JOURNAL OF QUATERNARY SCIENCE (2008) **23**(3) 203–212

Published online 14 September 2007 in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/jqs.1134

Late Quaternary vegetation, climate and fire dynamics inferred from the El Tiro record in the southeastern Ecuadorian Andes

HOLGER NIEMANN* **and HERMANN BEHLING**
Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Göttingen, Germany

Niemann, H. and Behling, H. 2007. Late Quaternary vegetation, climate and fire dynamics inferred from the El Tiro record in the southeastern Ecuadorian Andes. *J. Quaternary Sci.*, **Vol. 23** pp. 203–212. ISSN 0267-8179.

Received 8 September 2006; Accepted 15 March 2007

ABSTRACT: In order to study the stability and dynamics of mountain rainforest and paramo ecosystems, including the biodiversity of these ecosystems, the Holocene and late Pleistocene climate and fire variability, and human impact in the southeastern Ecuadorian Andes, we present a high-resolution pollen record from El Tiro Pass (2810 m elevation), Podocarpus National Park. Palaeoenvironmental changes, investigated by pollen, spores and charcoal analysis, inferred from a 127 cm long core spanning the last ca. 21 000 cal. yr BP, indicate that grass-paramo was the main vegetation type at the El Tiro Pass during the late Pleistocene period. The grass-paramo was rich in Poaceae, *Plantago rigida* and *Plantago australis*, reflecting cold and moist climatic conditions. During the early Holocene, from 11 200 to 8900 cal. yr BP, subparamo and upper mountain rainforest vegetation expanded slightly, indicating a slow warming of climatic conditions during this period. From 8900 to 3300 cal. yr BP an upper mountain rainforest developed at the study site, indicated by an increase in *Hedyosmun*, Podocarpaceae, *Myrsine* and *Ilex*. This suggests a warmer climate than the present day at this elevation. The modern subparamo vegetation became established since 3300 cal. yr BP at El Tiro Pass. Fires, probably anthropogenic origin, were very rare during the late Pleistocene but became frequent after 8000 cal. yr BP. Copyright © 2007 John Wiley & Sons, Ltd.

KEYWORDS: late Pleistocene; Holocene; palynology/pollen; Tropics; climate change; South America.

Introduction

In this paper we discuss vegetation, climate and fire dynamics inferred from a fossil pollen and charcoal record from the southeastern Ecuadorian Andes, with particular focus on landscape development and human impact. This study has been carried out under the framework of the 'Deutsche Forschungsgemeinschaft' (DFG) research group 'Tropical Mountain Ecosystems'.

Despite the importance of understanding the landscape history, especially in hotspots of biodiversity, some pollen records are available from the Ecuadorian Andes (e.g. Bush *et al.*, 1990; Colinvaux, 1997; Hansen *et al.*, 2003).

The pollen record from Lake Surucucho (Las Cajas National Park, 3200 m) at the eastern flank of the western Ecuadorian Andes shows treeless vegetation in glacial times and Holocene development of modern Andean forests (Colinvaux, 1997).

In northeastern Ecuador, records of the road cut sites at Mera (ca. 34 000–31 000 yr BP) and San Juan Bosco (31 000–26 000 yr BP) show a significant presence of mountain taxa such as *Alnus* and *Podocarpus* at low elevations of 1100 m and 970 m, respectively, suggesting a cooling of ca. 7.5°C below present during the middle of the last glacial period (Bush *et al.*, 1990).

In southwestern Ecuador in Las Cajas National Park in the western Cordillera (3700 m elevation), studies indicate for the Lateglacial period (17 000–11 000 cal. yr BP) a herb paramo, reflecting colder and moister climatic conditions relative to these of today. Fires were rare at that time. The beginning of the Holocene is marked by the expansion of moist mountain forest. During the Holocene *Polylepis* became more frequent and reached its maximum during the mid Holocene period. Fires were much more frequent during the early and mid Holocene than during the Lateglacial period. After 4000 cal. yr BP vegetation changes and the decrease in charcoal particles suggest a change to moister conditions (Hansen *et al.*, 2003).

Other palynological studies, from a similar landscape, are available from the eastern Andes of northern Peru (Hansen *et al.*, 1994; Hansen and Rodbell, 1995; Berrio *et al.*, 2002; Bush *et al.*, 2005), from the eastern Andes of southern Colombia (Hooghiemstra and Van der Hammen, 1993; Wille *et al.*, 2001;

* Correspondence to: H. Niemann, Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany.
E-mail: holnie@web.de

Velez *et al.*, 2006) and from the eastern Andes of Venezuela (Rull *et al.*, 2005).

The pollen record from Laguna Baja in northern Peru (3575 m elevation) indicates a marked vegetation and timberline oscillation during the Lateglacial period. A warm and moist climate was responsible for an open mixed mountain forest at ca. 12 000 yr BP (13 970 cal. yr BP) in northern Peru. This was followed by the expansion of paramo at the expense of the mixed mountain forest, suggesting a cooler and/or more arid interval between ca. 11 600 and 10 000 yr BP (13 478 and 11 480 cal. yr BP). During the Holocene, both temperature and precipitation increased, resulting in the replacement of paramo vegetation with wet mountain forest. The record from Laguna Baja also suggests a drier climate between ca. 9000 and 6000 yr BP (10 200 and 6830 cal. yr BP) (Hansen and Rodbell, 1995).

At Laguna Chochos (3285 m) in the eastern Andes of northern Peru, the Lateglacial period was cool and moist, and the vegetation was sparse on the glacial forelands. A warm and wet early Holocene was interrupted by a dry event that lasted from ca. 9500 to 7300 cal. yr BP (Bush *et al.*, 2005).

The Fuquene Lake record, on the eastern Andean Cordillera of Columbia (2580 m), records dry and cold conditions found during the late Pleistocene between 19 700 and 14 200 yr BP (23 350–17 030 cal. yr BP). A return to dry conditions is indicated by a hiatus between 13 110 and 8680 yr BP (15 600–9560 cal. yr BP). Very humid conditions prevailed during the early–mid Holocene, from 8680 to 7070 yr BP (9560–7870 cal. yr BP), and the lake reached its maximum extent during that period. A dry mid–late Holocene period is reflected by a decreasing lake level between 7070 and 4300 yr BP (7870–4900 cal. yr BP). Minimum lake levels were reached between 3700 and 1550 yr BP (4230–1770 cal. yr BP). From 1550 yr BP (1770 cal. yr BP) to the present the lake was relatively shallow (Velez *et al.*, 2006).

