stable during this period. The late Holocene, from ca. 1200 cal yr BP to present, was characterized by páramo; however, mountain forest and subpáramo presented significantly abundance compared to the previous periods. Fires became frequent since the late Holocene. The marked increased local and regional fire intensity during the wetter late Holocene strongly suggests that were of anthropogenic origin. During the late Glacial and early Holocene, the upper forest line was located at low elevations; but shifted slightly upslope to higher elevations during the mid-Holocene.

Key words. Palaeoecology, páramo, late Glacial, Holocene, climate and fire dynamics.

RESUMEN

Para reconstruir la historia ambiental, incluyendo la dinámica de la vegetación, el fuego y el clima, del área del valle de Cajanuma (3.285 m de altitud) en el Parque Nacional Podocarpus, sur del Ecuador, nos planteamos las siguientes preguntas de investigación: (1) ¿Cómo fue el desarrollo de la vegetación de montaña durante el último glacial y el Holoceno? (2) ¿Acaso el fuego jugó un control importante sobre el cambio de la vegetación y fue éste de tipo natural o de origen antropogénico? Se investigaron cambios paleoambientales mediante múltiples proxy tales como polen, esporas, los análisis de carbón y la datación por radiocarbono. Datos del polen resaltan que durante la parte final del último glacial y la transición al Holoceno temprano (*ca.* 16,000-10,500 cal yr BP) el páramo herbáceo fue el principal tipo de vegetación alrededor de la zona de estudio, mientras que el subpáramo y el bosque montano se encuentran con una baja representación. El Holoceno temprano y medio (*ca.* 10.500 a 5.600 años cal BP) se encuentran marcados por la alta abundancia de páramo, durante el Holoceno temprano, seguido de una ligera expansión del bosque montano, durante el Holoceno medio. Durante el Holoceno medio y tardío (*ca.* 5.600-1.200 años cal BP) hay una presencia significativa de páramo y subpáramo mientras que el bosque montano bajo disminuyó sustancialmente. Sin embargo, el bosque montano alto se mantuvo relativamente estable durante este período. El Holoceno tardío (*ca.* 1200 años AP hasta la actualidad) se caracterizó por vegetación de páramo, aunque, el bosque montano y el subpáramo presentaron una abundancia significativa en comparación con los períodos anteriores. Los incendios se hicieron frecuentes a partir del Holoceno tardío. El aumento marcado de la intensidad del fuego local y regional durante Holoceno tardío, período húmedo, sugiere fuertemente que eran de origen antropogénico. Durante el Último Glacial y Holoceno temprano, la línea superior del bosque se encontró en elevaciones bajas, ésta subió a elevaciones más altas durante el Holoceno medio.

Palabras clave. Paleoecología, páramo, Último Glacial, Holoceno, dinámica del clima y el fuego.

INTRODUCTION

The tropical northern Andes are among the hot spots of global vascular plant diversity due to their high structural and geological diversity. Especially, the Ecuadorian Andes harbour the most species rich ecosystems on earth (Barthlott *et al*. 2005; Rangel 2006). Among these bioma, the most characteristic one is páramo, due to its floristically unique, which is found above the upper forest line. The páramo is thought to have expanded downslope, while extensive burning and grazing prevented forest recovery. Some researchers suggest that the grass páramo below 4300 – 4100 m represents, at least partially, secondary vegetation in formerly forested areas (Lægaard 1992). It is especially subject to overgrazing, burning and cultivation, which leads to reduction of biodiversity (Podwojewski *et al*. 2002). Moreover, Ecuador currently suffers the highest deforestation rate of 198 000 ha year^{-1} between 1990 and 2005 (FAO 2006), because of the long occupation history and increasing human impact during last decades.

In this context, natural vegetation regeneration and sustainable management, as well as conservation of less degraded areas is urgently needed. The knowledge of palaeoecological conditions is very important to understand the natural composition and dynamics of modern ecosystems for proper management and conservation. Despite the need, of this knowledge only a limited number of palaeoecological studies are available from the Ecuadorian Andes (Bush *et al*. 2007). The available pollen records for the southeastern Andes, Andean Depression, were provided by the German-Ecuadorian Research Unit (www.tropicalmountainforest.org) focusing on the Podocarpus National Park (PNP) area and its surroundings (Niemann *et al*. 2013; Rodríguez & Behling 2012; Villota *et al*. 2012). Several investigations from sites between 2000 and 3300 m a.s.l. provide reconstructions of the environmental history, mostly of the northern PNP (Brunschön & Behling 2009; 2010; Jantz *et al*. 2013; Niemann & Behling 2008; 2009; 2010; Niemann *et al*. 2009; Rodríguez & Behling 2011).

In this paper, we present the investigation results of a core from the Cajanuma valley area in the western slope of the PNP, southern Ecuadorian Andes. Our main objective is the reconstruction of the local environmental history including vegetation, fire and climate dynamics in an attempt to identify mechanisms of past ecosystem change and human impact during the late Glacial. For that reason in this study we want to address the following main questions: (1) How did the vegetation develop at Cajanuma during the late Glacial and Holocene? (2) Did fire provide an important control over the vegetation and was it natural or anthropogenic? (3) How dynamic or stable were the UFL during the late Glacial and Holocene in the upper region of the PNP?

STUDY SITE

Location. The study area, Cajanuma, is located at the western slope of the eastern cordillera (Cordillera Real) in the Podocarpus National Park (PNP), southeastern Ecuadorian Andes (Fig. 1). The eastern Andean Cordillera is mainly formed by Paleozoic metamorphic rocks (Baldock 1982). The basin margins contain conglomerates of metamorphic debris, semipelites, quartzites and black phylites with some granitic intrusions (Litherland *et al*. 1994).

Particularly, the Andes of southern Ecuador are part of the Andean depression region (Depression of Giron-Cuenca in southern Ecuador and Huancabamba in northern Peru), where the highest peaks reach no more than 4000 m a.s.l., and active volcanoes and glaciers are absent (Schubert & Clapperton 1990). However, indications of Pleistocene glaciations are found. During the Last Glacial Maximum (LGM) lower moraine limits at 3750–3500 m a.s.l. in the eastern Ecuadorian Andes were estimated (Heine 2000), as well as, cirque lakes (remnants of the latest glaciations) between 2900 and 3400 m a.s.l. in the central PNP (Emck 2007).

The core analyzed “Cajanuma valley”(CV) was derived from a small peat bog, 30 m in diameter, located at 3285 m elevation (4°08’59’’ South, 79°09’25’’ West). The surrounding landscape is characterised by páramo with small forest patches at lower slopes. The area around the study site is not disturbed.

Climate. Inside the PNP at 3100 m a.s.l., rainfall up to 6000 mm a^{-1} was measured (Emck 2007; Bendix *et al*. 2008). The main rainy season lasts from April to August (austral winter), although rainfall is high throughout the year. On average, 9-10 humid months are recorded for the western slopes and temperature varies according to the time of day and season (Bendix *et al*. 2008). The coldest period of the year is generally the main rainy season. In the Cajanuma area the mean annual temperature registered is ca. 6.9 ºC and the annual precipitation rate is about 5700 mm (Emck 2007).

