

**RECONSTRUCTION OF LATE QUATERNARY  
LANDSCAPE DYNAMICS IN THE  
PODOCARPUS NATIONAL PARK REGION  
SOUTHERN ANDES OF ECUADOR**

**Dissertation**

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## Summary

The Ecuadorian Andes harbor ecosystems with the highest biodiversity on earth. Background information on past environmental dynamic is needed to understand, conserve and manage the ecosystems and their biodiversity.

Three radiocarbon dated sediment archives, Rabadilla de Vaca (RVM), at 3244 m elevation, and Valle Pequeño (VP), at 3200 m elevation, both in the central part of the Podocarpus National Park (PNP) region, as well as Lagunas Natasas Forest (LNB), at 3495 m elevation, south of the PNP in southern Ecuador in the so-called Andean depression, have been studied by pollen, spore and charcoal analysis. The results reveal vegetation changes in the LNB area during the past ca. 16,000 years and in RVM and VP area during the past ca. 2100 years. During late Pleistocene (15,930-11,660 cal yr BP), grass páramo vegetation dominated the area and the occurrence of *Plantago rigida* suggests cold and wet environmental conditions in the LNB region. *P. rigida* population decreased markedly during last Glacial period, especially during the Younger Dryas, a short cold interval (12,800 to 11,500 years ago), and the upper forest line (UFL) was most probably lower than present-day. Between 11,660 - 4280 cal yr BP, a marked decrease of páramo vegetation occurred, accompanied by an expansion of subpáramo (woody dwarf shrub) vegetation. In the LNB record south of PNP, an upslope shift of the UFL is documented. The LNB record provides for the first time evidence of large populations of *Polylepis* in this area of the southern part of the Andean depression. Around 4200 cal yr BP a return to cooler and more humid conditions favoured the increase of páramo vegetation. The late Holocene until present-day is characterized by a continuous fluctuation between páramo and subpáramo vegetation. However, around 1200 cal yr BP subpáramo vegetation (dwarf shrubs) was frequent, suggesting a moderate increase in temperature and moisture. In RVM area a stronger occurrence of subpáramo suggest wetter and warmer climatic conditions from 2100 until 1720 cal yr BP. In the LNB area an increase of páramo taxa indicate moister conditions after 500 cal yr BP. In the RVM and VP core, páramo vegetation expanded strongly and reduced the presence of forest vegetation since 800 to 310 cal yr BP. Influenced by wetter conditions and frequent fires, *Polylepis* became rare and was almost absent during the late Holocene in the LNB area. Although charcoal remains indicate human influence since more than 4000 years ago, maxima of charcoal particle concentration indicate an increased fire frequency from 1800 to 1600 cal yr BP and from 600 to 400 cal BP.

Comparing vegetation and fire records of the three studied sites, it is evident that fires favoured the expansion of grass páramo vegetation and curtailed the expansion of subpáramo and UMF. Fire probably played an important role in controlling changes of the upper forest limit during the late Holocene. However, it is difficult to detect whether climate change also played an important role during these periods. The fire events occurred diachronously between sites, suggesting anthropogenic influence. It is possible to infer regional changes influenced by climate variability. However, local conditions of temperature, precipitation, wind regimes, radiation and geomorphological features also have a strong impact on vegetation patterns, determining the structure, heterogeneity and distribution of the ecosystems.

## Resumen

Los Andes ecuatorianos albergan ecosistemas con la más alta biodiversidad sobre la tierra. Información preliminar sobre la dinámica de los ecosistemas en el pasado es necesaria para entender, conservar y manejar los ecosistemas y su biodiversidad.

Tres muestras de sedimentos fueron datadas, Rabadilla de Vaca (RV) a 3244 m de altura y Valle Pequeño (VP) a 3200 m de altura, ambas en la parte central del Parque Nacional Podocarpus (PNP), y Lagunas Natosas Bosque (LNB) a 3495 m de altura, al sur del PNP al sur del Ecuador en la región llamada Depresión Andina. Estas muestras fueron estudiadas con base en análisis de polen, esporas y partículas de carbón. Los resultados revelan cambios en la vegetación en la zona de LNB durante los últimos 16,000 años, y en RVM y VP desde hace 2100 años. Durante el Pleistoceno tardío (15,930 – 11,660 cal yr BP), la vegetación de páramo dominó el área y la presencia de *Plantago rigida* sugiere condiciones ambientales frías y húmedas en el área de LNB. La población de *P. rigida* disminuyó drásticamente durante el último período glacial y especialmente durante el “Younger Dryas”, que es un corto período frío (hace 12,800 a 11,500 años), y el límite superior del bosque (UFL) muy probablemente fue mas bajo que en la actualidad. Entre 11,660 – 4280 cal yr BP, ocurrió una marcada reducción de cobertura de páramo, acompañada por una expansión de la vegetación de subpáramo (arbusto enano leñoso). En la región de LNB, al sur del PNP, se evidenció un cambio altitudinal hacia arriba del UFL. En este sitio se evidencia por primera vez la presencia de grandes extensiones de *Polylepis* en la región de la Depresión Andina. Alrededor de 4200 cal yr BP el regreso a condiciones climáticas frías y húmedas favoreció la expansión de los páramos. El Holoceno tardío hasta el presente se caracteriza por la continua fluctuación entre vegetación de páramo y subpáramo. Sin embargo, alrededor de los 1200 cal yr BP, vegetación de subpáramo (arbustos enanos) fueron frecuentes, lo que sugiere un incremento moderado en temperatura y humedad. En el área de RVM desde los 2100 hasta los 1720 cal yr BP, la dominancia de subpáramo sugiere condiciones climáticas más húmedas y cálidas. En el área de LNB después de los 500 cal yr BP, el incremento de vegetación de páramo indica condiciones más húmedas. Esto también se registró en la zona de RVM y VP desde 800 a 310 cal yr BP, donde la vegetación de páramo se expandió ampliamente y redujo la posibilidad de crecimiento de bosque. Influenciada por condiciones más húmedas y fuegos (incendios) frecuentes, en el área de LNB, *Polylepis* estuvo casi ausente durante el Holoceno tardío. Aunque, restos de partículas de carbón indican la presencia humana desde hace

más de 4000 años. La máxima concentración de partículas de carbón indican alta frecuencia de fuegos desde 1800 hasta 1600 cal yr BP y desde 600 a 400 cal yr BP.

Comparando la vegetación y los registros de carbón entre los tres sitios, es evidente que el fuego favoreció la expansión de vegetación de páramo en detrimento de la vegetación de subpáramo y bosque montano alto (UMF). El fuego probablemente tuvo un rol importante en el control de los cambios del límite del bosque durante el Holoceno tardío. Sin embargo, es difícil establecer si cambios en las condiciones del clima también tuvieron un rol importante durante este período. Los fuegos se presentaron a distintos momentos entre los diferentes sitios, esto sugiere que existió influencia antropogénica. Es posible inferir cambios a nivel regional ocasionados por la variabilidad de clima; sin embargo, condiciones locales como temperatura, precipitación, vientos, radiación solar y geomorfología, también tienen un impacto fuerte en los patrones de la vegetación, los mismos que pueden determinar la estructura, heterogeneidad y distribución de los ecosistemas.

## Zusammenfassung

Die Anden Ecuadors beherbergen Ökosysteme, die weltweit zu den Gebieten höchster Biodiversität zählen. Paläoökologische Studien über vergangene Vegetationsveränderungen liefern wichtige und notwendige Kenntnisse, um diese Ökosysteme ganzheitlich zu verstehen. Nur so können die Gebiete und ihre wertvolle Biodiversität wirksam geschützt werden.

Anhand von drei Sedimentkernen, deren Altersbestimmung mittels Radiokohlenstoffdatierung vorgenommen wurde, sind neue palynologische Daten in den Anden Süd-Ecuadors erhoben worden. Die zwei Sedimente Rabadilla de Vaca (RVM) aus 3244 m Höhe und Valle Pequeño (VP) aus 3200 m Höhe stammen aus der zentralen Region des Podocarpus Nationalparks (PNP). Der dritte Sedimentkern Lagunas Natasas Forest (LNB) aus 3495 m Höhe ist aus dem Gebiet der Andinen Depression südlich des PNP. Die Ergebnisse der Analysen geben Aufschluss über Vegetationsveränderungen der letzten ca. 16,000 Jahre im Gebiet von LNB und der letzten ca. 2,100 Jahre in den Gebieten von RVM und VP.