The pollen record from Laguna Verde Alta at the eastern Andean Cordillera of Venezuela (4215 m) remained a periglacial desert, practically unvegetated between 15 500 and 11 000 cal. yr BP. Since about 11 000 cal. yr BP a lycopod assemblage (for example, cf. *Huperzia*) bearing no modern analogue colonized the superparamo. Although this community persisted until about 6000 cal. yr BP, it began to decline somewhat earlier, in synchrony with cooling following the Holocene thermal maximum of the Northern Hemisphere. At this time, the pioneer assemblage was replaced by a low-diversity superparamo community that became established 9000 cal. yr BP. This replacement coincides with regional declines in temperature and/or available moisture. Modern, more diverse superparamo assemblages were not established until about 4600 cal. yr BP, and were accompanied by a dramatic decline in *Alnus* (Rull *et al.*, 2005).

During the last glacial maximum (LGM) most Andean glaciers moved downslope, reaching lowermost positions from about 3000 m in the eastern Andes of Colombia, Ecuador and northern Peru (Clapperton, 1993; Rodbell, 1992, 1994).

Glaciers in the Ecuadorian Andes advanced before 12 500 yr BP and between 10 500 and 9000 yr BP. Rapid climatic fluctuations during the last deglaciation are documented by glacier advances, but they are not synchronous with European events (Heine and Heine, 1996).

The early and mid Holocene periods were marked by a widespread recession of glaciers in most parts of the Andes, but a return to cooler and more humid conditions apparently occurred after about 5000 yr BP. The present-day equilibrium snowline in the eastern Ecuadorian Andes is near 4800 m and glaciers terminate at 4400 m elevation. The moraine frontier of the last glaciation is found between 2800 and 3350 m elevation (Clapperton, 1993).

Similar time periods for major changes have been identified in the Amazon lowland, by the expansion of the Amazon rainforest north and south of the Equator (Behling and Hooghiemstra, 2000, 2001; Mayle *et al.*, 2000).

Glacier reconstruction at Cerro Chirripo, Costa Rica, indicated that deglaciation occurred some time after 12 360 cal. yr BP and before 9600 cal. yr BP (Orvis and Horn, 2000).

Two ice cores from Huascaran in north–central Andes of Peru contain glacial-stage conditions at high elevation (6048 m) from as much as 8°C to 12°C cooler than today. The climate was warmest from 8400 to 5200 yr BP (9455–5960 cal. yr BP) (Thompson *et al.*, 1995).

Very cold climatic conditions prevailed during the LGM, with temperatures suggested to be at least 5–8°C cooler than at present (Paduano *et al.*, 2003).

In a regional study the depression of mean annual temperature in the southern tropical Andes glaciated alpine areas was ca. 5.4 ± 0.8°C during the last glaciation (Porter, 2001).

Site description

Location

The Andes are a mountain chain, with peaks up to an altitude of more than 6000 m. The Andes of southern Ecuador and northern Peru include the so-called Andean depression (Depresion de Giron-Cuenca in Ecuador and Huancabamba in Peru). The main peaks of the mountains in this region only reach to about 4000 m. Active volcanoes are absent. The study area is part of the western slope of the eastern Cordillera in the southern Ecuadorian Andes, east of Loja in the inter-Andean valley.

The El Tiro Pass is located at 2810 m elevation in the eastern Cordillera, north of the Podocarpus National Park, adjacent to the main road from Loja to Zamorra (Fig. 1). The El Tiro Pass is about 10 km from Loja. The small bog at the El Tiro Pass (co-ordinates: 03° 50′ 25.9″ S, 79° 08′43.2″ W) is about 800 m from the summit, which has an elevation of about 3200 m. The 1.3 m deep bog is located in a small depression about 30 m wide and 60 m long.

Modern vegetation

The different vegetation types in the study area are mainly related to altitudinal gradients. The lower mountain rainforest is found at an elevation between 1800 and 2150 m, with an extremely diverse, two-storeyed tree stratum and is composed of numerous 20–35 m tall tree species. Undisturbed communities of this type can be found particularly on steep slopes of 30–50° inclination, as well as up to elevations of 2300 m at the bottom of wind-protected riverine valleys. Characteristic species include *Alzetea verticillata* (Alzataceae), *Graffenrieda miconioides* (Melastomataceae) and *Myrcianthes* sp. (Myrtaceae) (Bussmann, 2001; Lozano *et al.*, 2003).

The upper mountain rainforest is found at elevations between 2100 and 2750 m. This forest is being replaced by a much lower, monotypic formation, with only one tree stratum between 5 and 10 m, rarely up to 15 m tall. Characteristic trees are *Purdiaea nutans* (Cyrillaceae), *Myrica pubescens* (Myricaceae) and *Myrsine andina* (Myrsinaceae) (Bussmann, 2001).

