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Late Quaternary vegetation, fire and climate history reconstructed from two cores at Cerro Toledo, Podocarpus National Park, southeastern Ecuadorian Andes

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ABSTRACT

The last ca. 20,000 yr of palaeoenvironmental conditions in Podocarpus National Park in the southeastern Ecuadorian Andes have been reconstructed from two pollen records from Cerro Toledo (04°22′28.6″S, 79°06′41.5″W) at 3150 m and 3110 m elevation. Páramo vegetation with high proportions of *Plantago rigida* characterised the last glacial maximum (LGM), reflecting cold and wet conditions. The upper forest line was at markedly lower elevations than present. After ca. 16,200 cal yr BP, páramo vegetation decreased slightly while mountain rainforest developed, suggesting rising temperatures. The trend of increasing temperatures and mountain rainforest expansion continued until ca. 8500 cal yr BP, while highest temperatures probably occurred from 9300 to 8500 cal yr BP. From ca. 8500 cal yr BP, páramo vegetation re-expanded with dominance of Poaceae, suggesting a change to cooler conditions. During the late Holocene after ca. 1800 cal yr BP, a decrease in páramo indicates a change to warmer conditions. Anthropogenic impact near the study site is indicated for times after 2300 cal yr BP. The regional environmental history indicates that through time the eastern Andean Cordillera in South Ecuador was influenced by eastern Amazonian climates rather than western Pacific climates.

Introduction

The tropical eastern Andes and the northern parts of western Amazonia are among the hot spots of global vascular plant diversity due to their high structural and geological diversity (Mutke and Barthlott, 2005). Although the Ecuadorian Andes harbour ecosystems with one of the highest levels of biodiversity on Earth, the country also suffers the highest annual deforestation rates (0.5–2.4%) of South America, which is causing serious biodiversity loss (Josse, 2001). Especially for the hot spots of species richness, however, the historical environmental development is not well-known. Such knowledge is needed as background information to conserve and manage the ecosystems and their biodiversity.

Only a few palaeoecological studies are available from Ecuadorian Amazonia (Liu and Colinvaux, 1985; Colinvaux, 1987; Bush and Colinvaux, 1988; Liu and Colinvaux, 1988; Colinvaux et al., 1988a; Bush et al., 1990; Weng et al., 2002). Prior investigations from the Andes of Ecuador are restricted to northern locations on the Inter-Andean Plateau (Colinvaux et al., 1988b) and to southern locations in the western Cordillera (Colinvaux et al., 1997; Hansen et al., 2003). The only available pollen records for the southeastern Andes were provided by recent studies within a large research unit focusing on the Podocarpus National Park (PNP) and its megadiverse mountain ecosystems (Beck et al., 2008a). Several investigations from sites between 2000 and 3300 m a.s.l. provide reconstructions of the environmental history, mostly of the northern PNP (Niemann and Behling, 2008b; Niemann and Behling, 2009; Niemann et al., 2009).

Here we present the investigation results of two cores from the Cerro Toledo site in the southern part of the PNP area (4°S, 79°W). Our main objective is the reconstruction of the local environmental history including vegetation, fire and climate dynamics in an attempt to identify mechanisms of past ecosystem change and human impact. Together with previous studies in the northern part of the PNP, an extended environmental history for the PNP area will be reconstructed. A comparison with investigations from nearby sites in the Amazon and western Andes of Ecuador facilitates a regional interpretation of the environmental changes at the southeastern Andes.

Study site

Location

The study site Cerro Toledo is located in the southern part of the eastern Ecuadorian Andes, the so-called Cordillera Real (Fig. 1). It is situated in the Girón-Cuenca and Huancabamba Andean depression between southern Ecuador and northern Peru (lat. 3–7°S), where the highest peaks reach no more than 4000 m and active volcanoes are absent. Cerro Toledo is situated inside the PNP, some 45 km southeast of the town of Loja. The two analysed cores Cerro Toledo (CT) and Cerro Toledo B (CTB) are situated close to the exposed crest near the Cerro Toledo pass, which is today a paved road. The core CT

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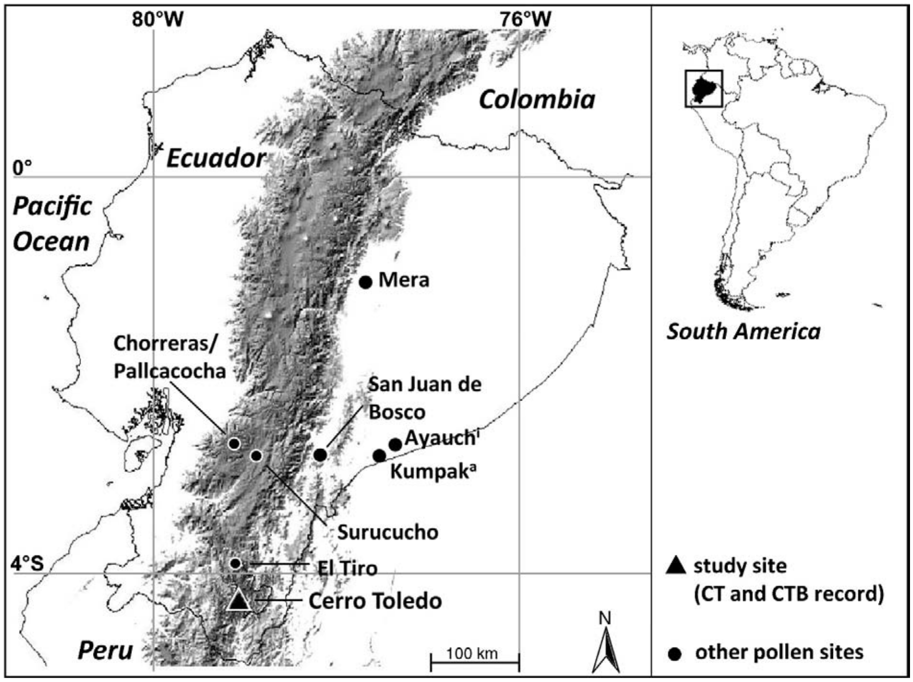

Figure 1. Map showing the location of Ecuador, the Andean mountain range as shaded area and study site Cerro Toledo located in the Podocarpus National Park (PNP). In addition relevant pollen record sites in the PNP area (El Tiro) and farther north in the Andes and Amazon basin of Ecuador are displayed.

(04°22'28.6"S, 79°06'41.5"W) was taken at 3150 m elevation and the core CTB at a distance of ca. 200 m and ca. 40 m lower. Both core sites are characterised by small depressions occupied by peat bogs.

Climate

The climate of Ecuador is dominated by the tropical trade wind regime with strong year-round easterlies (Beck et al., 2008b). Main weather types of the southern Cordillera Real are easterly conditions carrying moist air masses from the Amazon basin (Emck, 2007). Prevailing pressure systems in this region are the subtropical highs over the Atlantic Ocean and southeastern Pacific. The Cordillera Real acts as a climatic divide in Ecuador, separating humid climate on the Amazon-exposed eastern side from arid and semi-arid climate on the west (Emck, 2007). Thus, the study area is located between the humid Amazon basin and the dry Inter-Andean valley (Fig. 1). East of the Cordillera, precipitation and humidity rise continuously to the crests accompanied by increasing wind speed. Inside the PNP at 3100 m a.s.l., rainfall up to 6000 mm a^{-1} was measured. In contrast, the Inter-Andean basin receives generally less than 1000 mm a^{-1} (Emck, 2007; Bendix et al., 2008a). The main rainy season lasts from April to August but rainfall is high throughout the year.

Major factors governing air temperature are topography and altitude (Beck et al., 2008b). Temperature varies according to the time of day and season (Bendix et al., 2008a). The coldest period of the year is generally the main rainy season. Mean annual temperature for the páramo is ca. 6.5°C. Temperatures below 0°C are rare and only occur under anomalous weather conditions (Emck, 2007).

The research area is situated in the region where ENSO events cause strong weather anomalies. The coastal plains of southern Ecuador are severely affected by either floods (El Niño) or droughts (La Niña). The effects on the Andean highland are less clear. On the eastern escarpment there is a slight tendency toward reduced rainfall and enhanced temperatures during El Niño. However, ENSO seems not to cause extraordinary weather anomalies due to the fact that the Andes shelter the eastern slopes from Pacific air masses (Bendix et al., 2008b).