Im späten Pleistozän vor ca. 15,930-11,660 Jahren war Gras-Páramo die vorherrschende Vegetation im Gebiet von LNB und das Vorkommen von *Plantago rigida* weist auf kalte und feuchte klimatische Bedingungen in dieser Zeit hin. Die Abundanz von *P. rigida* nimmt im Spätglazial und vor allem während der Jüngerer Dryaszeit, die ein kurzes Kälte-Intervall vor ca. 12,800 - 11,500 Jahren darstellt, stark ab. Zu dieser Zeit befand sich die obere Waldgrenze in niedrigeren Höhenlagen als heute. Im Zeitraum vor ca. 11,660 - 4,280 Jahren hat sich Subpáramo-Vegetation (zumeist Zwergsträucher) ausgebreitet und Páramo zurückgedrängt. Zur gleichen Zeit hat sich die Waldgrenze in höhere Lagen verschoben. Die Pollenfunde aus dem Sedimentkern LNB belegen erstmals große Vorkommen von *Polylepis* in diesem Gebiet im südlichen Bereich der Andinen Depression.

Vor ca. 4,200 Jahren hat ein Wandel zurück zu kühleren und feuchteren Verhältnissen die Ausbreitung von Páramo begünstigt. Seit dem späten Holozän bis heute breiten sich kontinuierlich und im Wechsel Páramo und Subpáramo immer wieder aus, wobei vor ca. 1,200 Jahren Subpáramo die vorherrschende Vegetation war, was auf einen leichten Anstieg der Temperatur und Feuchtigkeit hindeutet.

Im Gebiet von RVM deutet ein hohes Vorkommen von Subpáramo vor ca. 2,100 bis ca. 1,720 Jahren auf feuchtere und wärmere klimatische Bedingungen hin. Im Gebiet von LNB zeigt ein vermehrtes Auftreten von Páramo-Taxa ein Wechsel zu feuchteren Verhältnissen vor ca. 500 Jahren an. Auch die Analysen der beiden Sedimente von RVM und VP ergeben, dass sich Páramo-Vegetation vor ca. 800 bis vor ca. 310 Jahren ausbreitete und den Wald zurückdrängte. Durch feuchtere Bedingungen, aber auch durch häufigere Feuerereignisse, ging das Vorkommen von *Polylepis* im Gebiet von LNB so weit zurück, dass im späten Holozän kaum mehr *Polylepis* vorzufinden ist. Vorgefundene Rückstände von Holzkohle deuten auf einen anthropogenen Einfluss seit mehr als 4000 Jahren hin. Besonders häufige Funde von Holzkohlepartikeln weisen auf ein erhöhtes Feuervorkommen vor ca. 1800 bis vor ca. 1600 Jahren und vor ca. 600 bis vor ca. 400 Jahren hin.

Vergleicht man die vegetations- und feuergeschichtlichen Ergebnisse der drei Untersuchungsgebiete miteinander wird deutlich, dass Feuer die Ausbreitung von Páramo-Vegetation begünstigt hat und im Gegenzug die Ausbreitung von Subpáramo und Bergregenwald an der oberen Waldgrenze verhindert hat. Den Feuerereignissen wird demnach im späten Holozän eine entscheidende Rolle für die Höhenverschiebungen der oberen Waldgrenze zugeteilt. Es bleibt schwierig zu ermitteln, ob auch wechselnde, klimatische Bedingungen in dieser Zeit eine Rolle gespielt haben. Da die Feuer an den verschiedenen Orten nicht zeitgleich vorkamen, ist die Ursache der Feuer aufgrund menschlicher Aktivitäten wahrscheinlich. Neben regionaler Klimavariabilität bestimmen im Untersuchungsgebiet vor allem lokale Unterschiede in Temperatur, Niederschlag, Wind- und Strahlungsverhältnissen sowie kleinräumige, geomorphologische Bedingungen die Vegetation und vorkommende Strukturen, Heterogenität und Verbreitung der Ökosysteme.

## Chapter I

### 1. General context

The tropical eastern Andes and the northern parts of western Amazonia are among the global hot spots of vascular plant diversity related to their high variety in relief and geomorphology (Mutke and Barthlott, 2005). Using data on vertebrates and vascular plants, Brummitt and Lughadha (2003) ranked the region as the top global biodiversity area. Regarding many groups of organisms, the Neotropical region is more speciose than any other region of the world. Two large-scale diversity patterns overlap in tropical mountains in general and in the Andes in particular: species richness of most groups of organisms peaks around the equator and declines towards the poles (Gaston, 2000), and species turnover is high along altitudinal gradients and usually shows a peak of richness not at lowest, but at medium elevations (Herzog et al., 2005; Krömer et al., 2005; Rahbek, 2005). Many hypotheses have been formulated to explain these patterns. Some of the most frequently used explanations are: evolution and biogeography; climate history; biotic and abiotic factors; stochastic effects. Each of the concepts is plausible to some extent, and it seems most probable that a combination is actually responsible for the observed richness patterns with all their group-specific variations (Brehm, 2007).

The present condition of the Andean ecosystems is mainly a consequence of past ecological processes, influenced by past environmental changes including climate, fire and land use. Vegetation history is, therefore, essential for understanding ecosystem dynamics. The actual position of this forest line is interpreted as remnants of high altitude forests now destroyed by human-made fires and forest clearing (Ellenberg, 1958; Laegaard, 1992; Sarmiento and Frolich, 2002). Studies on deforestation calculate that only 4% of the forests on the western Andean slope remain and almost no natural forests of the Central Valley are left because of the long occupation history and increasing human impact during last decades in particular (Dodson and Gentry, 1991).

Due to the lack of scientific information from this ecosystem, an Ecuadorian - German research cooperation group has been generating scientific knowledge from the eastern Andes tropical mountain forest. This research group started late 1990s, and since the year 2000 the DFG (Deutsche Forschungsgemeinschaft) research unit 402 ("Functionality in a Tropical Mountain Rainforest:

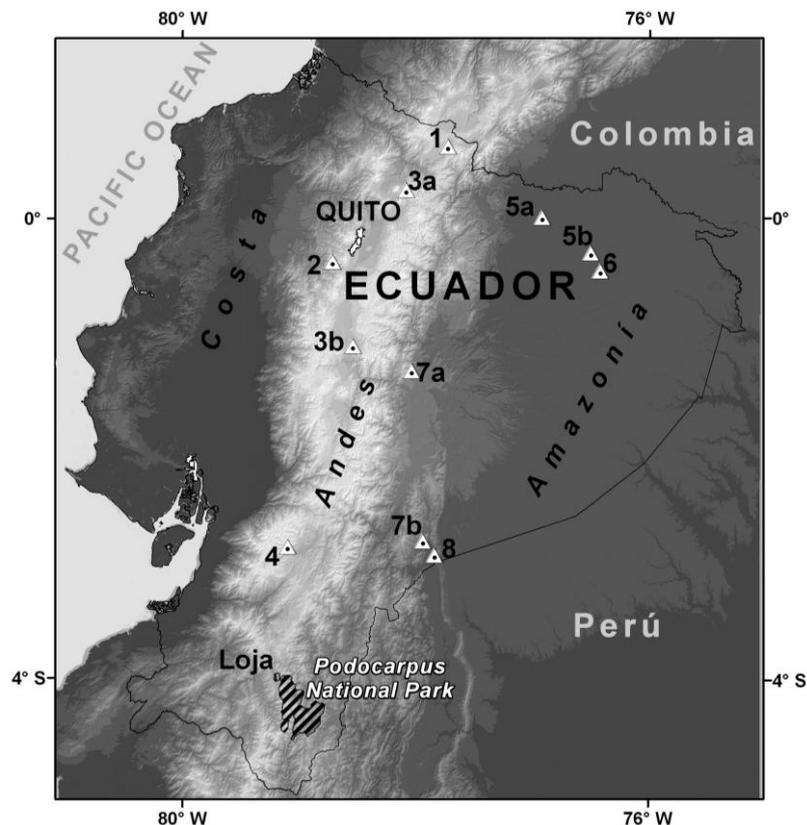
Diversity, Dynamic Processes and Utilization Potentials under Ecosystem Perspectives”) joined them to combine several working groups. In 2007, the new DFG research unit 816 (“Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador”) was launched to support additional research in the same area focusing on ecosystem functioning and sustainable land use management strategies in a biodiversity hotspot, which will continue until 2013. The research group has been investigating in an area of about 11.2 km<sup>2</sup> (Reserva Biológica San Francisco - RBSF), at the northern border of the Podocarpus National Park (PNP), southern Ecuador (Fig. 1.1).

