

LATE QUATERNARY VEGETATION, CLIMATE, AND FIRE DYNAMICS: HUMAN IMPACT AND EVIDENCE OF PAST *POLYLEPIS* POPULATIONS IN THE NORTHERN ANDEAN DEPRESSION INFERRED FROM THE EL CRISTAL RECORD IN SOUTHEASTERN ECUADOR

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Abstract. Late Pleistocene and Holocene vegetation, climate, and fire dynamics, as well as human impact, were studied in the El Cristal region, which is part of the Andean Depression in southeastern Ecuador. The sediment core from a small basin at 2056 m a.s.l. was analyzed by pollen and charcoal analysis and dated by six radiocarbon dates. The record indicates that during the late Pleistocene (*ca.* 19 750–12 500 cal yr BP) the Upper Mountain Rainforest (UMF), with some smaller areas of páramo and subpáramo were the main vegetation type in the study area. Additionally, there is evidence for *Polylepis* woodland in the region during this period, which does not exist in the area today. During the transition from the late Pleistocene to the early and mid-Holocene between *ca.* 12 500 to 3600 cal yr BP, there is a significant presence of mountain rainforest and stable proportions of subpáramo and páramo taxa. The early Holocene from *ca.* 11 500 to 7800 cal yr BP is characterized by UMF vegetation at the study site. *Polylepis* became more frequent and reached its maximum. During the mid-Holocene between 7800 to 3600 cal yr BP, the composition of the UMF changed. *Polylepis* decreased after *ca.* 4000 cal yr BP, probably due to higher fire frequency. During the mid- to late Holocene, human landscape disturbance is evident, especially between *ca.* 2000 and 1380 cal yr BP, with Asteraceae, *Muehlenbeckia/Rumex*, *Osmunda* and *Huperzia* all increasing in abundance. The late Holocene, from *ca.* 1380 cal yr BP, was characterized by an increased abundance of páramo taxa and a decrease in mountain rainforest taxa. The expansion of grassland during the late Holocene is interpreted as a result of an increase in human activity, which limited forest vegetation to isolated patches. However, between *ca.* 1200 and 900 cal yr BP the UMF expanded, probably due to forest recovery after the high frequency of fire. Between *ca.* 900 cal yr BP to present times, the UMF vegetation decreased markedly and grasslands (páramo taxa) expanded.

Key words: Late Pleistocene, Holocene, palynology, páramo, mountain rainforest, fire history, human impact, *Polylepis*, Andean Depression, southern Ecuador.

INTRODUCTION

The tropical northern Andes are among the hot spots of global vascular plant diversity due to its high structural and geological diversity (Mutke & Barthlott 2005). Mountain forests in particular contribute to this extraordinarily high level of biodiversity (Richter *et al.* 2008). According to Webster (1995), half of all species of the flora of Ecuador are found in the mountain rainforests. Despite the significance of these mountain ecosystems in terms of biodiversity, the mountain rainforests of the Ecuadorian

Andes represent the most threatened (Myers *et al.* 2000) and poorly studied habitat (Gentry 1995, Webster 1995, Beck *et al.* 2008a). Official sources report that of all South American countries, Ecuador currently suffered the highest deforestation rate of 198 000 ha year⁻¹ between 1990 and 2005 (FAO 2006), because of its long occupation history and increasing human impact during recent decades (Dodson & Gentry 1991). Even during pre-Columbian times, a long-lasting deforestation in the mountain regions contributed to the reduction of forest areas (Wunder 2000). The páramo vegetation is thought to have expanded downslope, while extensive burning and grazing prevented forest recovery.

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Some researchers suggest that the grass páramo below 4300–4100 m represents, at least partially, secondary vegetation in formerly forested areas (Ellenberg 1979, Lægaard 1992). Studies by Podwojewski *et al.* (2002) suggest that páramo areas, especially at lower altitudes, are subject to overgrazing, fire, or cultivation. In general, human activity has a strong impact on the vegetation of the Ecuadorian Andes, as land use patterns frequently involve grazing, burning, and deforestation (Ramsay & Oxley 1996).

In this context, the knowledge of palaeoecological conditions is very important, as the composition of past natural vegetation as well as pre-Columbian anthropogenic landscapes and climate conditions are often not well known. Despite the importance of this knowledge, only a limited number of palaeoecological studies are available from the Ecuadorian Andes, mainly because of the steep slopes and scarcity of natural archives in this region (Bush *et al.* 2007). In the Andean Depression region, which includes our study area, studies on vegetation history and upper forest line changes are increasing. Pollen records from the southern Ecuadorian Andes are provided by the German-Ecuadorian Research Unit (www.tropicalmountainforest.org), focusing on the Podocarpus National Park (PNP) area and its surroundings. These studies demonstrate marked past vegetation changes, as well as climate changes. The glacial period in general is marked by cold and wet conditions. A warm and dry early to mid-Holocene is shown, while wetter conditions are recorded in the late Holocene. The available studies also demonstrate changing environments, e.g. by differing fire intensity and human impact regimes, and their influence on local and regional ecosystem dynamics during the late Quaternary (Niemann & Behling 2008, 2010; Brunschön & Behling 2009, 2010; Niemann *et al.* 2009, 2013; Brunschön *et al.* 2010; Jantz & Behling 2012, Rodríguez & Behling 2011, Villota *et al.* 2012).

The upper forest line (UFL) is the maximum elevation where continuous forest occurs (Bakker *et al.* 2008). In the Andean Depression region, the UFL is highly variable and still poorly defined compared with other UFLs in the Andes. In the Andean Depression, the UFL is comparatively low between 2800 and 3300 m a.s.l. (Richter & Moreira-Muñoz 2005, Beck *et al.* 2008b), while (e.g.) north of the Andean Depression the UFL is located at ~3600 m (Richter *et al.* 2008, Moscol Olivera & Hooghiemstra 2010). In the Andean Depression the UFL is

characterized by high species richness, consisting of about 20 tree species (e.g. *Weinmannia*, *Clusia*).

Of particular interest is the genus *Polylepis*, often forming the UFL in the northern and central Andes (Wille *et al.* 2002, Hansen *et al.* 2003, Bakker *et al.* 2008), but interestingly missing in the Andean Depression (Beck *et al.* 2008c, Peters 2009). *Polylepis* is represented by eight species distributed throughout the Ecuadorian Andes (Simpson 1979, Schmidt-Lebuhn *et al.* 2006). Apparently, *Polylepis* forest would naturally occur primarily on the slopes and more protected ridges of the area, and might have had a greater range in the past (Simpson 1986, Romoleroux 1992, Kessler 1995, Purcell & Brelsford 2004). Moisture and temperature have been identified as controlling factors on *Polylepis* distribution in the Andes (Rada *et al.* 1996). Moisture from clouds permits *Polylepis* to survive in areas of otherwise low moisture availability (Gosling *et al.* 2009a). However, frequent strong winds and the extremely high precipitation are thought to be the main factors for the absence of *Polylepis* on the eastern Andean slope in Ecuador, because the genus tends to avoid perhumid regions (Kessler 1995, Richter & Moreira-Muñoz 2005). The *Polylepis* forests represent one of the world's most threatened ecosystems (Kessler 2006). Indeed, the current patchy distribution pattern of *Polylepis* woodland has been widely attributed to human activity with the onset of fire (Kessler 2002, Renison *et al.* 2002, Cierjacks *et al.* 2008, Urrego *et al.* 2011). Due to its patchy distribution and location at the highest elevations of the forest limit, this genus has become the focus of several ecological studies (Enrico *et al.* 2004, Cierjacks *et al.* 2007, Kessler *et al.* 2007, Seltmann *et al.* 2007).

In this paper, we present the palaeoecological results from the mountain rainforest of the El Cristal region located in the eastern part of the Cordillera Real of southern Ecuador. Unfortunately, nowadays the eastern slopes of the Ecuadorian Andes are under increasing anthropogenic pressure. Consequently, the vegetation displays patterns directly attributable to human intervention as well as traces of former natural habitats. This enhances our knowledge of how past processes, e.g. past vegetation, human impact as well as climate change, have influenced ecosystem dynamics and the development of the outstanding diversity in the study region. The point of special interest is how did anthropogenic or climatic conditions influence the occurrence and absence of *Polylepis* in the study area?