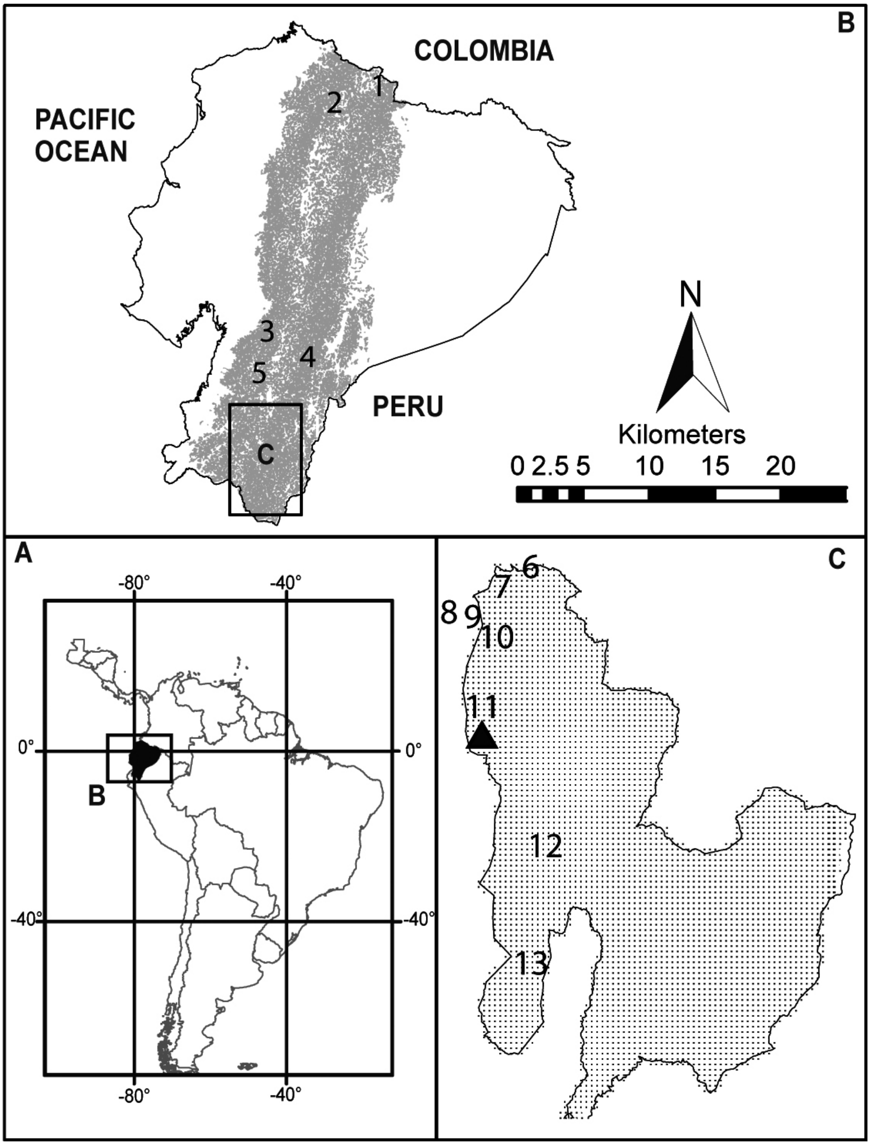

Figure 1. A. Map of Ecuador in South America. B. Map of the Andes of Ecuador, showing the location of the different studies sites. 1, Guandera Biological Reserve; 2, Laguna Yaguarcocha; 3, Lagunas Chorreras; 4, Lake Surucucho; 5, Tres Lagunas. C. Map of Podocarpus National Park and surrounding area, showing the location of the different studies sites. 6, Laguna Zurita; 7, El Tiro; 8, Laguna Daniel Álvarez; 9, Laguna Campana; 10, Cocha Caranga; 11, Valle Pequeño; ▲ Cajanuma valley; 12, Laguna Rabadilla de Vaca; 13, Cerro Toledo.

Vegetation. The most appropriate vegetation description by Homeier *et al*. (2008) classifies four different escarpment vegetation types in the PNP, which are relevant for our investigation area: lower and upper mountain rainforest, subpáramo and páramo. The coring site is situated in the páramo (including shrub and herb páramo) between ca. 3100-3700 m a.s.l.

According to Homeier *et al*. (2008) and additional information provided by Lozano *et al*. (2003), the lowest vegetation type is the lower mountain rainforest (LMF) between ca. 1300-2100 m a.s.l. with canopy heights of 30 m. Undisturbed communities of this type can be found particularly on steep slopes with 30º to 50º inclination, as well as up to ca. 2300 m at the bottom of wind-protected river valleys. Characteristic species are *Alzetea verticillata*, *Cedrela montana*, *Graffenrieda miconioides*, *Heliocarpus americanus*, *Mikania* sp., *Morus insignis*, *Myrcianthes* sp. and *Piper* sp. The upper mountain rainforest (UMF) is located between ca. 2100-2700 m a.s.l. and the canopy attains heights up to 25 m. Some of the main key species are *Clethra revoluta*, *Clusia* sp., *Dioicodendron dioicum*, *Hedyosmum racemosum*, *Ilex rimbachii*, *Macrocarpaea revoluta*, *Myrica pubescens*, *Myrsine andina*, *Myrsine coriacea*, *Podocarpus oleifolius*, *Prumnopitys montana*, *Purdiaea nutans* and species of *Weinmannia* At upper elevation between ca. 2700-3100 m a.s.l. the elfin-forest or subpáramo vegetation occurs. This vegetation type forms the upper forest line ecotone with a canopy height of 6-8 m. Characteristic species are, e.g. *Brachyotum rotundifolium*, *Clethra ovalifolia*, *Gaultheria reticulata*, *Gaiadendron punctatum*, *Graffenrieda harlingii* and *Hesperomeles lanuginosa*. The páramo (including shrub and herb páramo) occurs in the crest regions of the Cordillera Real above the upper forest line between ca. 3100 and 3700 m a.s.l. Páramo vegetation is characterised by plants with a maximum height of 2 m. Some key species are *Arcytophyllum setosum*, *Blechnum cordatum*, *Calamagrostis macrophylla*, *Chusquea neurophylla*, *Gynoxis buxifolia*, *Halenia weddelliana*, *Huperzia kuesteri*, *Ilex andicola*, *Monnina arbuscula*, *Neurolepis nana*, *Niphogeton dissecta*, *Oxalis spiralis*, *Puya eryngioides*, *Puya maculate*, *Rhynchospora vulcani* and *Valeriana microphylla*.

The present vegetation around the PNP is partially degraded due to deforestation and land conversion into pastures and cultivations (Beck *et al*. 2008). Currently, disturbance is primarily restricted to the surrounding areas and some border zones; a reason why the Podocarpus National Park still widely possesses well-protected natural vegetation including the study area of Cajanuma.

