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Three millennia of vegetation and environmental dynamics in the Lagunas de Mojanda region, northern Ecuador

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ABSTRACT. The pollen record from Lagunas de Mojanda, located at 3748 m a.s.l. (northern Ecuadorian Andes) reflects the vegetation and climate dynamics for the last ca 3400 cal yr BP. Páramo vegetation has been the main vegetation type since the beginning of the record. At Lagunas de Mojanda, from the last ca 3400 to 2200 cal yr BP, grass páramo was well represented mainly by Poaceae (40%) and the occurrence of *Valeriana* (5%), while montane forest taxa were poorly represented and subpáramo taxa were rare. The vegetation composition suggests cool and humid conditions. Between ca 2200 and ca 1300 cal yr BP, montane rainforest and subpáramo taxa had a higher presence but páramo taxa remained the main vegetation type in the study area, suggesting cool climatic conditions. From ca 1300 to ca 500 cal yr BP, páramo vegetation remained stable, with higher presence of *Phlegmariurus* and *Isoetes*, suggesting cool and humid conditions. The last ca 500 cal yr BP generally show lower frequency of montane rainforest and subpáramo taxa. Páramo vegetation reached the highest share, with the presence of Poaceae, *Plantago* and *Ranunculus* suggesting a trend of peat bog drying. Fires were present during the whole record, perhaps human-caused, but the study area does not show great disturbance except from ca 1300 to 500 cal yr BP, a period of an evident higher influx of charcoal particles coincidentally with nearby ancient human occupation.

KEYWORDS: palynology, late Holocene, páramo, interandean mountain range, northern Ecuadorian Andes

INTRODUCTION

The northern Andes have very high floristic biodiversity and endemism, due to the high structural and geological diversity of the region (Mutke & Barthlott 2005). The Ecuadorian Andes have a variety of ecosystems, of which the páramo, with its unique flora and high biodiversity, is one of the most characteristic. The páramo is found in the upper region of the northern Andes, between the upper forest line at ca 3500 m a.s.l. and the permanent snow line at ca 5000 m a.s.l. (Castaño 2002, Hofstede et al. 2003). This region consists of rugged, mostly glacier-formed valleys and plains with a large variety of lakes, peat bogs and wet grasslands, intermingled in tropical alpine grassland with shrub and low-stature forest patches (Buytaert et al. 2006). The isolated and fragmented occurrence of páramo over the top of the Andean highlands and repeated events of geographical isolation and reconnection have promoted unique plant radiation events, and the physiographic diversity of the area promotes high speciation and exceptionally high endemism (Cuesta et al. 2017, Hughes & Eastwood 2006, León-Yánez et al. 2011). The páramo hosts about 5000 different plant species, of which 60% are endemic to this ecosystem (Buytaert et al. 2006).

Despite the area's remoteness and the cold and wet climate, human activity in the páramo

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is not uncommon. The human presence in the tropical Andes dates to ca 12 500 years BP, and its impact on the landscape cannot be underestimated (Goldberg et al. 2016, Valencia et al. 2016). In the late Holocene the fire signal was heavily influenced by human activities (Valencia et al. 2016). For the last 500 years the density of human populations has increased (Pohle 2008) and more than 90% of the Andes fires could be anthropogenic (Román-Cuesta et al. 2011). Human activities such as cultivation, intensification of livestock grazing, *Pinus* cultivation and tourism have increased recently in the páramo (Hofstede et al. 2002, Buytaert et al. 2006), disturbing that area. Like other mountain ranges, the páramo is also subject to global climate change, because its distribution has been closely linked to temperature and precipitation patterns (Halloy & Mark 2003, Sklenář & Balslev 2005). Climate change, like rising temperatures, will lead to moisture stress on Andean ecosystems and will force taxa to move upslope or downslope depending on their ecological preferences (Cuesta et al. 2017) and will increase their risk of extinction (Feeley & Silman 2010). Empirical data documented warming of ca 0.33° C per decade over a 25-year period in the tropical Andes (Vuille & Bradley 2000). The páramo ecosystem is threatened by increasing temperature and greater variation of precipitation (Valencia et al. 2016).

Knowledge from palaeoecological studies about past climate conditions and anthropogenic impacts can give insight into vegetation changes and climate dynamics, and in turn these data can be used to develop and inspire conservation strategies to protect Ecuadorian landscapes. Only a limited number of palaeoecological studies on the páramo of the Ecuadorian Andes are available; these can be broken down based on the floras to those in the northern and central Ecuadorian Andes (e.g. Colinvaux et al. 1988, Hansen et al. 2003, van der Hammen et al. 2003, Bakker et al. 2008, Jantz & Behling 2012) and those in the southern Ecuadorian Andes (Niemann & Behling 2008, Nieman et al. 2009, Brunschön et al. 2010, Villota et al. 2012). Those studies have shown marked changes in the past vegetation and climate, as well as changing environments, from the Late Glacial to the Holocene. The early Holocene in the Ecuadorian Andes is marked by alternating wetter and drier phases (Hansen et al. 2003, Brunschön & Behling 2009). The mid-Holocene is characterized by warmer and drier conditions, especially in the western and central Ecuadorian Andes (Hansen et al. 2003, Jantz & Behling 2012). The late Holocene is generally marked by wetter and slightly cooler climatic conditions (Niemann & Behling 2008).

In this paper we present the results of a palaeoecological analysis of a core from the Laguna de Mojanda complex in the northern Andes of Ecuador. Our main objective is to reconstruct the vegetation and environmental dynamics, including fires and human impacts occurring in this interandean region during the last three millennia, in order to compare the data with studies from the northern tropical Andes. For management and conservation purposes, reconstruction of the past environment will provide important background information on the stage of the vegetation and the potential impact of fire.