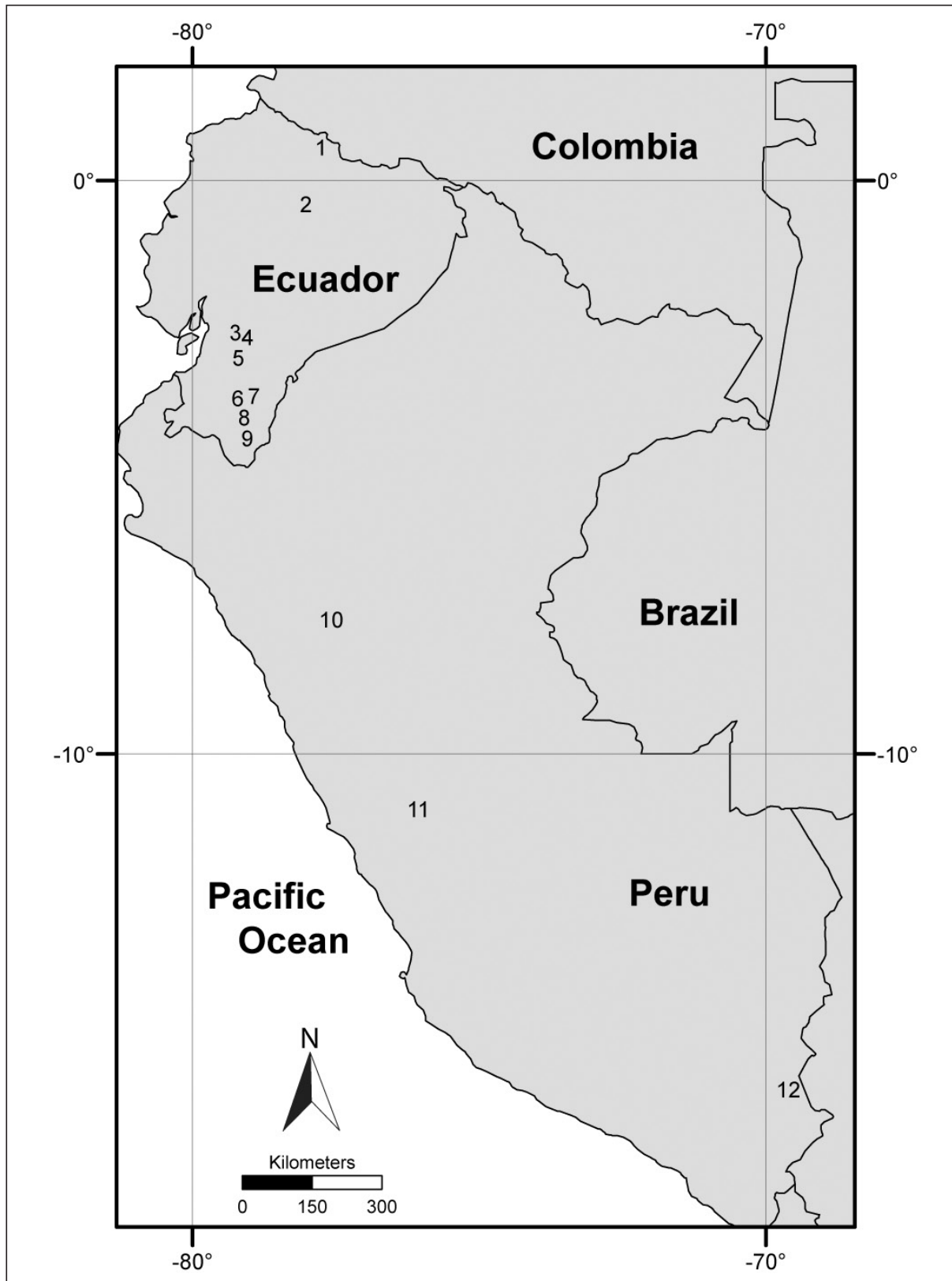


FIG. 1. Map of the Andes of Ecuador, Peru and Bolivia in South America, showing the location of the different study sites from the Ecuadorian Andes and neighboring countries. 1. Guandera Biological Reserve; 2. Laguna Yaguarcocha; 3. Lagunas Chorreras; 4. Lake Surucucho; 5. Tres Lagunas; 6. El Tiro; 7. Cocha Caranga; 8. Cerro Toledo; 9. El Cristal; 10. Laguna Junín; 11. Laguna de Chochos; 12. Lake Titicaca.

MATERIAL AND METHODS

The study area El Cristal is located on the eastern slope of the Cordillera Real between the Saraguro villages of El Tibio and El Cristal in the Protective Forest Corazón de Oro (Zamora Chinchipe Province) (Fig. 1). It is situated in the Girón-Cuenca (southern Ecuador) and Huancabamba (northern Peru) Andean Depression. Here, mountains barely reach heights of 4000 m and no active volcanoes are present.

The Protective Forest Corazón de Oro covers 54 000 ha and is located in the north of the Podocarpus National Park (PNP) between Loja and Zamora Chinchipe Provinces. At the time of its declaration in 2000, the Protective Forest Corazón de Oro encompassed more than 15 settlements, 30% of the area was already converted into pasture and another 30% of the forest cover was interspersed with pastures (UNL *et al.* 2006).

The sediment core analyzed was derived from the small swamp, 20 m in diameter, found in a shallow closed basin, which in this study is called "El Cristal" (EC). The core was taken at 2056 m a.s.l. (3°51'38.5" S, 79°03'40.1" W). The area around the study site is very disturbed. During fieldwork, much human activity was observed, mainly slash and burn fields, clear cuttings, fire, and paths. The path close to the swamp is used as the main connection between two villages.

Geology. The eastern Andean Cordillera is mainly built up of Paleozoic metamorphic rocks (Baldock 1982) of widely varying metamorphic grade. The local bedrock is dominated by white limestones, yellow sandstones, quartzites and black phyllites with some granitic intrusions (Litherland *et al.* 1994, Hungerbühler *et al.* 2002). The basin margins contain conglomerates of metamorphic debris and argillaceous sandstone in the Miocene layers (Sauer 1971).

Climate. The climate of the Ecuadorian Andes is dominated by the tropical trade wind regime, which is well established in the mid- and higher troposphere, with strong easterly winds throughout the year (Emck 2007, Bendix *et al.* 2008). The southeastern part of the country, encompassing the El Cristal area, is mainly influenced by easterly winds. Precipitation and humidity continuously rise on the eastern side to the crest regions, where rainfall can reach up to 2176 mm yr⁻¹ (Bendix *et al.* 2008). The main rainy season lasts from April to August, but

rainfall is high throughout the year. Temperature varies according to the time of day and season. The mean annual minimum temperature is -5°C and the maximum is -29.1°C, recorded in the weather station located 12 km from the study area at the Research Station San Francisco at 1960 m a.s.l. (Bendix *et al.* 2008).

Vegetation. The vegetation of the study area is mainly dominated by the lower mountain forest and upper mountain rainforest. The lower mountain forest (ca. 1500–2000 m a.s.l.) is characterized by *Alchornea glandulosa*, *Piptocomma discolor*, *Acalypha* sp., *Hyeronima macrocarpa*, *Vismia tomentosa*, *Miconia imitans*, *Cedrela montana*, *Ficus* sp., *Piper* sp. and *Celtis iguanaea* (Homeier *et al.* 2008). The upper mountain rainforest, between ca. 2000–2700 m, is characterized by *Hedyosmum* sp., *Weinmannia pinnata*, *Purdiaea nutans*, *Clethra revoluta*, *Clusia elliptica*, *Graffenrieda emarginata*, *Tibouchina lepidota*, *Heliocarpus americanus*, *Myrica pubescens*, *Myrsine andina*, *Podocarpus oleifolius* and *Prumnopitys montana*, and *Schefflera pentandra* (Homeier *et al.* 2008). However, due to human activity, the study site is also surrounded by taxa of páramo vegetation (mainly herbs), which is composed of *Puya eryngioides*, *Hypericum decandrum*, *Rhynchospora vulcani*, *Gaultheria amoena*, *Pernettya prostrata*, *Vaccinium floribundum*, *Calamagrostis macrophylla*, *Neurolepis elata*, *Chusquea neurophylla*, and *Valeriana plantaginea* (Homeier *et al.* 2008). There are also some types of subpáramo taxa, with vascular species such as *Gynoxis cuicochensis*, *Baccharis genistelloides*, *Chusquea jussieui*, *Diplostegium empetrifolium*, *Gaultheria reticulata*, *Hesperomeles ferruginea*, *Symplocos sulcinervia* (Homeier *et al.* 2008).

El Cristal is an area where tropical mountain rainforest has been highly modified by human activity. Forest remnants and secondary vegetation, pastures, small fields and other open areas dominate the landscape. However the borders of the settlements are covered with non-colonized disturbed primary forest on very steep, almost unreachable slopes (Gérique 2010).