MATERIAL AND METHODS

The "Cajanuma valley" (CV) sediment core was taken with a Russian Corer. The total length of the recovered core is 180 cm. Sections of 50 cm length were placed in splitted PVC tubes covered with plastic film and stored under dark and cold (+4 °C) conditions at Georg-August-University of Göttingen before processing.

For accelerator mass spectrometer (AMS) radiocarbon dating, four subsamples containing organic material were submitted to the University of Erlangen-Nürnberg (Germany). The ^{14}C dates were calibrated using the curve SHCal04. 14C SH terrestrial dataset of the Calib 6.0 software (Stuiver *et al*. 2005).

For palynological analysis, the CV core was sampled at four cm intervals along the core, resulting in 41 subsamples of 0.5 cm^3 each. All subsamples were processed using the standard pollen analytical methods (Fægri & Iversen 1989). One tablet of exotic *Lycopodium clavatum* spores, containing 18 583 ± 762 spores, was added to each sample before treatment as a marker for calculation of pollen and charcoal concentration as well as influx. A minimum of 300 pollen grains was counted for each sample. The pollen sum includes pollen of herbs, shrubs, trees and indeterminate taxa and excludes fern spores and pollen of aquatic taxa. The spores of Pteridophyta, *Isoëtes* and *Sphagnum* were counted and quantified as percentages based on the pollen sum.

The identification of pollen and spores is based on the reference published by Hooghiemstra (1984), as well as electronic pollen keys of Ecuador, kept at the department of Palynology and Climate Dynamics, and the South American Pollen Database (Bush & Weng 2007). Reference collections of recent material, held at the Department of Palynology and Climate Dynamics in Göttingen, were also used. They contain about 3000 neotropical taxa (Behling 1993) and ca. 620 Ecuadorian taxa, respectively. Identified taxa were classified into ecological groups that correspond to the prevailing vegetation types: Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo, Páramo and Pteridophyta. The pollen types that could not be identified were grouped in the indeterminate taxa. For charcoal analysis was used the technique developed by Finsinger *et al*. (2008), which estimated that charcoal particles correspond to the concentration of *Lycopodium clavatum* spores (marker). Charcoal particles were counted up to a total count of 100 *Lycopodium clavatum* spores. The counted charcoal particles were separated in two groups of different particle sizes (10 - 50 µm and 50 - >100 µm) to be able to give more detailed information about the fire history (Sadori & Giardini 2007). Fragments between 10 and 50 µm indicate regional fires, and fragments 50 - >100 µm local fire (Whitlock & Larsen 2001).

The software TILIA was used for data calculation of percentages, sums, as well as pollen and charcoal concentration and influx. TILIAGRAPH software was used to illustrate the data, as well as stratigraphy and the calibrated and uncalibrated dates (Grimm 1987). The program CONISS was used to conduct a cluster analysis of the pollen data which were included in the pollen sum to generate a dendrogram (Grimm 1987), helping to identify the pollen zones.

RESULTS

Stratigraphy. The 180 cm long peat bog sediment core from Cajanuma Valley (CV) consists of clay and organic material. Between 180 and 160 cm core depth clayey material is dominant with a dark/light greyish colour. From 160 to the top of the core the sediments are more compact and there is presence of organic material. Between 160 and 130 cm the organic material is highly decomposed and has a dark brown colour. Between 130 and 100 cm is found less decomposed organic material with presence of a few fine roots and has a light brownish colour. Between 100 and 35 cm the organic material is little decomposed with many plant remains and has a brown colour. Between 35 and 0 cm little decomposed organic material with humus layer is present and has a light brown colour. A detailed description of the stratigraphic units is given in Table 1.

Table 1. Stratigraphic description of the sediment core Cajanuma Valley (CV).

Depth (cm)	Description
0 – 10	Not decomposed plant material, with plant remains (roots)–humus layer
10 – 35	Very little decomposed plant material, with plant remains (roots), light brown coloured
35 – 50	Little decomposed organic material with roots, light brown coloured
50 – 75	Little decomposed organic material with little roots, light brown coloured
75 – 100	Little decomposed organic material, dark brown coloured
100 – 125	Less decomposed organic material, light brownish coloured
125 – 130	Less decomposed organic material, dark brownish coloured
130 – 160	Highly decomposed organic material, dark brownish coloured
160 – 175	Clayey material, dark-greyish coloured
175 – 180	Clayey material, with little stones; light-greyish coloured

Chronology and pollen zonation. Four AMS radiocarbon dates (Table 2) were performed at the AMS laboratory at the University of Erlangen/Nürnberg, Germany, providing the chronological control of the sediment core from Cajanuma valley (CV). Extrapolation of the dates suggests that the base of the core has an age of ca. 16 000 cal yr BP that probably reflects the beginning of sediment accumulation.

The series of four AMS dates shows a consistent age-depth model (Fig. 2), which indicates that sediments accumulated continuously without any gaps since the late Glacial. The average sediment accumulation rate is 0.69 mm yr^{-1}. In detail it is 0.04 mm yr^{-1} (16 000 to 10 500 cal yr BP), 0.04 mm yr^{-1} (10 500 to 5600 cal yr BP), 0.11 mm yr^{-1} (5600 to 1200 cal yr BP), 0.71 mm yr^{-1} (1200 to 350 cal yr BP), 1.68 mm yr^{-1} (350 to 200 cal yr BP), 1.68 mm yr^{-1} (200 to 50 cal yr BP) and 1.68 mm yr^{-1} (50 to -59 cal yr BP). The CONISS cluster analysis and major changes in the pollen assemblages suggest five main pollen zones (CV-I to CV) with subzones (CV-Va-c).

Description of the pollen diagram. A detailed pollen percentage diagram displays 21 different pollen taxa with a representation of >2% out of 77 pollen types and two spores types with a representation of >2% out of eleven identified (Fig. 3).

Table 2. List of AMS radiocarbon ^{14}C dates and calibrated ages from the Cajanuma Valley (CV) core using the curve SHCal04. 14C SH terrestrial dataset of the Calib 6.0 software.

Lab. Code	Depth (cm)	Dated Material	^{14}C age (yr BP)	1-σ (cal yr BP)
Erl-16087	80 – 81	Organic material	378 ± 48	402 ± 90
Erl-16586	104 – 105	Organic material	1538 ± 107	1396 ± 218
Erl-16086	135.5 – 136.5	Organic material	4803 ± 66	5515 ± 82
Erl-16587	160 – 161	Wood	9933 ± 86	11440 ± 153