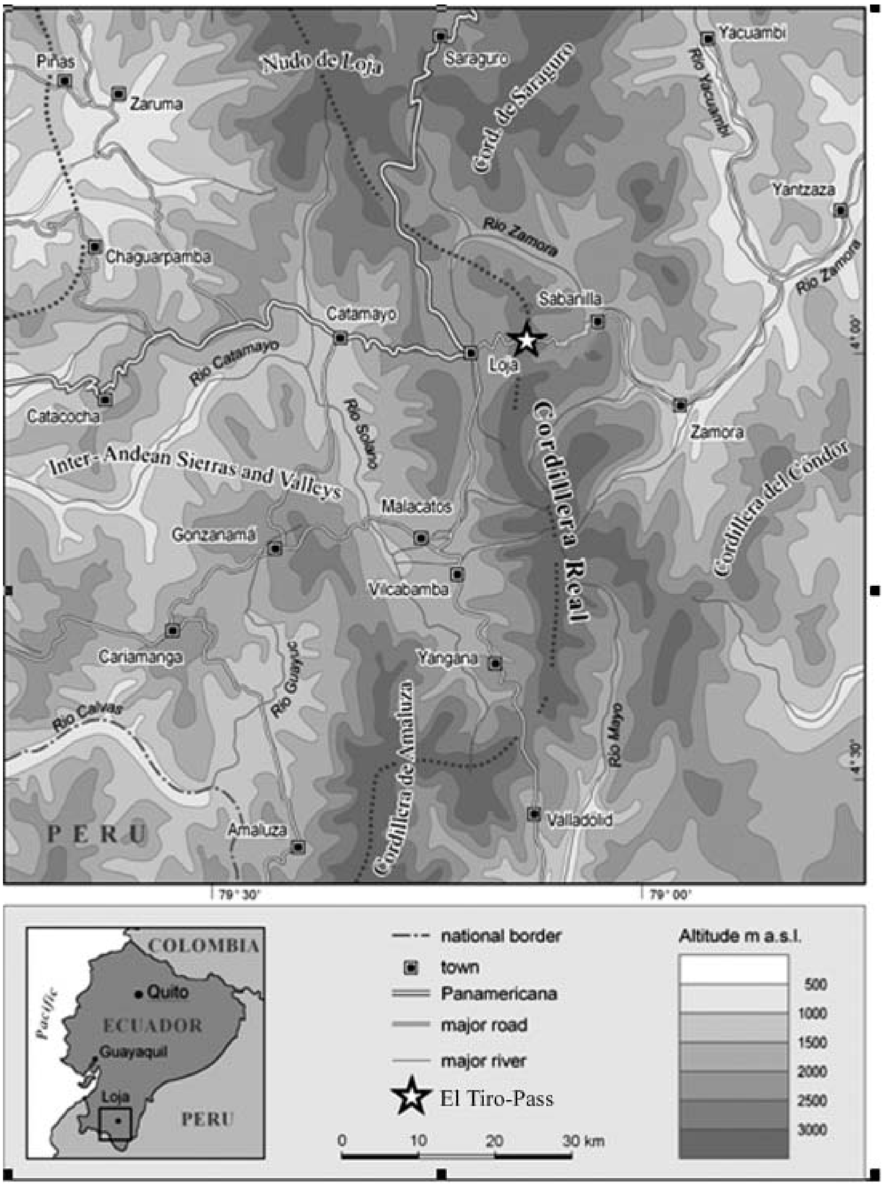

Figure 1 Map of Ecuador, showing the location of El Tiro Pass in southeastern Ecuador near Loja (modified after Richter, 2003)

The subparamo is present at altitudes between 2800 and 3100 m, characterised by *Puya nitida* (Bromeliaceae), *Brachyotum rotundifolium* (Melastomataceae) and *Oritrophium peruvianum* (Asteraceae). The shrubs and herbs grow up to 1 m (individual shrub species 2–3 m) in height (Lozano *et al.*, 2003).

The paramo is found at elevations from 2900 to 3400 m and is characterised by species such as *Arcytophyllum setosum* (Rubiaceae), *Blechnum cordatum* (Blechnaceae), *Puya maculate* (Bromeliaceae) and *Gynoxis buxifolia* (Asteraceae) (Lozano *et al.*, 2003).

The modern timberline in the Loja region is at about 3200 m. This is about 800 m lower than in the central and the northern Ecuadorian Andes, probably as a result of the so-called Andean depression (Richter and Moreira-Munoz, 2005). The high human activity (periodic burning was often observed) in the Loja region may influence the elevation of the timberline.

Climate

The climate in the southeastern Ecuadorian Andes is influenced by warm moisture-laden air from the Amazon lowland, which collides with cold mountain air masses. This produces much of the rainfall in the eastern Andean mountains. The high rainfall rates establish the mountain rainforest to the east and west of the Cordillera. The climate of the paramo/subparamo is the humid tropical diurnal type with cold nights and cool days. There is a short, drier period lasting from December until March (Bosmann *et al.*, 1994). As part of the Andean depression, all summits in the southern Ecuadorian Andes are below the snowline.

The eastern Andean mountains form a divide that separates the moist eastern slopes of the Andes from the dry inner Andean basins (e.g. the Loja and Catamayo basins). Between the eastern slopes of the eastern Cordillera and the dry valley of Catamayo, which are only 70 km apart, annual rainfall rates drop from over 4000 mm to 300 mm (Bendix *et al.*, 2004). The average precipitation rate (in the years 2003–2005) near the El Tiro Pass (2880 m) is about 3500 mm yr^{-1} (Emck, 2007).

Methods

The peat deposit at the El Tiro Pass was cored using a Russian corer. The total length of the core is 127 cm. Sections of 50 cm length were extruded on-site with split PVC tubes, wrapped

DOI: 10.1002/jqs

with plastic film and stored under dark and cold (+4°C) conditions before processing.

Five subsamples (organic material and charcoal fragments) were taken for accelerator mass spectrometer (AMS) radiocarbon dating from the El Tiro core. Radiocarbon ages have been calibrated using CalPal (CalCurve 50 k cal. yr BP to modern) (Weninger *et al.*, 2004).

For pollen and charcoal analysis 64 subsamples (0.25 cm^3) were taken at 2 cm intervals along the sediment core. All samples were processed using standard analytical methods (Faegri and Iversen, 1989). Exotic *Lycopodium* spores were added to each sample before treatment for calculation of pollen concentration and accumulation rates. 300 pollen grains were counted for each sample. The pollen sum includes trees, shrubs and herbs, and excludes fern spores and aquatic pollen taxa. Pollen identification relied on the reference collection of about 3000 neotropical species from the second author, on literature studies (Behling, 1993; Hooghiemstra, 1984) and on a reference collection collected during the fieldwork. Ecological grouping of the identified pollen taxa into lower and upper mountain rainforest, subparamo and paramo has been carried out according to available data in the literature (Bussmann, 2001; Lozano *et al.*, 2003; Homeier and Werner, 2005; Richter and Moreira-Munoz, 2005). Pollen and spore data are presented in pollen diagrams as percentages of the pollen total. Carbonized particles (2–150 μm) were counted on pollen slides and presented as influx (particles cm^{-2} yr^{-1}). Larger carbonized particles (250–700 μm) were observed, but not counted, from 73 cm to the top of the record. The software TILIA, TILIAGRAPH and CONISS were used for illustration of the pollen and spore data (Grimm, 1987). In total, 90 pollen and spore types were recognised. The pollen diagram (Fig. 3) shows records of the most abundant pollen and spore taxa. Figure 4 illustrates records of the ecological groups, pollen concentration and pollen influx as well as charcoal influx.

Results

Stratigraphy

The 127 cm long sediment core from the El Tiro Pass consists of organic material with roots (0–7 cm depth), decomposed organic rich material (7–49 cm) and well-decomposed organic rich material with silt and clay (49–74 cm). In the transition zone (74–83 cm) the organic matter content decreases. The lowermost part of the core consists of silty clay (83–127 cm). A detailed description of stratigraphic changes follows:

0–7 cm	dark brown decomposed organic material with fine roots,
7–49 cm	brown decomposed organic rich material,
49–74 cm	light brown strongly decomposed organic rich material with some silt and clay,
74–83 cm	light brown to grey organic material with increasing amounts of silt and clay,
83–127 cm	light grey silty clay.

Table 1 AMS radiocarbon ^{14}C dates and calibrated ages for sediment core from El Tiro Pass

Lab. code	Dated material	Core depth (cm)	^{14}C yr BP	cal. yr BP
Erl-8371	Leaf	31	1828 ± 55	1767 ± 63
Erl-8899	Organic material	48	2972 ± 43	3155 ± 70
Erl-8898	Organic material	77	7850 ± 71	8713 ± 131
Erl-9454	Organic material	97	11187 ± 104	13082 ± 139
Erl-8372	Organic material	126	16517 ± 128	19836 ± 306

Chronology and pollen zonation

Five AMS radiocarbon dates (Table 1) provide a detailed chronological control of the sediment core of El Tiro Pass. The AMS date near the base of the core at 127 cm depth documents that the bog contains deposits which cover the last 20 100 cal. yr BP.