Human settlement. Human-environment relationships have a long and diverse history in the region of the northern Andes. The earliest record of human occupation in the region of the southern Ecuadorian Andes close to El Cristal is Cubilán (10 000 cal yr BP), where scant traces of hunter-gatherers, nomads or semi-nomads have been found (Temme 1982).

The first human activity in the region of Loja and Zamora is dated at around 4000 cal yr BP, but human activities may have occurred in the dry inter-Andean valley much earlier (Guffroy 2004).

The present-day Mestizo and Saraguro settlers came from neighboring regions over the last 80 years and colonized the area of the Protective Forest Corazón de Oro. The El Cristal village was founded in the 1970s during the timber boom (Gerique 2010). Both Saraguros and Mestizos make little use of forest resources. The forest supplies them with timber for their own use (houses, buildings) or for sale, with a few species used mainly for food, medicine, or fuel. However, forest areas are in the main considered a reserve for new pastures and as plots for maize production; what is important in productive terms is the potential for agricultural use of the underlying soil (Wunder 1996).

Sediment extraction. The “El Cristal” (EC) sediment core was recovered using a Russian corer. The total length of the recovered core was 170 cm. Sections of 50 cm were placed in PVC tubes which had been split in half longways and covered with plastic film and stored under dark and cold (+4 °C) conditions at Georg-August University before processing.

Accelerator mass spectrometer (AMS) radiocarbon dating of 6 subsamples containing organic material was undertaken at the Radiocarbon Laboratory at the University of Erlangen-Nürnberg (Germany). The ¹⁴C dates were calibrated using the curve CalPal 2007 HULU for the northern hemisphere of the CalPal software (Weninger *et al.* 2004).

Palynological analysis. The EC core was sampled at 4 cm intervals along the core, resulting in 41 subsamples of 0.5 cm³. All samples 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 concentrations 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, but excludes fern spores and pollen of aquatic taxa. The spores of Pteridophyta, *Isoetes* and Bryophyta 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 Palynol-

ogy and Climate Dynamics, University of Göttingen, and the South American Pollen Database (Bush & Weng 2007). Reference collections of recent material, held at the Department of Palynology and Climate Dynamics, 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. In particular, for the Holocene period of the core Páramo also includes taxa that correspond to anthropogenic grasslands. The pollen types that could not be identified were grouped in the indeterminate taxa. A full list of identified pollen and spore taxa from the El Cristal core can be found in Table 1. For charcoal analysis, the technique used was 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 into two groups of different particle sizes (10-50 µm and 50- >100 µm) to give more detailed information about the fire history (Sadori & Giardini 2007). Fragments between 10 and 50 µm indicate regional fires, and fragments between 50 and >100 µm local fires (Whitlock & Larsen 2001).

Data analysis. The software TILIA was used for data calculation of percentages and sums, as well as pollen and charcoal concentration and influx. TILIA-GRAPH 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 includes taxa of the pollen sum, to generate a dendrogram (Grimm 1987), which helped to identify the pollen zones.

RESULTS

Stratigraphy. The sediment core EC mainly consists of silt, clay, and organic material. Between 170 and 120 cm core depth, the sediment has little organic material; silty and clayey material is dominant with a dark/light grayish color. From 120 cm to the top of the core the sediments are more compact and with decomposed material. Between 120 and 80 cm, the organic material is highly decomposed and has a dark/light brown color. Between 80 and 26 cm less

44 TABLE 1. List of identified pollen and spore taxa from the El Cristal (EC) core.

LMF	UMF	Subpáramo	Páramo	Other	Pteridophyta
<i>Acalypha</i>	<i>Alnus acuminata</i>	<i>Ambrosia</i> type	Apiaceae	<i>Alternanthera</i> type 1	<i>Isoetes</i>
<i>Alchornea</i>	<i>Clethra</i>	Asteraceae subf. Cichorioideae	<i>Arcytophyllum</i>	Amaranthaceae/Chenopodiaceae	<i>Blechnum</i> type
<i>Celtis</i>	<i>Clusia</i> type	<i>Baccharis</i> type	Brassicaceae	Euphorbiaceae	Cyatheaceae
<i>Hyeronima</i>	<i>Dodonea</i>	Ericaceae	Caryophyllaceae	cf Euphorbiaceae	<i>Huperzia</i>
Mimosaceae	<i>Escallonia</i>	cf <i>Ericaceae psilate</i>	<i>Centropogon</i>	<i>Palicourea</i>	<i>Jamesonia</i>
Moraceae/Urticaceae	<i>Hedyosmum</i>	<i>Gunnera</i>	Cyperaceae		<i>Osmunda</i>
<i>Oreopanax</i>	<i>Ilex</i> type	<i>Hypericum</i>	<i>Eryngium</i> type		
<i>Piper</i>	Melastomataceae	Lorantaceae	Fabaceae type 1		
Proteaceae	<i>Myrica</i>	<i>Monnina</i>	cf Fabaceae		
<i>Trema</i> type	<i>Myrsine</i>	<i>Muehlenbeckia/Rumex</i> type	Gentianaceae		
<i>Verbena</i>	Podocarpaceae	<i>Oxalis</i>	Geraniaceae		
	<i>Polylepis-Acaena</i> type		Iridaceae		
	<i>Purdiaca nutans</i>		<i>Macropypaea</i>		
	<i>Solanum</i> type		<i>Plantago rigida</i> type		
	<i>Symplocos</i> (type 3p)		Poaceae		
	<i>Symplocos</i> (type 2p)		<i>Puya</i>		
	<i>Vallea</i>		<i>Ranunculus</i>		
	<i>Weinmannia</i>		<i>Senecio</i> type		
			<i>Valeriana</i>		
			<i>Xyris</i>		

TABLE 2. Stratigraphic description of the sediment core El Cristal (EC).

Depth (cm)	Description
0 – 26 cm	Very little decomposed organic material; with plant remains (roots); light brown color
26 – 80 cm	Little decomposed organic material with roots, dark brown color
80 – 90 cm	Decomposed organic material, dark brown color
90 – 100 cm	Highly decomposed organic material, dark brown color
100 – 122 cm	Highly decomposed organic material; brownish colored; some darker belt between 120-125 cm
122 – 130 cm	Clayey material with little organic material, dark-grayish color
130 – 134 cm	Silt material compact, light-grayish color
134 – 140 cm	Clayey material compact, dark-grayish color
140 – 170 cm	Silt material compact, light-grayish color

decomposed organic material is found with the presence of a few fine roots. Between 26 and 0 cm the organic material is little decomposed with many plant remains. A detailed description of the stratigraphic units is given in Table 2.

Chronology and pollen zonation. The chronology of the core EC is based on six radiocarbon dates (Table 3). Extrapolation of the dates suggests that the base of the core has an age of 19 750 cal yr BP that probably reflects the beginning of sediment accumulation. The six radiocarbon dates suggest that the sediments have accumulated since the late Pleistocene.

The age-depth model (Fig. 2) reveals that the average sediment accumulation rate of the complete core is 0.32 mm yr⁻¹. The different intervals rates are: 0.05 mm yr⁻¹ (19 750 to 14 500 cal yr BP), 0.10 mm yr⁻¹ (14 500 to 3500 cal yr BP), 0.24 mm yr⁻¹ (3500 to 1300 cal yr BP), 0.34 mm yr⁻¹ (1300 to 380 cal yr BP) and 0.93 mm yr⁻¹ (380 to -57 cal yr BP).

The CONISS cluster analysis and major changes in the pollen assemblages suggest five main pollen zones (EC-I to EC-V) with subzones (EC-IIa, EC-IIb; EC-IIIa, EC-IIIb, and EC-IVa, EC-IVb).

Description of the pollen diagram. A detailed pollen percentage diagram displays 22 different pollen taxa with a representation of >2% out of 70 pollen types, and 5 spores types with a representation of >2% out of 11 identified taxa (Fig. 3). The summary percentage diagram (Fig. 4) shows the pollen and spores grouped into vegetation types: Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo, Páramo, and Pteridophyta, and concentration and influx of pollen and charcoal.

Pollen concentration and influx vary between 100 000 and 800 000 grains/cm³ and between 3000 and 15 000 grains/cm²/yr, respectively, with a very high pollen concentration and influx in subzone EC-IIIa with 1 400 000 grains/cm³ and 28 000 grains/cm²/yr, respectively.

TABLE 3. List of AMS radiocarbon ¹⁴C dates and calibrated ages from the El Cristal (EC) core using the curve CalPal 2007 HULU of the CalPal software.