Vegetation

The most appropriate vegetation description by Homeier et al. (2008) classifies 4 different eastern escarpment vegetation types in the PNP, which are relevant for our investigation area: páramo, subpáramo, lower and upper mountain rainforest.

The coring sites are situated in the páramo (including shrub and herb páramo) between ca. 3100–3600 m a.s.l. above the forest line. Páramo vegetation is characterised by plants with a maximum height of 2 m. Some key species are *Puya eryngioides*, *Chusquea neurophylla*, *Monnina arbuscula* and *Valeriana microphylla*. A detailed description of the herb páramo in the Cerro Toledo area (Lozano et al., 2003) lists *Neurolepis nana*, *Niphogeton dissecta*, *Calamgrostis macrophylla*, *Halenia weddelliana*, *Valeriana convallarioides* and *Huperzia kuesteri*.

Subpáramo vegetation, a subtype of elfin forest forming the forest line, occurs between ca. 2700–3100 m a.s.l. covering most of the Cerro Toledo region. Canopy heights are 6–8 m or somewhat lower. Characteristic species are *Clethra ovalifolia*, *Gaultheria reticulata*, *Gaiadendron punctatum* and *Hesperomeles ferruginea*.

Upper mountain rainforest (UMF) is located between ca. 2100–2700 m a.s.l. and the canopy attains heights up to 25 m. Some of the main key species are *Hedyosmum* sp., *Clethra revoluta*, *Weinmannia* sp., *Myrsine coriacea* and *Podocarpus oleifolius*.

The lowest vegetation type is the lower mountain rainforest (LMF) between ca. 1300–2100 m a.s.l. with canopy heights of 30 m. Characteristic species are *Cedrela montana*, *Morus insignis*, *Piper* sp. and *Heliocarpus americanus*.

Upper forest line

The upper forest line (UFL) is defined as the maximum elevation where continuous forest occurs (see also Bakker et al., 2008). In the Andean depression the UFL is highly variable and not as well understood as other neotropical forest lines (Richter et al., 2008). North and south of the depression, the UFL is located at 4000 m a.s.l. or even higher, while the South Ecuadorian UFL is comparatively low between 2800–3300 m a.s.l. (Richter and Moreira-Muñoz, 2005; Beck et al., 2008b). The low position of the UFL in South Ecuador is characterised by the absence of *Polylepis*. Frequent strong winds and the extremely high precipitation are considered to be the main factors for the absence of *Polylepis*, because the genus tends to avoid regions of perhumid conditions (Kessler, 1995; Richter and Moreira-Muñoz, 2005). The higher located UFL is mainly formed by a *Polylepis* belt sometimes joined by *Gynoxis* trees, while the lower one represents an ecotone consisting of about 20 tree species (Beck et al., 2008c).

Methods

The cores were taken with a Russian Corer and stored under dark and cold (4°C) conditions. For AMS radiocarbon dating, 7 subsamples were submitted to the University of Erlangen-Nürnberg and Poznan Radiocarbon Laboratory. The ^{14}C dates were calibrated using CalPal Online and the CalPal 2007 HULU curve (Weninger et al., 2004). For palynological analysis the CT core was sampled at 2-cm intervals, the CTB core at 4-cm intervals and from 160 cm to the base every 8 cm. All samples were processed using standard pollen analytical methods (Fægri and Iversen, 1989). For calculations of concentration and influx *Lycopodium* spores were added as marker. A minimum of 300 pollen grains were counted for each sample. The pollen sum includes pollen of trees, shrubs and herbs. Pteridophyta, *Isoëtes* and moss spores were counted and quantified as percentages relative to the pollen sum. Carbonised particles (5–150 µm) were counted on pollen slides and presented as charcoal concentration and influx.

Identification of pollen and spores was based on a published pollen reference from Colombia (Hooghiemstra, 1984) and the reference collections (Behling, 1993) kept at the Department of Palynology and Climate Dynamics, University of Göttingen, containing approximately 3000 Neotropical and 300 Ecuadorian pollen and spore types. Identified pollen and spores were classified in ecological groups regarding the vegetation types of Homeier et al. (2008). TILIA, TILIAGRAPH and CONISS (Grimm, 1987) were used for data calculation, illustration and cluster analysis. In addition, non-destructive magnetic susceptibility (κ) was measured for the CT core with a Bartington MS2F point sensor in 1-cm intervals.

Results

Stratigraphy

Detailed sediment descriptions of both cores are presented in Tables 1 and 2. The CT core consists of a ca. 50-cm-thick silty clayey base followed by a gradual transition (134–107 cm) to highly decomposed peaty material. From 107 to 31.5 cm, the sediment consists of black or brown decomposed peaty material. A thick sand layer between 31.5 and 6 cm disrupts the core, while the top 6 cm are characterised by organic material with a high proportion of *Sphagnum*. The base of the CTB core is formed by moist and decomposed material (235–100 cm). Upwards the core the sediment gets less decomposed and compact. The top 27 cm consist of brown and moist peat.

Table 1
Stratigraphic description of the Cerro Toledo CT core.

Depth (cm)	Description
0–6	Dark-brown/green plant remains with high proportion of *Sphagnum*
6–14	Yellow, clayey mixed erosion material
14–31.5	Yellow greyish coarse-grained sand erosion material
31.5–45	Dark-brown, highly decomposed peaty material, with plant remains and rootlets
45–82	Black-brown, highly decomposed peaty material, with plant remains and rootlets
82–96	Dark-brown highly decomposed peaty material, with plant remains and rootlets
96–107	Black-brown, highly decomposed peaty material, with plant remains and rootlets
107–134	Brown, highly decomposed peaty material, no plant remains, gradually transition zone from brown to light brown coloured material (conspicuous transition beginning at 125 cm)
134–182	Light brown/grey and very compact silty clay

Table 2
Stratigraphic description of the Cerro Toledo CTB core.

Depth (cm)	Description
0–27	Brown peaty material with less-decomposed plant remains (rootlets)
27–75	Dark-brown/black decomposed peat with plant remains, more compact
75–100	Brown compact peat with many plant remains
100–142	Dark-brown/black decomposed peat with plant remains, more compact
142–235	Black-brown, highly decomposed and compact peat

Chronology

The chronologies of the two cores are based on 7 radiocarbon dates, 5 for the CT core and 2 for the CTB core (Table 3). The ages for the CT core are consistent (Fig. 2) and the basal age of 16,778 ± 137 ^{14}C yr BP indicates that the core extends back to the last glacial maximum (LGM). The sand layer in this core was probably deposited when the road along the Cerro Toledo pass was constructed 15–20 yr ago (Richter, M., personal communication, 2007). Deposition most likely occurred almost instantaneously. Accordingly, top and bottom of the sand layer were defined with the age of −37 cal yr BP, excluding the layer from the age scale. The age–depth model reveals a sedimentation rate of 0.04–0.25 mm yr^{-1} up to the sand layer. The top of the core shows comparatively high accumulation rates of 3.33 mm yr^{-1} (Fig. 3). The CTB core covers the Holocene, as extrapolated from the lower age at 122 cm of 4435 ± 35 ^{14}C yr BP. Extrapolation of ages to the core base were considered feasible because of analogy with the CT core and uniform stratigraphy suggesting continuous sediment accumulation.

Description of pollen diagrams of the CT core

A detailed percentage diagram (Fig. 4) displays 32 of the most frequent and important taxa out of 131 pollen and 52 spore types encountered. The summary percentage diagram (Fig. 5) shows the pollen and spores grouped into the different vegetation types. The dendrogram indicates 5 different zones (CT-I to V, Fig. 4).

Pollen concentrations (14,600–1,326,000 grains cm^{-3}) as well as pollen influx (400–19,000 grains cm^{-2} yr^{-1}) do not vary markedly throughout the core. Exceptions are high pollen concentration and influx just above the sand layer at 6 cm of 42,000 grains cm^{-2} yr^{-1}. Charcoal concentrations (5000–1,338,000 particles cm^{-3}) and charcoal influx (200–25,000 particles cm^{-2} yr^{-1}) are relatively low throughout the lower part of the core. Significantly higher values up to 239,000 particles cm^{-2} yr^{-1} are found in the uppermost part close to the sand layer at 32 and 6 cm (Fig. 5).