STUDY SITE

LOCATION

The Mojanda complex is at 3748 m a.s.l. (0°7′48.894N; 78°15′26.101W) within the páramo of Lagunas de Mojanda, a tourist site in an interandean mountain range 50 km north of Quito, between the provinces of Pichincha and Imbabura. The Mojanda area was declared a protected municipal area in 2015. The Mojanda-Fuya Fuya volcanic complex reaches 4362 m a.s.l. and consists of a stratovolcano (Mojanda) and a composite volcano (Fuya Fuya) (Robin et al. 1997, 2009). The Mojanda caldera is nowadays occupied by a large lake named Caricocha, also known as Laguna Grande de Mojanda (Fig. 1). The volcanism is mainly of pre-Holocene age, but the Upper Fuya Fuya volcanic centre is probably Holocene in age (Robin et al. 1997). The studied sediment core was extracted from the edge of a lake called Huarmicocha, close to Lake Cariococha (Fig. 1). The area is occupied by páramo vegetation and *Polylepis* forests. Some years ago the páramo used to be burned to allow grazing of cattle. The native pre-hispanic inhabitants, whose remains persist at the Cochasquí archaeological site (*cocha* meaning lake, and *qui* meaning middle in reference to the equator), lived downslope in the surroundings of the area. The Cochasquí occupation dates from 950 to 1550 A.D. (Ugalde 2015). The inhabitants cultivated

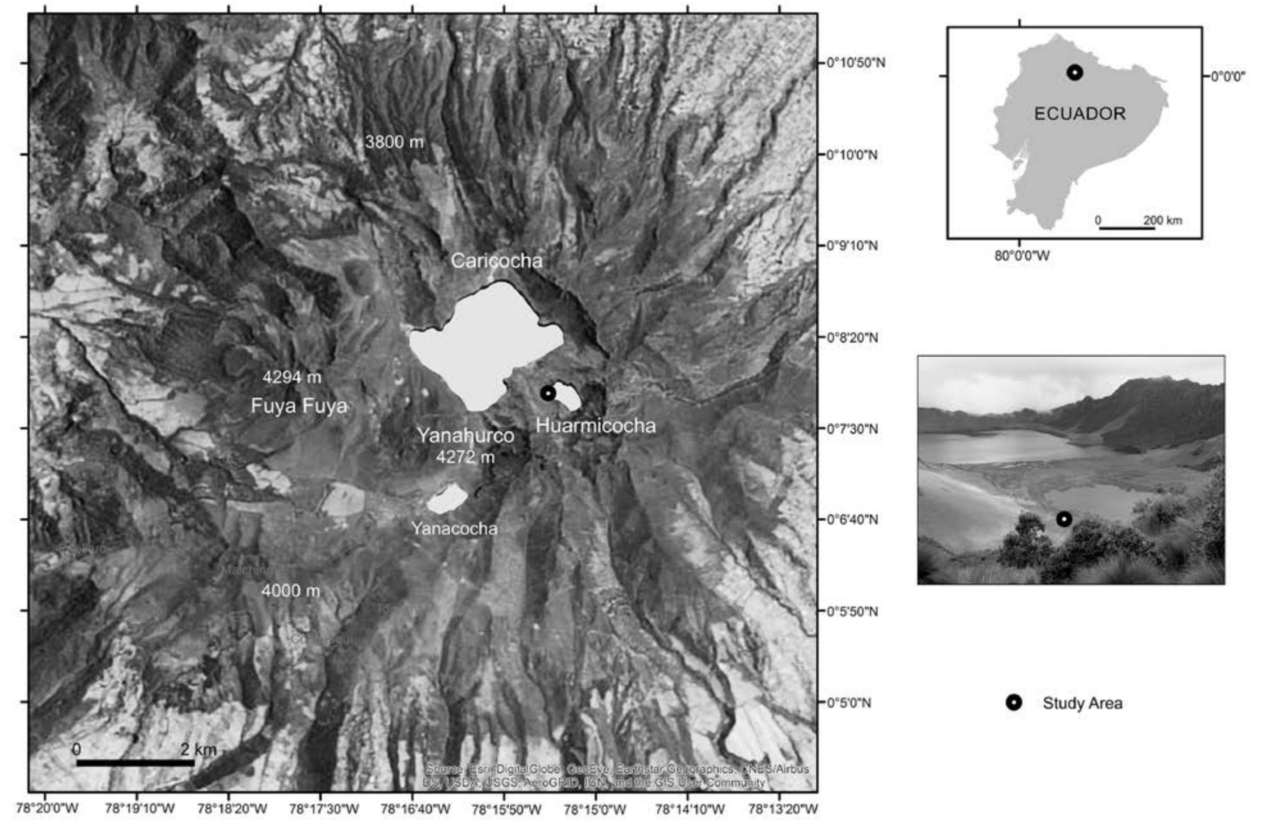

Fig. 1. Map showing the study site including the Laguna de Mojanda complex and photographs of the coring site at the edge of the small lake called Huarmicocha

potatoes and other Andean tubers as well as *Chenopodium quinoa*, *Lupinus* and *Zea mays*, used local fish and ducks from the lakes, and sometimes hunted deer and rabbits (CIDAP 2007, Ugalde 2015).

CLIMATE

Climate data from Lagunas de Mojanda are very sparse, but according to data from the weather stations at nearby sites (Tabacundo H. Mojanda M022 and Cochasquí-Hda. INAMHI M605) there is a drier season from July to September and two rainy seasons, one from October to November and a second from February to April (IEE et al. 2013). The average annual temperature is ca 12°C and the average annual precipitation is between 1000 and 1300 mm (Ecociencia 2008, IEE et al. 2013). To understand the climate regime at Lagunas de Mojanda it is necessary to consider the location of the area, which is in neither the east or nor the west Andean chains, but within the drier interandean valleys that connect the eastern and western ranges of the cordillera. Mojanda is closest to the western mountain chain of the Andes, which receives more precipitation at the western flank than at its eastern or inner flank, because a rain shadow is produced. Typically, precipitation over the eastern slope of the Andes is higher due to the easterly trade winds blowing from the Amazon basin (Emck 2007). The El Niño Southern Oscillation (ENSO) also affects the climate of Andean ecosystems at interannual timescales (Garreaud 2009, Vuille et al. 1999).