The series of five AMS dates shows a regular down-core increase of age, which indicates that sediments accumulated continuously. Cluster analysis of terrestrial pollen taxa produces a dendrogram that permits zonation of the record into zones ET-1 to ET-7 (Fig. 4).

The average sedimentation rate of the El Tiro Pass sediment core is shown in Fig. 2. The sediment accumulation rate is relatively constant (average about 0.08 mm yr^{-1}).

Description of the pollen diagram (Figs 3 and 4)

Zone ET-1 (126–108 cm, ca. 20 100–15 800 cal. yr BP) is marked by a high representation of paramo herb pollen (65–85%), primarily Poaceae (40–50%), *Plantago rigida*

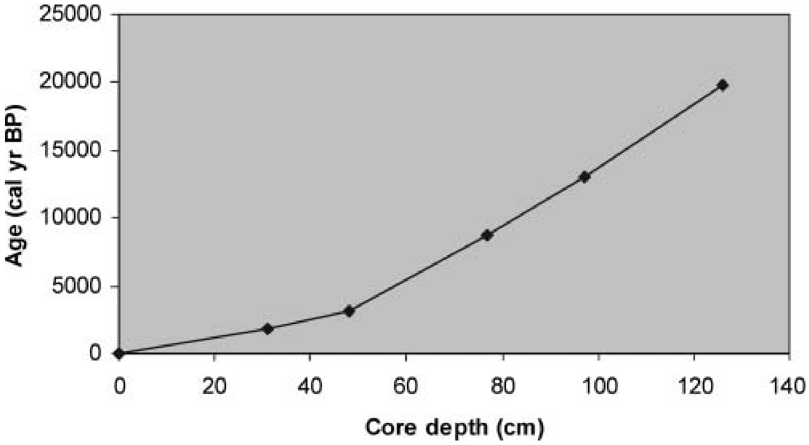

Figure 2 Average sedimentation rate of El Tiro Pass sediment core (yr BP/core depth in cm)

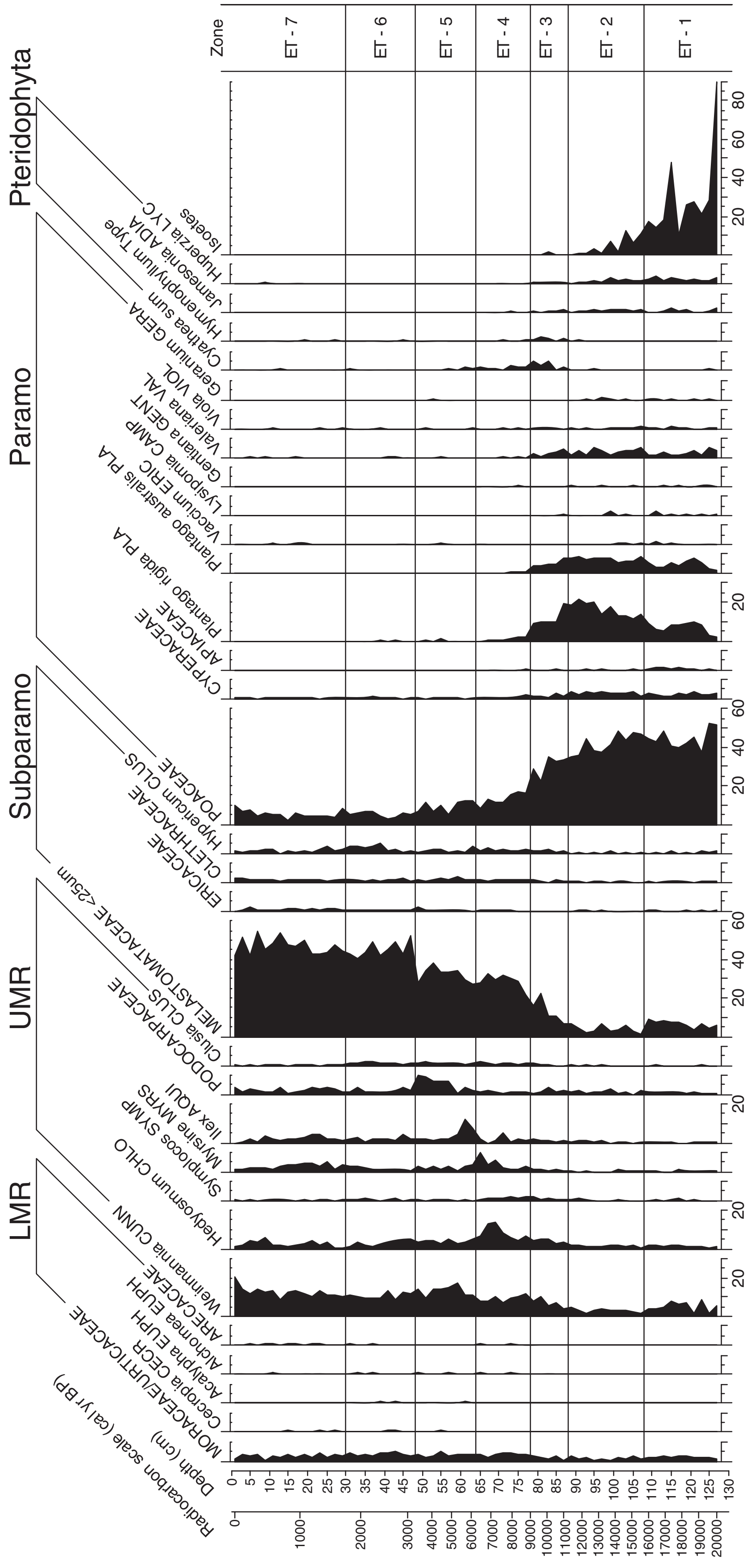

Figure 3 Pollen percentage diagram of core El Tiro Pass (2810 m elevation) showing selected fossil pollen and spore taxa grouped into lower mountain rainforest (LMF), upper mountain rainforest (UMR), subparamo, paramo and Pteriodophyta