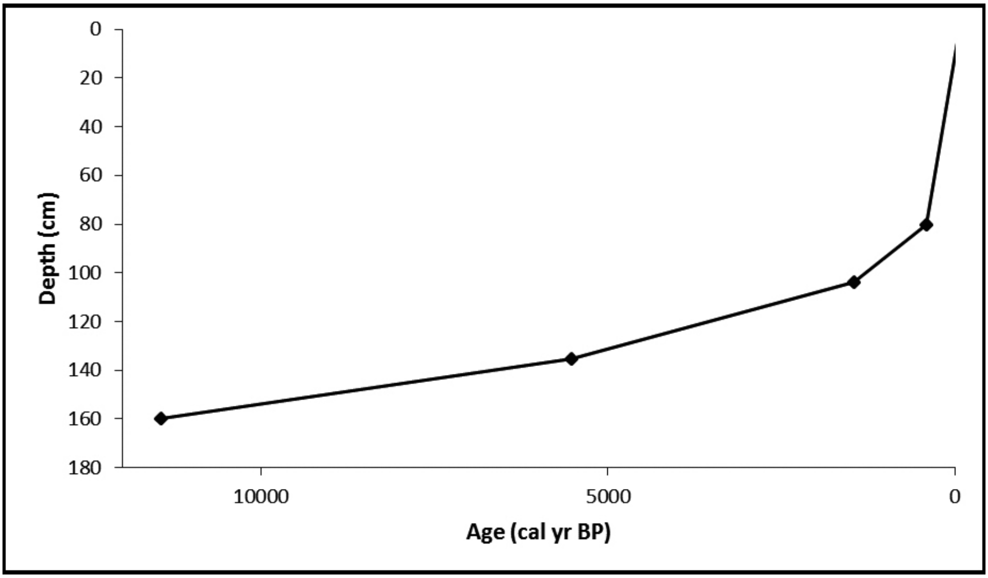

Figure 2. Age–depth model (core depth in cm/cal yr BP) for the Cajanuma Valley (CV) core based on 4 radiocarbon dates.

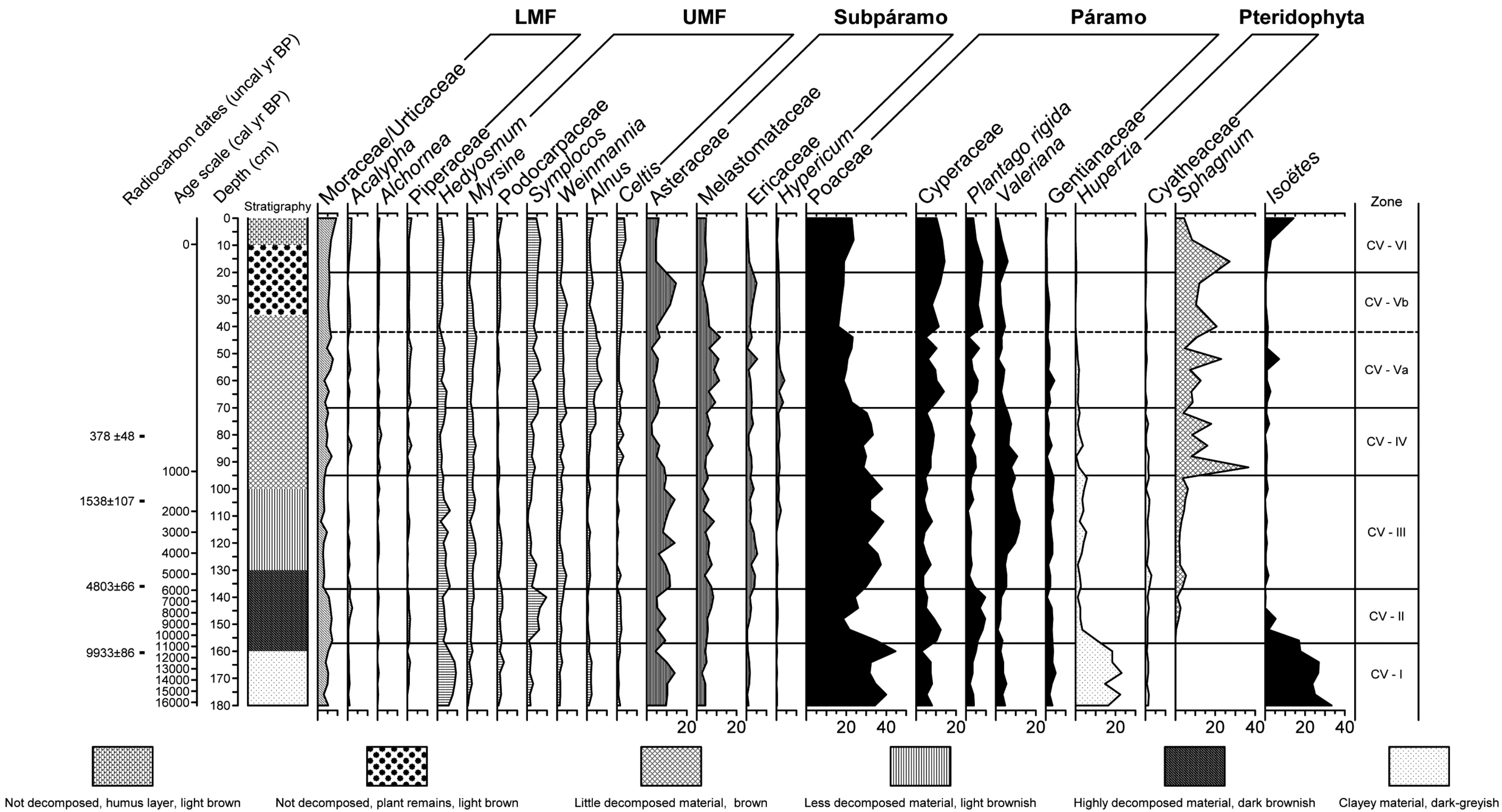

Figure 3. Pollen percentage diagram of the Cajanuma Valley (CV) core showing selected fossil pollen and spore taxa grouped into Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo, Páramo and Pteridophyta.

The summary percentage diagram (Fig. 4) shows the pollen and spores grouped into the vegetation types: Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo, Páramo and Pteridophyta (without *Isoëtes*), *Sphagnum* and concentration and influx of pollen and charcoal particles.

Pollen concentration and influx vary between 25 000–530 000 grains/cm^3 and between 250–12 000 grains/cm^2/yr, respectively. The charcoal concentration of the two counted fraction vary between 3 500 000–14 000 000 particle/cm^3 (small fraction) and 100 000–600 000 particle/cm^3 (large fraction). The charcoal influx for both counted fractions varies between 40 000–1 200 000 particle/cm^2/yr (small fractions) and between 100–95 000 particle/cm^2/yr (large fraction).

Zone CV–I (180–156 cm; ca. 16 000–10 500 cal yr BP, six samples), is characterized by low proportion of LMF pollen taxa (10%) mainly due to low values of Moraceae/Urticaceae (7%) and *Acalypha* (1%). UMF taxa (15–20%) are mainly represented by *Hedyosmum* (9%), which presents the highest value of the record in this zone, *Myrsine*, Podocarpaceae, *Symplocos*, *Weinmannia* and *Alnus acuminata* (2–3%). Subpáramo pollen taxa show stable values (20%), mainly by Asteraceae (10%) and Melastomataceae (5%). This zone is marked by relatively high values of páramo taxa (60%), especially by Poaceae (40%) and Cyperaceae pollen (10%). Also, pollen of Gentianaceae (5%) presents the highest values of the record. In this zone Pteridophyta spores (20–25%) are mainly represented by *Huperzia* (15–20%), which presents the highest value of the record in this zone. *Isoëtes* spores (up to 25%), which are not included in the sum of Pteridophyta, are very frequent in this zone.

