Holocene climate variability and vegetation dynamics inferred from the (11 700 cal. yr BP) Laguna Rabadilla de Vaca sediment record, southeastern Ecuadorian Andes

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Abstract: Palaeoenvironmental changes, inferred from a 492 cm long lake sediment core from Laguna Rabadilla de Vaca (3312 m) in Podocarpus National Park, southeastern Ecuadorian Andes, were investigated using multiple proxies. Pollen, spore and charcoal analyses, as well as x-ray fluorescence and magnetic susceptibility scanning reflect the last c. 11 700 cal. yr BP of climate and vegetation history. Pollen data indicate that the herb-paramo was the main vegetation type at Laguna Rabadilla de Vaca during the early-Holocene period, before c. 8990 cal. yr BP. The herb-paramo was rich in Poaceae, Cyperaceae, *Valeriana* and *Huperzia*, reflecting cold and relatively wet climatic conditions. During the middle Holocene from c. 8990 to 3680 cal. yr BP *Weinmannia* increases markedly, indicating warmer climatic conditions than present-day, probably related to the Holocene thermal optimum, because of a spread of shrub-paramo vegetation and/or a shift of mountain rainforest and sub-paramo vegetation zones to higher elevations. XRF data indicate a drier period from c. 8990 to 6380 cal. yr BP and a wetter period from c. 6380 to 3680 cal. yr BP. A Poaceae-dominated herb-paramo occurred from c. 3680 cal. yr BP until modern times, reflecting cooler climatic conditions relative to the middle Holocene. XRF and charcoal data indicate a decrease in precipitation during this period.

Key words: Ecuador, Andes, Holocene climate change, paramo, vegetation dynamics, pollen analysis, XRF-scanning, *Weinmannia*.

Introduction

The Ecuadorian Andes harbour the most species-rich ecosystems on Earth (Barthlott *et al.*, 2005). Despite its high biodiversity huge areas have been strongly affected by human activity (eg, industrial deforestation) during the last decades. Natural vegetation regeneration and sustainable management, as well as conservation of less degraded areas is urgently needed. To study the highly diverse mountain forest and paramo ecosystems in southeastern Ecuador, extended research has been carried out in the framework of the

‘Deutsche Forschungsgemeinschaft’ (DFG) research group ‘Tropical Mountain Ecosystems’ focusing on Podocarpus National Park (Beck *et al.*, 2008). Currently (2007–2010) more than 25 different research groups are working in this area. Palaeoecological work analysing more than ten different lake, peat and soil cores in the Podocarpus National Park region started in 2005. Palaeoecological information is needed to understand the natural composition and dynamics of modern ecosystems for proper management and conservation.

Among the few palaeoenvironmental records available from the southeastern Ecuadorian Andes are those from the El Tiro-Pass (2810 m), c. 30 km north of the core site (Niemann and Behling, 2008a) and from Laguna Cocha Caranga (2710 m), c. 25 km north of the core site (Niemann and Behling, 2008b). Neighbouring regions in South

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Figure 1 Map of central northwestern tropical South America, showing Laguna Rabadilla de Vaca (star) and other locations discussed in the text (circles)

America offer archives, for example from the Colombian inter-Andean Cauca Valley (1020 m) (Berrio *et al.*, 2002), from Laguna Loma Linda (310 m), located in the transition zone between the savannah of the Llanos Orientales and the Amazon rainforest in Colombia (Behling and Hooghiemstra, 2000), from the Yasuni National Park (220 m) in the Ecuadorian Amazonia (Weng *et al.*, 2002), from Laguna Chochos (3285 m) in the eastern Peruvian Andes (Bush *et al.*, 2005), from Laguna Tuctua in the central Peruvian Andes (4000 m) (Hansen *et al.*, 1994), from Lake Titicaca (3810 m) in the central Peruvian Andes (D'Agostino *et al.*, 2002; Paduano *et al.*, 2003), from Lake Aricota at 2800 m in the central Peruvian Andes (Placzek and Quade, 2001) and from Huascarán (*c.* 6050 m) in the central Peruvian Andes (Thompson *et al.*, 1995). Locations of greater interest for this study are shown in Figure 1.

In this study we seek to address the following main questions: (1) how did climate and vegetation develop at Laguna Rabadilla de Vaca during the Holocene period in comparison with preceding studies from the Podocarpus National Park region; and (2) is there an interregional coherence with studies from outside Ecuador?