### **1.1. Previous research in palaeoecology in the northern Andean region**

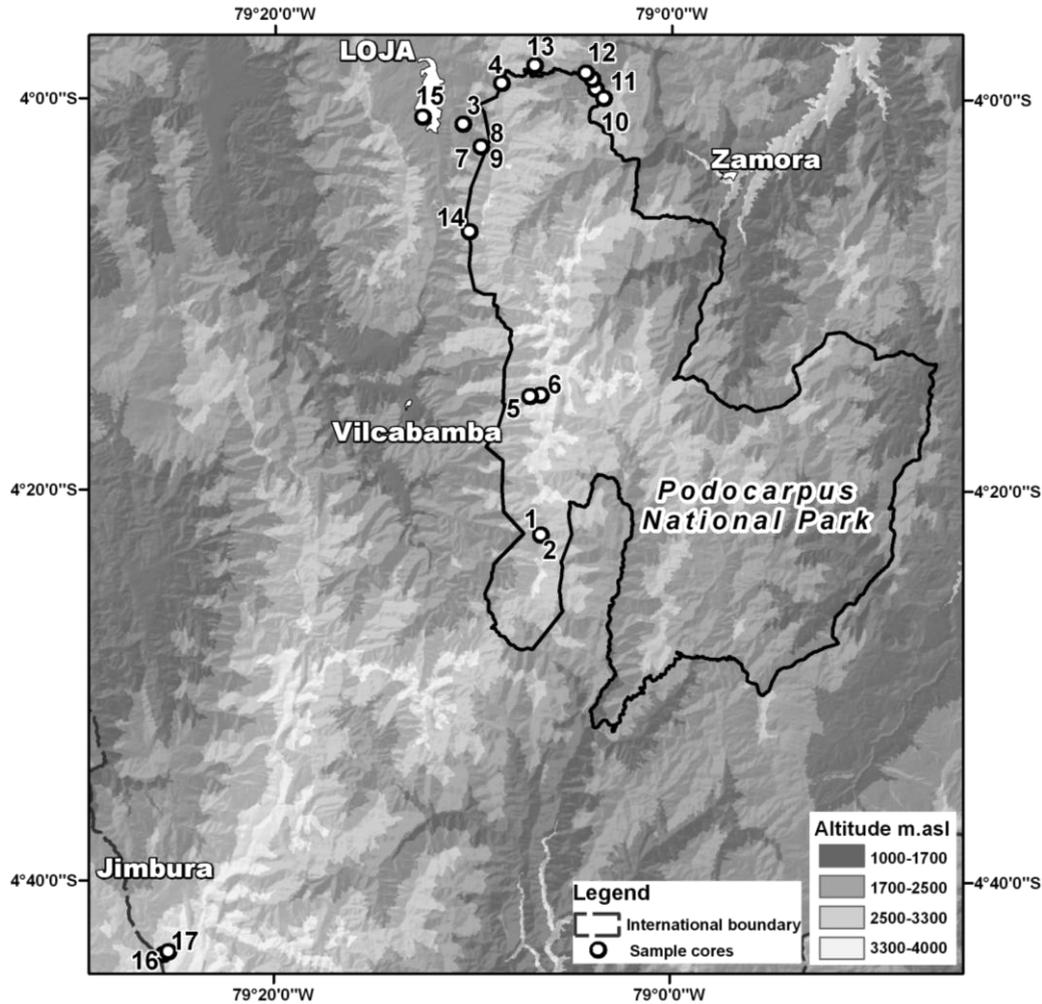
The Andean mountain forest has not been well studied regarding its palaeoecology. Because of the very difficult topography and accessibility, as well as the limited availability of botanical reports and databases for these areas, records are scattered (Bush et al., 2007). There are several records from the Colombian Andes (e.g. Berrío et al., 2002; Hooghiemstra and van der Hammen, 1993; van der Hammen and Hooghiemstra, 2003; Vélez et al., 2006; Wille et al., 2001) which indicate the presence of colder and drier conditions during the late Pleistocene (ca. 20,000-10,000 yr BP) than today. For the Colombian Andes a decrease of the annual temperature of 6 to 8° C with a downward shift of the upper forest line of approximately 800 – 1400 m compared to today was estimated for the last glacial maximum (LGM). At the beginning of the Holocene (ca. 11,500 cal yr BP) in the Peruvian Andes show higher UFL because of increase in temperature and precipitation (Hansen and Rodbell, 1995; Bush et al., 2005).

In Ecuador few palynological studies have been carried out. Hansen et al. (2003) demonstrate that cooler and moister climate occurred at the end of last glacial (17,000 to 11,000 cal yr BP) in the páramos of southwest of Ecuadorian Andes. Colinvaux et al. (1997) also noted cooler conditions and an absence of woody vegetation in regions of the southern Ecuadorian Andes where forest is present today. During the last decades, additional studies to understand the upper forest line dynamics during the late Holocene have been carried out in northern Ecuador. Results suggest that since ca. 6000 years ago the UFL was 100 to 200 m higher than today. (Bakker et al., 2008; Di Pasquale et al., 2008; Wille et al., 2002) (Fig. 1.1 and 1.2).

Since 2005 the DFG project has been supporting preliminary investigation on palaeoenvironmental topics in the PNP region and its surroundings. Different environments and ecosystems have been studied based on core, bog and monolith pollen samples (Fig. 1.2 and Table 1.1). These records have been integrated to determine past ecosystem function and dynamic. Climate, fire and human impact since the late Quaternary have been analyzed to generate knowledge about environmental factors which led to the modern landscape conditions. Additional samples, including modern pollen rain records, are now analyzed by the new research team, but are not included in this thesis.



**Figure 1.1** Maps showing the Podocarpus National Park (PNP) in the southeastern Ecuadorian Andes and other palynological study sites in the Andes and Amazon basin of Ecuador: (1) Guandera - Bakker et al., 2008/Di Pasquale et al., 2008; (2) Pantano de Pecho - Wille et al., 2002; (3 a/b) Lake Yaguarcocha - Colinvaux et al., 1988b; (4) El Cajas - Colinvaux et al., 1997/Hansen et al., 2003; (5 a/b) Tena – Orellana Colinvaux et al., 1988a; (6) Yasuni - Weng et al., 2002; (7 a) Mera - Bush et al., 1990/Liu and Colinvaux, 1985; (7 b) San Juan Bosco - Bush et al., 1990; (8) Lake Ayauch - Bush and Colinvaux, 1988.



**Figure 1.2:** Topographic map of the Podocarpus National Park showing the fossil pollen record sites within the region: (1, 2) Cerro Toledo, (3) Laguna Campana, (4) El Tiro, (5) Laguna Rabadilla de Vaca, (6\*) Rabadilla de Vaca mire, (7, 8, 9) Cocha Caranga, (10) ECSF-Cerro del Consuelo, (11) ECSF-Refugio, (12) ECSF-T2/250, (13) Laguna Zurita, (14\*) Valle Pequeño (Cajanuma), (15) Laguna Daniel Álvarez, Lagunas Natosas bog (16), Lagunas Natosas Forest (17\*). Numbers with asterisk (\*) are sites presented in this thesis. Detailed information on the pollen record locations is listed in Table 1.1.