Zone CV–II (156–136 cm; ca. 10 500–5600 cal yr BP, five samples). LMF taxa show stable values (10%) by Moraceae/Urticaceae (7%) and the presence of *Acalypha* (2%). Proportions of UMF pollen taxa increase slightly (25%) by *Myrsine* and Podocarpaceae (2–3%). *Symplocos* pollen represents the highest values (6–10%) of the record in this zone. *Alnus acuminata* values decrease (0%). Pollen of subpáramo taxa increases slightly (20%) at the top of the zone mainly by Melastomataceae (10%). Páramo taxa decreased slightly from 60 to 50%, especially due to lower representation of Poaceae (30%). However, *Plantago rigida* pollen has higher values (8%) in this zone. Pteridophyta group strongly decrease (10%); mainly due to the low representation of *Huperzia* spores (3%). In this zone *Isoëtes* spores occur with lower values (5%).

Zone CV–III (136–96 cm; ca. 5600–1200 cal yr BP, eleven samples), is characterized by low representation of LMF pollen (6%), due to the lowest values of Moraceae/Urticaceae pollen (3%). Proportion of UMF taxa decreased slightly (15%), mainly due to low percentages of *Symplocos* (4%). Subpáramo pollen taxa show a stable proportion (25%) such as Asteraceae (15%) and Melastomataceae (6%). Ericaceae are represented by higher values (5%) in this zone. Páramo pollen taxa are frequent and show highest values in this zone (65%), mainly due to Poaceae (35%) and *Valeriana* (10%). Compared to the previous zone, Pteridophyta show stable proportions (10%), mainly due to *Huperzia* (5%); also by spores of Cyatheaceae (3%) which present the highest value of the record. In this zone spores of *Isoëtes* are absent. Proportion of *Sphagnum spores* (5%) increases in this zone.

Zone CV–IV (96–72 cm; ca. 1200–350 cal yr BP, six samples), is marked by a slightly higher representation of LMF pollen (11%), e.g. Moraceae/Urticaceae (6%) and *Acalypha* (2%) compared to the previous zone. UMF taxa increase slightly (20%) at the top of the zone; mainly by *Weinmannia* (4%) and

Alnus acuminata (4%) at the top of the zone. A slight increase is found in pollen of *Celtis* (3%). However, Podocarpaceae pollen represents lower values (1%) in this zone. Subpáramo pollen taxa decreased from 25 to 15%, especially due to lower representation of Asteraceae (8%) and Ericaceae (3%). Páramo taxa vary between 65 and 55%, especially due to lower values of Poaceae pollen (30%) at the bottom of the zone. *Valeriana* pollen presents the highest values (10%) of the record at the bottom of this zone. Compared to the previous zone Pteridophyta decreased strongly (5%) and *Sphagnum* spores (35%) present the highest values of the record.

Subzone CV–Va (72–44 cm; ca. 350–200 cal yr BP, seven samples), is characterized by a stable representation of LMF taxa, mainly due to Moraceae/Urticaceae (4–7%); also *Acalypha* and Piperaceae with (2%). UMF taxa reach highest values between 20 and 28% of the record, mainly due to pollen of *Myrsine* (4%) and *Symplocos* and *Alnus acuminata* with (5%). Percentages of subpáramo taxa increase slightly, such as Ericaceae (4%). Highest representation of pollen of Melastomataceae (15%) and *Hypericum* (4%) is found in this subzone. Compared to the precious zone proportion of páramo taxa decreased (45%), mainly due to Poaceae (20%) and *Valeriana* (4%). Pollen of Cyperaceae represents higher proportion (10%) at the bottom of this subzone. In this subzone Pteridophyta spores (2%) decreased mainly by the low presence of *Huperzia* spore (1%) and the absence of Cyatheaceae spores. *Isoëtes* values increase slightly (7%) at the top of this subzone. Spore of *Sphagnum* (15%) decrease at this subzone.

Subzone CV–Vb (44–20 cm; ca. 200–50 cal yr BP, three samples), shows a stable proportion of LMF pollen (11%). UMF taxa remain stable (20%); however *Weinmannia* show higher values (5%) in this subzone. Subpáramo pollen shows the highest amounts within this subzone, especially by Asteraceae (15%) and Ericaceae pollen (5%). Compared to the previous subzone, páramo taxa show stable percentage, especially by Poaceae (20%). In this subzone Pteridophyta show stable values (2%).

Zone CV–Vc (24–0 cm; ca. 50 cal yr BP to -59 cal yr BP, three samples), is characterized by slightly increase proportion of LMF pollen taxa; mainly Moraceae/Urticaceae taxa slightly increase (6–10%) at the top of this zone. UMF taxa remain stable between 20 and 25%; however *Celtis* show highest values (5%) of the record in this zone. Subpáramo taxa show the lowest values of the record (13%), mainly by Asteraceae, Melastomataceae (5%) and Ericaceae (1%). Compared to the previous subzone, pollen of páramo increase from 40 to 50%. This is mainly due to increasing values of Poaceae (25%), Cyperaceae (15%) and *Valeriana* (6%). Compared to the previous subzone Pteridophyta spores show stable values (2%). *Isoëtes* value increase slightly (14%). Proportion of S*phagnum* spores (25%) slightly increased at the bottom of this zone.

INTERPRETATION AND DISCUSSION OF THE ENVIRONMENTAL RECORD

During the Last Glacial Maximum (LGM), most Andean glaciers moved down slope and reached their lowermost positions at about 3000 m in the eastern Andes of Colombia, Ecuador and northern Peru (Rodbell 1994). Lower glacier margins are estimated at ca. 3100 m for the PNP region, with glaciers terminating at elevations of ca. 2750–2800 m (Rozsypal 2000). At the end of the LGM, the volume of glaciers decreased creating moraines, lakes and bogs. The moraine frontier at the PNP is found between 2800 and 3350 m elevation, after the glacial retreat deposits accumulated at the study site at about 16 000 cal yr BP.