DOI: 10.1002/jqs

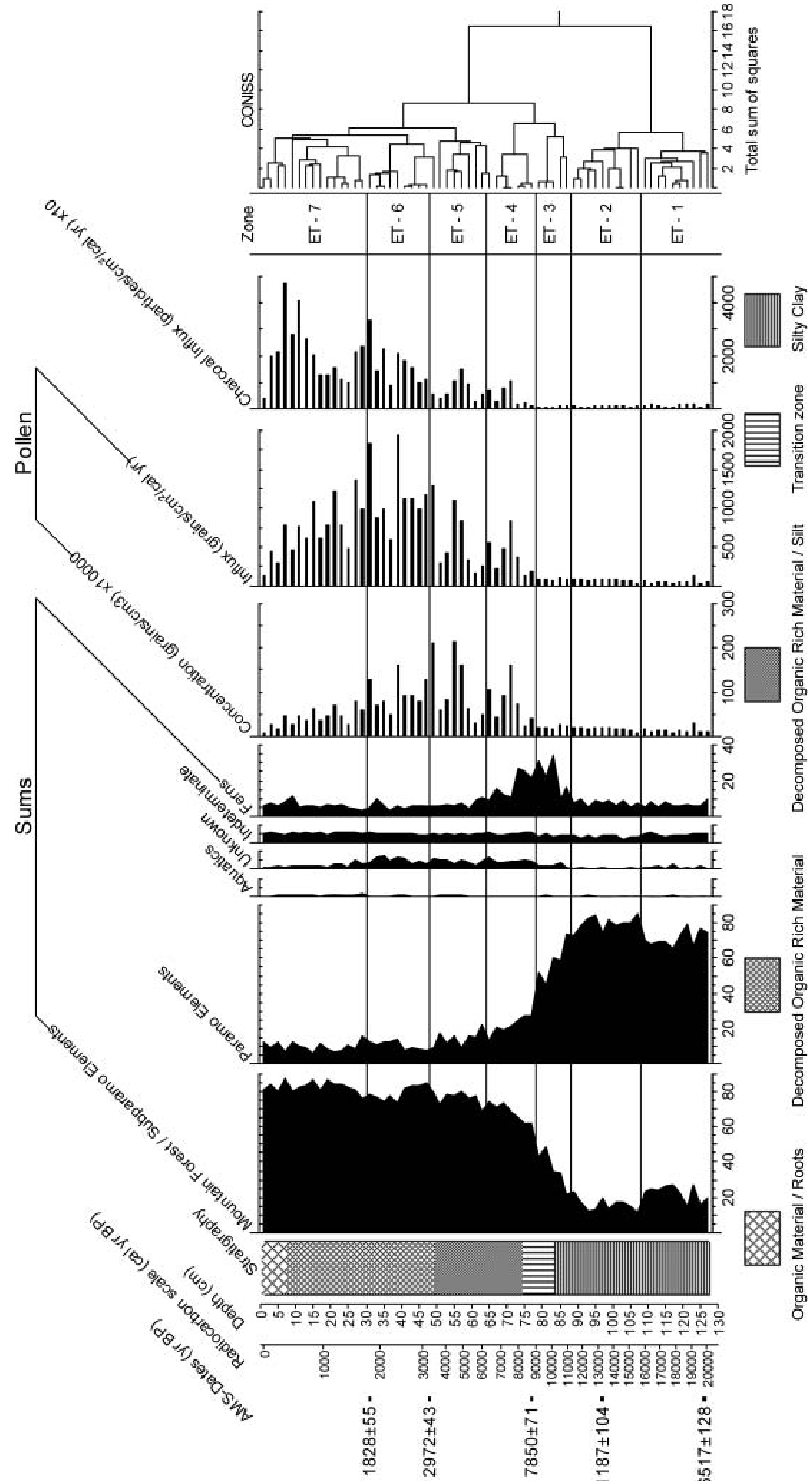

Figure 4 Pollen percentage diagram of core El Tiro Pass (2810 m elevation) showing radiocarbon dates, sums of ecological groups, records of pollen concentration, pollen influx, charcoal influx and the CONISS dendrogram

and *P. australis* (10–15%), rare *Valeriana* (2–5%) and spores of *Huperzia* (5%). Spores of *Isoetes* comprise 15–90%. Taxa of subparamo and upper mountain rainforest total 15–25%, primarily represented by Melastomataceae and *Weinmannia*. Charcoal influx was very low, <2500 particles cm^{-2} cal. yr^{-1}.

Zone ET-2 (108–88 cm, ca. 15 800–11 200 cal. yr BP) is characterised by a high number of paramo herb pollen (75–85%), primarily Poaceae (35–45%), increasing *Plantago rigida* and *Plantago australis* (20–30%) and minor *Valeriana* (4–7%). Fern spores of *Huperzia* decrease little (3–5%). Spores of *Isoetes* decrease from 20% to 0%. Taxa of

DOI: 10.1002/jqs

subparamo and upper mountain rainforest total 10–18%, primarily represented by Melastomataceae and *Weinmannia* (both 5–10%). Charcoal influx values remain low.

Zone ET-3 (88–78 cm, ca. 11 200–8900 cal. yr BP) is characterised by a strong decrease in paramo herb pollen (65–30%). Taxa of subparamo and upper mountain rainforest increase to 25–45%, primarily represented by Melastomataceae (10–20%), *Weinmannia* (10–12%), Podocarpaceae and *Hedyosmum* (both 5–8%). Fern spores increase markedly from 10% up to 35%, especially *Cyathea* (5–8%) and *Hymenophyllum* type (3–5%). The lowest charcoal influx rates occur in this zone: <2000 particles cm^{-2} cal. yr^{-1}.

Zone ET-4 (78–64 cm, ca. 8900–6200 cal. yr BP) is also marked by a continuous decrease in pollen of paramo herbs (30–15%). Taxa of subparamo and upper mountain rainforest increase strongly (45–75%), represented by Melastomataceae (15–25%), *Weinmannia* (10–15%), *Hedyosmum* (5–15%), *Myrsine* (3–10%) and *Ilex* (3–8%) as well as *Clusia*, *Symplocos* and Podocarpaceae. Taxa of lower mountain rainforest are represented in low amounts, Moaceae/Urticaceae (5–8%), *Alchornea* and Arecaceae (0–2%). Fern spores decrease markedly from 35% to 10%. Charcoal influx increase from <2000 up to 10 000 particles cm^{-2}/cal. yr^{-1}.

Zone ET-5 (64–48 cm, ca. 6200–3300 cal. yr BP) is characterised by high amounts of pollen from subparamo and upper mountain rainforest taxa (60–75%), represented by Melastomataceae (25–35%), *Weinmannia* (10–12%), *Hedyosmum* (5–8%), Podocarpaceae (5–10%), *Myrsine* (3–8%), *Ilex* (3–12%) and *Symplocos* (2–3%). Lower mountain rainforest elements are rare, Moaceae/Urticaceae (5–8%) and *Alchornea* (0–2%). Herb taxa total 12–20%, fern spores 8–15%. The charcoal influx varies from 5000 to 15 000 particles cm^{-2} cal. yr^{-1}.