**Table 1.1:** Pollen record sites within the Podocarpus National Park region and the surroundings

<i>Pollen record</i>	<i>Coordinates</i>	<i>Elevation (m a.s.l.)</i>	<i>Age (cal yr BP)</i>	<i>Reference</i>	<i>Site (Shown in Fig. 1.2)</i>
Cerro Toledo (CT)	04°22'47.7" S 79°06'69.2" W	3150	20,000	Brunschön and Behling, 2009	1
Cerro Toledo (CTB)	04°22'47.7" S 79°06'69.2" W	3110	10,000	Brunschön and Behling, 2009	2
Laguna Campana	04°01'28 S 79°10'40" W	2488	500	Brunschön et al., 2010	3
El Tiro	03°59'23.2" S 79°08'42.7" W	2811	20,000	Niemann and Behling, 2007	4
Laguna Rabadilla de Vaca	04°15'19.7" S 79°06'43.7" W	3312	11,500	Niemann et al., 2009	5
Rabadilla de Vaca bog (*)	04°15'23.7" S 79°07'15.3" W	3200	2100	Rodríguez and Behling, 2010	6
Laguna Cocha Caranga	04°02'37.5" S 79°09'45.2" W	2710	14,000	Niemann and Behling, 2009	7
Cocha Caranga Mire	04°02'37.5" S 79°09'45.2" W	2710	1500	Niemann and Behling, 2009	8
Cocha Caranga Forest	04°02'37.5" S 79°09'45.2" W	2700	150	Niemann and Behling, 2009	9
ECSF-Cerro del Consuelo	04°00'08.8" S 79°03'34.5" W	3155	1350	Niemann and Behling, 2010	10
ECSF-Refugio	03°59'40.1" S 79°03'59.1" W	2520	1050	Niemann and Behling, 2010	11
ECSF-T2/250	03°58'51.3" S 79°04'28.1" W	1990	1250	Niemann and Behling, 2010	12
Laguna Zurita	03°58'28.8" S 79°07'03.4" W	2590	1300	Niemann and Behling, 2010	13
Valle Pequeño Cajanuma (*)	04°06'57.9" S 79°10'19.4" W	3244	1600	Rodríguez and Behling, 2010	14
Laguna Daniel Alvarez	04°01'07.3" S 79°12'42.1" W	2203	1500	Matthias, 2008	15
Lagunas Natasas Bog	04° 43' 56.6" S 79° 25' 41.2" W	3482	15,000	Villota and Behling, in process	16
Lagunas Natasas Forest (*)	04°43'49.5" S 79°25'26.63" W	3495	16,000	Rodríguez and Behling, 2012	17

(\*) Cores presented in this thesis

## 1.2. Research goals and chapter structure

The present investigation is contributing to the scientific goal to gain a better understanding about the environmental conditions since late Quaternary period in the Podocarpus National Park region of the southern Ecuadorian Andes. The reconstruction of past vegetation and climate changes as well as of human impact enhance our knowledge of how past processes have influenced ecosystem dynamics during late Quaternary period.

The main goals are to generate new paleoecological information for areas which have not been studied and to complement previous knowledge generated by the research group so far. The reconstruction of environmental condition for new studied sites presented in this thesis, provide additional and detailed information about the climatic conditions inferred from past vegetation dynamics.

Main question are: 1) What was the nature of vegetation, fire and climate dynamics in the Podocarpus National Park during the late Quaternary? (2) How dynamic or stable were vegetation and upper forest line during the late Quaternary in the southern part of the Andean Depression? (3) Which environmental factors have driven possible changes in vegetation and upper forest line dynamics? (4) Has fire, natural or anthropogenic, played a role in the dynamics of the upper forest line during the late Quaternary? 5) How widespread was *Polylepis* in the southernmost region of Ecuador during late Quaternary?

### Chapter structure

Chapters are presented in sequential order. There are differences in format (e.g. references) in order to follow the journal requirements for publication.

*Chapter I*, presents a general introduction of the area and highlights the most important aspects of this region as a “hotspot” for biodiversity. Also, some background information is given about previous investigation carried out in the Northern Andes region in general, and the Podocarpus National Park region specifically. The general achievements of the present study are explained and describe the

structure of this document. Environmental description (vegetation, geomorphology and climate) provide specific knowledge about the research area.

*Chapter II*, provides general aspects of palynological methods (fieldwork and laboratory techniques) followed for all samples collected at the three sites.

*Chapter III*, an investigation and comparison between two cores (Rabadilla de Vaca mire and Valle Pequeño bog) is presented, which describes the last 2100 cal yr BP. The landscape and vegetation changes produced by climate and human impact, and their relation to the upper forest line dynamics are analyzed.

*Chapter IV*, enhances the understanding of the regional effects of the environmental changes and the ecosystem responses for the last 16,000 cal yr BP, carried out near the Peruvian border at the southernmost part of the Ecuadorian Andes. Special attention is given for *Polylepis* dynamic and human impact on landscape conditions.

*Chapter V*, summarizes the findings based on the three cores analyzed in this research in the context of previous studies.

*Chapter VI*, contains the synthesis of palaeoecological conditions and vegetation history based on fossil pollen and spore analysis for Rabadilla de Vaca mire, Valle Pequeno bog and Lagunas Natasas Forest spanning the Late Quaternary period.

*Appendix A and B*, a list of identified pollen and spores taxa are listed according to the four major vegetation types. Pollen and spores photo plates for the most common taxa identified are presented and a short description is given.

*Appendix C*, complete diagrams of identified pollen grains and spores for the three cores are presented.

### 1.3. Overview of the study region

The Podocarpus National Park (PNP) is located in the Cordillera Real, an eastern range of the South Ecuadorian Andes (Fig. 1.1), which is the weather division between the humid Amazonia and the dry Inter-Andean region. In southern Ecuador the Andes are not as high as in the central and northern part of the country, but the topography of that area, called the Huancabamba depression, is more complicated. Here, a mountain junction culminates in the “Nudo de Loja” at 3800 m a.s.l., from which the Inter-Andean Sierras stretch towards SW, S and SE, interrupted and dissected by valleys and basins. In spite of its dominance of the south Ecuadorian Andes the Cordillera Real only partly forms the watershed between the Pacific and the Atlantic Ocean.

The PNP contributes substantially to the biodiversity hotspot in Ecuador (Barthlott et al. 2005), for which a total of 16 000–20 000 species of vascular plants has been reported (Gentry, 1977; Jørgensen and Ulloa Ulloa, 1994; Jørgensen and Leon-Yanez, 1999). The hotspot character is especially true for the divergence zone of the ranges south of the “Nudo de Loja” with its highly complex structures from xeric to hygric vegetation types within a short distance, where a rapid genetic interchange is guaranteed (Gentry and Dodson, 1987).

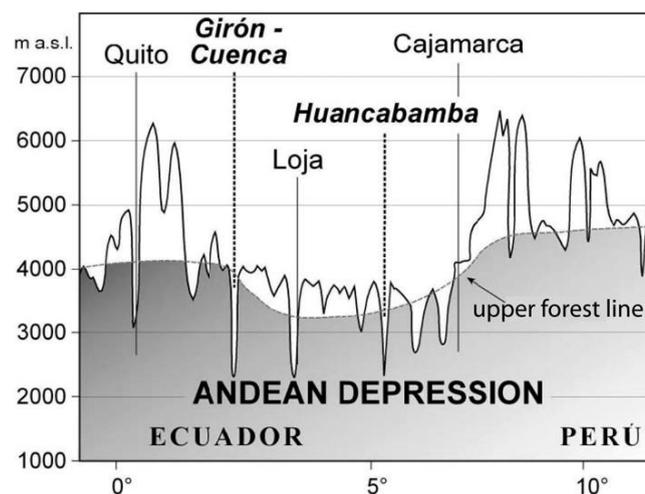
The three study sites are located on the western slope of the Andean Cordillera or Cordillera Real Oriental, southern Ecuador (Fig. 1.2). The first site is Rabadilla de Vaca mire (RVM), a peat bog located on a slope at the transition from the upper montane rainforest (UMF) to subpáramo vegetation, situated at 04° 15' 23,7" S, and 79° 07' 15,3" W at 3,200 m a.s.l. about 10 km east of the small village of Vilcabamba. The second site is Valle Pequeño bog (VP), a small isolated valley filled with organic rich sediment deposits, located 16.5 km north from the RVM site and about 12 km south of the town of Loja, at 04°06' 57,9" S, and 79°10'19,4" W at 3,244 m a.s.l. near the Cajanuma entrance close to the border of the PNP, also located within subpáramo vegetation. The third site is Lagunas Natosas, a small peat bog next to a forest patch, situated at 04°43'49.5" S and 79°25'26.63" W at 3495 m a.s.l., 125 km south of the city of Loja and about 12 km south of the town of Jimbura at the Peruvian border.