Zone CT-I (182–125 cm, ca. 20,000–16,200 cal yr BP, 17 samples) is characterised by a high proportion (65–85%) of páramo taxa, primarily *Plantago rigida* (30–60%) and *P. australis* (1–6%), Apiaceae (8–20%), Poaceae (7–15%), Cyperaceae (2–9%) and *Valeriana* (1–3%). Much less frequent (1–11%) are taxa of the subpáramo vegetation, mainly represented by pollen of Melastomataceae and Asteraceae (0–2%). A slight increase in subpáramo taxa to the top of this zone is due to the increase in Melastomataceae pollen to 9%. The group of UMF with values between 5% and 15% is mainly represented by *Alnus* (2–7%), *Hedyosmum* (0–4%), *Weinmannia* (0–3%), *Myrsine* (0–2%) and Podocarpaceae pollen (1–2%). The Podocarpaceae group consists most probably of *Podocarpus*, but *Prumnopitys* pollen not distinguished so far has to be considered as well. LMF taxa are poorly

Table 3
List of radiocarbon dates of samples from the Cerro Toledo cores CT and CTB.

Core	Lab. — no.	Depth (cm)	^{14}C age (yr BP)	Calibrated age[a] (cal yr BP)	1-σ range (cal yr BP)	Dated material
CT	Erl-11029	42–43	271 ± 48	356 ± 68	287–424	Organic material
	Poz-24271	65–65.5	4280 ± 35	4854 ± 13	4841–4867	Organic material
	Erl-11397	83–84	8101 ± 52	9056 ± 56	9000–9112	Organic material
	Erl-11030	108–109	12,627 ± 100	14,984 ± 324	14,659–15,308	Organic material
	Erl-8373	179.5–180.5	16,778 ± 137	19,999 ± 311	19,687–20,310	Organic material
CTB	Poz-24270	58–58.5	2245 ± 30	2257 ± 64	2192–2321	Organic material
	Poz-24272	122	4435 ± 35	5094 ± 122	4972–5216	Piece of wood

[a] Calibration of ^{14}C ages is based on CalPal Online (CalPal 2007 HULU curve). The calibrated ages stand for the mean probability of the 1-σ upper and lower age ranges.

represented (0–4%), as percentages of Moraceae/Urticaceae (0–2%), *Acalypha* (0–2%) and *Alchornea* pollen (0–1%) are low. Pteridophyta, mostly spores of *Huperzia*, vary between 7% and 14%.

Zone CT-II (125–107 cm, ca. 16,200–14,700 cal yr BP, 6 samples) is marked by a strong decrease in páramo taxa at the top of this zone from 65% to 44%, reflected by decreasing pollen types of *Plantago rigida*, *P. australis*, Apiaceae and Cyperaceae to levels of 2% or even lower. However, Poaceae pollen increases as an important páramo taxa from 11% to 45%. The subpáramo group reaches high values between 14% and 16% mainly due to Melastomataceae pollen (8–13%). UMF taxa increase within this zone to 24% mostly due to higher percentages of *Hedyosmum* (1–5%), *Weinmannia* (1–6%) and Podocarpaceae pollen (1–4%). LMF taxa increase from 6% to 12% with higher proportions of Moraceae/Urticaceae (1–6%) and *Celtis* pollen (0–3%). *Isoëtes* spores appear with a strong increase to 433% (relative to the pollen sum) at 108 cm core depth.

Zone CT-III (107–81 cm, ca. 14,700–8600 cal yr BP, 9 samples) shows a decrease to 39% in páramo taxa, due to a decrease in Poaceae pollen from 43% to 23%. Pollen types of *Plantago rigida*, *P. australis* and Apiaceae disappears, while Cyperaceae pollen increases to 13% in the lower part of the zone. The highest value (14%) of *Valeriana* pollen is reported at the top of this zone. Subpáramo taxa remain stable between 8% and 14% with only one peak of 24% at 92 cm depth, mainly represented by maxima of Melastomataceae (12%) and Asteraceae pollen (10%). Compared to the previous zone, UMF taxa decrease from 24% to 10%. This is mainly due to decreasing values of *Alnus*, *Hedyosmum* and *Weinmannia* pollen to 2% or 1%. LMF taxa increase markedly and reach the maximum proportion of 32% most notably by the strong increase of Moraceae/Urticaceae pollen from 4% to 24%. Pteridophyta spores fluctuate like previously but show generally higher values. Spores of Cyatheaceae (1–5%) are more frequent, whereas *Huperzia* spores become less important (1–4%) in this zone. Spores of *Isoëtes* first decrease and subsequently disappear.

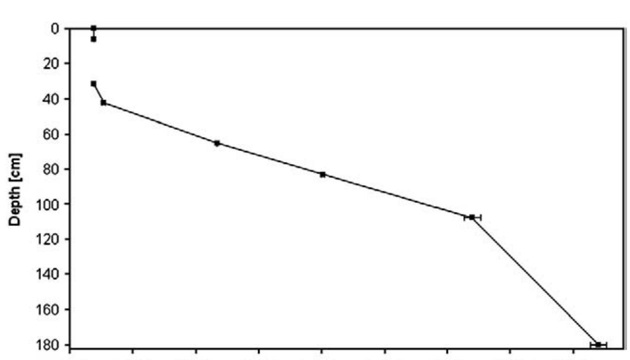

Figure 2. Age–depth model for the CT core based on 5 radiocarbon dates illustrating core ages (x-axis) compared to core depth (y-axis).

Zone CT-IV (81–46 cm, ca. 8600–1100 cal yr BP, 10 samples) shows an increase in páramo taxa, primarily represented by high occurrence up to 65% of Poaceae pollen. Compared to former zones a constant lower frequency of subpáramo taxa (ca. 10%) is mainly represented by pollen of Melastomataceae and Asteraceae. At the top of this zone, *Hypericum* pollen appears with 5%. Compared to decreasing values of the previous zone, the UMF group shows slightly higher and stable proportions between 13% and 19%, mainly due to higher values up to 11% of Podocarpaceae pollen. Lower frequencies between 3% and 12% of LMF taxa are mainly due to the decrease of Moraceae/Urticaceae pollen to a low value of 1% at the top of this zone. *Sphagnum* spores first appear in this zone and increase to values of 18%. Pteridophyta, primarily *Huperzia* spores, increase up to the highest value of 69% and decrease subsequently to 18%.

Zone CT-V (46–0 cm, ca. 1100 cal yr BP to recent times, 10 samples) shows first lower values (25%) of páramo taxa than in the previous zone, but towards and above the sand layer proportions increase up to 70%. Páramo composition changes within this zone as Poaceae pollen decreases to 2% and Cyperaceae pollen increases from 1% to 18%. Pollen of *Moritzia* appears for the first time and reaches high proportions between 10% and 50% in the upper 4 cm. Concurrently *Valeriana* pollen re-occurs and reaches high values of 13%. Subpáramo taxa increase at the beginning of this zone, primarily because of the high value (39%) of *Hypericum* pollen, and subsequently decrease from 53% to 9%. UMF and LMF taxa do not exceed 20% or 14%, respectively. *Sphagnum* spores decrease compared to the previous zone and fluctuate between 0% and 17%, with one exception of the highest peak (87%) before the sand layer. Pteridophyta spores vary from 3% to 18%.

Description of pollen diagrams of the CTB core

The most abundant 28 taxa from a total of 133 pollen and 42 spore types are shown in a detailed percentage diagram (Fig. 6). Identified pollen and spores grouped into different vegetation types are illustrated by a summary percentage diagram (Fig. 7). Five zones are distinguished by cluster analysis (CTB-I to V, Fig. 6). Pollen concentration (56,000–760,000 grains cm^{-3}) and pollen influx (1400–19,000 grains $cm^{-2}\,yr^{-1}$) remain relatively stable but increase in the upper part of the core (zone CTB-V). The relatively low values of charcoal concentration (31,000–800,000 particles cm^{-3}) and charcoal influx (700–20,000 particles $cm^{-2}\,yr^{-1}$) increase in zone CTB-V (Fig. 7).