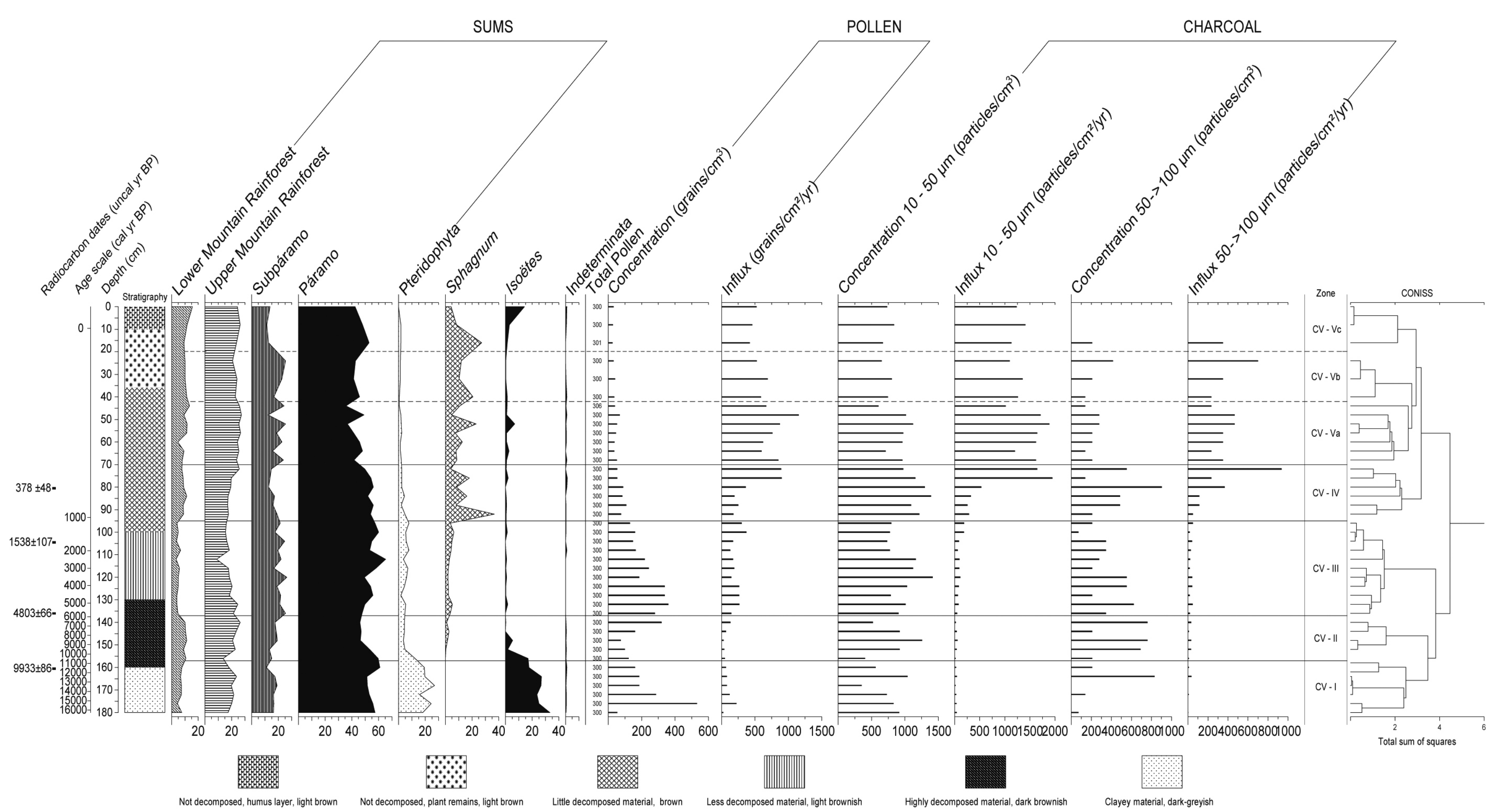

Figure 4. Summary pollen percentage diagram of the Cajanuma Valley (CV) core showing radiocarbon dates (uncal yr BP), age scale (cal yr BP), vegetation groups, pollen sum, pollen concentratin and influx, charcoal concentration and influx, and the CONISS dendrogram.

The pollen record from the Cajanuma valley (CV) at 3285 m elevation, in general reflects the local development and vegetation dynamics on the drier western slope of the Podocarpus National Park (PNP) in the Andean Depression. Pollen and spores data suggest that páramo vegetation, which today naturally covered the area, exists around the core site since the late Glacial from ca. 16 000 cal yr BP.

Late Glacial and transition to the early Holocene. The pollen record from Cajanuma valley (CV) indicates that herb páramo was the main vegetation type around the study area during the recorded period from ca. 16 000-10 500 cal yr BP (zone CV–I), while the subpáramo and mountain rainforest were low represented. The low presence of mountain forest taxa is probably related to low temperatures at that time which did not allow the development of mountain forest near the study site.

During this period, is also recorded the low pollen input into the basin with presence of clayey material; which could reflect that the páramo vegetation was sparse and forest occurred in some distance to the coring site. Such conditions of low local productivity coupled with input from long distance dispersal serves to elevate a few anemophilous pollen types in the percentage data, yielding proportions that do not reflect local vegetation (Hansen *et al*. 1984).

Pollen of Lower Mountain Rainforest (LMF) taxa (e.g., Moraceae/Urticaceae, *Alchornea* and *Acalypha*) tends to be over-represented due to wind transport to higher elevations (Jantz *et al*. 2013). At Laguna Baja in northern Peru over representation of forest taxa (e.g., Moraceae/Urticaceae) in páramo samples is attributed to low pollen productivity of local plants at high elevations resulting in higher values of long distance wind transported pollen (Hansen & Rodbell 1995). Main components of the Upper Mountain Rainforest (UMF) were *Hedyosmum*, Podocarpaceae and *Alnus acuminata*. The occurrence of *Hedyosmum*, which is abundant during this period, indicates relatively wet conditions. Representation of *Alnus acuminata* pollen in páramo was observed also in the superpuna of the Junín area in central Peru and was assumed due to long distance transport (Hansen *et al*. 1984). The subpáramo at CV was dominated by shrubby vegetation composed of Asteraceae and Melastomataceae. The herb páramo was rich in Poaceae, Cyperaceae and Gentianaceae, reflecting cool conditions, associated with a high presence of *Huperzia* and *Isoëtes*. The occurrence of Pteridophyta and high values of *Isoëtes* suggest wetter conditions. *Isoëtes* mostly occurs submerged in páramo lakes and is sensitive to strong frosts (Bosman *et al*. 1994). It indicates that there must have been a shallow water body at the study site. Similarly, cooler climates are indicated by the occurrence of treeless vegetation during glacial times in the southern Ecuadorian Andes (Colinvaux *et al*. 1997). Also in southwestern Ecuadorian Andes (3700 m elevation), studies indicate for the late Glacial period (17 000–11 000 cal yr BP), a herb páramo surrounded the area, reflecting colder and moister climatic conditions (Hansen *et al*. 2003).

During the late Glacial and transition to the early Holocene, the low charcoal influx indicates rare fire and suggests the absence of human activity in the study area.

Early to mid–Holocene. The early to the mid-Holocene period between ca. 10 500 to 5600 cal yr BP (zone CV–II), is marked by gradual change indicated by high abundance of páramo vegetation during the early Holocene, followed by a slight expansion of mountain forest into higher elevations and a partial replacement of páramo during the mid-Holocene. Páramo vegetation began to decrease while subpáramo and mountain rainforest increased (9000–5600 cal yr BP).