VEGETATION

The Mojanda lakes are surrounded by páramo vegetation and high Andean forest remnants possessing high biodiversity. Three main types of vegetation have been distinguished around the coring site and around the other lakes: lake marshes and bogs, tussock páramo vegetation and high mountain forest. Some of the most important trees are *Polylepis pauta* (Rosaceae), *Polylepis incana* (Rosaceae), *Hedyosmum angustifolium* (Chloranthaceae), *Miconia latifolia* (Melastomataceae), *Miconia salicifolia* (Melastomataceae), *Oreopanax andreanus* (Araliaceae), *Gynoxys acostae* (Asteraceae), *Vallea stipularis* (Elaeocarpaceae), and *Buddleja pinchinchensis* (Buddlejaceae). Some shrubs present in the area are *Valeriana microphylla* (Caprifoliaceae), *Loricaria thuyoides* (Asteraceae), *Pentacalia* *andicola* (Asteraceae), *Brachyotum laedifolium* (Melastomataceae) and *Otholobium brachystachyum* (Fabaceae). Near the lakes we found *Juncus arcticus* (Juncaceae), *Plantago rigida* (Plantaginaceae), *Carex pichinchensis* (Cyperaceae), and small herbs such as *Ranunculus* spp. (Ranunculaceae), *Phlegmariurus spp.* (neotropical segregate of *Huperzia*), and *Lachemilla*. In the tussock páramo the common herbs include *Calamagrostis intermedia* (Poaceae), *Cortaderia jubata* (Poaceae), *Valeriana adscendens* (Caprifoliaceae), Plantago spp., *Lupinus pubescens* (Fabaceae), *Azorella aretioides* (Apiaceae), *Ranunculus peruvianus* (Ranunculaceae), *Geranium* spp., and *Epilobium denticulatum* (Onagraceae). Many bryophyte species also occur in the study area.

MATERIAL AND METHODS

The Mojanda core (MOJ) was taken with a Russian corer from the marshes surrounding Lake Huarmicocha. The total length of the core is 200 cm. Sections 50 cm long were placed in split PVC tubes, covered with plastic film and stored in dark and cold (+4°C) conditions at the Pontificia Universidad Católica del Ecuador before processing.

Age estimates for the sediments were obtained by accelerator mass spectrometry (AMS) radiocarbon dating. Two subsamples of organic material were submitted to the Department of Geosciences, National Taiwan University. The ^{14}C dates were calibrated using the CalPal 2007 HULU curve of CalPal Online (Weninger et al. 2004) (Tab. 1).

For palynological analysis the Mojanda core was sampled at 4 cm intervals, yielding 52 subsamples (1.0 cm^3 each). All samples were processed by standard pollen analysis methods (Fægri & Iversen 1989). Additionally, for calculations of pollen and charcoal concentrations and influx, one tablet of exotic *Lycopodium clavatum* spores (20848 ± 1546) was added as a marker to each sample before treatment. A minimum 300 pollen grains were counted for each sample. The total pollen sum includes pollen of herbs, shrubs and trees, and excludes fern spores and pollen of aquatic taxa. The spores of Cyatheaceae, *Phlegmariurus*, *Isoetes*, *Jamesonia*, *Osmunda* and *Sphagnum* were counted and quantified as percentages of the total pollen sum.

The pollen and spore were identified against the reference collections held at the Pontificia Universidad Católica del Ecuador and the Department of Palynology and Climate Dynamics, University of Göttingen, as well as published literature (Hooghiemstra 1984).

Carbonized particles were counted up to a total count of 100 *Lycopodium clavatum* spores using Finsinger et al.'s (2008) technique and represented as concentration and influx. The counted charcoal particles were divided into two groups of different particle sizes (10–50 µm and 51–100 µm) to provide more detailed information about the local and regional fire history (Sadori & Giardini 2007).

Identified taxa were classified in ecological groups corresponding to the prevailing vegetation types: lower montane rainforest (LMF), upper montane rainforest (UMF), subpáramo and páramo.

Data calculations and illustration employed TILIA and TILIAGRAPH software, respectively (Grimm 1987). The obtained data were expressed as percentages in two different diagrams: the first is a detailed pollen diagram with the most representative taxa (Fig. 2); the second is a summary diagram of the pollen taxa grouped by vegetation type (Fig. 3). The CONISS program was used to make a cluster analysis of the pollen data and to generate a dendrogram (Grimm 1987) to help identify the pollen zones.

RESULTS

STRATIGRAPHY

The MOJ sediment core consists mainly of clay combined with volcanic ash and decomposed organic material. Between 200 and 103 cm core depth the sediment contains clay with decomposed organic material. From 103 to 71 cm the clay is mixed with some volcanic ash and little decomposed organic material. Volcanic ash is the main material between 71 and 69 cm. From 69 to 23 cm, clay occurs with volcanic ash and decomposed organic material. Finally, between 23 and 0 cm the core consists of clay with very little decomposed organic material and some plant remains.

CHRONOLOGY

The chronology of the Mojanda core is based on two radiocarbon dates (Tab. 1, Fig. 4). The dated sample near the base of the core at 199 cm depth is dated to 3380 ± 20 cal yr BP, indicating that the studied site contains deposits from the late Holocene. The two radiocarbon dates suggest that sediment accumulated continuously without gaps. The dating suggests an average

Table 1. List of AMS radiocarbon ^{14}C dates and calibrated ages from the Mojanda peat bog core (MOJ) using the CalPal 2007 HULU curve of CalPal software

Lab. code	Dated material	Core depth (cm)	^{14}C (yr BP)	1–σ (cal yr BP)
NTUAMS-1450	Organic material	126–127	2024 ± 12	1975 ± 20
NTUAMS-1451	Organic material	199–200	3144 ± 24	3380 ± 20