Zone CTB-I (235–196 cm, ca. 10,000–8400 cal yr BP, 5 samples) is characterised by high proportions (35–51%) of páramo taxa consisting mainly of Poaceae pollen between 29% and 47% and Cyperaceae pollen up to 14%. Subpáramo taxa are relatively stable with 9% to 14%, represented by pollen of Melastomataceae (6–8%) and Asteraceae (1–4%). UMF taxa vary between 8% and 17%, primarily due to Podocarpaceae (3–7%), *Hedyosmum* (1–6%) and *Weinmannia* (1–3%) pollen. LMF taxa increase slightly to the top of this zone and reach proportions up to 27% mostly consisting of Moraceae/Urticaceae pollen (14–20%). Spores of pteridophyta are represented by slightly

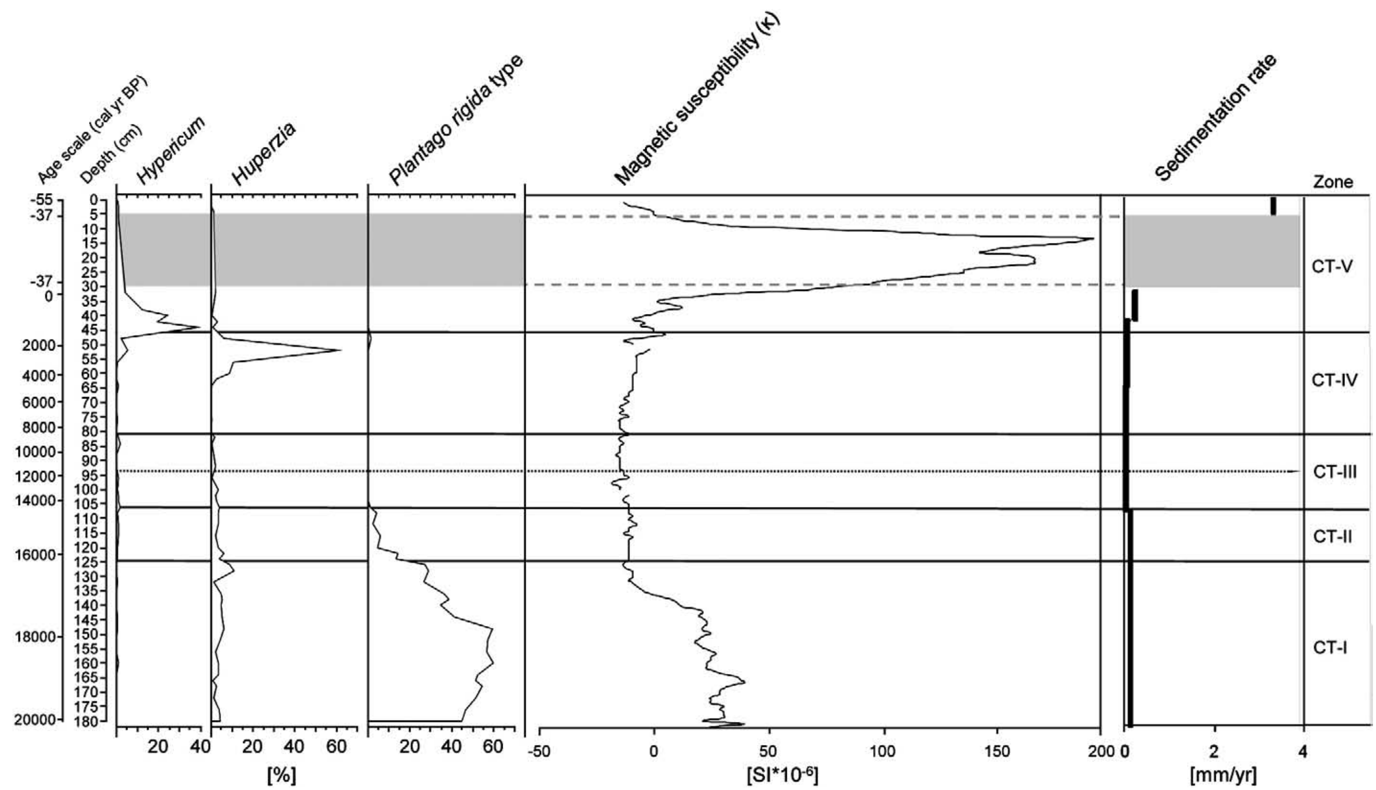

Figure 3. Magnetic susceptibility (κ) and sedimentation rate of the CT core compared to abundances of selected pollen types: *Hypericum*, *Huperzia*, *Plantago rigida* type.

increasing values from 7% to 10%, while Cyatheaceae spores show a decreasing trend from 3% to 9%. Moss spores, mainly *Sphagnum*, increase up to 6% toward the top of the zone. *Isoëtes* spores are rare with a maximum of 4%.

Zone CTB-II (196–164 cm, ca. 8400–6900 cal yr BP, 4 samples) shows a further increase in páramo up to 55%, dominated by pollen of Poaceae (40–52%). Cyperaceae pollen decreases markedly compared to the previous zone to values between 0% and 2%. *Xyris* pollen (1–7%) appears mostly in the second part of this zone. Subpáramo taxa show no marked changes. The same is true for UMF taxa, except for Podocarpaceae pollen that reaches higher percentages between 6% and 10% in this zone. A decrease in LMF taxa from 27% to 14% is indicated by the decrease of Moraceae/Urticaceae pollen from 20% to 9%. The decreasing trend of pteridophyta spores continues and Cyatheaceae spores (2–5%) are less important. Moss spores (1–3%) stay at low percentages and spores of *Isoëtes* are absent.

Zone CTB-III (164–112 cm, ca. 6900–4700 cal yr BP, 7 samples) shows lower proportions of minimum 28% of páramo taxa in the first part of the zone, but they recover in the top of the zone reaching values of 41%. This is mainly due to Poaceae pollen varying between 21% and 36%. Pollen of Cyperaceae and *Xyris* increases upwards from 140 cm core depth and reaches 8%. Subpáramo taxa are represented in this zone by higher percentages between 17% and 28%, mainly because of higher values of Asteraceae (4–19%) and Ericaceae (1–4%) pollen. Also, UMF taxa reach higher frequencies between 14% and 22%, in particular shown by pollen of Podocarpaceae (7–15%) and Myrtaceae (1–3%). Spores of pteridophyta increase first to 18% at 132 cm core depth and decrease afterwards to 7%. Mosses, namely *Sphagnum* spores, first increase markedly to the highest value of 142% and subsequently decrease to low percentages comparable to the previous zones.

Zone CTB-IV (112–46 cm, ca. 4700–1800 cal yr BP, 10 samples) is marked by an increase in páramo taxa to their highest value of 64%, attributed primarily to high proportions of Poaceae pollen (34–50%) and increasing percentages of Cyperaceae pollen to highest values of 25%. Subpáramo taxa decrease again from 15% to 8% but pollen of Melastomataceae remains at same levels. UMF taxa show a slight decrease to 11% in this zone, primarily due to the decrease of Podocarpaceae pollen to 4%. A more significant decrease occurs for LMF taxa from 13% to 6%, mainly due to the low values (3%) of Moraceae/Urticaceae pollen. Pteridophyta spores vary between 6% and 10% and spores of mosses remain at low frequencies (1–11%).

Zone CTB-V (46–0 cm, ca. 1800 cal yr BP to recent times, 12 samples) shows a stable proportion of páramo taxa (48–57%) at slightly lower levels than in the prior zone. Poaceae pollen (38–50%) remains stable, while Cyperaceae pollen decreases significantly to 1%. Subpáramo taxa increase slightly and vary from 7% to 17%, mainly by pollen of Melastomataceae (4–10%) and Asteraceae (1–4%). UMF taxa increase markedly to the highest value of 25% at the top of the core, primarily due to higher pollen frequencies of *Hedyosmum* (3–7%) and *Weinmannia* (1–6%). LMF taxa show slightly higher proportions between 9% and 15%, represented mainly by Moraceae/Urticaceae (3–8%) and *Alchornea* (1–6%) pollen. The highest proportions of pteridophyta spores up to 20% are reached in this zone due to higher values up to 6% of *Huperzia* spores and increasing Cyatheaceae spores from 2% to 9%. Moss spores vary between 2% and 24%. *Isoëtes* spores are sparsely present (<1%).