Zone ET-6 (48–30 cm, ca. 3300–1700 cal. yr BP) is marked by a high representation of pollen from upper mountain rainforest and subparamo taxa (70–80%), represented by Melastomataceae (40–50%), *Weinmannia* (10–15%) and *Hedyosmum* (5–7%). Podocarpaceae, *Myrsine*, *Ilex* and *Symplocos* (0–6%). Taxa of lower mountain rainforest are represented in low amounts, Moaceae/Urticaceae (5–8%), *Alchornea* and Arecaceae (0–2%). Herb taxa total 12–20%, fern spores 8–10%. This zone is characterised by a high charcoal influx rate from 10 000 to 23 000 particles cm^{-2} cal. yr^{-1}, with a maximum at ca. 1700 cal. yr BP (35 000 particles cm^{-2} cal. yr^{-1}).

Zone ET-7 (30–0 cm, ca. 1700 cal. yr BP–present) shows the highest percentages of upper mountain rainforest and subparamo taxa (75–85%), represented by Melastomataceae (40–50%) *Weinmannia* (10–20%), *Hedyosmum*, Podocarpaceae, *Myrsine* and *Ilex* (all with 3–5%). Taxa of lower mountain rainforest are represented in low amounts, Moaceae/Urticaceae (5–8%), *Alchornea* and Arecaceae (0–2%). Herb taxa total 12–20%, fern spores 8–12%. The highest charcoal influx rate is represented in this zone 10 000–30 000 particles cm^{-2} cal. yr^{-1}. A maximum is found at ca. 600 cal. yr BP (45 000 particles cm^{-2} cal. yr^{-1}). Thereafter influx rates decrease to 5000 particles cm^{-2} cal. yr^{-1} at the core top.

Past vegetation, climatic and fire dynamics

During the late Pleistocene since ca. 20 100 cal. yr BP (Zones ET–1 and ET-2) the pollen spectra document a landscape dominated by grass-paramo, rich in Poaceae and *Plantago*. The most identified *Plantago* pollens are *P. rigida* and *P. australis*. Pteridophyta spores and spores of *Huperzia* are relatively rare. High percentages of *Isoetes* indicate that the small basin was filled with shallow water before the mire started to develop. The occurrence of paramo vegetation at this elevation indicates cold and the high frequency of *Plantago rigida* suggests wetter conditions. Fires were apparently absent or very rare during the Pleistocene.

Only a small increase in tree and shrub pollen is recorded during the early Holocene from ca. 11 200 to 8900 cal. yr BP (Zone ET-3). Subparamo expanded slightly, and different ferns including tree ferns (*Cyathea*) became frequent. These changes indicate a moderate change to warmer and wetter conditions during this period. Fires were still very rare during this early Holocene period.

During the early–mid Holocene from ca. 8900 to 3300 cal. yr BP (Zones ET-4 and ET-5), the upper mountain rainforest was predominant where today subparamo vegetation exists. A succession of *Hedyosmum*, Podocarpaceae, *Myrsine*, *Ilex* and the relatively low occurrence of Melastomataceae compared to present-day reflect the formation of the upper mountain rainforest at the coring site. A marked increase in charcoal influx values may indicate the beginning of human influence in the region at about 8000 cal. yr BP.

During the late Holocene period, from ca. 3300 cal. yr BP (Zones ET-6 and ET-7), upper mountain rainforest vegetation decreased and the modern subparamo vegetation with a high occurrence of Melastomataceae became established and was relatively stable. This vegetational change reflects a change to wetter and probably also cooler conditions than during the early–mid Holocene. Charcoal concentration increased and showed two main peaks at ca. 1700 and 600 cal. yr BP before decreasing significantly after 500 cal. yr BP. The increase in fire frequency even during this wetter period probably indicates that fires were man-made. Different fire intensities may also suggest changes in human activity.

Discussion

The pollen record indicates that the El Tiro Pass, which is today naturally covered with subparamo, was covered with grass-paramo during the recorded Pleistocene period since 20 100 cal. yr BP. *Plantago australis* and the cushion plant *Plantago rigida* were frequent during the late Pleistocene, especially during the period from 15 800–11 200 cal. yr BP. In particular *Plantago rigida* reflects cold and wet, rather than dry conditions. According to Cleef (1978) *Plantago rigida* constitutes cushion bogs at high elevation (3000–5200 m) in the puna and paramo. They are common in the grass-paramo (ca. 3600–4200 m elevation) of the Colombian Andes and occur in boggy valleys, on former lakes or even float on glacial lakes in the humid bamboo-paramo. *Plantago australis* ssp. *oreades* is a common taxon in wet subparamo and wet grass-paramo vegetation. In the eastern Cordillera of Colombia this subspecies was recorded with low cover in different azonal moist paramo communities (Cleef, 1978). The pollen data from Holocene mire in the Chingaza National Park at 3730 m elevation, in the eastern Cordillera of middle Colombia in the grass-paramo zone, show a high occurrence of *Plantago rigida* pollen. Cushions of *Plantago rigida* date from the early Holocene, 9000 yr BP (10 200 cal. yr BP) until today, and experienced several periods of expansion and re-expansion. Expansion of the *Plantago rigida* cushion took place under cool and humid conditions. Under warmer and drier conditions the expansion stopped (Bosman *et al.*, 1994). At Laguna Chochos (3285 m), in the eastern Andes of northern Peru, the low pollen influx and charcoal values indicate that the initial deglacial conditions were markedly cooler than today, with low to moderate precipitation, and that there was not enough vegetation biomass to sustain fire (Bush *et al.*, 2005).

Huperzia became less frequent at the end of the Pleistocene. This is also documented in the pollen record of Laguna Chorrereas at an elevation of 3700 m (Las Cajas National Park, western Cordillera). There, *Huperzia* sp. spores decrease during the transition from the late Pleistocene–Holocene period. *Huperzia* spp. and *Lycopodium* spp. characterise the upper cold wet paramo (Hansen *et al.*, 2003).

Fires were rare during the late Pleistocene in the El Tiro region. This has been also found in the record from Lake Surucucho in the Las Cajas National Park (Colinvaux *et al.*, 1997). At Laguna Chochos fires were rare until 11 500 cal. yr BP (Bush *et al.*, 2005).

A relatively low increase in mountain rainforest and subparamo shrubs and trees is observed during the early Holocene period from 11 200 to 8900 cal. yr BP, suggesting that the formation of forest vegetation in the upper Andean regions was slow and took a long period of about 2300 years. This might be due to a slow increase in temperature and a slow retreat of the glaciers in the northern Andes. Results from fossil pollen records from the central Peruvian Andes (4000 m) point to increased moisture as well as higher temperatures from about 11 000 to 7000 yr BP (12 910–7850 cal. yr BP) (Hansen *et al.*, 1994). At Cerro Chirripo, Costa Rica (about 3500 m), deglaciation occurred some time after 12 360 cal. yr BP and before 9600 cal. yr BP (Orvis and Horn, 2000). The dates from the pollen record of Lake Surucucho (3200 m) indicate a much earlier establishment of mountain rainforest and subparamo by an increase in *Weinmannia* and *Hedyosmum* at 10 300 yr BP (12 260 cal. yr BP) (Colinvaux, 1997).