Site description

Location

Laguna Rabadilla de Vaca (04°15'19.7"S, 079°06'43.7"W, 3312 m) is located on the western slope of the eastern Cordillera (Cordillera Real) in the southeastern Ecuadorian Andes (Figure 1), about 10 km east of the small village of Vilcabamba (1700 m) and about 15 km south of Cajanuma (Podocarpus National Park entrance). Laguna Rabadilla de Vaca is part of the so called Lagunas de Compadre, a group of 15 lakes formed by glaciers, located east and west of the eastern Cordillera in the middle of the Podocarpus National Park.

Figure 2 Photograph (from southwest) of Laguna Rabadilla de Vaca, with the east Andean divide in the background. The slopes are covered with shrub-paramo vegetation and the lake shore covered with herb-paramo vegetation. The coring position is marked with an arrow

Geomorphology and geology

The Andes of southern Ecuador and northern Peru include the so-called Andean depression (Depression de Giron-Cuenca in Ecuador and Huancabamba in Peru). The highest peaks reach about 4000 m elevation; and there are no active volcanoes in the region (Richter and Moreira-Munoz, 2005).

Laguna Rabadilla de Vaca (Figure 2) is located toward the west, very close to the eastern Andean divide at the base of a cliff created by a large valley glacier originating on higher elevations of the divide. Slopes east of the lake shore reach 3600–3700 m. To the west, the 6 ha in size and *c.* 5 m deep lake is dammed by a recessional moraine. The catchment of the westward-draining lake is about 2 km².

The southern Cordillera Real is mainly built up by the 'Zamora series', consisting of Palaeozoic metamorphic rocks of widely varying metamorphic grade. Local bedrock is dominated by semipelites, quartzites and black phylites with some granitic intrusions (Litherland *et al.*, 1994).

Modern vegetation

Laguna Rabadilla de Vaca is located in the paramo vegetation zone. Two different types of paramo ecosystems are identified for the Podocarpus National park region (Lozano *et al.*, 2003). The herb-paramo (Paramos herbaceos), located at *c.* 3200–3400 m, is rich in *Neurolepis nana*, *Calamagrostis macrophylla* (Poaceae) and *Niphogeton dissecta* (Apiaceae). The herbs and shrubs grow from 0.2 m to 1 m in height. This paramo type is found along flat slopes and concave sections, as well as along ridges. This herb-paramo is dominant around Laguna Rabadilla de Vaca. The shrub-paramo (Paramos arbustivos bajos), located at *c.* 2900–3400 m, is rich in *Weinmannia rollottii* (Cunoniaceae), *Oxalis spiralis* (Oxaliaceae) and *Ilex andicola* (Aquifoliaceae). The shrubs and herbs grow from 0.5 m to 1.2 m in height. This paramo type is found mainly along steep slopes (Lozano *et al.*, 2003), which is confirmed by the fact that the slopes above Laguna Rabadilla de Vaca are dominated by this paramo type.

At lower altitudes between *c.* 2800 and 3100 m, subparamo vegetation is present, characterized by *Puya nitida* (Bromeliaceae), *Brachyotum rotundifolium* (Melastomataceae) and *Oritrophium peruvianum* (Asteraceae). The shrubs and herbs mainly grow to 1 m in height; some individual shrub species can be 2–3 m tall (Lozano *et al.*, 2003).

The modern treeline in northern and central Ecuador is at about 3400–3600 m. At the El Tiro-Pass, 30 km north of the core site, the modern treeline is at *c.* 2800 m, which is about 600–800 m lower. A shift of vegetation zones to lower elevation is probably a result of the so-called Andean depression (Bader, 2007).

Table 1 AMS-radiocarbon dates and calibrated ages for the lake core from Laguna Rabadilla de Vaca

Core name	Laboratory code	Dated material	Core depth	^{14}C yr BP	Median calibrated age (cal. yr BP)	2 σ age range (cal. yr BP)
Lag. Rabadilla de Vaca	Erl-8896	Bulk sample	96 cm	1887 $\pm$ 38	1770	1630–1875
Lag. Rabadilla de Vaca	Erl-8895	Bulk sample	278 cm	4603 $\pm$ 45	5170	4990–5445
Lag. Rabadilla de Vaca	Erl-11032	Bulk sample	360 cm	6822 $\pm$ 88	7620	7460–7790
Lag. Rabadilla de Vaca	Erl-8375	Bulk sample	450 cm	9262 $\pm$ 81	10 380	10 225–10 555