### ***Geomorphology and Geology***

The Andes of southern Ecuador and northern Peru include the Andean depression (Depression de Girón-Cuenca in Ecuador and Huancabamba in Peru). The main peaks of the mountains in this region only reach up to about 4000 m. Active volcanoes are absent (Richter and Moreira-Muñoz, 2005). 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).

### ***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 páramo is the humid tropical diurnal type with cold nights and cool days. There is a drier period lasting 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 (e.g., 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)(Fig. 1.3).



**Figure 1.3** Position of the Girón-Cuenca and Huancabamba Andean depression region and the upper forest line depression in this low section of the Andes; source: Richter et al., 2009 (modified).

## **Ecosystems**

Characterized by altitudinal gradient and the varying climatic situations, the Andes comprise alone eight of the total 15 vegetation types recorded for Ecuador (Patzelt, 1996). A general trait of the area is its extraordinary high endemism which is typical for southern Ecuador (Quizhpe et al., 2002). The vegetation above the treeline is called “páramo” (Monasterio, 1980; Balslev and Luteyn, 1992; Hofstede et al., 2003). The most common type of páramo is tussock grass páramo, dominated by large tussock grasses interspersed with various shrubs and herbs (Ramsay and Oxley, 1997; Mena Vásconez and Medina, 2001). Most páramos in Ecuador are burned regularly, especially where they are used for livestock grazing (Laegaard, 1992). These fires may have increased the dominance of tussock grasses at the expense of shrubs loss, especially in the lower parts of the páramo (Van Der Hammen and Cleef, 1986; Ramsay and Oxley, 1997; Suarez and Medina, 2001). Below the treeline we find upper montane forest, comprising several forest types, including dwarf forests (Cleef and Hooghiemstra, 1984). Some synonyms or sub classifications of these forests are sub-alpine rain forest, andean cloud forest, elfin forest, mossy forest, dwarf cloud forest, “bosque alto-andino” or “ceja andina” (see e.g. Webster, 1995; Jørgensen et al., 1999). These forests are characterized by low stature trees with small sclerophyllous leaves, and abundant moss cover on both the trees and the forest floor. They are species-poor compared to tropical rain forests at lower altitudes (Gentry, 1995), but very species-rich compared to upper montane forests in temperate regions. While in the very north and south of that depression the treeline climbs to 4000 m a.s.l. and even higher, the south Ecuadorian treeline is located between 2800 m and 3300 m a.s.l. The upper forest line (around 4000 m) in the north is formed by only two woody genera, namely *Polylepis* and *Gynoxis*. In contrast, the lower tree line in southern Ecuador exhibits extraordinary species diversity, indicating a kind of a timberline ecotone which is affected not by temperature or dryness but by the permanent strong wind and exceptional high moisture causing water-logging of the soils. Common tree genera are *Weinmannia*, *Ilex*, *Ocotea*, *Oreopanax*, *Hedyosmum*, *Clusia*, *Clethra*, *Miconia*, *Podocarpus*, *Myrsine*, *Brunellia*, *Hesperomeles*, *Gaiadendron*, *Polylepis*, *Escallonia*, *Gynoxys*, etc. (Cleef and Hooghiemstra, 1984; Van Der Hammen and Cleef, 1986; Gentry, 1995).

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## Chapter II

### 2. General aspects on palynological methods

#### 2.1. Field excursion

Palynological studies have been carried out on sediments cores taken mainly from peat bogs. Samples taken in previous studies also include lakes, lagoons and other shallow water bodies (Fig. 2.1a). For the three cores analyzed during this study, a Russian corer was used to extract the cores (Fig. 2.1b). This corer helped to take a sediment core in sections of 50 cm length of 5 cm diameter (Fig. 2.1c). Sediment sections were extruded on-site with split PVC tubes and wrapped with plastic film. Cores taken in the field were stored under dark and cool (4°C) conditions to minimize drying, oxidation and light effects.



**Fig. 2.1 a.b.c.** Example of areas where the cores were taken, sediments extraction using Russian corer, sediment stored in 50 cm tube, respectively.

#### 2.2. Laboratory process

All the sediments were treated uniformly during lab procedures, according to analytical methods after Fægri and Iversen (1989). The samples obtained during fieldwork were sub-sampled (0.25 or 0.5 cm<sup>3</sup>) every 2 to 4 cm, which depend for the length of the core and detailed information for special

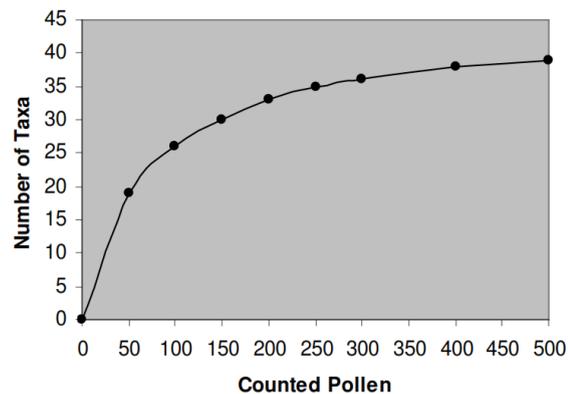
section. One tablet of *Lycopodium clavatum* marker spores was added to each sample for determination of pollen, spores and charcoal concentration (grains or particles/cm<sup>3</sup>) and influx (grains or particles/ cm<sup>2</sup>/year). Then, samples were treated with hydrofluoric acid (HF) to dissolve silicate minerals and hydrochloric acid (HCl) to remove carbonates. A mesh (150 µm) was used to filter the samples and Acetic Acid (CH<sub>3</sub>COOH) for dehydration, and the final step, was the application of acetolysis to stain the grains, remove cellulose and clear the exine. Every sample was mounted onto a plate with glycerine gelatine to be analyzed under a light microscope.

### 2.3. Radiocarbon dating

In order to determine the age of the sediments, material from core samples (organic matter and charcoal fragments) were sent for Accelerator Mass Spectrometer (AMS) radiocarbon dating to the University of Erlangen/Nürnberg. Age-depth model were generated based on radiocarbon dates with specified error ranges, calibrated with CalPal (Cal Curve 50 ka cal BP to modern) (Weninger et al., 2004), or with Calib 5.0.2 (Stuiver and Reimer, 1993) using the southern hemisphere calibration curve (McCormac et al., 2004). There are some commonly used models, which include linear interpolation (used in this research), spline and linear regression models (Bennett, 1994).

### 2.4. Pollen and spores identification

Tropical regions are characterized by a high plant diversity, but the pollen and spore reference collection is still very poor in the case of Ecuador, which makes the grain identification much more difficult. For the analyzed samples a minimum of 300 pollen grains were counted, beyond that, the biodiversity accumulation curve stabilized (Fig. 2.2).



**Figure 2.2** Taxa accumulation curve for plant diversity in the Podocarpus National Park area. Around 300 pollen grains are needed to reach the almost maximum taxa diversity (Niemann 2008).

For pollen identification, the morphology guide of Hooghiemtra (1984) for Colombia, and Behling (1993) for the Neotropics and Ecuador, were used. A contribution of near 400 new pollen records to this reference collection has been accomplished during this project, which amplifies the pollen database for the area. Additionally, *Lycopodium* (marker for pollen and charcoal percentage calculation) and charcoal particles were also taken into account to include them in the data interpretation.