Lab. Code	Depth (cm)	Dated Material	¹⁴ C age (yr BP)	1-σ (cal yr BP)
Erl-16584	45 – 46	Organic material	346 ± 50	404 ± 65
Erl-16084	95 – 96	Organic material, with recent roots	1927 ± 41	1780 ± 224
Erl-16083	132 – 133	Charcoal	3527 ± 45	3743 ± 128
Erl-16977	141 – 142	Organic material, with recent roots	4335 ± 50	4923 ± 55
Erl-16976	153 – 154	Organic material	11318 ± 84	13221 ± 123
Erl-16585	166 – 168	Organic material	14928 ± 123	18214 ± 254

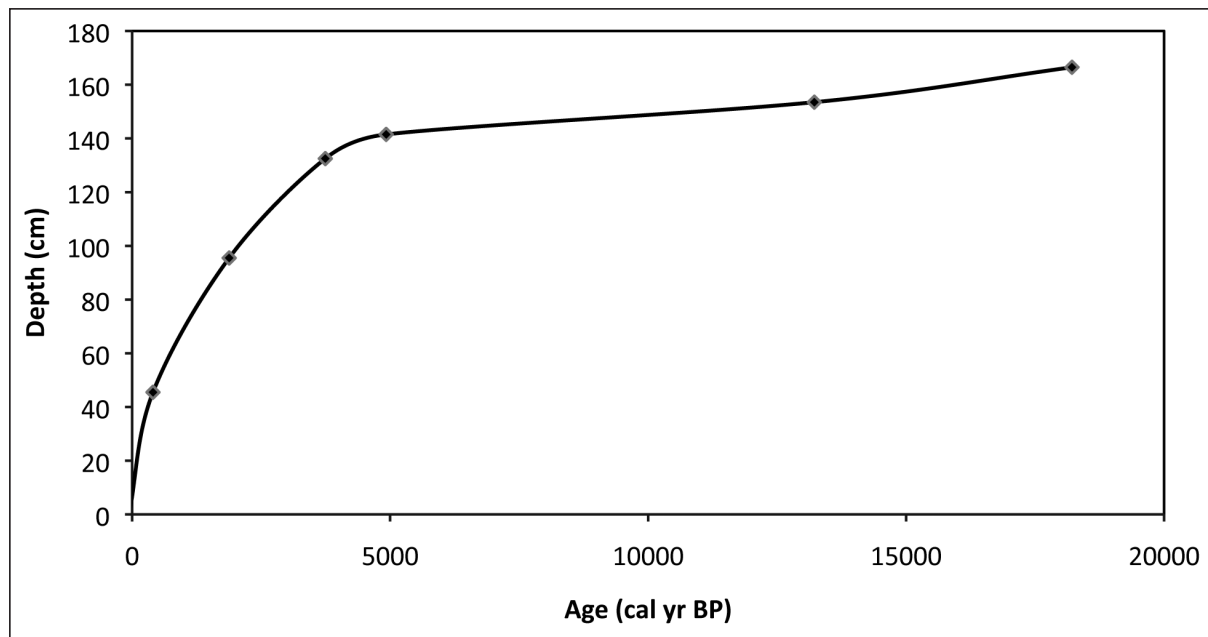


FIG. 2. Age–depth model (core depth in cm/cal yr BP) for the El Cristal (EC) core based on 6 radiocarbon dates.

The charcoal concentration of the two counted fractions varies between 6 000 000–20 000 000 particles/cm³ (small fraction) and 100 000–600 000 particles/cm³ (large fraction), with a high concentration for the small fraction at zones EC-V and EC-III with 30 000 000 particles/cm³, and for the large fraction at zone EC-III with 900 000 particles/cm³. The charcoal influx for both counted fractions varies in the sediment core between 100 000–500 000 particles/cm²/yr (small fractions) and 30 000–10 000 particles/cm²/yr (large fraction). Charcoal influx for small and large fractions at zone EC-V shows a high value with 2 000 000 and 60 000 particles/cm²/yr, respectively.

Zone EC-I (170–152 cm; 7 samples, ca. 19 750–12 530 cal yr BP) is characterized by a low pollen representation of LMF taxa (5–8%) mainly due to low values of *Alchornea*, *Acalypha* and *Clusia* (0–1%). This zone is marked by relatively high values of UMF taxa (45–55%), with an increase during this zone especially in *Hedyosmum* and *Myrica* (from 10 to 15%), *Alnus* (2–4%) and *Polylepis-Acaena* type (5%). Subpáramo taxa show the lowest values of the record (6–8%), mainly by Asteraceae and the *Muehlenbeckia/Rumex* type (1–3%). Páramo pollen taxa show stable values (30%) such as Poaceae (10–15%). In this zone Pteridophyta spores (10–14%) are mainly represented by Cyatheaceae (5–8%) and *Jamesonia* (4%). *Isöetes* spores (up to 50%), which are not in-

cluded in the sum of Pteridophyta, are very frequent in this zone.

Subzone EC-IIa (152–140 cm; 3 samples, ca. 12 530–7800 cal yr BP). LMF shows a stable representation (9%) by Moraceae/Urticaceae (3–5%), *Alchornea* (2%) and *Acalypha* and *Clusia* (0–1%). As well as LMF, UMF pollen taxa show stable representation (55–60%) with *Hedyosmum* (15%), *Myrica* (12%), *Polylepis-Acaena* type (5–8%) and Melastomataceae (2–5%). Subpáramo taxa increase slightly (16%) mainly by Ericaceae pollen (5–10%) and the *Muehlenbeckia/Rumex* type present the highest values (5–7%) of the record in this subzone. Páramo taxa vary between 18 and 28%, especially due to values of Poaceae pollen from 10 to 15% and *Plantago* sp. (5–7%). Pteridophyta spores show stable values (10–16%), mainly by Cyatheaceae 10% and *Jamesonia* (3–5%). *Isöetes* values decrease slightly (20%).

Subzone EC-IIb (140–128 cm; 3 samples, ca. 7800–3600 cal yr BP) is characterized by a slightly higher representation of LMF pollen (15%), e.g. *Alchornea* (3–5%) compared with the previous subzone. UMF taxa decreased from 60 to 45%, especially due to lower representation of *Hedyosmum* (2–4%) and the absence of *Alnus*. At the lower part of this zone the *Polylepis-Acanena* type present the highest percentages (8%) of the record as well as *Myrsine* (5–10%). Subpáramo pollen taxa show a