Figure 3 Age–depth model (cal. yr BP/core depth in cm) of Laguna Rabadilla de Vaca lake sediment core

Two different mountain rainforest ecosystems exist in the Podocarpus National Park region. The upper mountain rainforest, located between *c.* 2100 and 2750 m, consists of low, monotypic formation, with only one tree stratum between 5 and 10 m; rarely up to 15 m. Characteristic trees include *Purdiaea nutans* (Cyrillaceae), *Myrica pubescens* (Myricaceae) and *Myrsine andina* (Myrsinaceae). The lower mountain rainforest is located between *c.* 1800 and 2150 m with an extremely diverse, two-storied tree stratum and is composed of numerous 20–35 m tall tree species. Characteristic species include *Alzetea verticillata* (Alzateaceae), *Graffenrieda miconioides* (Melastomataceae) and *Myrcianthes* sp. (Myrtaceae); (Bussmann, 2001, 2005; Lozano *et al.*, 2003).

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 climate of the paramo is classified as humid tropical diurnal with cold nights and cool days. There is a dry season that lasts from December until March (Bosman *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 division that separates the moist eastern slopes of the Andes from the dry inner-Andean basins (eg, the Loja- and Catamayo Basin). 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).

Laguna Rabadilla de Vaca is located close to the eastern Andean divide and highly influenced by easterly trade winds (average annual speed 9.3 m/s) from the Amazon lowland. In the

winter months (June–August), this trade wind system is very strong and stable, occasionally interrupted by westerly winds in the summer months (November–March). Annual precipitation at Cajanuma, located on the western slope (3400 m) is about 5700 mm and the average annual temperature is about 6.9°C (Emck, 2007).

Material and methods

A 492 cm long sediment core was recovered with a Livingstone piston-corer near the centre of the lake (*c.* 5 m water depth) from an inflatable rubber raft (Figure 2). Core sections of 1 m were recovered in tubes and stored under dark and cold (+4°C) conditions before processing.

Four bulk subsamples (organic) were submitted for Accelerator Mass Spectrometer (AMS) radiocarbon dating (Table 1). Radiocarbon dates were performed at the University of Erlangen/Nürnberg, Germany. There is no carbonate bedrock in the catchment, which might contaminate the bulk samples. Radiocarbon ages were calibrated using Calib 5.0.2 (Stuiver and Reimer, 1993), performed with the Southern Hemisphere calibration curve (McCormac *et al.*, 2004). Median ages of the 2 σ distribution were used for the age–depth model (Figure 3).

A total of 52 subsamples (0.25 cm³) were taken from the sediment core for palynological and charcoal analyses mainly at 10 cm (5 cm) intervals. All samples were processed with standard analytical methods (Faegri and Iversen, 1989). Exotic *Lycopodium* spores were added to each sample before treatment for calculation of pollen and charcoal concentration. Approximately 300 pollen grains were counted for each sample. The pollen sum includes tree, shrub and herb pollen and excludes spores. Pollen identification

was based on the reference collection of H. Behling, which includes about 3000 neotropical species, and on the literature (Hooghiemstra, 1984; Behling, 1993). A reference collection with about 300 species, collected during fieldwork and at the herbarium of the (ECSF) research station is also available.

The grouping of the identified pollen taxa into lower and upper mountain rainforest, subparamo and paramo has been carried out according to available data from the literature (Bussmann, 2001, 2005; Lozano *et al.*, 2003; Homeier and Werner, 2005). Pollen and spore data are presented in pollen diagrams as percentages of the terrestrial pollen sum. Pollen concentration (grains/cm³) and influx (grains/cm² per yr) were also calculated. Carbonized particles (10–150 µm) were counted on pollen slides and presented as influx (particles/cm² per yr). Pollen diagrams were created with TILIA, TILIAGRAPH and CONISS (Grimm, 1987).

Non-destructive magnetic susceptibility (κ) scanning was performed, on split cores with a Bartington MS2F point sensor at 1 cm resolution. An Avaatech XRF-scanner provided semi-quantitative analyses of Al, Si, S, K, Ca, Ti, Mn and Fe (Richter *et al.*, 2006; Tjallingii *et al.*, 2007) at 1 cm depth intervals (see Figure 6). Values are given in total counts (cnts).