**Table 2.1:** Identified palynomorphs (pollen and spores), subsamples and age for the tree pollen records

<i>Pollen record</i>	<i>Pollen types</i>	<i>Spore types (pteridophyta)</i>	<i>No. of subsamples</i>	<i>Record age (yr BP)</i>
Rabadilla de Vaca	123	35	21	2100
Valle Pequeño	128	29	40	1630
Lagunas Natasas Forest	105	25	48	15930

## 2.5. Data presentation and visualization

Diagrams are the most efficient way to represent pollen and spore data, usually in percentages with respect to the total pollen count. Diagrams also present stratigraphy, age and depth of the core to easily correlate the palynological data. Sums of herbs and woody taxa, as well as of carbonized particles (10-150  $\mu\text{m}$ ), were represented as concentration ( $\text{grains}/\text{cm}^3$ ) and influx ( $\text{grains}/\text{cm}^2/\text{yr}$ ) rates in the pollen diagrams. Due to the complexity/variety of the pollen and spores grains, not all of the identified grains are represented but the most significant and important for the interpretation.

For a better understanding, single pollen taxa were grouped into four general vegetation types or ecosystems: Lower Mountain Forest (LMF), Upper Mountain Forest (UMF), Subpáramo and Páramo. The classification has been adopted and defined according to Hommeier et al. (2008). Taking this vegetation classification into account, the pollen assemblages were easy to understand.

The software TILIA, TILIAGRAPH and CONISS were used to plot pollen and spore data (Grimm 1987). Cluster analysis (CONISS) of terrestrial pollen (and spore) taxa produced dendrograms which helped to identify the pollen zones.

## 2.6. Considerations for palynological data interpretation

Palynological data has been used to reconstruct environmental conditions, past events and human impact, and to determine the factors which caused these landscape modifications. Pollen data based on visual identification using a light microscope limited the possibility to reach species level. The most frequent pollen grains were identified to a family level, genus level was not often reached and only very few grains were identified to a species level. Bio-indicators for some environmental conditions are usually based on species level, and there are some families (e.g., Melastomataceae, Asteraceae, Rubiaceae) which are widely distributed and thus not indicative of an specific ecosystem. The complexity of the biodiversity in the area, the lack of reference material, as well as the absence of local expertise, made this work very hard to achieve. However, a better knowledge and reference collection has been built in order to provide a more detailed databank for the biodiversity of the area.

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## Chapter III

### 3. Late Holocene vegetation, fire, climate and upper forest line dynamics in the Podocarpus National Park, south-eastern Ecuador

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**Abstract:** Late Holocene vegetation, fire, climate and upper forest line dynamics were studied based on detailed pollen and charcoal analyses. Two sediment cores, from the Rabadilla de Vaca mire (RVM) and the Valle Pequeño bog (VP), with an age of about 2100 and 1630 cal yrs B.P., respectively, were taken at the modern upper forest line in the Parque Nacional Podocarpus (Podocarpus National Park) in southeastern Ecuador. The two pollen records reflect relatively stable vegetation with slight changes in floral composition during the recorded period. Changes of the proportion between subpáramo and páramo vegetation are related to lower and higher frequency of fires. The RVM records show that the upper forest line moved to a higher elevation between 1630 and 880 cal yrs B.P., stabilising after 310 cal yrs B.P. Human impact is suggested by a high fire frequency, mainly between 1800–1600 and 880–310 cal yrs B.P. The VP records indicate no marked changes in the upper forest line. The charcoal records suggest an increased human impact from 230 cal yrs B.P. to the present. The results indicate that high fire frequency is an important factor in reducing the expansion of subpáramo vegetation and upper montane rainforest and in favouring the distribution of grass páramo. Since there is a clear correlation between fire and vegetation dynamics, it is difficult to detect how far climate change also played a significant role in upper forest line changes during the late Holocene.

**Keywords:** Ecuador Upper forest line Fire history, Climate change Palynology Late Holocene

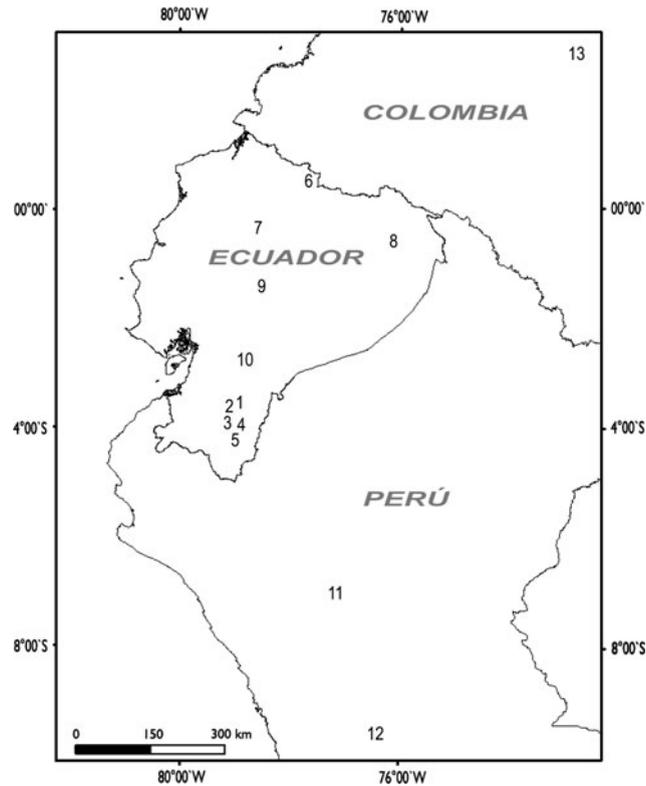
### 3.1. Introduction

The current altitudinal position of the Andean upper forest line (UFL) indicated by the uppermost forest patches is, to a large extent, the result of past ecological processes influenced by environmental changes including climate, fire and land use. These forest patches are interpreted as remnants of high altitude forests now destroyed by anthropogenic fires and forest clearance (Ellenberg 1958; Laegaard 1992; Sarmiento and Frolich 2002). Reconstruction of vegetation history is therefore an essential tool for understanding the dynamics of the UFL positions. The limit between montane rainforest and páramo grassland has important ecological and socioeconomic relevance. Studies on deforestation in Ecuador have estimated that only 4% of the forests on the western Andean slope are left. In the central valley, almost no natural forests are left because of the long occupation history and, in particular, increasing human impact during recent decades (Dodson and Gentry 1991). The potential position of the UFL is still not known due to a lack of both ecological and historical information about tropical ecosystems. According to some authors, the uppermost forest patches found above the actual tree line indicate the potential UFL. However, there is no evidence that these highest forest patches have ever been connected (Islebe and Hooghiemstra 1997; Wille et al. 2002), and present patches are mostly restricted to special micro-sites such as ravines and boulder slopes (Troll 1959; Walter and Medina 1969). The situation of forest patches at lower altitudes, close to the actual UFL, is not well known. These may also rely on unique local conditions or they may be remnants of formerly more extensive forest (Miehe and Miehe 1994; Kessler 2002; Bakker et al. 2008).

A few palaeoenvironmental records are available from southern Ecuador and neighbouring countries (Fig. 3.1). Studies from southwestern Ecuador in the Cajas National Park on the Western Cordillera at 3,700 m indicate that there was a herb páramo there in the Late-glacial period (17000–11000 cal yrs B.P.), reflecting climatic conditions colder and moister than those of today (Hansen et al. 2003). During the Holocene, *Polylepis* became more frequent and reached its maximum during the mid Holocene period. The climate was warmer with a more moderate seasonality during the early Holocene than it is nowadays. Fires were much more frequent during the early and mid Holocene than during the Late-glacial period. However, after 4000 cal yrs B.P., the vegetation changed and the decrease of charcoal particles suggests a change towards moister conditions (Hansen et al. 2003). The results of the 17000 yrs B.P. old record of the Paso El Tiro, which is today covered by subpáramo

vegetation, provide important insights on past vegetation, climate and fire history (Niemann and Behling 2008a).