Fern spores including tree ferns (*Cyathea*) expanded markedly, reflecting a change to more humid conditions at the study site during this early Holocene period. The record from Laguna Baja also shows an increase in fern spores between ca. 12 000 and 11 000 yr BP (13 970 and 12 910 cal. yr BP) (Hansen and Rodbell, 1995).

During the later early–mid Holocene period from ca. 8900 to 3300 cal. yr BP, a succession of *Hedyosmun*, Podocarpaceae, *Myrsine* and *Ilex* may indicate the formation of the upper mountain rainforest at the study site. It is quite possible that upper mountain rainforest vegetation reflects a warmer climate, as indicated by the more strongly decomposed organic material during this period. At Fuquene Lake on the Eastern Andean Cordillera of Colombia (2580 m), very humid conditions are suggested during the early–mid Holocene from 8680 to 7070 yr BP (9560–7870 cal. yr BP) (Velez *et al.*, 2006). From 8850 yr BP (10 010 cal. yr BP) the record from La Teta, Cauca Valley in central Colombia (1020 m), indicates dry climatic conditions relative to the present, these prevailing up to 2880 yr BP (3010 cal. yr BP) (Berrio *et al.*, 2002).

According to Homeier and Werner (2005) elevational distribution data (taken about 10 km to the east of El Tiro Pass at the Estacion Cientifica San Francisco (ECSF), next to Sabanilla) indicate the following taxa elevation relationships: *Hedyosmum* 1800–2600 m, Podocarpaceae 1800–2700 m, *Myrsine* 1900–3100 m and *Ilex* 1800–3100 m. However, this suggestion has to be examined in detail when other additional records are available from the southeastern Ecuadorian Andes. Melastomataceae is the most dominant family in the subparamo today (Lozano *et al.*, 2003; Richter, personal communication). During the early–mid Holocene period, Melastomataceae pollen was recorded at about 15% lower than during the late Holocene. This suggests also the formation of the upper mountain rainforest rather than subparamo at the coring site.

Fern spores decrease during the period 8900–6200 cal. yr BP (Zone ET-4), while charcoal influx increase markedly, indicating that fires became quite frequent during this period. Macroscopic charcoal has been observed from 73 cm (ca. 8000 cal. yr BP) up to the top of the record. This may suggest that fires occurred near the El Tiro Pass on the slopes of the El Tiro mountains and may have reduced the frequency of different fern species in the vegetation. So far, it has been difficult to determine whether fires were of natural or anthropogenic origin. The first human activity in the region of Loja is dated at around 4500 cal. yr BP (Guffroy, 2004), but human activities may have occurred in the dry inter-Andean valley much earlier. For example, in the Sabana de Bogota (Colombia) the presence of Amerindians could be established from 12 500 yr BP (14 800 cal. yr BP) onward and possibly even before that time (Van der Hammen and Urrego, 1978). It is somewhat speculative, but it is possible that fires on the El Tiro mountain slopes originate from anthropogenic fires by hunting activities in the savanna or dry forest area of the dry Loja basin after 8000 cal. yr BP.

During the mid–late Holocene period since 3300 cal. yr BP, the pollen data suggest, by the increase in Melastomataceae, the formation of relatively stable subparamo vegetation at the study site. Fires remained frequent during the mid Holocene period and increased during the late Holocene in the El Tiro region. The increased fire intensity during the wetter late Holocene strongly suggests that frequent fires were of anthropogenic origin. We assume that by the increased use of fire for hunting proposes and by slash and burning activities in the drier lower valleys (e.g. in the Loja area), fires spread into the mountains during drier phases of the year. The pollen record from Lake Surucucho in Las Cajas National Park (3200 m) also shows a strong increase in fires during the late Holocene (Colinvaux, 1997). Fire frequency decreased during the last ca. 600 years. The reduction or absence of human activities in the study region during the last centuries might be related to the dramatic decrease in the human population between the 14th and 17th centuries. The decrease probably reflects the Inca invasion northwards and subsequent occupation of the Loja region by the Incas. Another reason for the decreased population was probably the Old World diseases which the Spanish occupants brought to Ecuador (Alchon, 1991). By analysis of additional cores from the lower regions we wish to verify this hypothesis.

Conclusions

- The El Tiro Pass bog core at 2810 m elevation provides a detailed radiocarbon-dated record of the late Pleistocene and Holocene environment dynamics close to the modern upper forest limit in the subparamo vegetation zone on the eastern Andean flank in southern Ecuador.
- During the recorded late Pleistocene period since ca. 20 100 cal. yr BP grass-paramo, rich in Poaceae and *Plantago rigida*, indicates cold and moist conditions.
- During the early Holocene from ca. 11 200 to 8900 cal. yr BP subparamo and montane rainforest developed slightly in the upper region of the El Tiro mountain, probably due to the relatively cold conditions.

- During the early–mid Holocene from ca. 8900 to 3300 cal. yr BP the upper mountain rainforest was predominant, suggested by the less frequent occurrence of Melastomataceae and the successional stages of *Hedyosmun*, Podocarpaceae, *Myrsine* and *Ilex*. The occurrence of the upper montane rainforest at the coring site and the stronger decomposition of the organic material during that time suggest relatively warm and also somewhat drier conditions.
- During the late Holocene period since 3300 cal. yr BP the modern subparamo dominated by Melastomataceae became established, suggesting a somewhat cooler and wetter climatic condition than during the early–mid Holocene.
- Fires were rare during the Late Pleistocene and became frequent only after 8000 cal. yr BP. It is suggested that fires on the El Tiro mountain slopes originated from anthropogenic activities. During the last 500 cal. yr BP fire frequency decreased, probably due to a decrease in the human population.

Acknowledgements The project FOR 402/D1 is kindly funded by the Deutsche Forschungsgemeinschaft (DFG). Felix Matt (research station leader) is thanked for his logistical support and for information concerning the Loja region. Thanks are also due to Jürgen Homeier for use of his species lists and collected flower samples.

References

Alchon SA. 1991. *Native Society and Disease in Colonial Ecuador*. Cambridge University Press: Cambridge, UK.

Behling H. 1993. Untersuchungen zur spätpleistozänen und holozänen Vegetations- und Klimageschichte der tropischen Küstenwälder und der Araukarienwälder in Santa Catarina (Südbrasilien). In *Dissertationes Botanicae*, Vol. 206 . J Cramer: Berlin.

Behling H, Hooghiemstra H. 2000. Holocene Amazon rain forest–savanna dynamics and climatic implications: high resolution pollen record Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science* **15**: 687–695.

Behling H, Hooghiemstra H. 2001. Neotropical savanna environments in space and time: late Quaternary interhemispheric comparisons. In *Interhemispheric Climate Linkages*, Markgraf V (ed.). Academic Press: New York; 307–323.