Results

Stratigraphy

The 492 cm long lake sediment core from Laguna Rabadilla de Vaca consists of dark brown fine detrital mud (see Figure 5). The organic material is interrupted by three light brown 3–4 cm thick clay layers at 190, 280 and 295 cm sediment depth. The clay layers have sharp erosive bases.

Chronology

Four AMS radiocarbon dates (Table 1) provide the chronological control for the sediment core from Laguna Rabadilla de Vaca. The AMS date close to the base of the core (450 cm core depth) indicates Holocene deposits. Extrapolation of the age–depth model shows an age of 11 700 cal. yr BP at the base of the sediment record.

The series of four AMS dates indicates a consistent sedimentation rate (Figure 3). The average sediment accumulation rate for the entire core is 0.41 mm/yr. In detail it is 0.52 mm/yr (recent–1770 cal. yr BP), 0.53 mm/yr (1770–5170 cal. yr BP), 0.34 mm/yr (5170–7620 cal. yr BP) and 0.32 mm/yr (7620–11,700 cal. yr BP) (see Figure 6).

Description of the pollen diagram

The total number of identified different pollen and spore types is 108. The pollen diagram (Figure 4) shows records of the most abundant pollen and spore taxa. Figure 5 illustrates records of the ecological groups, the pollen sum, the pollen concentration, and the pollen and charcoal influx. A cluster analysis of terrestrial pollen taxa produces a dendrogram that permits zonation of the record into the zones RV-1, RV-2 and RV-3 (Figure 5).

Zone RV-1 (490–405 cm; c. 11,700–8990 cal. yr BP)

This zone is marked by a stable representation of lower mountain rainforest (LMF) and upper mountain rainforest (UMF) pollen taxa such as *Weinmannia* (8–12%), *Hedyosmum* (5–10%) and Moraceae/Urticaceae (3–8%). Subparamo taxa is slightly less than in other zones, Melastomataceae (5–10%) and Asteraceae (3–8%) percentages are low. Paramo pollen are well represented, especially Poaceae (30–40%). Cyperaceae, Liliaceae, *Valeriana* and *Thalictrum* (all 1–5%) percentages are low. Fern spore (12–25%) percentages are highest in this zone, especially *Huperzia* (2–8%). Pollen concentrations (150 000–320 000 grains/cm³) are stable.

Figure 4 Pollen percentage diagram of the Laguna Rabadilla de Vaca record, showing selected pollen and spore taxa grouped into lower mountain rainforest (LMF), upper mountain rainforest (UMF), subparamo and paramo

Figure 5 Pollen summary diagram of the Laguna Rabadilla de Vaca record, showing radiocarbon dates, lithology, sums of ecological groups, pollen sum, records of pollen concentration, pollen and charcoal influx and the CONISS dendrogram (based on pollen taxa)

Figure 6 XRF-data, physical properties and charcoal influx for Laguna Rabadilla de Vaca

Pollen influx (6000–8000 grains/cm² per yr) is low and charcoal influx (6000–13,000 particles/cm² per yr) is high with a decreasing trend, in this zone.

Zone RV-2 (405–197.5 cm; c. 8990–3680 cal. yr BP)

This zone is marked by low percentages of LMF pollen (eg. Moraceae/Urticaceae; 3–8%). UMF pollen reach their highest percentages in this zone, especially *Weinmannia* (12–25%). *Hedyosmum* (3–10%) is low in abundance. Subparamo taxa such as Melastomataceae (5–8%) and Asteraceae (3–8%) percentages are stable. Paramo pollen are well represented, especially Poaceae (35–45%). Cyperaceae, Liliaceae and *Valeriana* (all 1–3%) percentages are low. Fern spore (8–15%) percentages are lower than in previous zone. Pollen concentrations (120 000–420 000 grains/cm³) are high. Pollen influx (5000–20,000 grains/cm² per yr) is high with an increasing trend throughout this period. Charcoal influx (3000–14 000 particles/cm² per yr) is high, peaking between 395 and 365 cm.