The Holocene history of UFL dynamics in the northern Andes has been addressed by an increasing number of palynological studies since the 1960s (van der Hammen and González 1960; van Geel and van der Hammen 1973; Hooghiemstra 1984; Colinvaux 1997; Hansen et al. 2003).



**Fig.3.1** Map of South America showing the study sites mentioned in the text. 1, Laguna Zurita; 2, Paso El Tiro; 3, Cocha Caranga; 4, Laguna Rabadilla de Vaca; 5, Cerro Toledo; 6, Guandera; 7, Pantano de Pecho; 8, Río Napo; 9, Laguna Yambo; 10, Lago Surucucho; 11, Laguna Chochos; 12, Huascarán; 13, Laguna Loma Linda

However, there is no consensus about what happened there during the Holocene, as different pollen studies and their interpretations are often contradictory, and the timing of events is somewhat uncertain (Markgraf 1989; van 't Veer et al. 2000; Marchant et al. 2001).

Vélez et al. (2003) studied areas situated between the western and central Andean Cordilleras in

Colombia, showing the dynamics of forest expansion/reduction with a clear increase in wetness during the mid Holocene. On the eastern Andean Cordillera, pollen records also show dry and cold conditions during the Late Pleistocene, very wet conditions for the early to mid Holocene, and dry conditions during the mid to late Holocene, while on the eastern savannas, records suggest dry conditions during the early Holocene and generally wet conditions for the mid and late Holocene (Behling and Hooghiemstra 1998, 2000).

Predictions of future global change suggest that changes in biodiversity composition and distribution are likely to occur in these ecosystems (IPCC 2007). Higher temperatures together with human influence will allow fires to occur more frequently and will increasingly transform the landscape.

Two sediment cores were collected at the modern upper forest limit (UFL) and studied by pollen and charcoal analysis, in order to obtain long-term records of vegetation dynamics in the study area. Four main questions will be addressed: (1) What was the nature of vegetation, fire and climate dynamics in the Parque Nacional Podocarpus (Podocarpus National Park, PNP) during the late Holocene? (2) How dynamic or stable were the vegetation and UFL during the late Holocene in the upper region of the PNP? (3) Which environmental factors have driven possible changes in vegetation and UFL dynamics? (4) Has fire, natural or anthropogenic, played a role in the dynamics of the UFL during the late Holocene? See also Brunschön et al. (2010) who studied a reconstruction of local environmental conditions over the past 500 years with a high-resolution multiproxy approach using pollen, spore, charcoal and XRF analyses at Laguna Campana in the PNP.

## **3.2. Study area**

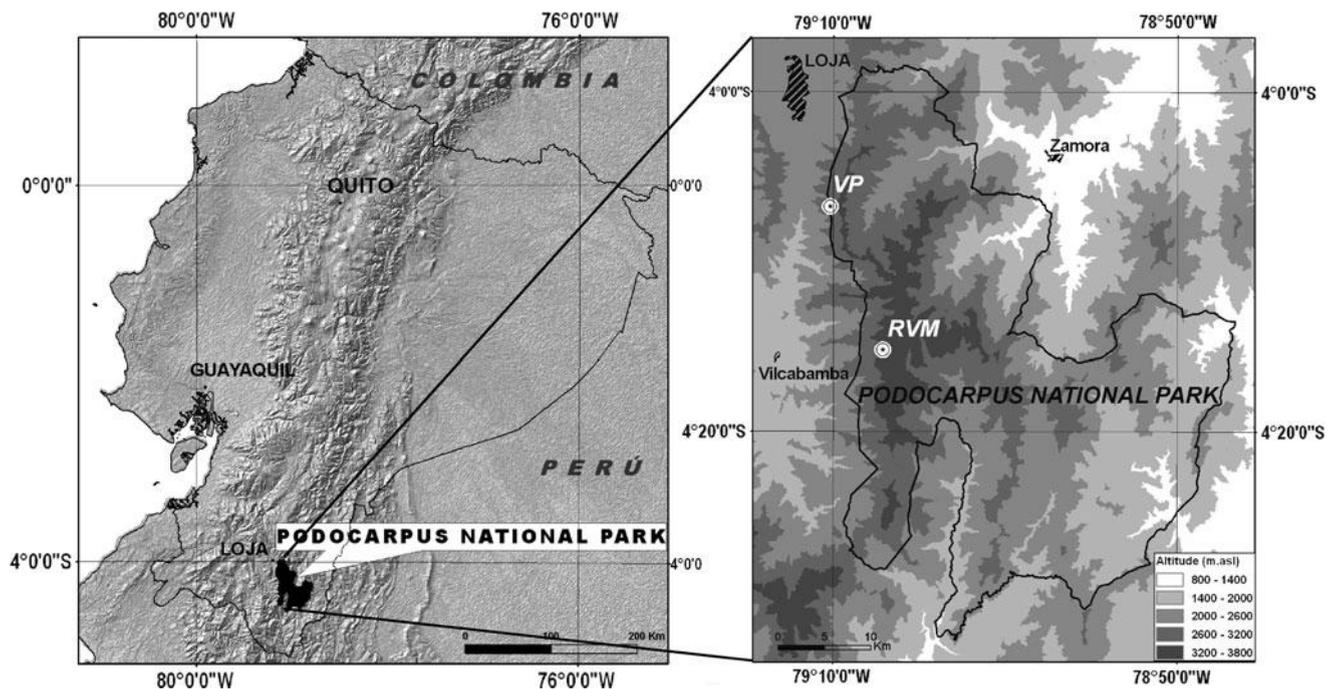
### ***Location***

The Parque Nacional Podocarpus (PNP) region is located in the southeastern Ecuadorian Andes, and occupies 1,460 km<sup>2</sup> between ca. 04° 00' to 04° 30'S and 79° 10' to 78° 34' W (Fig.3.2). Two study sites were selected on the western slope of the eastern Cordillera (Cordillera Real) at the modern upper forest limit. The first, Rabadilla de Vaca mire (RVM), is a 30 x 20 m<sup>2</sup> peat bog located on a slope at the transition from upper montane rainforest (UMF) to subpáramo vegetation, situated at 04 15' 23,7"S, and 79° 07' 15,3"W at 3,200 m a.s.l. about 10 km east of the small village of Vilcabamba at 1,700 m. The second site is Valle Pequeño bog (VP), a small isolated valley 4 x 20 m<sup>2</sup>

filled with organic-rich sediment deposits. The site is located 16.5 km north from the RVM site and about 12 km south of the town of Loja, at  $04^{\circ}06' 57,9''$  S, and  $79^{\circ}10'19,4''$  W at 3,244 m a.s.l. near the Cajanuma entrance close to the border of the PNP, also located within subpáramo vegetation.

### ***Geomorphology and geology***

The Andes of southern Ecuador and northern Peru encompass the so-called Andean depression (Depression de Girón-Cuenca in Ecuador and Huancabamba in Peru). The main peaks of the mountains in this depression reach about 4,000 m in the Nudo de Loja, from which the inter-Andean Sierras stretch towards the southwest, south and southeast, all interrupted and dissected by valleys and basins. Active volcanoes are absent (Richter and Moreira-Muñoz 2005). The southern Cordillera Real is mainly part of the Zamora series, consisting of Palaeozoic metamorphic rocks of widely varying metamorphic grades. Local bedrock is dominated by semipelites, quartzites and black phylites with some granitic intrusions (Litherland et al. 1994).