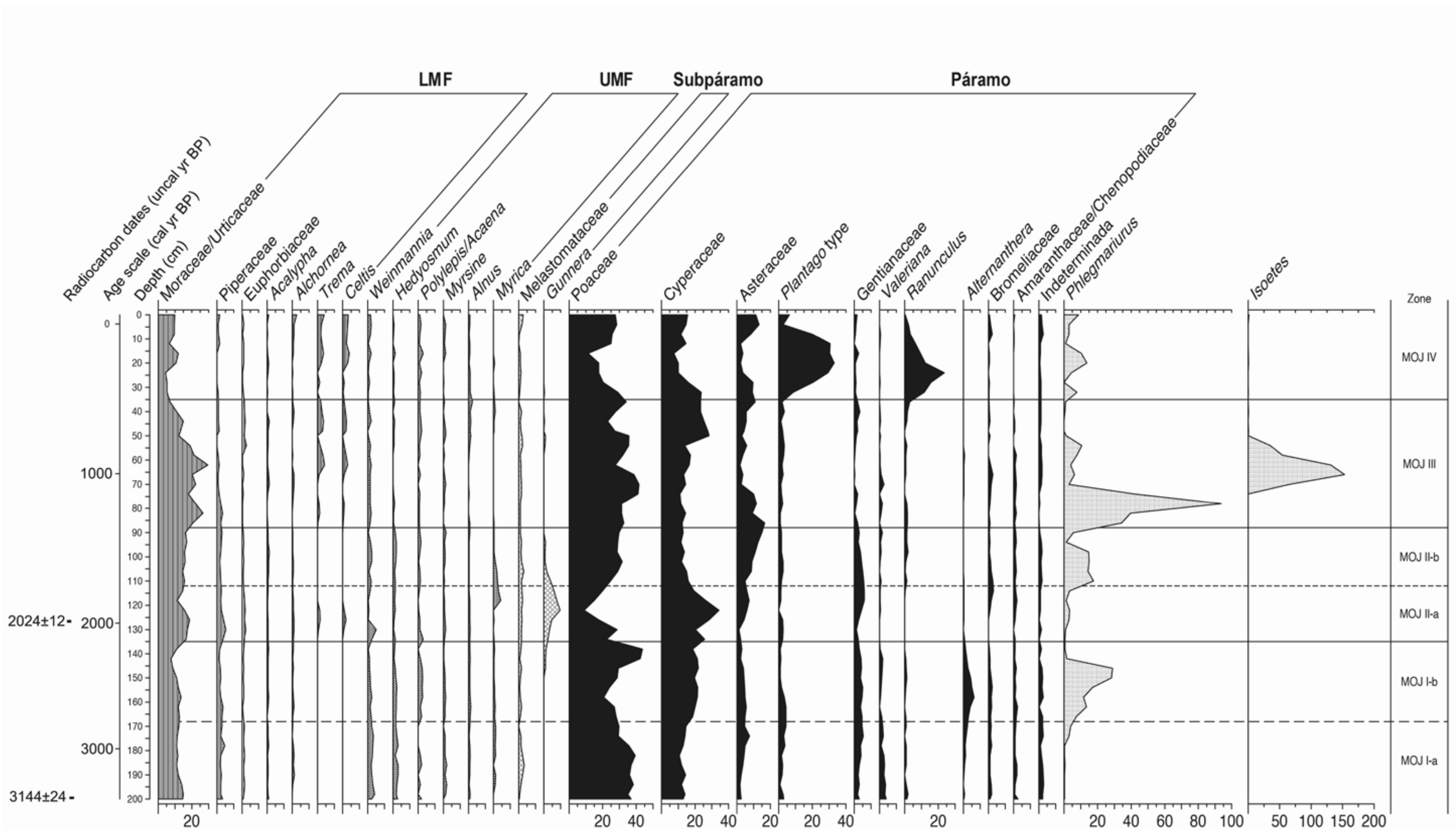

Fig. 2. Pollen percentage diagram of the Mojanda core (MOJ) showing radiocarbon dates (uncal yr BP), age scale (cal yr BP), depth (cm), selected fossil pollen and spore taxa grouped into lower montane rainforest (LMF), upper montane rainforest (UMF), subpáramo and páramo

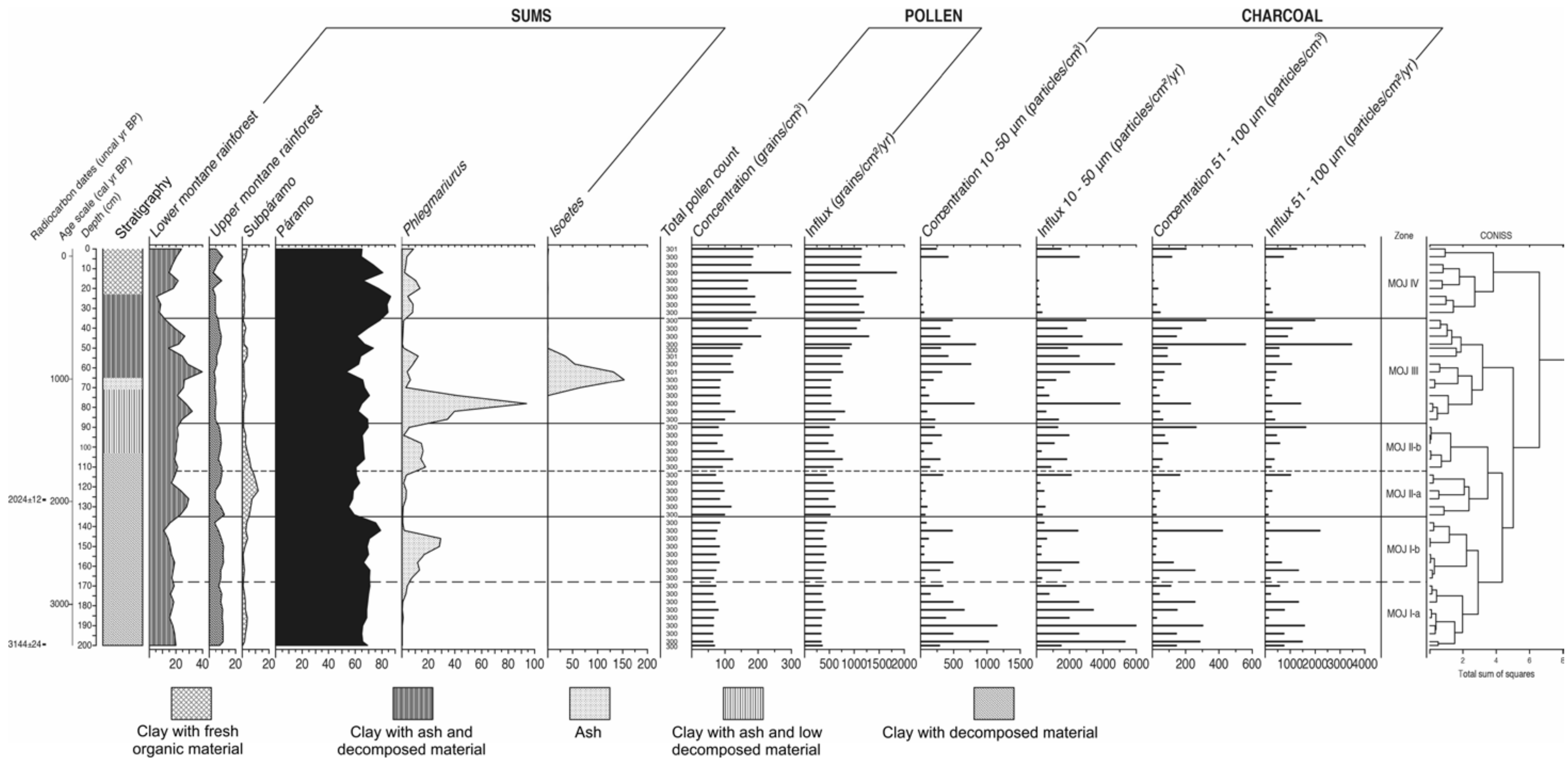

Fig. 3. Summary pollen percentage diagram of the Mojanda core (MOJ) showing radiocarbon dates (uncal yr BP), age scale (cal yr BP), stratigraphy, ecological groups, pollen sum, pollen concentration and influx, charcoal concentration and influx, and the CONISS dendrogram