Magnetic susceptibility of the CT core

Magnetic susceptibility (κ) analysis of core CT reveals proportions of minerogenic input and can be related to the vegetation development. Although the data have low values not exceeding 200 $SI \times 10^{-6}$ (Fig. 3), there is a good correlation between changes in magnetic susceptibility and the trends in the abundance of several pollen types. Relatively high values (on average 26 $SI \times 10^{-6}$) in the lower part of the core, reflecting high minerogenic input, coincide with high proportions of the *Plantago rigida* pollen type. After ca. 17,000 cal yr BP, decreasing κ-values are related to a decrease in minerogenic input

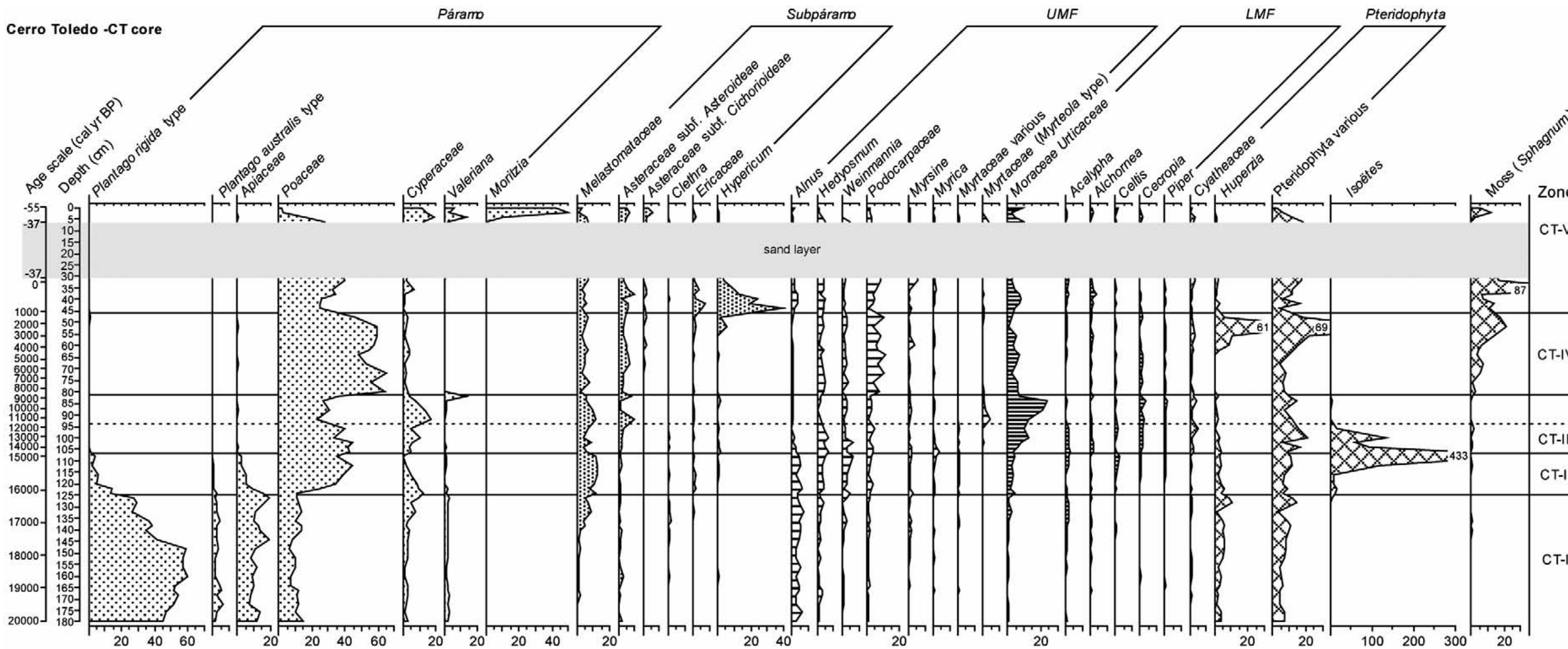

Figure 4. Pollen percentage diagram of the most important and frequent taxa of the Cerro Toledo (CT) core, southeastern Ecuadorian Andes.

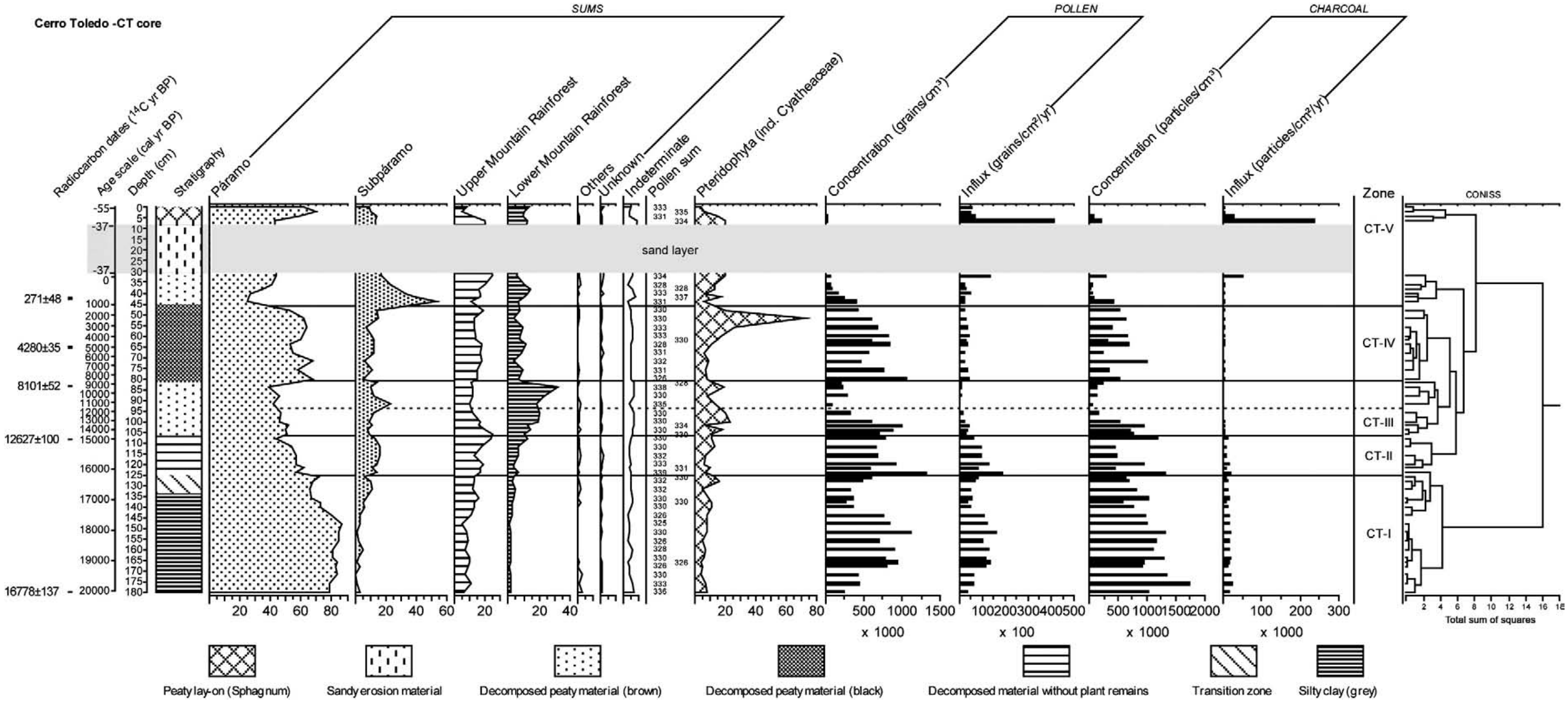

Figure 5. Summary pollen diagram showing radiocarbon dates, age scale, stratigraphic data, vegetation groups, concentration and influx of pollen and charcoal and CONISS cluster analysis of the Cerro Toledo (CT) core.