Zone RV-3 (197.5–0 cm; c. 3680–0 cal. yr BP)

This zone is marked by low percentages of LMF pollen (eg. Moraceae/Urticaceae; 1–5%). UMF pollen such as *Weinmannia* (4–12%) and *Hedyosmum* (3–8%) decrease compared with the previous zone. Subparamo taxa such as Melastomataceae (5–10%) and Asteraceae (1–8%) are stable. Paramo pollen types peak in this zone, especially Poaceae (40–55%). Liliaceae and *Valeriana* (both 1–3%) percentages are low. Fern spore percentages (8–15%) are stable. Pollen concentrations (180 000–260 000 grains/cm³) are lowest in this zone. Pollen influx (8000–16 000 grains/cm² per yr) is high. Charcoal influx (4000–14 000 particles/cm² per yr) is high with peaks at the beginning of this period.

XRF-scanning and physical properties

The main zonation of the pollen diagram (RV-1, RV-2 and RV-3) is also used for XRF data. Zone RV-2 is subdivided into a lower part (405–330 cm, 8990–6380 cal. yr BP) and an upper part (330–197.5 cm, 6380–3680 cal. yr BP) (Figure 6). The high peaks at 190, 280 and 295 cm core depth occur at the same depth as the thick clay layers.

A correlation matrix (Spearman Rank Order Correlation) showed positive correlations of Ti to K and Si ($r = 0.863$ and 0.809 , K to Si $r = 0.817$, $p < 0.001$). Al was also correlated significantly to all three elements (Si: $r = 0.723$, K: $r = 0.675$, Ti: $r = 0.633$, $p > 0.001$) as well as Ca (K: $r = 0.583$, Si: $r = 0.579$, Al: $r = 0.539$, Ti: $r = 0.501$, $p < 0.001$). As correlations among the mentioned elements are significant and show high correlation coefficients. Only Ti and Si are plotted for palaeoenvironmental reconstruction. Fe showed little correlation to these elements (Al: $r = 0.149$, Ti: $r = 0.160$, Si: $r = 0.226$, K: $r = 0.240$, $p < 0.001$). All other element concentrations were too low for accurate interpretation. In zone RV-1 Ti and Si counts reach their highest concentrations with a maximum between 465 and 440 cm. In contrast, in the lower part of zone RV-2 Ti and Si values are low. The transition between zone RV-2 and zone RV-1 is characterized by high concentrations of Ti and Si, with maxima at 295, 280 and 190 cm before a sharp decrease to the lowest values of the record in zone RV-3.

Magnetic susceptibility (κ) shows only moderate correlation to the elements mentioned above (Ti: $r = 0.44$, $p = 0.006$, K: $r = 0.468$, $p = 0.003$, Si: $r = 0.422$, $p = 0.009$, Ca: $r = -0.28$, $p = 0.088$ and Fe: $r = 0.215$, $p = 0.194$), but generally follows the peaks of the elements it is best correlated with, especially at the depths of the clay layers.

Interpretation and discussion

The pollen record from Laguna Rabadilla de Vaca (3312 m) indicates that paramo vegetation has surrounded the lake throughout the Holocene. The bottom of the sediment core shows an extrapolated age of *c.* 11 700 cal. yr BP. As it was impossible to recover deeper sediments, we conclude that material was too coarse for recovery and might reflect the deglaciation of the basin. During last glacial maximum (LGM), the maximum equilibrium line of the glaciers is estimated at *c.* 3100 m for the Podocarpus National Park region, with glaciers terminating at elevations of *c.* 2750–2800 m (Rozsypal, 2000). After Clapperton (1987), a moraine low stand is described at 2800 m for the Las Cajas National Park (Figure 1) in western central Ecuador. At the El Tiro-Pass (2810 m, Figure 1), *c.* 30 km north of the core site, the bottom of the sediment core shows an age of *c.* 20 100 cal. yr BP, indicating early deglaciation or lack of glaciation (Niemann and Behling, 2008a). At Laguna Chochos (3285 m, Figure 1), eastern Peruvian Andes, deglaciation was locally completed at *c.* 11 700 cal. yr BP (Bush *et al.*, 2005).