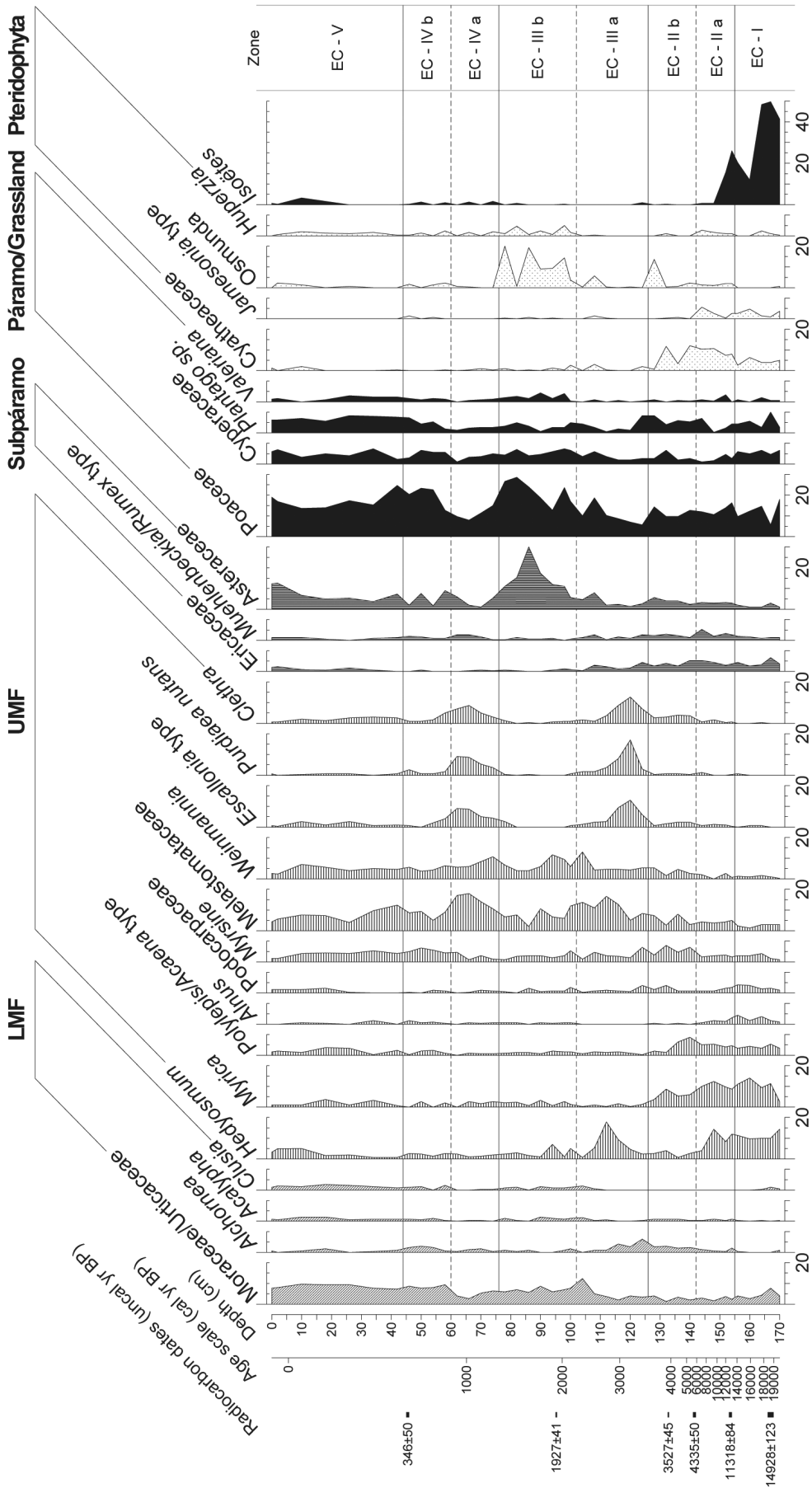


FIG. 3. Pollen percentage diagram of the El Cristal (EC) core showing selected fossil pollen and spore taxa grouped into Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo, Páramo/grassland, and Pteridophyta.

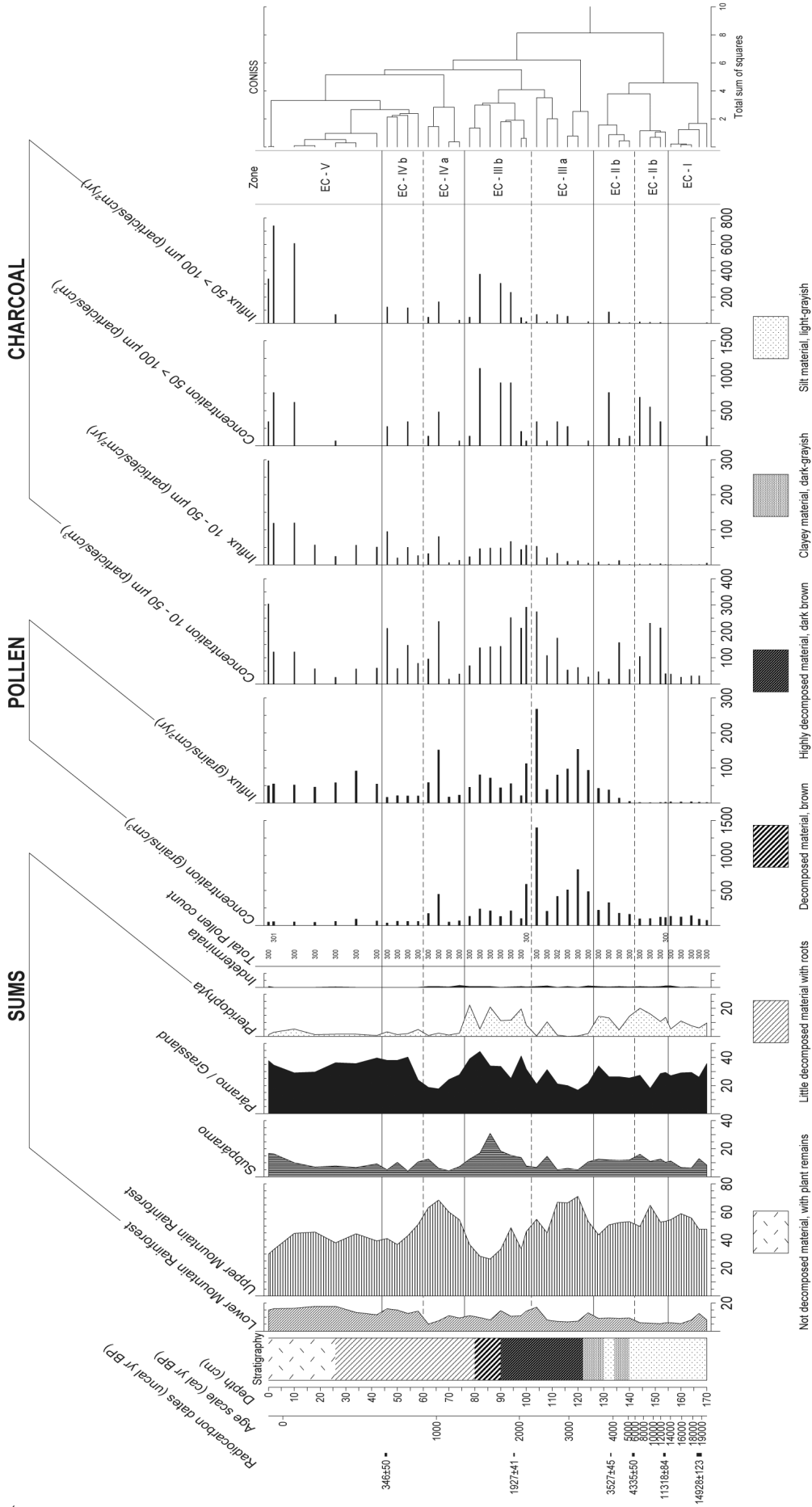


FIG. 4. Summary pollen percentage diagram of the El Cristal (EC) core showing radiocarbon dates (uncal yr BP), age scale (cal yr BP), vegetation groups, pollen sum, pollen concentration and influx, charcoal concentration and influx, and the CONISS dendrogram.

stable proportion (15%) such as Ericaceae (6%) and Asteraceae (4–6%). Páramo pollen taxa increase slightly from 28 to 35%, mainly by *Plantago* sp. (10%) and Cyperaceae (4–7%). At the top of this subzone Pteridophyta show stable values (15%), primarily by Cyatheaceae 13% and *Osmunda* spores (14%). In this subzone spores of Isoetes are absent.

Subzone EC-IIIa (128–94 cm; 9 samples, ca. 3600–1850 cal yr BP) is marked by a stable representation of LMF taxa (13%), especially by pollen of Moraceae/Urticaceae (5–12%) and *Alchornea* (4–6%). UMF taxa reach highest values between 60 and 70% of the record, mainly due to pollen of the *Escallonia* type, *Purdiaea nutans* and *Clethra* (5–15%); also *Weinmannia* and Melastomataceae pollen taxa with (8–12%). Subpáramo taxa such as the *Muehlenbeckia/Rumex* type and Ericaceae (2–5%) show stable values and Asteraceae with (6–12%). Compared to the previous subzone, páramo pollen decreased from 20% to 15%. This is mainly due to decreasing values of Poaceae (5–10%) and Cyperaceae (2–3%). The *Plantago* sp. show increased values (8%) at the lower part of the subzone. In this subzone the Pteridophyta group shows the lowest value of the record (5%), mainly due to the absence of *Huperzia*, Cyatheaceae and *Jamesonia*.

Subzone EC-IIIb (94–78 cm; 4 samples, ca. 1850–1380 cal yr BP) is characterized by a stable representation of LMF taxa, mainly due to Moraceae/Urticaceae (5–15%); also *Alchornea*, *Acalypha* and *Clusia* with (1%). UMF pollen shows lowest amounts within this subzone, especially *Hedyosmum* (2–4%), the *Escallonia* type, *Purdiaea nutans* and *Clethra* (1–3%) are represented at low levels; however *Weinmannia* (4–7%) and Melastomataceae (6–10%) show stable amounts. Subpáramo taxa show highest values in this subzone (20–30%), mainly due to Asteraceae pollen (15–30%). Compared to decreasing values of the previous subzone, páramo taxa show slightly higher proportions (35–40%), mainly due to higher values of Poaceae (30%) and Cyperaceae (5–10%). Compared with the previous subzone, Pteridophyta increased strongly, mainly due to *Osmunda* spores, which increased to higher values between 15% and 20%; also *Huperzia* (5%).

Subzone EC-IVa (78–62 cm; 4 samples, ca. 1380–900 cal yr BP) shows a stable proportion of LMF pollen (10%). UMF taxa increase slightly and vary from 55 to 60%, mainly by pollen of *Escallonia* type, *Purdiaea nutans* and *Clethra* (5–10%), and also

Melastomataceae (10–18%). Subpáramo shows lower values of Asteraceae (2–5%). Compared with the previous subzone, páramo taxa show stable percentages, especially by Poaceae (15–25%). Strong decrease in Pteridophyta (2%) is found.