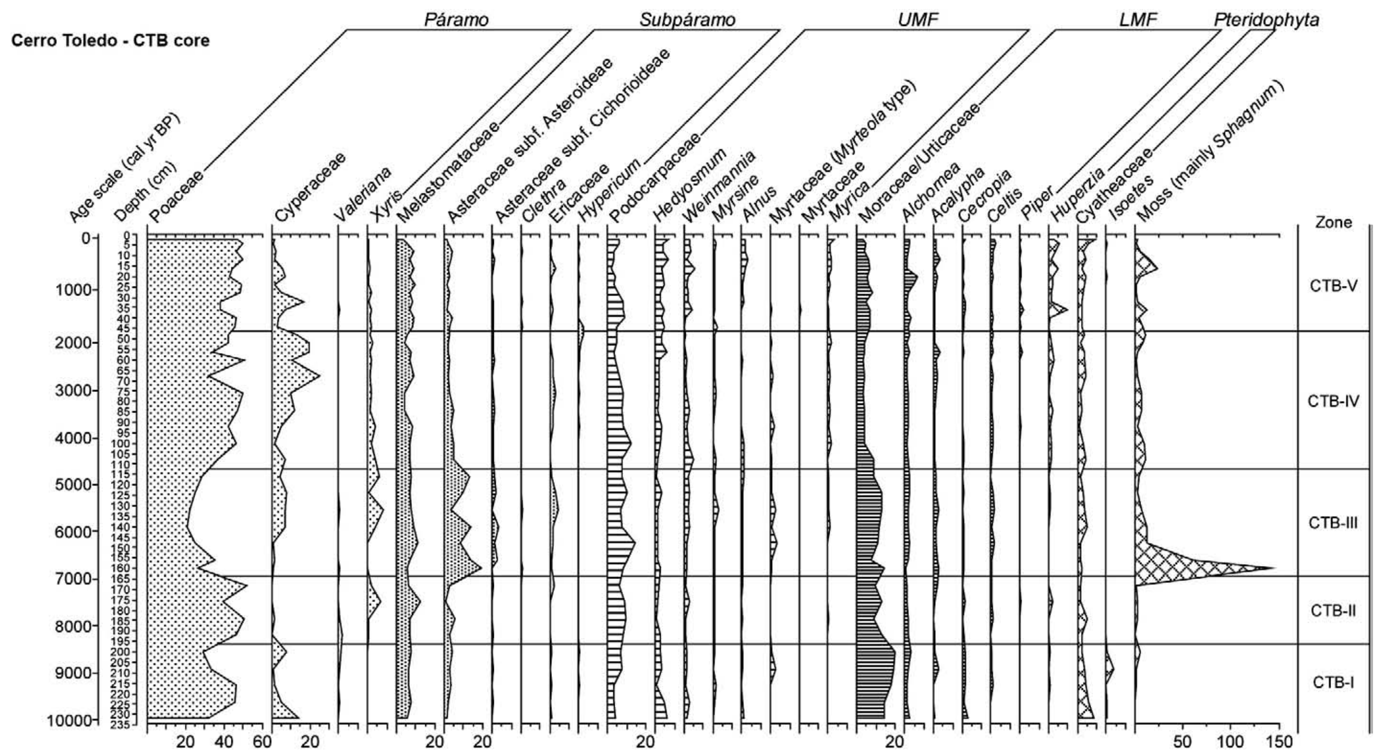

Figure 6. Pollen percentage diagram of the most important and frequent taxa of the Cerro Toledo (CTB) core, southeastern Ecuadorian Andes.

at the time when *Plantago rigida* disappeared. Synchronous with the first peaks of *Huperzia* spores and *Hypericum* pollen after 2300 or 750 cal yr BP, respectively, the κ-values are higher and reach a maximum of almost 200 $SI \times 10^{-6}$ in the upper part of the core reflecting the sand layer. The values markedly decrease above the sand layer to negative values.

Interpretation and discussion

Environmental conditions of the LGM

Pollen assemblages from the period between ca. 20,000–16,200 cal yr BP (zone CT-I) indicate páramo vegetation dominated by *Plantago*, mainly *P. rigida*, together with Apiaceae and Poaceae. The azonal páramo species *P. rigida* most likely formed cushion mires in depressions. *P. rigida*, along with *P. australis* and *Huperzia*, reflect locally cold and humid conditions that likely prevailed during the LGM (Cleef, 1978; Bosman et al., 1994). The low temperatures were probably responsible for the low abundance of forest taxa, suggesting that mountain rainforests were restricted to lower elevations. The UFL must have been markedly lower compared to the present.

The only Andean Alder species is considered to be *A. acuminata* (Furlow, 1979). High pollen abundances of *A. acuminata* recorded for the LGM at Cerro Toledo are interpreted to reflect high abundances of *A. acuminata* trees. The same was found in records from the eastern Bolivian Andes, where it marked cold and dry conditions (Mourguiart and Ledru, 2003). At Cerro Toledo *A. acuminata* declined during late-glacial times, when submersed growing *Isoëtes* indicates a change to wetter conditions than previously. But this does not indicate explicit dry conditions for times with higher *A. acuminata* abundance at our study site. Since *A. acuminata* is also favoured by disturbances resulting in open areas like landslides (Weng et al., 2004), erosion may have facilitated the growth of *A. acuminata*. The high minerogenic content of the clayey sediment during this period suggests that the vegetation cover was not complete, resulting in unstable soils and erosion.

Glaciation apparently did not affect our study site at 3150 m elevation since ca. 20,000 cal yr BP, even if sufficient humidity could have facilitated glacier formation. Evidence for glacier extents during Marine Isotope Stage 2 in northern parts of Ecuador (Schubert and Clapperton, 1990; Clapperton and Seltzer, 2001; Mark et al., 2004) give only limited support for LGM glaciations in South Ecuador. Lower glacier margins at 2750 m a.s.l. in the Andean depression region (lat. 3–6°S) were reconstructed by geomorphologic analyses in the central area of the PNP (Rozsypal, 2000). Here cirque lakes are found at 3200 m elevation. Consequently, glaciers may have existed in the Cerro Toledo area until 20,000 cal yr BP.

From the beginning of the following period (16,200–14,700 cal yr BP, zone CT-II) páramo vegetation began to decrease while subpáramo and mountain rainforest increased. This represents an upslope shift of mountain rainforest and UFL in the study area indicating increasing temperatures. The persistent occurrence of pteridophyta and high values of *Isoëtes* suggest a change to wetter conditions than previously. *Isoëtes*, a (semi-) aquatic genus mostly occurring submerged in páramo lakes (Cleef, 1978; Bosman et al., 1994), indicates that there must have been shallow water bodies in the small basin of the study site. This is also suggested by below zero κ-values (Fig. 3) and higher Cyperaceae occurrence at this time, which reflect wet conditions or riverine vegetation. Likewise the wet assemblage of shrubby subpáramo vegetation composed of Melastomataceae, Asteraceae and Ericaceae suggests high moisture levels (Cleef, A., personal communication, 2008). The marked decrease of *Plantago* and increase of Poaceae might indicate that grass páramo surrounded the small basin.

Environmental conditions of the late-glacial period

The decrease of páramo continued from ca. 14,700–11,500 cal yr BP (zone CT-III). *Plantago* and Apiaceae disappeared recording a change-over to a grass páramo with alternating Poaceae and Cyperaceae. Pollen of LMF taxa (e.g., Moraceae/Urticaceae, *Alchornea* and *Acalypha*) tends to be over-represented due to wind transport to higher elevations (Bosman et al., 1994; Bush and Rivera, 2001). In our study