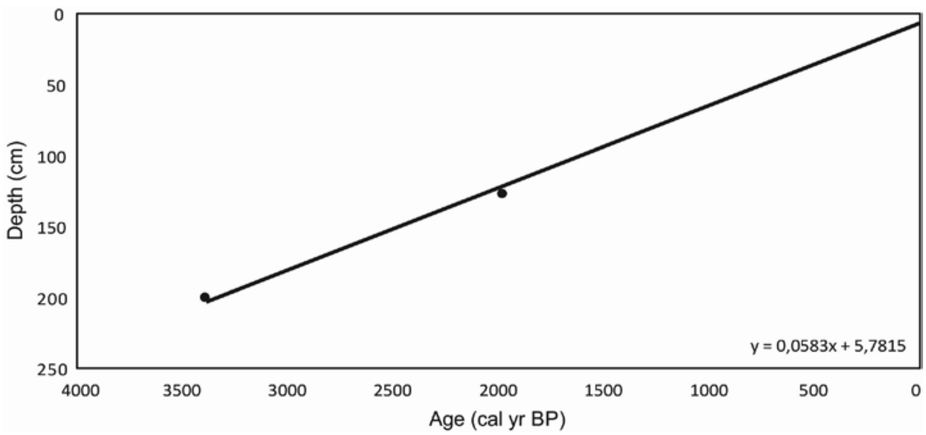

Fig. 4. Age-depth model of the Mojanda core based on two calibrated radiocarbon dates

sedimentation rate of 0.58 mm/yr, varying between 0.52 mm/yr from 3400 to 1980 cal yr BP and 0.62 mm/yr from 1980 to –60 cal yr BP.

DESCRIPTION OF THE POLLEN DIAGRAM

We identified 58 pollen taxa and 11 spore taxa. The pollen diagram displays only the 25 most common and important pollen and spore taxa (occurrence >1%; Fig. 2). The summary pollen diagram groups the pollen and spores into ecological groups: lower montane rainforest (LMF), upper montane rainforest (UMF), subpáramo, páramo and *Phlegmariurus* and *Isoetes* spores. The diagram also shows the concentration and influx of pollen and charcoal particles.

Cluster analysis by CONISS demarcates four main pollen zones: MOJ I-a and MOJ I-b; MOJ II-a and MOJ II-b; MOJ III and MOJ IV.

The pollen concentrations (6500–29 800 grains cm^{-3}) and pollen influx (330–1800 grains cm^{-2} yr^{-1}) remain relatively stable but increase towards the upper part of the core (zone MOJ III). The charcoal concentrations in the two counted fractions vary from 1250 to 115 000 particles/cm^3 (10–50 µm) and from 230 to 55 800 particles/cm^3 (51–100 µm). The charcoal influx for both counted fractions varies from 110 to 5900 particles/cm^2/yr (10–50 µm) and from 13 to 3400 particles/cm^2/yr (51–100 µm). The concentration and influx of both particles are highest in zones MOJ I-a and MOJ III (Fig. 3).

Subzone MOJ I-a (200–170 cm, ca 3400–2800 cal yr BP, 9 samples) shows a value of 20% for lower montane rainforest (LMF) taxa, dominated by Moraceae/Urticaceae (12–15%) and Piperaceae (2–3%); Euphorbiaceae type, *Acalypha* and *Alchornea* pollen occur at low values (1% each). Upper montane rainforest (UMF) taxa have a 10% share, consisting mostly of *Weinmannia* and *Hedyosmum* (2–4%) and *Polylepis/Acaena* (2%); *Myrsine*, *Alnus*, and *Myrica* pollen have stable values of 1% each. The low share of subpáramo (3%) consists mainly of Melastomataceae (3%), reaching its highest value of the whole record. This subzone is also marked by high values of páramo pollen (65–70%), represented mainly by Poaceae (30–40%) and Cyperaceae (15%). Pollen taxa of Asteraceae, *Plantago* type Gentianaceae (2–5% each) and *Valeriana* (4%) have their highest values of the record in this zone. *Ranunculus*, *Alternanthera*, Bromeliaceae, and Amaranthaceae/Chenopodiaceae have small shares (1%) in this subzone, as do *Phlegmariurus* spores (4%).

Subzone MOJ I-b (170–138, ca 2800–2200 cal yr BP, 8 samples) is marked by stable shares of LMF taxa (20%), including Moraceae/Urticaceae (9–13%), Piperaceae (2–3%), Euphorbiaceae type, *Acalypha*, and *Alchornea* (1% each). The abundance of UMF taxa remains stable at 10%, with *Weinmannia*, *Hedyosmum* and *Polylepis/Acaena* (2% each), and *Myrsine*, *Alnus*, and *Myrica* (1% each). Subpáramo pollen taxa decreases slightly to 2%, with mainly Melastomataceae (2%). The representation of páramo pollen increases slightly at 70%, with higher values for Poaceae (45%) at the upper part of the subzone; Cyperaceae (20%) reaches its highest value in this subzone. Pollen of Asteraceae, *Plantago* type, Gentianaceae, and *Valeriana* show stable values (5% each); pollen of *Ranunculus*, Bromeliaceae, and Amaranthaceae/Chenopodiaceae each have 1% shares. The highest share of *Alternanthera* (5%) was recorded in this subzone. Spores of *Phlegmariurus* increase markedly (15–30%).