Subzone EC-IVb (62–46 cm; 4 samples, ca. 900–500 cal yr BP) is characterized by stable proportions of LMF pollen taxa, mainly Moraceae/Urticaceae (9%). Compared with the previous subzone, proportion of UMF taxa decreased, mainly due to *Escallonia* type, *Purdiaea nutans* and *Clethra* (2–4%). The values of *Myrsine* (4–7%) within this subzone are higher. Melastomataceae (13%) show stable values. Percentages of subpáramo taxa remain stable, such as *Muehlenbeckia/Rumex* type (5%). Páramo taxa show stable values and are dominated by pollen of Poaceae (12–20%).

Zone EC-V (46–0 cm; 7 samples, ca. 500 to -60 cal yr BP) is characterized by high representation of LMF pollen (15 to 20%) compared with the previous zone. Mainly Moraceae/Urticaceae pollen increased to 12%, as well as *Clusia* and *Acalypha* (1–3%). UMF taxa remain stable between 30 and 40%, with *Weinmannia* (2–5%) and *Myrsine* (3–6%), while *Hedyosmum* increases from 3 to 6% at the top of the zone. Pollen of Melastomataceae (6–11%) shows decreasing values. Compared with the previous zone, pollen of subpáramo decreases from 17 to 10%. This is mainly due to decreasing values of *Muehlenbeckia/Rumex* type and Ericaceae (1%). Páramo taxa increase in this zone, especially Poaceae pollen from 20 to 25% at the lower part of this zone. Pteridophyta spores (1–2%) show the lowest values of the complete record.

INTERPRETATION AND DISCUSSION OF THE POLLEN DATA

Mountain regions provide excellent conditions for the study of past climatic changes because of the close relationship between climate and environment (Gosling and Bunting 2008). Especially the “El Cristal” (EC) core, at 2056 m elevation, reflects the local development and vegetation dynamics of the eastern slope of the Cordillera Real (Protective Forest Corazón de Oro) over the last 19 750 cal yr BP.

Late Pleistocene. The late Pleistocene period, from about 19 750 to 12 500 cal yr BP (zone EC-I), shows a significant presence of mountain rainforest taxa (ca. 60% of all pollen) in the study area, especially of taxa of the Upper Mountain Rainforest (UMF) and a

smaller proportion of Lower Mountain Rainforest (LMF) taxa. Subpáramo (*ca.* 10% of pollen) and páramo vegetation (30% of pollen) are present during this period. A high proportion of UMF, as well as a relatively high proportion of páramo taxa suggest that an open mountain rainforest occupied the region during this period. The high proportion of silt within the sediment deposits during this period could indicate that the soils were unstable and vegetation cover incomplete, resulting in higher rates of erosion.

The LMF was represented mainly by Moraceae/Urticaceae probably located at lower elevations. Despite that, Moraceae/Urticaceae pollen can be wind-transported over longer distances, especially in the study area where the easterly winds are dominant (Hansen & Rodbell 1995, Bush & Rivera 2001, Weng *et al.* 2004, Gosling *et al.* 2009b, Moscol Olivera *et al.* 2009). Studies by Niemann *et al.* (2010) based on pollen rain transects reveal that the altitudinal distribution of the present vegetation types and certain taxa are well reflected in the modern pollen rain data. Also a pollen trapping study by Jantz *et al.* (2013) reveals that the distinct pollen spectrum of modern pollen rain reflects local to regional vegetation conditions. Main components of the UMF during the late Pleistocene were *Hedyosmum*, *Myrica*, *Polylepis*, *Alnus* and *Podocarpaceae*. The occurrence of *Hedyosmum*, which is abundant during this period, indicates relatively wet conditions. Also, the presence of *Myrica*, which occurs in sloping humid ground and eroded Andes slopes, and *Alnus*, which occurs in marshy and disturbed areas (Marchant *et al.* 2002), indicates humid conditions and eroded soils.

Evidence of small populations of *Polylepis* at low elevation in the northern part of the Andean Depression is interesting, since it does not occur today (Fig. 3). Recently, populations of *Polylepis* have also been reported in the southern part of the Andean Depression in southernmost Ecuador next to the border of Peru (Rodríguez & Behling 2012, Villota *et al.* 2012). However, *Polylepis* population were absent in the records of the central part of the Andean Depression where the Podocarpus National Park (PNP) is located (Brunschön & Behling 2009, Niemann & Behling 2008), probably due to high precipitation and strong winds. Similar proportions of *Polylepis* to those in El Cristal have been described in the record from Lake Surucucho during the late glacial outside of the Andean Depression at 3180 m on the eastern face of the Cordillera Occidental (Colinvaux *et al.* 1997). A comparable distribution of *Polylepis* popu-

lation has been reported from the high Andes of Peru, Laguna Junin record, at 4100 m in the central Peruvian Andes, which suggests that between 16 000 and 12 000 yr BP a forest line dominated by *Polylepis* and Asteraceae covered the plain (Hansen *et al.* 1984). The results from the northern as well as from the southern part of the Andean Depression indicate the movement of *Polylepis* populations into the Andean Depression during glacial times, which have apparently not reached the central part.

Subpáramo taxa were dominated mainly by Ericaceae and páramo mainly by Poaceae in the study area. Studies suggest that the relatively high pollen proportion of Poaceae in the UMF vegetation zone possibly relates either to wind transport from higher elevations of the surrounding higher mountains or to the occurrence of forest grasses with high pollen production in the study area (Hansen *et al.* 1984, Bush *et al.* 1990, Niemann *et al.* 2010). The high abundance of páramo taxa and the presence of *Polylepis* provide a robust overall image of cold conditions during this period. During this time *Isoëtes* was abundant in the basin at the study site. *Isoëtes* is a good proxy for the existence of a shallow lake, or extensive shallow margins, and it is sensitive to hard freezes (Cleef 1978, Ybert 1988, Bosman *et al.* 1994).

In addition, in the El Cristal record there is no marked shift of the upper forest line (UFL). The study site is located at lower altitudes and forest taxa dominate the area with relatively stable values during the late Pleistocene and Holocene (Fig. 4). As already mentioned, the UFL in the southern part of Ecuador ranges from 2800 to 3300 m a.s.l. and the study area is located at 2056 m elevation. However, the presence of páramo taxa at lower elevations during the late Pleistocene shows that the UFL was at markedly lower elevation, reflecting cold conditions.

During the late Pleistocene, the low charcoal influx, i.e. below 50 710 particles/cm²/yr for both counted fractions (Fig. 4), indicates that fire is rare and suggests the absence of human activity in the study area. Absence or relatively low occurrence of fire during the glacial period has also been documented in other records from southern Ecuador (Brunschön & Behling 2009, Niemann *et al.* 2009). Given that fire is the major control on woodland abundance in the Andes (Kessler 1995, Bush *et al.* 2008), it could be expected that a low frequency of fires might have allowed a much higher proportion of mountain forest in the study area.

Transition from the late Pleistocene to the early and mid-Holocene period. The transition from the late Pleistocene to the early and mid-Holocene period between ca. 12 500 and 3600 cal yr BP (zone EC-II), is mostly characterized by the high abundance of mountain forest taxa (60% of all pollen) with small fluctuations between the LMF and the UMF. The UMF in particular shows a high proportion (55% of pollen) during the early Holocene (from 11 500 to 7800 cal yr BP), whereas during the mid-Holocene (from 7800 to 3600 cal yr BP) the proportion of UMF decreased slightly while the proportion of LMF showed a small increase (15% of pollen). Relatively stable proportions of subpáramo taxa (ca. 15% of pollen) and páramo vegetation (ca. 30%) are found during this period. The high abundance of forest taxa coupled with more open subpáramo and páramo taxa suggests that open mountain forest still occupied the study area.