During this period stable proportion of LMF was shown in the pollen record; but there is evidence of a slight increase of *Acalypha*, which probably reflects slow and continuous increasing temperatures. UMF vegetation increases slightly mainly by the strong increase of *Symplocos* taxa. Also by, *Myrsine* and Podocarpaceae. Nevertheless, *Hedyosmum* starts to decline in abundance ca. 10 500 cal yr BP. The stable proportion of LMF and the increase of UMF suggest an establishment of mountain rainforest vegetation and a rise in temperature during this period. Subpáramo was dominated mainly by Asteraceae and Melastomataceae. Relatively high proportion of páramo was reached during this period, mainly by high abundance of Cyperaceae and *Plantago rigida*. The frequent occurrences of *P. rigida* and Cyperaceae indicate locally humid conditions (Moscol Oliveira & Hooghiemstra 2010). In particular *P. rigida* constitutes cushion bogs at high elevation (3000–5200 m) in grass páramo (Bosman *et al*. 1994; Niemann & Behling 2008). Pteridophyta were rare during this period, *Huperzia* decreased during the transition from the late Pleistocene–Holocene period (Hansen *et al*. 2003). However, abundance of Cyatheaceae slightly increased during this period. Also, *Isoëtes* became rare at the study site. In the Cajas National Park (western Ecuadorian Andes), the pattern was similar, the early Holocene showed warmer conditions than at present (Colinvaux *et al*. 1997; Hansen *et al*. 2003). At Fuquene Lake (eastern Colombian Andes), very humid conditions are suggested during the early Holocene (Vélez *et al*. 2006). At Laguna Chochos and Laguna Baja (eastern Peruvian Andes) a warm and wet condition is shown by the arrival of cloud forest taxa to both sites at 11 500 cal yr BP (Hansen & Rodbell 1995; Bush *et al*. 2005). Also, studies in the west and central Andes region of Ecuador, Peru and Bolivia in general show a trend of a relative warm and dry mid-Holocene (Hansen *et al*. 2003; Paduano *et al*. 2003; Weng *et al*. 2006).

Relatively low values of charcoal influx during the early and mid-Holocene suggest rare fires in the study area.

Mid- to late Holocene. During the mid- to late Holocene (ca. 5600–1200 cal yr BP, zone CV–III), the LMF decreased, in particular Moraceae/Urticaceae. Whereas the LMF decreased, the UMF presence remained relatively stable; with a particular high abundance of *Weinmannia* and *Hedyosmum* and a marked lower occurrence of *Symplocos*. However, it has to be considered that *Weinmannia* and *Hedyosmum* are anemophilous taxa (Hansen & Rodbell 1995; Weng *et al*. 2004). Anemophilus taxa are overrepresented in pollen spectra (Moscol Oliveira *et al*. 2009; Jantz *et al*. 2013). Subpáramo vegetation expanded due to the higher representation of Asteraceae, Ericaceae and *Hypericum* at the top of the zone; probably suggesting higher moisture conditions (Marchant *et al*. 2002). *Hypericum* is also a good proxy for the existence of landscape disturbance (Brunschön & Behling 2009). The páramo vegetation expanded, it was dominated mainly by Poaceae and Gentianaceae with increasing proportions of *Valeriana*; suggesting a change to cooler and wetter conditions. The marked decrease of *Plantago rigida* and increase of Poaceae might indicate that grass páramo surrounded the study site. In addition, the high presence of *Huperzia* and Cyatheaceae suggests wetter conditions.

Fires were slightly frequent during the mid- to late Holocene period. There is evidence of a slight increased influx of smaller charcoal fragments after 5600 cal yr BP. Studies from lake Titicaca and the surrounding altiplano as well as southern Ecuador suggest that once the mid-Holocene drought ends, human populations expand rapidly and are engaged in landscape modification (Brenner *et al*. 2001; Niemann & Behling 2008).

Late Holocene. The late Holocene since ca. 1200 cal yr BP (zone CV–IV to CV–V), was generally characterized by páramo vegetation, but mountain forest and subpáramo were similar or slightly stronger presented compared to the previous periods. Pteridophyta were almost absent during this period.

Between ca. 1200–350 cal yr BP (zone CV–IV) the LMF increased slightly, mainly by the increased proportion of *Alchornea* and Piperaceae. However, as mention before pollen of LMF taxa (e.g., Moraceae/ Urticaceae, *Alchornea*, *Acalypha* and Piperaceae) tends to be over-represented due to wind transport to higher elevations. The UMF increased slightly and was represented mainly by high occurrence of *Alnus acuminata* and *Celtis*. *Alnus acuminata* grows along river beds and follows landslides as a pioneer (Marchant *et al*. 2002). The presence of *A*. *acuminata* can be a result of anthropogenic disturbances (Weng *et al*. 2004), rather than by climatic changes. *A. acuminata* and *Celtis* are also a component of successional forests after human disturbance (Marchant *et al*. 2002). The subpáramo remained relatively stable during this period. Páramo vegetation was still well represented with a high occurrence of Poaceae and *Valeriana*; suggesting cooler and wetter conditions. Higher abundance of *Sphagnum* appeared during this period. *Sphagnum* moss probably reflects the formation of the peat bog the study area.

Between ca. 350–50 cal yr BP (subzone CV–Va and CV–Vb), the LMF vegetation remain stable. Slightly higher presence of UMF vegetation is due to the slight increase of *Symplocos*, *Weinmannia* and *Alnus acuminata*. Subpáramo vegetation slightly increased, mainly by higher proportion of Asteraceae and Melastomataceae. Especially, Asteraceae may reflect landscape disturbance (Chepstow-Lusty *et al*. 2003). Slightly lower presence of páramo vegetation is due to the lower occurrence of Poaceae and *Valeriana*. However, Cyperaceae slightly increased; suggesting cooler and wetter conditions. *Sphagnum* presence remained stable. Also, high occurrence of *Isoëtes* is recorded. Persistent humid conditions are suggested by high occurrences of Cyperacae and *Isoëtes*.

Between ca. 50 cal yr BP–to the present (subzone CV–Vc) LMF and UMF remained stable. Subpáramo vegetation decreased slightly due to lower presence of mainly Asteraceae and almost absence of Ericaceae. Poaceae together with Cyperaceae dominated in the herb páramo until modern times; reflecting cooler conditions where modern vegetation as well as modern climatic conditions became established.

In addition, there is evidence of a major influx of larger charcoal fragments after 1200 cal yr BP which may reflect local fires of anthropogenic origin. Since, the first stronger presence of human in this region was after 10 000 yr BP according to the Cubilán archaeological record, located about 100 km north of Loja at 3100 m of altitude (Valdez 2008). During the late Holocene human influence is reported throughout the Andes (Hansen *et al*. 2003; Bush *et al*. 2005; Weng *et al*. 2006). Nevertheless, it is important to point out that for the last years there is no evidence of local fires; as mention above disturbance is primarily restricted to the surrounding areas and the study site is since the last years well-protected.

Upper forest line (UFL) changes. The Upper Forest Line (UFL) dynamics is mainly reflected by fluctuations in the proportion of upper mountain rainforest (UMF) and subpáramo vegetation. During the late Glacial and transition to the early Holocene, from ca. 16 000-10 500 cal yr BP, the high proportion of páramo taxa comparably with the low presence of mountain rainforest and subpáramo indicate that páramo vegetation extensively covered the area and dominated the landscape. This probably reflects a downslope shift of UFL in the study area. During the LGM, the UFL position in the Podocarpus National Park (PNP) area was at least ca. 700 m lower in the northernmost PNP area compared to today (Brunschön & Behling 2010).