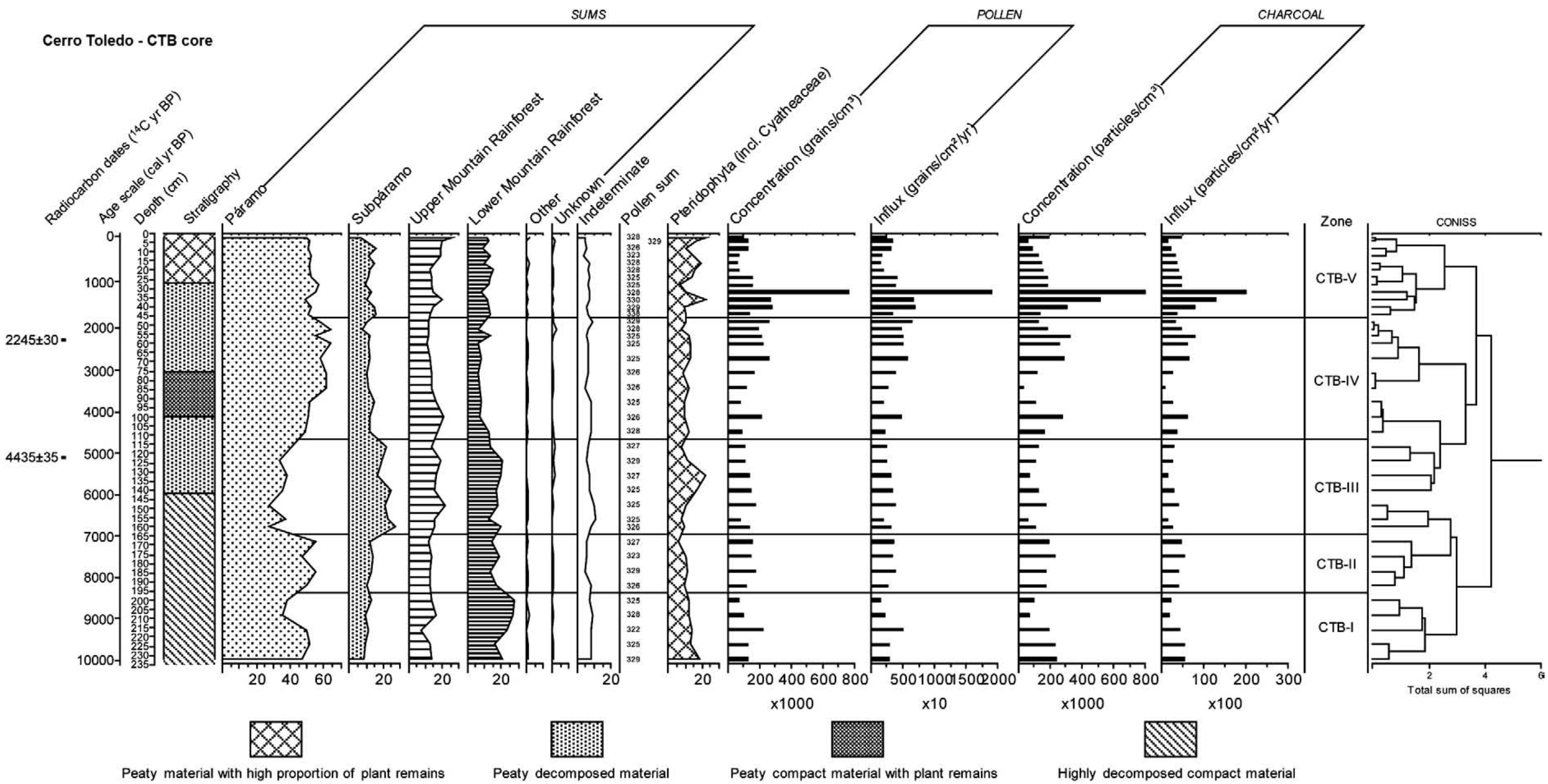

Figure 7. Summary pollen diagram showing radiocarbon dates, age scale, stratigraphic data, vegetation groups, concentration and influx of pollen and charcoal and CONISS cluster analysis of the Cerro Toledo (CTB) core.

Table 4
Summarised major vegetation changes and climate events since the late Pleistocene recorded for the western Cordillera and western Amazon basin in Ecuador in comparison with the interjacent Cerro Toledo study site in the eastern Cordillera.

Site	Western Cordillera, eastern flank		Eastern Cordillera	Western edge of Amazon basin, Andean foothill		
	Laguna Chorreras/ Pallcacocha [1]	Lake Surucucho (Llaviucu) [2]	Cerro Toledo	San Juan de Bosco [3]	Mera site [4]	Lake Ayauch[i] [5] /Lago Kumpak[a] [6]
Location	2°45' S, 79°10' W	3° S lat.	4°22' S, 79°06' W	3°3' S, 78°27' W	1°28' S, 78°06' W	No data/3°2' S, 77°49' W
Elevation	3700/4060 m	3180 m	3150 m	970 m	1100 m	500/700 m
Precipitation	East: >2000 mm yr^{-1}	750 mm yr^{-1}	Up to 6000 mm yr^{-1}	No data	>4800 mm yr^{-1}	2000–3000 mm yr^{-1}
Temperature	Day:12–18°C	14°C	6.5°C	No data	20.8°C	23–24°C
Time period (yr BP)	Major vegetation changes and climate events					
Late Holocene after 4000	Moist mountain rainforest increase		Páramo expansion continued		Precipitation event northeastern Andes: 1300–800 yr BP> flooding of western Amazonia	Dry period: 4200–3150 yr BP and 1500–800 yr BP, some taxa decline, no major forest change
Mid-Holocene ca. 7500–4000	Grass páramo expansion, *Polylepis* dominating the forest line		Expansion of páramo, decrease of lower mountain rainforest			Lake formation, Amazon rain forest, dry period: 4300–4800 yr BP
Early Holocene ca. 10,000–7500	Moist mountain rain forest elements remain stable		Lowest páramo and highest lower mountain rainforest distribution			
Holocene transition ca. 11,500–10,000	Moist mountain rain forest expansion, *Polylepis* become important	Development of modern Andean forest				
Late-glacial ca. 15,000–11,500	Persistent páramo dominance	Upslope advance of forest line	Decrease of páramo, changeover to grass páramo, increase of lower mountain rainforest			
LGM ca. 20,000–15,000	Páramo initially dominant and spread into higher elevations		Páramo dominance (moist *Plantago* association)			
Late Pleistocene ca. 30,000–26,000		Treeless vegetation (related to modern páramo)		Mixed lowland/ mountain community	Mixed lowland/ mountain community, Andean forest growth at least 700 m lower	

[1]Hansen et al. (2003); [2]Colinvaux et al. (1997); [3]Bush et al. (1990); [4]Liu and Colinvaux (1985), Bush et al. (1990), Colinvaux (1987); [5]Bush and Colinvaux (1988); [6]Liu and Colinvaux (1988).

only Moraceae/Urticaceae showed high presence, suggesting that a masking in the pollen record could be the case. Nevertheless, the conspicuous increase in LMF probably reflects slowly and continuously increasing temperatures. Persistent humid conditions suggested by high occurrences of Cyperacae and *Isoëtes* may be responsible for only minor upslope shift of rain forests.

Environmental conditions of the Holocene

The beginning of the Holocene (ca. 11,500 cal yr BP) is represented by a gradual change indicated by disappearance of *Isoëtes*, lower presence of páramo vegetation and a high proportion of subpáramo. The shallow water pond was replaced by a peat bog. During the early Holocene (ca. 11,500–8400 cal yr BP, including zone CT-III and CTB-I), relatively low proportion of páramo and highest expansion of LMF were reached between ca. 9300 and 8500 cal yr BP. Thus the highest temperatures during the last 20,000 yr were probably reached during this interval. This interpretation is supported by highly decomposed peat of the CTB core.

From ca. 8500 to 6900 cal yr BP (zone CT-IV and CTB-II), grass páramo vegetation expanded substantially while LMF decreased, suggesting a change to cooler conditions. Even though UMF presence remained relatively stable during this period, a particularly high abundance of Podocarpaceae probably reflects an upslope shift of UFL. Humid conditions persisted at the study site as pteridophyta continued to show high abundances and *Sphagnum* appeared for the first time.

During the mid-Holocene between ca. 6900 and 4700 cal yr BP (zone CTB-III), the abundance of subpáramo was notably higher while páramo were represented by a lower occurrence than earlier. This is interpreted to indicate a change to higher temperatures. However, temperatures did probably not exceed those of the warmest period between ca. 9300–8500 cal yr BP because UMF continued to persist at same abundances and Moraceae/Urticaceae occurrence was even lower as in the previous period. Persistent humid conditions are indicated by relatively high occurrence of pteridophyta and the presence of *Sphagnum* probably forming bogs with *Xyris* and grasses. After ca. 4700 cal yr BP (zone CTB-IV) the trend of páramo expansion continued under cooler conditions. The grass páramo composition was dominated by Poaceae with increasing proportions of Cyperaceae. Decreasing occurrences of subpáramo, UMF and particularly LMF suggest that the cooling continued until ca. 1800 cal yr BP.

During the late Holocene after ca. 1800 cal yr BP (zone CTB-V), a slight decrease in páramo and increase in subpáramo, UMF, and LMF suggest a change to warmer temperatures opposed to the previous interval of cooling. The very high occurrence of *Moritzia* (probably *M. lindenii*) dominated the páramo assemblage in the uppermost part of the CT core. Therefore, the notable páramo increase in recent times likely reflects an overrepresentation of *Moritzia* at the core site rather than vegetation changes (Cleef, A., personal communication, 2008).