During the transition to the Holocene and early Holocene period (subzone EC-IIa) stable proportions of LMF were present in the pollen record. The UMF was represented mainly by *Myrica* and *Polylepis*. *Myrica* as a pioneer species occurs in degenerated areas and along trails, probably reflecting disturbances in the study area (Marchant *et al.* 2002, Niemann & Behling 2009). *Polylepis* was still present and became even slightly more common during this period (Fig. 3). The Llaviucu record, at the southern part of the Cajas National Park (3180 m elevation) to the north outside of the Andean Depression, shows the highest proportion of *Polylepis* at the beginning of the Holocene (Colinvaux *et al.* 1997). Also, the Laguna Natosa Forest record, in the southern part of the Andean Depression (3495 m), shows the highest occurrence of *Polylepis* during the early and mid-Holocene, between 11 660 and 4300 cal yr BP (Rodríguez & Behling 2012). In addition, there is evidence of stronger distribution of *Myrsine* and Melastomataceae at the study site. *Myrsine* is a typical gap species and can be common in upper montane rainforest (Marchant *et al.* 2002). Melastomataceae is well represented in Ecuadorian secondary forest (Marchant *et al.* 2002). This stronger distribution probably facilitates the expansion of woody vegetation and suggests warmer and drier conditions. Stable proportions of subpáramo vegetation was shown in the pollen record. Mainly, the subpáramo was represented by *Muehlenbeckia/Rumex*, suggesting disturbed areas (Marchant *et al.* 2002). Slightly lower presence of páramo vegetation is due to the decrease

in Cyperaceae, also suggesting drier conditions. This climatic condition coincides with the records of the PNP, e.g. El Tiro and Cerro Toledo, in the central part of the Andean Depression (Niemann & Behling 2008, Brunschön & Behling 2009). In addition, a high occurrence of Pteridophyta was established, mainly due to the increase in Cyatheaceae and *Jamesonia* (páramo fern). This gives an indication of vegetation structure, as ferns may be characteristic of a wet understory but also show high occurrences on open soils after disturbance (Bussmann *et al.* 2008). The strong decrease of *Isoetes* and Cyperaceae reveals that a swamp probably replaced the shallow water pond.

Relatively low values of charcoal influx (i.e. below 33 000 particles/cm²/yr and 1000 particle/cm²/yr for small and large fragments respectively) during the early Holocene suggest a scarcity of fires in the study area (Fig. 4).

During the mid-Holocene (subzone EC-IIb), the LMF is mainly characterized by the increased proportion of *Alchornea* (i.e. from 2 to 5%). There is a change in the composition of the UMF. A decreased occurrence of *Hedyosmum*, *Myrica* and *Polylepis*, but an increased proportion of Podocarpaceae, *Myrsine*, *Weinmannia* and *Clethra* is found, possibly related to the Holocene thermal optimum which facilitated forest expansion (Hansen *et al.* 1994, Hansen & Rodbell 1995, Hansen *et al.* 2003, Bush *et al.* 2005, Niemann & Behling 2008, Niemann *et al.* 2009). The decrease in the *Polylepis* population after ca. 4000 cal yr BP (Fig. 3) is probably due to the first higher fire frequency which occurred during this dry period as it is a fire-sensitive tree (Cierjacks *et al.* 2007). The subpáramo remained stable during the mid-Holocene. Páramo vegetation was still well represented with a high occurrence of Poaceae. In addition, the Pteridophyta is represented by a high presence of *Osmunda* and Cyatheaceae. It is important to note that the presence of *Osmunda* often reflects disturbed areas (Brunschön & Behling 2009).

There is a slight increase in the influx of large particles (8600 particle/cm²/yr) which suggests a first local fire increase at around 4000 cal yr BP. Since the first stronger presence of human in this region was after 10 000 yr BP, according to the Cubilán archaeological record, located in the páramo of Loja at 3100 m a.s.l. (Valdez 2008). Also an initial strong increase in fire frequency was found in the El Tiro record after ca. 8000 cal yr BP (Niemann & Behling 2008).

Mid- to late Holocene. During the mid- to late Holocene (*ca.* 3600–1380 cal yr BP) the abundant montane forest taxa is split roughly between LMF (*ca.* 13%) and UMF (*ca.* 40–70%). In addition, subpáramo and páramo taxa became increasingly abundant between 2500 to 1300 cal yr BP, reaching a maximum of *ca.* 30% and *ca.* 40%, respectively. Also, higher values of charcoal influx of larger fragments (i.e. from 10 000 to 35 000 particles/cm²/yr) are evident after 3300 cal yr BP, suggesting local fire of anthropogenic origin.

Between *ca.* 3600 and 2500 cal yr BP (subzone EC-IIIa), the LMF taxa are well represented by Moraceae/Urticaceae and *Alchornea* throughout the period. The UMF expanded strongly, showing a compositional change in the vegetation. There is evidence of a vegetational succession. First with *Escallonia*, *Purdiaea nutans* and *Clethra*, which have the highest values in the record, and later with Melastomataceae, *Hedyosmum* and finally *Weinmannia*, suggesting that this vegetational composition possibly constituted a considerable part of the local vegetation. Moreover, subpáramo taxa remain stable. Páramo taxa make up a low proportion mainly because of the decrease of Poaceae. Also Pteridophyta were rare during this period, especially Cyatheaceae. The high proportion of mountain rainforest taxa and comparably low presence of páramo taxa and Pteridophyta may indicate that mountain rainforest vegetation covered the study region and dominated the landscape. Between *ca.* 2500–1380 cal yr BP (subzone EC-IIIb) the LMF taxa remain stable. The proportion of UMF decreases (30% of pollen), mainly due to the low frequency of *Hedyosmum* and the absence of *Escallonia*, *Purdiaea nutans* and *Clethra*. The higher proportion of subpáramo taxa, e.g. Asteraceae, between *ca.* 2000 and 1300 cal yr BP, reflects landscape disturbance (Chepstow-Lusty *et al.* 2003). Like Asteraceae, the presence of *Muehlenbeckia/Rumex* pollen throughout this period may record disturbance, e.g. agricultural activity (Colinvaux *et al.* 1997). Páramo-like vegetation is represented primarily by Poaceae, probably due to human activities. Moreover, after *ca.* 2000 cal yr BP *Valeriana* became quite common in the study area. In addition, there is the high presence of *Osmunda* and *Huperzia*. Especially *Huperzia* is a pioneer species common on landslides and along road cuts on open sandy soils (Brunschön & Behling 2009).

In addition, there is evidence of a major influx of larger charcoal fragments after 2000 cal yr BP (Fig. 4)

which may reflect local fires of anthropogenic origins, e.g. wood extraction, land use by slash and burn, and hunting (Niemann & Behling 2008), which may have resulted in grassland expansion and forest destruction. An abrupt decrease of arboreal taxa, coupled with high values of Poaceae, Asteraceae, and Pteridophyta reflects the reaction of the vegetation to increasing fires (Niemann & Behling 2009).

Late Holocene. The late Holocene, from *ca.* 1380 cal yr BP to the present, was generally characterized by a substantial expansion of páramo taxa, mainly caused by a higher abundance of Poaceae, forming anthropogenic grasslands and a reduction of mountain rainforest to forest patches. However between *ca.* 1200 and 900 cal yr BP, the UMF expanded, probably due to a forest recovery after a high frequency of fire during the previous period. Moreover, the LMF remained relatively stable during this period. The subpáramo was dominated mainly by Asteraceae.

Between *ca.* 1380 and 900 cal yr BP (subzone EC-IVa) there is a significant presence of mountain rainforest taxa. Especially certain taxa of UMF vegetation increased markedly, such as Melastomataceae, *Escallonia*, *Purdiaea nutans* and *Clethra* between *ca.* 1200–900 cal yr BP, which probably reflects a forest recovery. However the LMF taxa decrease slightly. The subpáramo taxa were dominated mainly by Asteraceae. The páramo taxa show a low proportion mainly due to the decrease of Poaceae. In addition, there is evidence of the absence of Pteridophyta spores after *ca.* 900 cal yr BP. There is low charcoal influx compared with the previous period.

Between *ca.* 900 cal yr BP and the present (subzone EC-IVb and zone EC-V) the UMF vegetation decreased markedly, mainly Melastomataceae, *Escallonia*, *Purdiaea nutans* and *Clethra*. There is evidence of an expansion of grassland (páramo taxa) mainly caused by the expansion of Poaceae and Cyperaceae (after ~ 500 cal yr BP) which may indicate locally humid conditions (Moscol Olivera & Hooghiemstra 2010). The occurrence *Plantago* reflects wet conditions (Bosman *et al.* 1994, Niemann & Behling 2008). This indicates a change to a moister and cooler environment. The increased fire intensity during the wetter late Holocene strongly suggests that frequent fires were of anthropogenic origin. Hence high influx of charcoal accompanies the expansion of páramo species (Colinvaux *et al.* 1997, Niemann & Behling 2008, Brunschön *et al.* 2009).

COMPARISON OF THE RESULTS WITH OTHER RECORDS

The new results from El Cristal, located in the northern Andean Depression, is here compared with nearby study sites in and outside the Andean Depression of the northern Andes in Ecuador (Colinvaux *et al.* 1997, Hansen *et al.* 2003, Bakker *et al.* 2008, Niemann & Behling 2008, 2009; Brunschön & Behling 2009, Jantz & Behling 2012), Peru (Hansen *et al.* 1984, Bush *et al.* 2005), and Bolivia (Paduano *et al.* 2003, Williams *et al.* 2011).