The early-Holocene period

During the early-Holocene period (RV-1, *c.* 11 700–8990 cal. yr BP) herb-paramo was the main vegetation type around Laguna Rabadilla de Vaca. The herb-paramo, associated with a high number of ferns, mainly *Huperzia*, was rich in Poaceae, Cyperaceae, *Valeriana* and Liliaceae, reflecting cool and relatively wet climatic conditions. A slow warming during this period is indicated by the pollen record from El Tiro-Pass (2810 m, Figure 1), which shows a slight expansion of subparamo and upper mountain rainforest vegetation into higher elevations during the early Holocene. Fern spores including tree ferns (*Cyathea*) expanded markedly, reflecting a change to more humid conditions (Niemann and Behling, 2008a). The pollen record from Laguna Cocha Caranga (2710 m, Figure 1), *c.* 25 km north of the core site, shows an increase of upper mountain forest taxa, mainly *Weinmannia*, during the late-Pleistocene to early-Holocene period (*c.* 14 500–9700 cal. yr BP), reflecting an increase in temperature and a shift of vegetation zones, as well as the treeline to higher elevations (Niemann and Behling, 2008b).

In contrast, at Laguna Chochos (3285 m, Figure 1), an already warm and wet early Holocene (*c.* 11 500–9500 cal. yr BP) was estimated (Bush *et al.*, 2005). Fossil pollen data from Laguna Tuctua in the central Peruvian Andes (4000 m, Figure 1) point to increasing moisture, as well as higher temperatures from about 12 910 to 7850 cal. yr BP (Hansen *et al.*, 1994).

High Ti values are commonly regarded as an indicator for detrital input (Haberzettl *et al.*, 2005, 2006, 2007, 2008; Mayr *et al.*, 2005; Haberzettl, 2006) and confirm the assumption of wet conditions during RV-1. This immobile element probably was delivered to the lake via fluvial processes resulting in enhanced Ti input during wetter, and reduced Ti input during drier, conditions (eg, Haberzettl *et al.*, 2005, 2007). Hence, Ti likely reflects hydrological variations in that area. However, input of Ti during RV-1 might also have been caused by more open vegetation cover relative to modern times, as it is also reflected by low pollen influx during this time. Probably both factors (increased humidity and erosivity) caused the high Ti values during the early Holocene period in the earliest part of the record, which are almost synchronous with the maximum herb and fern percentages.

The Fe record, which was also interpreted as an indicator for fluvial terrigenous sediment influx in other studies (eg, Richter *et al.*, 2006) cannot be applied as climate proxy at Laguna Rabadilla de Vaca. While Fe and Ti are closely related in the terrigenous fraction, reduced Fe is prone to diagenetic remobilization whereas Ti is inert to diagenetic processes (Granina *et al.*, 2004; Richter *et al.*,

2006) which probably explains the different patterns of Ti and Fe at Laguna Rabadilla de Vaca. However, the signal of clastic input of Fe can at least be traced at the depths of the clay layers. Though the correlation coefficient between Fe and κ is rather low the same seems to be the case for κ as reductive dissolution of ferric iron components also has a strong impact on the rock magnetic properties of the sediment (Kasten *et al.*, 2003) and rock-magnetic parameters are not palaeoclimate proxies *per se* (Geiss *et al.*, 2003). κ can only be used as an indicator for detrital input at obvious parts of the record, ie, at the depths of the clay layers.

The middle-Holocene period

The middle-Holocene period (RV-2, *c.* 8990–3680 cal. yr BP) at Laguna Rabadilla de Vaca is characterized by an increase of *Weinmannia*, reflecting a shift of vegetation zones, as well as the treeline into higher elevations. *Weinmannia* has a large altitudinal range in the Podocarpus National Park region, occurring from lower mountain rainforest up to paramo vegetation zone (Lozano *et al.*, 2003; Homeier and Werner, 2005). Table 2 shows the number of *Weinmannia* species, found in different vegetation zones. The highest numbers of *Weinmannia* species are found in the upper mountain rainforest vegetation zone.

Today, the slopes above Laguna Rabadilla de Vaca are covered with shrub-paramo vegetation, while herb-paramo vegetation occurs on the flat areas near the lake (Figure 2). It might be possible that the shrub-paramo vegetation spread around the whole lake during this period.