Alnus is conventionally thought to have increased simultaneous with the Holocene warming (Weng et al., 2004). In this record, however, no increase of *A. acuminata* was found with the onset of the

Holocene. Because *A. acuminata* presence also can be a result of anthropogenic disturbances (Weng et al., 2004), we suggest rather an increase of *A. acuminata* caused by human impacts in the area than by climatic changes. Human disturbances are supported by higher charcoal influx in the most recent pollen zones of both cores. The fact that charcoal influx increased twice as much than pollen influx in the CT core indicates heightened fire frequency. The undisturbed sediment of CTB core shows high charcoal influx and concentration between 1550 and 1220 cal yr BP (zone CTB-V), supporting human activities in the permanent humid area. Increased fires were probably due to human fire use in slash and burn farming or hunting activities (Niemann and Behling, 2008a). However, compared to charcoal influx values of nearby study sites, for example El Tiro (Niemann and Behling, 2008b), fire activity was comparably low at Cerro Toledo. This is supported by the heightened presence of *Weinmannia* despite higher fire frequencies, as this genus is highly sensitive to fire (Niemann and Behling, 2009).

Another indication of human disturbance are very high occurrences of *Huperzia* and *Hypericum* at ca. 2300 cal yr BP and ca. 750 cal yr BP (Fig. 3). *Huperzia* is a pioneer common on landslides and along road cuts on open sandy soils. *Hypericum* can replace degraded páramo vegetation (Cleef, A., personal communication, 2008). The synchronously increased minerogenic input may reflect erosion because of sparse vegetation favouring *Huperzia* and *Hypericum*.

Vegetation history of the Podocarpus National Park area

Environmental reconstruction for the PNP area is based on the comparison of the records presented here from the southern region at Cerro Toledo with the northernmost record from El Tiro site (Niemann and Behling, 2008b), ca. 43 km distant. For the LGM (ca. 21,000–15,800 cal yr BP) the record of El Tiro at 2800 m a.s.l. indicated grass páramo vegetation, mainly composed of Poaceae and *Plantago* reflecting cold and moist conditions. The UFL was at markedly lower elevations compared to present day. This agrees with Cerro Toledo results even though the páramo composition dominated by *Plantago* suggests more humidity at Cerro Toledo. Concerning the stronger signal of downslope eastern LMF at the higher elevation Cerro Toledo site, we assume that the southern part was more influenced by eastern Amazonia climates than the northern part of the PNP. Perhaps forest taxa from lower elevations had less effective (topographic) barriers allowing them to reach Cerro Toledo. Indications for slowly warming conditions were found at El Tiro from ca. 11,200 cal yr BP onwards. This is later than at the Cerro Toledo site, where first evidence of slightly rising temperatures occurred at 16,200 cal yr BP.

Páramo vegetation decreased continuously and almost disappeared during the warming interval at El Tiro, while UMF vegetation expanded from ca. 8900–3300 cal yr BP. After 3300 cal yr BP, modern subpáramo vegetation became established. Hence, the period from 8900–3300 cal yr BP was warmer and drier than the present at El Tiro. At Cerro Toledo, highest temperatures probably occurred between 9300 and 8500 cal yr BP. Thus, both lines of evidence suggest that the highest temperatures in the region were reached in the early Holocene.

For both sites, rare fires were recorded during the LGM and higher fire frequencies during the Holocene. At El Tiro fires began to increase already since 8000 cal yr BP and highest frequencies occurred since 3300 cal yr BP. Increased fire frequency at Cerro Toledo was indicated since 1550 cal yr BP. Fires during the late Holocene at both sites are suggested to be mostly of anthropogenic origin. However, El Tiro was probably more disturbed than the Cerro Toledo region as fires increased earlier and stronger.

Regional integration of the environmental history at Cerro Toledo

Cerro Toledo, located in the eastern Andes between the Amazonian basin and the western Andes, could experience both Pacific-type climates (from the west) and Amazonian-type climates (from the east). The present-day climate at the study site, with strong easterlies and particularly high precipitation, indicates a greater influence of Amazonian climates than Pacific. The eastern slopes thus appear sheltered from Pacific climates by the Andes. For the reconstruction of past conditions, however, further comparisons have to be made and vegetation changes of different sites have to be considered (Table 4). At first, two records at the western Cordillera allow a regional comparison. Lake Surucucho, ca. 150 km north from Cerro Toledo lies almost at the same altitude (3180 m a.s.l.). The record shows treeless vegetation during glacial times, an upslope advance of UFL in the late-glacial period, and the development of Andean forest during the Holocene (Colinvaux et al., 1997). Obviously forest could establish at a greater altitude than in the PNP area, and the UFL was located at higher elevations already during the early Holocene.

Furthermore, the signal of UFL shift is less evident in the PNP area than at other sites where the typical proxy *Polylepis* dominates the UFL. Studies from the southwestern Ecuadorian Cordillera at Laguna Chorreras (ca. 3700 m a.s.l.) indicate that *Polylepis* replaced other taxa during the Holocene and reached its maximum during the mid-Holocene period, reflecting a strong signal for UFL shift (Hansen et al., 2003).

A shift of UFL to higher elevations during the mid-Holocene at the Cerro Toledo is indicated by notably high presence of Podocarpaceae, even though other taxa (e.g., *Weinmannia* or *Hedyosmum*) constituting the UFL ecotone did not increase. This suggestion is supported by results of the El Tiro site inside the PNP, where the UFL shifted upslope after 8900 cal yr BP (Niemann and Behling, 2008b). The weaker signal of UFL shift in the PNP area can originate from the absence of *Polylepis*, due to high precipitation and strong winds, or reflect minor fluctuations of past UFL shifts. Hence, variant forest development and UFL positions reveal major differences between the western and eastern Cordillera, which is mainly due to different climatic conditions.

Records from the Ecuadorian Amazon basin are few and far between (Table 4). During the late Pleistocene (ca. 30,000–26,000 yr BP) at San Juan de Bosco (Bush et al., 1990) and the Mera site (Liu and Colinvaux, 1985), mixed lowland and mountain forest communities were present at ca. 1000 m elevation. During the late Holocene, flooding of the western Amazonia (ca. 1300–800 cal yr BP) was interpreted as a consequence of increased precipitation in the northeastern Andes. Accordingly, there is a certain connectivity of the eastern Andes and the Amazon basin. At Cerro Toledo no concurrent events were identified to the dry periods observed in western Amazonia during the mid- and late Holocene at Lake Ayauch[i] and Kumpak[a] (Bush and Colinvaux, 1988; Liu and Colinvaux, 1988). However, the drier climates only affected some lowland taxa and did not implicate a major forest change. Therefore it is likely that the dry periods of the Amazonian basin may not have affected the upper slopes and highland taxa of the eastern Andes. Despite the poor information available from the Amazon basin, a linkage between the eastern Cordillera and the Amazonia is much more appropriate even in the past than between the eastern and western Andes.

Conclusions

The two records at Cerro Toledo provide a detailed vegetation reconstruction including fire and climate history during the last 20,000 cal yr BP. The study site was not covered by glaciers at 3150 m elevation during the recorded period, even though it was persistently humid. However, páramo vegetation dominated by *Plantago* at the beginning of the record could have developed in moist and cold places following glacial retreat, which means glaciers could have existed before the recorded time. The transition to the Holocene was a gradual change with slow warming. Highest temperatures were probably reached in the early Holocene between 9300 and 8500 cal yr BP.

Increasing temperatures and the expansion of mountain rainforest during the Holocene caused an upslope UFL shift, but not consequent shifts of all vegetation types within the broad vegetation belts. The present peat bog with high proportions of *Sphagnum* began to develop during the mid-Holocene. Indications of human disturbances are found since ca. 2300 cal yr BP, but the study site was comparatively little affected by anthropogenic impact during the past.

It can be concluded that regional climate dynamics influenced the vegetation development over time in the PNP area. Continuous, very humid conditions of the study area indicate that the region was mostly influenced by eastern Amazonian-type climates. However, local site characteristics like slope and aspect can explain differences in microclimates between the sites that gave rise to differences in the local vegetation development through time. Furthermore, the Andean barriers for climatic conditions and upslope-moving taxa from the Amazon basin seem to be less effective in the southern part of the PNP area than in the northern part. Hence, the cordilleras presented not absolute but nonetheless considerable barriers for plant dispersal.

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