Subzone MOJ II-a (138–114 cm, ca 2200–1700 cal yr BP, 6 samples) is characterized by a high frequency of LMF taxa (20–25%), attributable to the shares of Moraceae/Urticaceae (15–20%), Euphobiaceae type, *Celtis* and *Trema* pollen (2% each); the highest values for Piperaceae were recorded in this zone. *Acalypha* and *Alchornea* pollen are stable at 1%. The percentage of UMF vegetation decreases slightly from 10% in the previous subzone to 5%, mostly due to a decline of *Hedyosmum* and *Polylepis/Acaena* (1% each). *Weinmannia* (2–5%) is more frequent in this subzone, reaching its highest values for the whole record. *Myrsine* pollen has low shares (1–2%). *Myrica* has its highest shares (2–5%) at the upper part of this subzone. Subpáramo has higher shares here (5–10%) than in the other subzones, formed mainly of *Gunnera* (10%) and Melastomataceae (2%). The abundance of páramo pollen taxa slightly decreases (60%) from the value in the previous subzone; it is represented by low shares of Poaceae (20%) and *Plantago* type (2%); pollen of *Valeriana*, *Ranunculus*, and *Alternanthera* taxa do not appear, but Cyperaceae pollen has a higher share (35%). Pollen of Asteraceae (6%), Gentianaceae (6%), and Bromeliaceae (3%) increase slightly at the upper part of the subzone. Amaranthaceae/Chenopodiaceae pollen have a stable share (1%). The share of *Phlegmariurus* spores is low (3%) in this subzone.

Subzone MOJ II-b (114–90 cm, ca 1700–1300 cal yr BP, 6 samples). LMF taxa remain stable (20%), consisting mainly of Moraceae/Urticaceae (15%), Piperaceae (2–3%), *Acalypha* and *Alchornea* (1% each). However, Euphobiaceae type has a low share (1%), and *Celtis* and *Trema* pollen do not appear. The values for UMF taxa slightly increase at 10%, represented by *Weinmannia*, *Hedyosmum*, *Polylepis/Acaena*, *Myrsine*, and *Myrica* (1–2% each). *Alnus* pollen is absent. The percentages for subpáramo pollen taxa decrease slightly (6%), with Melastomataceae (2%) and *Gunnera* (1–4%). Páramo pollen taxa show higher values (65%) and are especially well represented by Poaceae (30%) and Asteraceae (15%). *Valeriana* and *Ranunculus* pollen increase slightly (1–2%). Pollen of Cyperaceae (15%) and Bromeliaceae (1%) show lower values. *Plantago* type (2%), Gentianaceae (6%), and Amaranthaceae/Chenopodiaceae (2%) pollen have stable shares. Spores of *Phlegmariurus* increase in this subzone (15%).

Zone MOJ III (90–36 cm, ca 1300–500 cal yr BP, 14 samples) is characterized by higher representation of LMF pollen (20–35%), due to the higher shares of Moraceae/Urticaceae (20–25%), Euphorbiaceae type (2%) and *Trema* (2–4%), which reach their highest values at this zone. *Celtis* pollen (2%) shows high shares in this zone. Pollen of Piperaceae have lower shares (1–2%), and *Acalypha* and *Alchornea* are stable at 1%. UMF taxa remain stable at 10%, with *Weinmannia*, *Polylepis/Acaena*, and *Myrsine* (1–2%). Pollen of *Hedyosmum*, *Alnus* and *Myrica* (0–1%) decrease slightly. The share of subpáramo taxa falls steeply to 3%, with *Gunnera* (0–1%). The share of Melastomataceae pollen remains stable at 2%. Páramo pollen taxa increase their shares slightly (65–80%), including Poaceae (30–40%) and Cyperaceae (15–25%) in the upper part of the zone, and also *Plantago* type (3%). Pollen of Gentianaceae, *Valeriana*, and Amaranthaceae/Chenopodiaceae decrease slightly (1–2% each). Pollen of Asteraceae (15%) and *Ranunculus* and Bromeliaceae (1–2% each) remain stable. *Phlegmariurus* reaches its highest share (50–90%) in the lower part of the zone, and *Isoetes* (100–150%) in the middle of the zone (Fig. 2).

Zone MOJ IV (36–0 cm, ca 500 cal yr BP to present, 9 samples) is characterized by a lower representation of LMF pollen (20%), due to lower shares of Moraceae/Urticaceae (5–10%), Piperaceae and Euphorbiaceae type (1%). High values were recorded for pollen of *Alchornea* (2%) and *Trema* (4%). *Celtis* pollen reaches its highest values for the whole record (4%) in the upper part of this zone. Pollen of *Acalypha* remains stable (1%). UMF pollen taxa have a stable share (10%), with *Weinmannia* (2%), *Hedyosmum* (1%), *Polylepis/Acaena* and *Myrsine* (1–2% each), and *Alnus* (1%). Subpáramo taxa remain stable at 3%, comprised primarily of Melastomataceae (1–2%). Páramo taxa slightly increase to 85%, mainly represented by *Plantago* type (20–30%) and *Ranunculus* (10–20%) pollen, which reach their highest values for the record in this zone. Pollen of Poaceae (20–30%), Cyperaceae (10–20%) and Asteraceae (5–10%) have lower shares in this zone. Pollen of Gentianaceae and Bromeliaceae have stable shares (1–2% each). The share of *Phlegmariurus* spores decreases (5–10%).

INTERPRETATION AND DISCUSSION

The pollen record from Mojanda (MOJ) at 3748 m a.s.l. reflects the local and regional vegetation dynamics of the studied area. The area of the peat bog from which the sediments were recovered is a narrow fringe (less than 100 m wide) at the western edge of Lake Huarmicocha. The lake and its surrounding peat bog occupies ca 6.5 ha. The depression within which the Mojanda lakes and the peat bog sit corresponds to the old Mojanda caldera; the lakes are surrounded by very rugged terrain formed over volcanic debris and lava flows; steep hillsides of several volcanic summits increase the elevation from 3700 to 4000 m a.s.l. in less than 500 m, and even to 4300 m in 1 km. Therefore it is inferred that the sedimentary record recovered from the peat bog reflects mostly local vegetation dynamics and to a lesser extent regional dynamics (Jacobson & Bradshaw 1981). The fossil pollen data from MOJ suggest that for the last ca 3400 cal yr BP the vegetation dynamics were relatively stable, with páramo taxa as the main vegetation type around the coring site. From ca 2200 to ca 500 cal yr BP the vegetation dynamics underwent mild fluctuations: the abundance of montane rainforest slightly increased, correlated with climatic fluctuations.

Late Holocene from ca 3400 to ca 2200 cal yr BP (zone MOJ Ia-b)

During this period, páramo taxa, especially grassland páramo taxa, are well represented in the pollen record, suggesting that it was the main vegetation type around the Mojanda lakes. There was a low share of montane rainforest taxa, and subpáramo taxa were rare. This vegetation pattern probably reflects cool and humid conditions such as those of the present time. The presence of clay and organic material points to the presence of standing water in part of the basin (Hansen 1995, Wille et al. 2002), and sediment accumulation with high production of biomass (Bakker et al. 2008) suggests a transition from an open body of water (lake) to the peat bog as in the present day.