Consequently the strong increase of *Weinmannia* indicates warmer climatic conditions between *c.* 8990 and 3680 cal. yr BP, corresponding to the worldwide Holocene thermal optimum which is also visible in various regional archives. For example from *c.* 8900 to 3300 cal. yr BP an upper mountain rainforest developed at the El Tiro-Pass (2810 m, Figure 1), where nowadays subparamo vegetation occurs, suggesting a warmer climate than present, as well as a shift of the treeline to higher elevations (Niemann and Behling, 2008a). Ice cores from Huascaran (*c.* 6050 m, Figure 1) in the central Peruvian Andes show that the climate was warmest from *c.* 9455 to 5960 cal. yr BP (Thompson *et al.*, 1995). At Lake Titicaca (3810 m, Figure 1), central Peruvian Andes, a dry event between *c.* 9000 and 3100 cal. yr BP is inferred from changes in the vegetation composition (Paduano *et al.*, 2003), in combination with a well-documented early- to middle-Holocene lowstand, between *c.* 8000 and 3600 cal. yr BP (D'Agostino *et al.*, 2002). Pollen, charcoal and radiocarbon data from the Colombian inter-Andean Cauca Valley (1020 m, Figure 1), indicates drier climatic conditions than present from *c.* 9670 to 3030 cal. yr BP (Berrio *et al.*, 2002).

The Holocene climate development of Laguna Rabadilla de Vaca generally corresponds to the previous studies of the Podocarpus National Park region, as well as to other palaeoenvironmental records of tropical South America (discussed above). Additionally, our data also correspond to studies from outside tropical South America (Haug *et al.*, 2001; Kim *et al.*, 2002; Li *et al.*, 2002; Andersen *et al.*, 2004; Liew *et al.*, 2006).

Low Ti values suggest dry climatic conditions at Laguna Rabadilla de Vaca for the early middle Holocene (*c.* 8990–6380 cal. yr BP). At Laguna Cocha Caranga (2710 m, Figure 1) drier climatic conditions occurred from *c.* 9700 to 6900 cal. yr BP, characterized by high percentages of Cyperaceae and *Isoetes* coupled with low concentration of *Botryococcus*, reflecting a lower lake level and an enlarging of marshy lake shores, because of reduced precipitation (Niemann and Behling, 2008b). At Laguna Chochos (3285 m, Figure 1) a warm and wet early Holocene was interrupted by a warm-dry event that lasted from *c.* 9500 to 7300 cal. yr BP (Bush *et al.*, 2005). The pollen record Yasuni National Park (220 m, Figure 1), Ecuadorian Amazonia, shows a long-lasting plateau of *Cecropia* pollen (*c.* 8700–5800 cal. yr BP) which is tentatively

Table 2 Altitudinal range of different *Weinmannia* species for the Podocarpus National park region

	Lozano <i>et al.</i> (2003)	Homeier and Werner (2005)
LMF	2 species	5 species
UMF	7 species	4 species
Subparamo	5 species	2 species
Paramo	x	x
Shrub-paramo	4–5 species	x
Herb-paramo	2 species	x

x, no data available

interpreted to a period of increased tree mortality, indicating a drought period (Weng *et al.*, 2002). In contrast, the pollen record from Laguna Loma Linda (310 m, Figure 1), Colombian savannah, shows lower annual and stronger seasonal precipitation signals than today during the period from c. 9650 to 6850 cal. yr BP (Behling and Hooghiemstra, 2000).

High Ti values suggest wetter climatic conditions for the late middle Holocene (c. 6380–3680 cal. yr BP). Accordingly, at Laguna Cocha Caranga (2710 m, Figure 1) wetter climatic conditions occurred from c. 6900 to 4200 cal. yr BP. Low percentages of Cyperaceae and *Isoetes* coupled with high concentration of *Botryococcus* reflect an enlarging of the water body. Marshy lake shores were flooded at that time, because of higher precipitation (Niemann and Behling, 2008b). Maximum Holocene lake level at Lake Aricota (2800 m, Figure 1), central Peruvian Andes, was attained before c. 7000 cal. yr BP and ended c. 2800 cal. yr BP (Placzek and Quade, 2001). The pollen record from Laguna Loma Linda (310 m, Figure 1) shows that during the period from c. 6850 to 3900 cal. yr BP rainforest taxa increased markedly, reflecting an increase in precipitation (Behling and Hooghiemstra, 2000). The pollen record from Yasuni National Park (220 m, Figure 1) also indicates wet climatic conditions from c. 5800 to 4900 cal. yr BP (Weng *et al.*, 2002).