Likewise, the late Glacial period, during the early Holocene, (10 500–9000 cal yr BP), herb páramo was the main vegetation type around the study area. Subpáramo vegetation and mountain rainforest were low represented. Suggesting that, the UFL position was still low. On the contrary, within the whole PNP area, the UFL seems to have shifted upslope in the range of ca. 100–150 m (Brunschön & Behling 2010). During the mid- Holocene, (9000–5600 cal yr BP), a relatively high increase of mountain rainforest and subpáramo shrubs and trees is observed. Páramo vegetation was represented by a lower occurrence. This probably, suggests a shift of UFL to higher elevations. A ca. 400 m upslope is reconstructed for the PNP by Brunschön & Behling (2010).

During the mid- to late Holocene, (5600–1200 cal yr BP), the significant presence of páramo taxa comparably with the relatively low presence of mountain rainforest probably represents a downslope shift of UFL in the study area.

Between ca. 1200–350 cal yr BP high proportion of páramo taxa comparably with the low presence of mountain rainforest and subpáramo indicate a downslope shift of UFL in the study area. However, the suggested lower UFL should be interpreted in the context of local fires. Higher frequency of fires probably lowered the UFL position.

Between ca. 350 cal yr BP to present, the páramo vegetation seems to have been slightly depressed, while the mountain forest and subpáramo vegetation slightly expanded; suggesting an upslope of the UFL. The UFL shifted upslope to the highest elevations of ca. 2800 m a.s.l. in the PNP (Brunschön & Behling 2010).

Comparison with other records from the Podocarpus National Park. The Cajanuma valley record, located at 3285 m elevation in the western slope of the PNP, will be compared to close by study sites: El Tiro Pass (2811 m a.s.l.; 15 km north of the site), Cocha Caranga (2710 m a.s.l., ca. 10 km north), Valle Pequeño (3244 m a.s.l., ca. 3 km), Laguna Rabadilla de Vaca (3312 m a.s.l., ca. 15 km south of the study site) and Cerro Toledo (3150 m a.s.l., ca. 30 km south) (Fig. 1).

During the late Glacial and transition to the early Holocene (16 000–10 500 cal yr BP), a similar vegetation pattern as in Cajanuma valley is evident from the pollen record of El Tiro Pass which indicated grass páramo vegetation, mainly composed of Poaceae and *Plantago* reflecting cold and moist conditions (Niemann & Behling 2008). Nevertheless, a pollen record of Cocha Caranga suggests higher proportions of the UMF between ca. 14 500 to 9700 cal yr BP, indicating increased temperatures compared to earlier periods (Niemann & Behling 2009). Also the Cerro Toledo record suggests higher occurrence of subpáramo and mountain rainforest vegetation with relative wet conditions (Brunschön & Behling 2009).

A similar vegetation pattern, as in Cajanuma valley, during the early Holocene, (10 500–9000 cal yr BP), was recorded in El Tiro Pass between, 11 200 to 8900 cal yr BP, which indicates slowly warming conditions with a relatively low increase in mountain rainforest and subpáramo shrubs and trees (Niemann & Behling 2008). In the Laguna Rabadilla de Vaca record, between ca. 11 700–8990 cal yr BP, it is evident that herb páramo was the main vegetation type associated with a high number of ferns, reflecting cool and relatively wet climatic conditions (Niemann *et al*. 2009).

A drier mid-Holocene, as recorded in Cajanuma valley between ca. 9000 to 5600 cal yr BP, has been recorded throughout the PNP. As is the case of the El Tiro record in which, between ca. 8900 to 3300 cal yr BP, UMF was predominant and a succession of *Hedyosmum* and Podocarpaceae took place (Niemann & Behling 2008). The Laguna Cocha Caranga record indicates that the early to mid-Holocene was a drier period by the strong increase of Cyperaceae and *Isoëtes* and a marked increase of fire intensity (Niemann & Behling 2009). The strong increase of *Weinmannia* indicates warmer climatic conditions, between ca. 8990–3680 cal yr BP, at the Laguna Rabadilla de Vaca record (Niemann *et al*. 2009). The Cerro Toledo record between 6900 to 4700 cal yr BP shows a gradual change in the vegetation composition. The lower presence of páramo vegetation and high proportion of subpáramo; reflects warmer conditions (Brunschön & Behling 2009).

During the late Holocene (ca. 1200 cal yr BP to the present) the vegetation composition at the study area is somewhat similar to what has been found in the pollen records of the PNP. The Cocha Caranga record shows open grassy areas with forest after ca. 1300 cal yr BP (Niemann & Behling 2009). The record of Cerro Toledo after ca. 1800 cal yr BP shows a slight decrease in páramo and increase in subpáramo, UMF, and LMF suggesting warmer temperatures (Brunschön & Behling 2009). Also, the El Tiro record shows an increase of Melastomataceae, thus suggesting relatively stable subpáramo vegetation (Niemann & Behling 2008). Also, the Valle Pequeño record suggests a higher representation of mountain forest after ca. 1630 cal yr BP (Rodríguez & Behling 2011).

CONCLUSIONS

- The Cajanuma valley sediment core at 3285 m a.s.l. present a detailed palaeoenviromental record from the late Glacial to the Holocene, on the western slope of Podocarpus National Park of the eastern Cordillera in southern Ecuador.
- During the recorded late Glacial period and transition to the early Holocene, since ca. 16 000 to 10 500 cal yr BP, herb páramo, rich in Poaceae, Cyperaceae and Gentianaceae, associated with a high presence of *Huperzia* and *Isoëtes*, indicates cool and wet conditions.
- During the early to mid-Holocene from ca. 10 500 to 5600 cal yr BP, there was a high abundance of páramo vegetation followed by a slight expansion of mountain forest into higher elevations and a partial replacement of treeless páramo. High proportion of páramo was reached, mainly by high abundance of *Plantago rigida*, suggesting relatively cold conditions. The upper mountain rainforest (UMF) developed slightly due to higher abundance of *Symplocos* taxa. The high occurrence of the UMF at the coring site and the stronger decomposition of the organic material suggest relatively warm and also somewhat drier conditions.
- During the mid- to late Holocene (ca. 5600–1200 cal yr BP) there is a marked presence of páramo and subpáramo, while LMF decreased markedly. Even though, UMF presence remained relatively stable.
- The late Holocene period since 1200 cal yr BP was generally characterized by páramo vegetation. Even though, mountain forest and subpáramo presented a high abundance compared to the previous periods.
- Fires were rare during the late Glacial and became slightly frequent during the mid- late Holocene after 5600 cal yr BP. But since the late Holocene at about 1200 cal yr BP, fires became more common, reflecting fires of anthropogenic origin.

- The Upper Forest Line (UFL) dynamics fluctuated since the late Glacial to the Holocene. During the late Glacial, the UFL occurred at much lower elevation than today. During the early Holocene, the UFL position remains low. However, at the mid- to late Holocene, the UFL shifted upslope to higher elevations where it is today.

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