LMF is represented mainly by Moraceae/Urticaceae, whose ecological distribution is at lower elevations (Jørgensen & León-Yánez 1999). Moraceae/Urticaceae is anemophilus and can be overrepresented in the pollen record (Bush & Rivera 2001); it is an example of the long-distance pollen transport that has been studied along the Andes (Reese & Liu 2005, Ortuño et al. 2011, Jantz et al. 2013). The different taxa shown in the pollen record of the UMF ecological group indicate that it was diverse during the late Holocene. The presence of *Weinmannia* and *Hedyosmum* suggests humid climate. The low presence of *Polylepis* at the end of this period suggests that small populations surrounded the study area. A study by Urrego et al. (2011) suggests that *Polylepis* woodlands grew close to the lakes, as occurs at the Mojanda lakes now. Subpáramo taxa are poorly represented, suggesting that shrub vegetation, probably Melastomataceae, existed near the coring site. The share of páramo vegetation was higher during this period. The more than 50% share of Poaceae pollen and small amounts of Cyperaceae and *Valeriana* pollen indicate that the vegetation of Lagunas de Mojanda was grass páramo (Marchant et al. 2002), suggesting local conditions cooler than those of today. The low amounts of Cyperaceae and *Alternanthera* pollen may indicate the presence of standing water (Bakker et al. 2008). Poaceae and Cyperaceae are the dominant taxa and other páramo taxa are less represented, suggesting that the páramo was species-poor locally. The presence of *Phlegmariurus* at the end of this period testifies to cold wet páramo (Hansen et al. 2003).

From ca 3400 to ca 2800 cal yr BP, high influx of charcoal of both fractions indicates that fires occurred in the study area. Fires have occurred in the páramo during the whole Holocene (Sarmiento 2002). Most páramos in Ecuador are burned regularly, especially where they are used for livestock grazing (Laegaard 1992). A study by Niemann et al. (2009) revealed high charcoal influx at ca 3680 cal yr BP, accompanied by a higher share of Poaceae as a result of the burning.

Late Holocene from ca 2200 to ca 1300 cal yr BP (zone MOJ IIa-b)

This period of the late Holocene at Mojanda is characterized by a slightly higher share of montane rainforest. Subpáramo reaches its highest values for the whole record during this period. At the same time, the share of páramo vegetation declines slightly, but it remains the main vegetation type at the Lagunas de Mojanda.

LMF slightly increased, mainly due to a higher share of Moraceae/Urticaceae and the low abundance of Piperaceae, Euphorbiaceae and *Celtis* and *Trema* at the beginning of this period. The presence of Piperaceae probably suggests moister conditions (Marchant et al. 2002). UMF was stable, with a slight increase of *Weinmannia* and *Myrica* at the beginning of the period. The higher occurrence of Piperaceae and *Myrica* suggests humid conditions (Marchant et al. 2002). The slight and temporary increase of LMF and the stable proportion of UMF suggest better establishment of montane rainforest vegetation close to the coring site. During this period there is high abundance of subpáramo taxa, mainly *Gunnera* spp. pollen, perhaps attributable to humid locations (Bakker et al. 2008). The somewhat lower frequency of páramo taxa is due mainly to the relatively lower abundance of Poaceae, although Cyperaceae, Asteraceae, Gentianaceae, and Bromeliaceae slightly increased during this period. The higher presence of Asteraceae and Gentianaceae coupled with smaller amounts of charcoal may indicate a local reduction of human activity. The share of *Phlegmariurus* was stable during this period. The values of charcoal influx of both particle sizes, lower than in the previous period, suggest low frequency of fires in the study area.

Late Holocene from ca 1300 to ca 500 cal yr BP (zone MOJ III)

This period is marked by a slightly higher frequency of montane rainforest taxa, especially LMF. Subpáramo decreased and reached its lowest share for the whole record. Páramo vegetation remained stable. *Phlegmariurus* and *Isoetes* spores reached their highest shares during this period, probably suggesting cool and humid conditions in the study area.

LMF vegetation increased slightly, mainly due to the relatively high share of Moraceae/Urticaceae, and also the greater abundance of *Trema* which probably suggests disturbance of the Laguna de Mojanda area. As well as *Trema*, *Celtis* is considered a good indicator of disturbance (Marchant et al. 2002). *Acalypha* was slightly more frequent during this period. UMF taxa slightly increased from ca 1000 to 500 cal yr BP, essentially in the increased occurrence of *Alnus*. The presence of a pioneer tree, *Alnus*, which could have formed swampy forest on wet soils along watercourses, together with the presence of *Hedyosmum*, indicates that relatively wet conditions continued. In this period subpáramo taxa strongly decreased and reached their lowest share for the whole record. The pollen record shows a stable share of páramo vegetation, the main components of which were Poaceae, Cyperaceae, Asteraceae and *Plantago*. Grassland páramo is associated with a high share of *Phlegmariurus* (ca 1300–1100 cal yr BP) and later *Isoetes* (ca 1100–700 cal yr BP), suggesting cool and humid local conditions. Especially *Isoetes* occurs mostly submerged at the edges of páramo lakes and is a good proxy for the presence of a shallow lake (Bosman et al. 1994, Gosling et al. 2008).

During this period the evidence of both local and regional fires increased, as shown by the higher influx of carbonized particles. Higher frequency of fires and the presence of *Trema* and *Celtis* pollen taxa probably suggest an increase of disturbed areas due to human activities.

Late Holocene from ca 500 cal yr BP to present time (zone MOJ IV)

This most recent period of the Holocene shows a variable and in general lower frequency of montane rainforest taxa. Subpáramo taxa remained stable though sparsely represented. Páramo taxa reached their highest share for the whole record, confirming that páramo vegetation has been the main vegetation type in the study area since ca 3400 cal yr BP.

LMF decreased, particularly Moraceae/Urticaceae, but *Trema* remained stable and *Celtis* even increased; *Alchornea* became slightly more frequent in the forest during this period. UMF showed a low share with some fluctuations, mainly in the higher frequency of *Polylepis* and low frequency of *Hedyosmum*, *Alnus* and *Myrica*. Subpáramo taxa remained stable, as in the previous period. The higher share of páramo taxa was achieved mainly due to *Plantago* and *Ranunculus* reaching highest abundance. *Plantago* forms cushion mires at high elevations even on the superpáramo (Niemann & Behling 2008, Bosman et al. 1994), and some species of *Ranunculus* cover drying ponds in páramo areas. *Phlegmariurus* was present at low frequency and *Isoetes* was absent during this period, probably indicating desiccation of waterbodies. A study by Brunschön et al. (2010) at Laguna Campana (at ca 2488 m a.s.l. in the south-eastern Ecuadorian Andes) also reflects that conditions were dryer in the lagoon from 1900 to 1950 A.D.