During the late Pleistocene (19 700–12 500 cal yr BP) a similar vegetation pattern as in El Cristal is evident from the pollen records of the PNP located in central part of Andean Depression in southern Ecuador. The Cocha Caranga record, at an elevation of 2710 m, shows higher proportions of the UMF taxa between *ca.* 14 500 and 9700 cal yr BP, indicating increased temperatures compared with earlier periods (Niemann & Behling 2009). The Cerro Toledo record, at 3150 m, suggests a higher occurrence of subpáramo and mountain rainforest vegetation with relatively wet conditions (Brunschön & Behling 2009). The record from the central Ecuadorian Andes outside the Andean Depression, Lake Surucucho, at 3180 m, indicates an advance of the treeline during the late glacial period (Colinvaux *et al.* 1997).

Like the pollen records from the Ecuadorian Andes, the Peruvian and Bolivian Andes records show a similar vegetation pattern to the study area. For example, the Laguna Junin record, at 4100 m in the central Peruvian Andes, suggests that between 16 000 and 12 000 yr BP a forest line dominated by *Polylepis* and Asteraceae covered the plain areas (Hansen *et al.* 1984). The Laguna de Chochos record, located at an altitude of 3285 m near the upper forest limit of the eastern Peruvian Andes, suggests that the cloud forest replaced a glacial foreland habitat about 15 000 cal yr BP (Bush *et al.* 2005). Moreover, the Laguna Khomer Kotcha Upper record, at 4153 m in the eastern Bolivian Andes, shows that before *ca.* 14 500 cal yr BP, warming and relatively moist conditions were evident with an expansion of *Polylepis* woodland (Williams *et al.* 2011).

A drier early/mid-Holocene, as recorded in El Cristal between *ca.* 11 500 to 3600 cal yr BP, has been recorded throughout many regions of the northern and central Andes (Marchant *et al.* 2002). Studies by Bush and Gosling (2012) suggest that sites

closest to the equator became dry during the early Holocene (*ca.* 11 000 cal yr BP). Also, the mid-Holocene is characterized by a dry event (*ca.* 8000–5000 cal yr BP), where a reduction in precipitation in the northern to central Andes is evident (Urrego *et al.* 2009). However, new past environmental change studies describe this event as one of increased drought frequency punctuated with episodic wet events, rather than as a single dry 'event' (Paduano *et al.* 2003, Bush *et al.* 2005, Valencia *et al.* 2010). Especially in the southern Ecuadorian Andes in the PNP, pollen records show relatively warm and dry conditions. As is the case of the record of Laguna Cocha Caranga, which indicates that the early to mid-Holocene was a drier period, shown in the strong decrease of *Isoetes* and a marked increase of fire intensity giving rise to the establishment of open grassy vegetation (Niemann & Behling 2009). Also the El Tiro record, at 2810 m elevation, shows that mountain forest taxa, especially of the UMF, was predominant, with *Hedyosmum* and Podocarpaceae reflecting a warmer climate (Niemann & Behling 2008). The Cerro Toledo record shows a gradual change in the vegetation composition. The disappearance of *Isoetes*, lower presence of páramo vegetation, and high proportion of subpáramo reflect warmer conditions (Brunschön & Behling 2009).

Like those from the PNP, the record from the El Cajas National Park (southern Ecuador) Lagunas Chorreras, at 3700 m altitude outside of the Andean Depression, indicates that the beginning of the Holocene is marked by the expansion of mountain forest. During the Holocene especially *Polylepis* became commoner, reaching its maximum during the mid-Holocene period (Hansen *et al.* 2003). Other records from the central and northern Ecuadorian Andes (outside the Andean Depression) show the same vegetation pattern: Laguna Yaguarcocha, at 2200 m in central Ecuador, with *Alnus* and *Weinmannia* as representative taxa (Colinvaux *et al.* 1988), and Guandera Biological Reserve, 3400 m in the northernmost region of Ecuador, with a greater occurrence of *Hedyosmum* (Bakker *et al.* 2008).

Studies throughout the Ecuadorian Andes as well as in Peru and Bolivia indicate drier conditions during the early/mid-Holocene. The Lagunas de Chochos record suggests that a warm and wet early Holocene was interrupted by a dry period that lasted from *ca.* 9500 to 7300 cal yr BP, when, consistent with a drier and more fire-disturbed setting, *Alnus* became an important floral component. Moreover,

the Lake Titicaca record, 3810 m high in the northern portion of the Bolivian Altiplano, reflects a dry phase between *ca.* 6000 and 4000 cal yr BP, shown by a change in pollen composition that shows sharp declines of Cyperaceae and *Isoetes* (Paduano *et al.* 2003).

During the late Holocene (*ca.* 1380 cal yr BP to the present) the vegetation composition at the study area El Cristal was somewhat similar to what has been found in the pollen records of the PNP. The Cocha Caranga record shows open grassy areas with forest patches of mainly *Weinmannia*, Melastomataceae, *Myrsine*, *Clethra* and Moraceae/Urticaceae after *ca.* 1300 cal yr BP (Niemann & Behling 2009). The El Tiro record shows a decrease in upper mountain rainforest and an increase in Melastomataceae, thus suggesting relatively stable subpáramo vegetation (Niemann & Behling 2008). Unlike El Cristal, the Cerro Toledo record after *ca.* 1800 cal yr BP shows a slight decrease in páramo and increase in subpáramo, UMF, and LMF taxa, suggesting warmer temperatures (Brunschön & Behling 2009).

Other records from the southern and northern Ecuadorian Andes show a similar vegetation pattern. Studies by Jantz & Behling (2012), in the eastern ridge of the western Cordillera in southern Ecuador at 3780 m, indicated that after *ca.* 2240 cal yr BP vegetation changes suggest a moister and cooler environment, as *Plantago rigida* became very abundant as well as *Ranunculus* and *Hypericum*. Also, the data obtained from the Guandera Biological Reserve indicate an increase of páramo vegetation and a decrease in temperature between 2000 and 800 cal yr BP (Bakker *et al.* 2008).

SUMMARY AND CONCLUSIONS

The El Cristal sediment record from the eastern slope of the Cordillera in the Protective Forest Corazón de Oro of southern Ecuador provides a detailed history of the vegetation and fire dynamics since the late Pleistocene. Given the location of the study area in the Andean Depression, local climatic conditions vary considerably, influencing the vegetation structure.

During the late Pleistocene period (*ca.* 19 750–11 500 cal yr BP) Upper Mountain Forest (UMF) was the main vegetation type at the study area. In particular, there is evidence of the occurrence of *Polylepis* forests at low elevations in the northern part of the Andean Depression, which does not occur today. *Polylepis* populations were shifted into the northern part of the Andean Depression from the

higher Andean regions. The high occurrence of *Isoetes* indicates that the small basin was filled with shallow water. Due to the presence of páramo taxa at lower elevations during the late Pleistocene the upper forest line was at a markedly lower elevation.

The transition from the late Pleistocene to the early and mid-Holocene period between *ca.* 12 500 and 3600 cal yr BP was characterized by small fluctuations between the Lower Mountain Forest (LMF) and the UMF. The relatively stable proportion of subpáramo and páramo taxa suggests that an open mountain forest covered the study area. A substantial decline in *Isoetes* indicates that the shallow water pond was probably replaced by a swamp. Hence the relatively high proportion of mountain rainforest and low proportion of páramo taxa may reflect warmer conditions. After *ca.* 4000 cal yr BP, *Polylepis* forest decreased probably because of an increase in the frequency of fire during this dry period, as it is a fire-sensitive tree. The mid-to late Holocene (*ca.* 3600–1380 cal yr BP) is characterized by a high occurrence of UMF and a good representation of LMF. The landscape disturbance in the study area is reflected in a higher frequency of Asteraceae, *Muehlenbeckia/Rumex*, as well as the high presence of *Osmonda* and *Huperzia*. The late Holocene, from *ca.* 1380 cal yr BP to the present, was generally characterized by an expansion of páramo taxa and a low proportion of mountain rainforest. Hence the vegetation changed to an open grassy landscape with forest patches.

Fires, as recorded in small and large charcoal fragments, are found throughout the 19 750 years of the core studied, showing that fire is an important ecological factor even under humid conditions such as in the study area. In addition, increased fire intensity during the wetter late Holocene strongly suggests that frequent fires were of anthropogenic origin. However, the first presence of considerable anthropogenic activity is recorded at around 4000 cal yr BP.

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