Landslides on the slopes above Laguna Rabadilla de Vaca, contemporaneous with the peaks in Ti, and probably caused by strong precipitation events, may be responsible for the thick clay layers at 190, 280 and 295 cm sediment depth (between 5800 and 3600 cal. yr BP), consistent with an increase in humidity. This may also explain the increase in sedimentation rate from 0.34 to 0.52 mm/yr. The clay layer at 280 cm was counted for pollen and spores. The high occurrence of shrub pollen, c. 75%, especially *Weinmannia* (30%), *Hedyosmum* and Melastomataceae (both 8–10%), low values of Poaceae (10 %) and ferns (2 %), as well as the absence of *Isoetes* point to the slopes as the source of this sediment. The clay layers display sharp erosive bases, suggesting rapid sedimentation events.

The late-Holocene period

From the beginning of the late-Holocene period (RV-3, c. 3680 cal. yr BP to present) a Poaceae-dominated (40–55%) herb-paramo expanded at Laguna Rabadilla de Vaca, reflecting cooler climatic conditions relative to the middle-Holocene period. A decrease of Si and Ti points to less erosion, probably resulting from drier climatic conditions throughout the late Holocene. This is also consistent with the record from El Tiro-Pass (2810 m, Figure 1) where modern subparamo vegetation became established after 3300 cal. yr BP, indicating a shift of vegetation zones into lower elevation, because of cooler climatic conditions during the late-Holocene period (Niemann and Behling, 2008a). At Laguna Cocha Caranga (2710 m, Figure 1) drier climatic conditions occurred from c. 4200 to 1300 cal. yr BP. Percentages of fern spores decrease, low concentration

of *Botryococcus* coupled with a strong increase of Cyperaceae indicates a lake level low stand, owing to a reduction in precipitation. The water body shrank, and marshy lake shores developed. From c. 1300 cal. yr BP to the present, a peat bog became established, reflecting wetter conditions during this period (Niemann and Behling, 2008b). At the Cariaco Basin, a trend toward drier conditions is evident from c. 5400 cal. yr BP to present, with a precipitation minimum during the time interval from c. 3800 to 2800 cal. yr BP (Haug *et al.*, 2001).

In contrast, a moist late Holocene is described elsewhere. The pollen record from Laguna Loma Linda (310 m, Figure 1) shows a continued increase of rainforest taxa from c. 3900 to 2300 cal. yr BP, precipitation was still increasing and the length of the annual dry period possibly shortened. From c. 2300 cal. yr BP onwards, grass savannah expanded, likely as a result of increased human impact on the vegetation (Behling and Hooghiemstra, 2000). The pollen record of the Yasuni National Park (220 m, Figure 1) shows wet climatic conditions from c. 3700–1000 cal. yr BP and dry climatic conditions from c. 1000 cal. yr BP to present (Weng *et al.*, 2002).

The very high charcoal influx at the beginning of this zone may suggest human activities by uncontrolled burning near Laguna Rabadilla de Vaca. The high number of Poaceae may be a result of these burning activities in conjunction with the cooler and drier climatic conditions. At Laguna Cocha Caranga (2710 m, Figure 1) *Myrica* strongly expands from c. 4800 cal. yr BP which may also indicate settlement in the Loja region. The first known human activity in the region of Loja (Figure 1), indicated by ceramic fragments, has been dated around 4000 cal. yr BP. Since then the native Palta culture established around Loja (Guffroy, 2004).

Conclusions

During the early Holocene (11 700–8990 cal. yr BP) climatic conditions were cool and relatively wet. Herb-paramo was the main vegetation type at the Laguna Rabadilla de Vaca. The herb-paramo, associated with a high number of ferns, mainly *Huperzia*, was rich in Poaceae, Cyperaceae, *Valeriana* and Liliaceae. The middle Holocene (8990–3680 cal. yr BP) is characterized by warmer climatic conditions than modern times (Holocene thermal optimum). Drier climatic conditions for the early middle Holocene (8990–6380 cal. yr BP) and wetter climatic conditions for the late middle Holocene (6380–3680 cal. yr BP) are inferred. A strong increase of *Weinmannia* reflects a shift of vegetation zones into higher elevation and/or a spread of a shrub-paramo vegetation type around the whole lake. Cooler and drier climatic conditions relative to the late middle-Holocene period become established since the beginning of the late Holocene (3680 cal. yr BP). A Poaceae-dominated (40–55%) herb-paramo expanded until modern times.

The data from Laguna Rabadilla de Vaca reflect Holocene climate and vegetation development that is consistent in comparison with preceding studies from the Podocarpus National Park region. The Holocene thermal optimum assumed in this study fits well with the interregional climate development.

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