The human presence in the tropical Andes began at the early Holocene but for the last 500 years or so there has been an evidently low influx of carbonized particles of both size ranges at Lagunas de Mojanda, indicating that fires have been rare and that the impact of human activity has been low – that is, until the last few decades, when an increase of fire events became apparent. Using only charcoal data it is impossible to separate natural from anthropogenic fires, but there clearly was a lower incidence of human activity at the site beginning at ca 500 cal yr BP, which coincides with the end of occupation at Cochasquí (Ugalde 2015). Fires are unlikely to occur naturally at present because regular rains keep the vegetation wet and there are few sources of natural ignition (Di Pasquale et al. 2008); the fires that occur are likely to be anthropogenic in origin.

COMPARISON WITH OTHER STUDY SITES

Here we compare the Mojanda (MOJ) pollen record from the northern Ecuadorian Andes with nearby sites located in the Ecuadorian, Colombian, Peruvian, and Bolivian Andes.

The Mojanda (MOJ) pollen record suggests that the climate during the last 3400 cal yr BP was relatively cool and moist. This result can be compared with numerous studies done throughout South America. As noted by Marchant & Hooghiemstra (2004), the last 4000 yr BP of South America presents a more humid climate than in other regions such as Africa.

Late Holocene from ca 3400 to ca 2200 cal yr BP

During this period, pollen records throughout the Ecuadorian Andes mostly present cooler and moister conditions. As shown in the Guandera Biological Reserve (northern Ecuadorian Andes), from ca 5300 to 2100 cal yr BP the presence of peat bog plants indicates cool and moist conditions (Bakker et al. 2008). In the pollen record from Laguna de Anteojos in the central Ecuadorian Andes, between ca 4100 to 2100 cal yr BP the presence of páramo taxa shows cooler conditions (Villota et al. 2014). A study by Wille et al. (2002) at Pantano de Pecho reflects cooler climatic conditions since ca 3700 cal yr BP. Many palaeoecological studies from the southern Ecuadorian Andes present vegetation and climatic dynamics similar to those in the Mojanda record. For example, a study by Hansen et al. (2003) at Laguna Chorreras shows high abundance of *Sphagnum* followed by cool and moister conditions after ca 4000 cal yr BP. Pollen records from Podocarpus National Park reflect a vegetation and climate reconstruction similar to that from the Mojanda pollen core. The Laguna Ravadilla de Vaca pollen record shows that Poaceae was the main vegetation taxa from ca 3600 cal yr BP to the present (Niemann et al. 2009).

Like the pollen records from the Ecuadorian Andes, the vegetation at numerous Colombian sites record a shift between 4000 and 3500 cal yr BP to relatively moist environmental conditions (Marchant et al. 2001). This is evident in the Llano Grande II record, which after 3000 uncal yr BP shows a cool and wet environment (Velásquez 2005). Several studies from the central Peruvian Andes show in detail declining temperatures from ca 3000 to ca 1000 yr BP (Hansen & Rodbell 1995). For example, the pollen record at Laguna La Compuerta (western Peruvian Andes) at ca 2600 cal yr BP shows a cooling event with a wetter oscillation (Weng et al. 2006). Wetter conditions have persisted from 3900 yr BP to the present day on the Bolivian Altiplano (Abbott et al. 2000). This is also seen in the pollen record of Lake Titicaca, where wetter environmental conditions have been dated slightly earlier to 3900 years BP (Argollo & Mourguiart 2000).

Late Holocene from ca 2200 cal yr BP to present

During this period the pollen records from the northern and southern Ecuadorian Andes show mostly cooler and moister climatic conditions. A study by Colinvaux et al. (1988) from Laguna Yaguarcocha and Yambo (northern Ecuador) suggests wet conditions from ca 1600 to 800 yr BP. In southern Ecuador the record from Laguna Zurita shows high occurrence of Cyperaceae and *Isoetes* before 1200 cal yr BP, which indicates the presence of a marshy lake shore and cooler conditions (Niemann & Behling 2010).

Fires

Fires during the late Holocene are evident all over the northern Andes, as human activity in the highlands is not uncommon. The human presence in the upper Andes dates to prehistoric times (Chepstow-Lusty et al. 1996). The first increased presence of humans at the Ecuadorian Andes appears after 9000 yr BP according to the Inga archaeological record (Bell 1971). Palaeoecological studies of the southern Ecuadorian Andes show that fires occurred in the páramo region during the whole Holocene (Niemann & Behling 2008). The pollen record from Lake Surucucho in Cajas National Park shows a strong increase in fires during the late Holocene (Colinvaux 1997).

CONCLUSIONS

– Páramo vegetation is well represented during the whole record, mainly with Poaceae, Cyperaceae, Asteraceae, *Plantago*, Gentianaceae, and *Ranunculus*, confirming that páramo vegetation has been the main type in the study area for the last ca 3400 cal yr BP.

– Montane rainforest is relatively rare through the whole record. From ca 2200 to ca 500 cal yr BP its share was slightly higher, suggesting better establishment of montane rainforest in areas near the coring site.

– Most of the fires during the late Holocene probably were human-caused. At present, natural fires are not likely to occur because regular rainfall keeps the vegetation wet. The charcoal record indicates two periods, from ca 3399 to ca 2800 cal yr BP and from ca 1300 to ca 500 cal yr BP, in which fires were frequent around the study area.

– Disturbance is not highly evident during the whole record, but from ca 1300 to ca 500 cal yr BP the higher influx of carbonized particles and the presence of *Trema* and *Celtis* pollen taxa suggest disturbance of forested areas.

– Based on the vegetation dynamics during the last three millennia, permanent cool and moist conditions are reflected in the study area. The last 500 years show marked shifts in the vegetation composition, perhaps reflecting desiccation of lakes at the coring site, related to regional changes in climate toward a drier situation.

– The study results underline the importance of maintaining the study area as a protected municipal area in order to conserve the natural páramo and forest vegetation around Lagunas de Mojanda, avoiding anthropogenic impacts such as fires which may severely alter the vegetation.

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