Bendix J, Fabian P, Rollenbeck R. 2004. Gradients of fog and rain in a tropical montane cloud forest of southern Ecuador and its chemical composition. In *Proceedings of the 3rd International Conference on Fog, Fog Collection and Dew*, 11–15 October 2004, Cape Town, South Africa.

Berrio JC, Hooghiemstra H, Marchant R, Rangel O. 2002. Late-glacial and Holocene history of the dry forest area in the south Colombian Cauca Valley. *Journal of Quaternary Science* **17**: 667–682.

Bosman AF, Hooghiemstra H, Cleef AM. 1994. Holocene mire development and climatic change from a high Andean *Plantago rigida* cushion mire. *The Holocene* **43**: 233–243.

Bush MB, Colinvaux PA, Wiemann MC, Piperno DR, Liu KB. 1990. Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Research* **34**: 330–345.

Bush MB, Hansen BCS, Rodbell DT, Seltzer GO, Young KR, Leon B, Abbott MB, Silman MR, Gosling WD. 2005. A 17 000-year history of Andean climate and vegetation change from Laguna de Chochos, Peru. *Journal of Quaternary Science* **20**: 703–714.

Bussmann RW. 2001. The montane forests of Reserva Biologica San Francisco (Zamora-Chinchipe, Ecuador):vegetation zonation and natural regeneration. *Erde* **132**: 9–25.

Clapperton CW. 1993. *Quaternary Geology and Geomorphology of South America*. Elsevier: Amsterdam.

Cleef AM. 1978. Characteristics of neotropical paramo vegetation and its subantarctic relations. In *Geoecological Relations between the Southern Temperate Zone and the Tropical Mountains*, Troll C, Lauer W (eds). Erdwissenschaftliche Forschung XI. Franz Steiner: Wiesbaden; 365–390.

Colinvaux PA. 1997. Glacial and postglacial pollen records from the Ecuadorian Andes and Amazon. *Quaternary Research* **48**: 69–78.

Emck P. 2007. *A climatology of south Ecuador - with special focus on the major Andean ridge as Atlantic-Pacific climate divide*. PhD thesis, Universität Erlangen-Nürnberg, Bavaria.

Faegri K, Iversen J. 1989. *Textbook of Pollen Analysis*. Wiley: New York.

Grimm EC. 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of the incremental sum of squares. *Computer and Geosciences* **13**: 13–35.

Guffroy J. 2004. *Catamayo precolombino: Investigaciones arqueologicas en la provincia de Loja (Ecuador)*. IRD: Paris.

Hansen BCS, Rodbell DT. 1995. A late-glacial/Holocene pollen record from the eastern Andes of northern Peru. *Quaternary Research* **44**: 216–227.

Hansen BCS, Seltzer GO, Wright HE. 1994. Late Quaternary vegetation change in the central Peruvian Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**: 263–285.

Hansen BCS, Rodbell DT, Seltzer GO, Leon B, Young KR, Abbott M. 2003. Late-glacial and Holocene vegetation history from two sides in the western Cordillera of southwestern Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**: 79–108.

Heine K, Heine JT. 1996. Late Glacial fluctuations: glacier retreat during Younger Dryas time. *Arctic and Alpine Research* **28**: 496–501.

Homeier J, Werner FA. 2005. *Preliminary Checklist of the Spermatophytes of the Reserva San Francisco (Province Zamora-Chinchipe, Ecuador)*. Department of Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen: Göttingen.

Hooghiemstra H. 1984. Vegetation and climatic history of the High Plain of Bogota, Colombia: a continuous record of the last 3,5 million years. *Dissertationes Botanicae* **79**. J. Cramer Verlag: Vaduz; 1–368.

Hooghiemstra H, Van der Hammen T. 1993. Late Quaternary vegetation history and paleoecology of Laguna Pedro Palo (subandean forest belt, Eastern Cordillera, Colombia). *Review of Palaeobotany and Palynology* **77**: 235–262.

Lozano P, Delgado T, Aguirre Z. 2003. *Estado actual de la flora endemica exclusive y su distribucion en el Occidente del Parque Nacional Podocarpus*. Funbotanica & Herbario y Jardin Botanico: Loja, Ecuador.

Mayle F, Burbridge R, Killeen TJ. 2000. Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**: 2291–2294.

Orvis KH, Horn SP. 2000. Quaternary glaciers and climate on Cerro Chirripo, Costa Rica. *Quaternary Research* **54**: 24–37.

Paduano GM, Bush MB, Baker PA, Fritz SC, Seltzer GO. 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**: 259–279.

Porter SC. 2001. Snowline depression in the tropics during the last glaciation. *Quaternary Science Reviews* **20**: 1067–1091.

Richter M. 2003. Using epiphytes and soil temperatures for eco-climatic interpretations in southern Ecuador. *Erdkunde* **57**: 161–181.

Richter M, Moreira-Munoz A. 2005. Climatic heterogeneity and plant diversity in southern Ecuador experienced by phytoindication. *Review of Peruvian Biology* **12**: 217–238.

Rodbell DT. 1992. Late Pleistocene equilibrium-line reconstructions in the Northern Peruvian Andes. *Boreas* **21**: 43–52.

Rodbell DT. 1994. The timing of the last deglaciation in Cordillera Oriental, Northern Peru based on glacial geology and lake sedimentology. *Geological Society of America Bulletin* **105**: 923–934.

Rull V, Abbott MB, Polissar PJ, Wolfe AP, Bezada M, Bradley RS. 2005. 15.000-yr pollen record of vegetation change in the high altitude tropical Andes at Laguna Verde Alta, Venezuela. *Quaternary Research* **64**: 308–317.

Thompson LG, Mosley-Thompson E, Davis ME, Lin PN, Henderson KA, Cole-Dai J, Bolzan JF, Liu KB. 1995. Late glacial stage and Holocene tropical ice core records from Huascaran, Peru. *Science* **269**: 46–50.

Van der Hammen T, Urrego CG. 1978. Prehistoric man on the Sabana de Bogota: data for an ecological prehistory. *Palaeogeography, Paleoclimatology, Palaeoecology* **25**: 179–190.

Velez MI, Hooghiemstra H, Metcalfe S, Wille M, Berrio JC. 2006. Late Glacial and Holocene environmental and climatic changes from a limnological transect through Colombia, northern South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **234**: 81–96.

Weninger B, Jöris O, Danzeglocke U. 2004. Calpal: The Cologne radiocarbon CALibration and PALaeoclimate research package http://www.calpal.de [18 June 2007].

Wille M, Hooghiemstra H, Behling H, van der Borg K, Jose Negret A. 2001. Environmental change in the Colombian subandean forest belt from 8 pollen records: in the last 50 kyr. *Vegetation History and Archaeobotany* **10**: 61–77.