**Fig. 3.2** Map of Ecuador showing the location of Parque Nacional Podocarpus (Podocarpus National Park) and detailed site location of the cores Rabadilla de Vaca mire (RVM) and Valle Pequeño bog (VP) in the southern Andes of Ecuador

***Climate***

The climate in the southeastern Ecuadorian Andes Cordillera is influenced by warm moisture-laden air from the Amazon lowland, which collides with cold mountain air masses (Emck 2007). The study area is located between the humid Amazon basin and the dry inter-Andean valley. East of the Cordillera, precipitation and humidity rise continuously to the mountain crests accompanied by increasing wind speed. Inside the PNP, at 3,100 m, rainfall up to 6,000 mm a<sup>-1</sup> has been measured. In contrast, the inter-Andean basin receives generally less than 1,000 mm a<sup>-1</sup> (Emck 2007; Bendix et al. 2008). The main rainy season lasts from April to August, but rainfall is high throughout the year. As part of the so-called Andean depression, all summits in the southern Ecuadorian Andes are below the present-day snowline. The eastern Andean mountains form a division that separates the moist eastern slopes of the Andes from the dry inner Andean basins such as 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, the annual rainfall drops from over 4,000 to 300 mm (Bendix and Rollenbeck 2004).

The windward area around Lagunas del Compadre (Cajanuma), eastwards of the main crest, receives an annual precipitation of about 5,700 mm and the average annual temperature is about 6.9 °C (Emck 2007). Furthermore, the long dry period of the inter-Andean section is very pronounced in the west, while the eastern escarpment experiences only a slight dry peak restricted to November. Relative humidity is permanently high with mean values over 90%, except for a short period in November (Bendix and Lauer 1992). The annual precipitation rate on the western slope ridge at 3,400 m is about 5,700 mm and the average annual temperature is about 6.9 °C (Emck 2007). There are two weather stations located at 3,240 m within the UFL ecotone, one in a mixed elfin forest, the other 120 m away in a nearby dwarf bamboo páramo (Richter 2003).

***Modern vegetation***

The modern upper forest limit (UFL) in northern and central Ecuador is at ca. 3,400 m at La Libertad, at ca. 3,500 m at Atillo and at ca. 3,600 m at Guandera (Di Pasquale et al. 2008). Like most parts of the Cordillera Real, the lower parts of the deeply incised valley of the Río San Francisco below 2,150 m are covered by an evergreen rainforest, and the upper parts by a broad-leaved montane rain forest that extends up to the UFL between 2,700 and 3,000 m (Beck et al. 2008). In the Loja region, the modern UFL is at about 3,200 m (Richter and Moreira-Muñoz 2005). At the Paso

El Tiro, 30 km north of the core site, the modern UFL is at ca. 2,800 m. The movement of vegetation zones to lower elevations is probably a result of the so called Andean depression (Bader 2007). Cores RVM and VP are located in the lower subpáramo close to the UFL. In the montane rainforest, we recognise two kinds, the lower and upper mountain rainforest. The lower montane rainforest (LMF) is present between ca. 1,800–2,150 m with an extremely diverse, two-storied tree stratum composed of trees up to 20–35 m height. Characteristic taxa are *Alzatea verticillata* (Alzataceae), *Graffenrieda miconioides* (Melastomataceae) and *Myrcianthes sp.* (Myrtaceae) (Bussmann 2001, 2005; Lozano et al. 2003).

The upper montane rainforest (UMF) is present between ca. 2,100–2,750 m and is represented by a low, monotypic formation with only one tree stratum between 5–10 m, rarely up to 15 m. Characteristic trees are *Morella pubescens* (Myricaceae) and *Myrsine andina* (Myrsinaceae). Two different types of modern páramo ecosystems are found within the Parque Nacional Podocarpus (PNP) region. The herbaceous páramo (páramo herbáceo) located at ca. 3,100–3,400 m is rich in *Neurolepis nana*, *Calamagrostis macrophylla* (Poaceae) and *Niphogeton dissecta* (Apiaceae). These herbs and shrubs are 0.2–1 m in height.

This páramo type is found on flat slopes and concave sections, as well as in ridge areas, and occurs around RVM. The shrub páramo (páramo arbustivo bajo), located at ca. 2,900–3,400 m, is rich in *Weinmannia rollottii* (Cunoniaceae), *Oxalis spiralis* (Oxalidaceae) and *Ilex andicola* (Aquifoliaceae). The shrubs and herbs grow from 0.5 to 1.2 m height, and this páramo type is found mainly on steep slopes (Lozano et al. 2003).

The subpáramo is present between ca. 2,800–3,100 m, characterised by *Puya nitida* (Bromeliaceae), *Brachyotum rotundifolium* (Melastomataceae) and *Oritrophium peruvianum* (Asteraceae). Shrubs and herbs grow up to 1 m height, while individual shrubs can be 2–3 m tall (Bussmann 2001, 2005; Lozano et al. 2003).

The area is characterised by a mixture of dense elfin forest and uniform *Chusquea* bamboo stands, *Neurolepis* dwarf bamboo patches and mixed shrub páramo interspersed with tree stands, forming a complicated ecotone complex (Richter et al. 2008).

### ***Human occupation***

The first human activity in the region of Loja began around 4500 cal yr B.P. (Guffroy 2004), but human activities may have occurred in the dry inter-Andean valley much earlier. For example, in the Sabana de Bogotá in Colombia, the presence of Amerindians could be established from 12500 yrs B.P. (14800 cal yrs B.P.) onward and possibly even before that time (Van der Hammen and Urrego 1978). Niemann and Behling (2008a) found at Paso El Tiro, located 10 km east of Loja, an increased fire intensity during the wetter late Holocene that suggests frequent fires of anthropogenic origin through an increased use of fire for hunting purposes and for slash and burning activities in the drier lower valleys, for example in the Loja area; fires spread into the mountains during drier phases of the year. Fire frequency decreased during the last ca. 600 years. The reduction or the absence of human activities in this region during recent centuries might be related to the dramatic decrease in human population between the 14th and 17th century. The decrease probably reflects the invasion northwards by the Inca and their occupation of the Loja region. Another probable reason for the decreased population is the arrival of Old World diseases brought by the Spaniards (Alchon 1991).

## **3.3. Materials and methods**

### ***Coring***

Cores were taken from the central part of the two study sites, RVM and VP, using a Russian type corer. At both sites, 80 cm of core were collected. For further transport, sections of 50 cm length were extruded on site, covered with plastic film and placed in split PVC tubes. In the laboratory, cores were stored under cold (+4° C) and dark conditions.

### ***Sample processing and analysis***

For accelerator mass spectrometer (AMS) radiocarbon dating, three (1 cm thick) samples were taken from the RVM core, and two from the VP sediment core.

Forty subsamples were taken from the RVM core and 21 from VP (0.25 cm<sup>3</sup>) for pollen and charcoal analyses at 2 and 4 cm intervals, respectively. Standard pollen analytical methods were used to process the samples (Fægri and Iversen 1989). Lycopodium spores were added to each sample before treatment for calculation of pollen and charcoal concentration in grains or particles/cm<sup>3</sup> and

influx in grains or particles/cm<sup>3</sup> yr. A minimum of 300 pollen grains was counted for each sample. Tree, shrub and herb pollen were included in the pollen sum, but spores and aquatic taxa were excluded. For pollen identification, we used the reference collection of the Department of Palynology and Climate Dynamics in Göttingen for neotropical taxa, and related literature (Hooghiemstra 1984; Behling 1993). The amount of charcoal particles in sediment deposits reflects the frequency of past fires. Charcoal particles (5–150 µm) were counted in each sample on the pollen slides and analysed as described in the literature (Clark 1988; Clark et al. 1997, 1998).

Pollen types were grouped according to the ecosystem or habitat type for which they are most characteristic. Four main vegetation types were defined: lower montane forest, upper montane forest, subpáramo and páramo. Pollen and spore data were converted to percentages based on the pollen sums using the programs TILIA and TILIAGRAPH for calculation, drawing the diagrams and zonation (Grimm 1987). Two different pollen diagrams were generated for each core. First, a percentage diagram with the most important or representative taxa for each ecosystem, and second, a summary diagram of the pollen taxa expressed in percentages for each vegetation type (Figs. 3.3, 3.4, 3.5, 3.6). The zonation of the pollen record is based on cluster analysis by CONISS (Grimm 1987) and important changes in the pollen assemblages.

## 3.4. Results

### 3.1.1 Stratigraphy

The 80 cm long sediment for RVM core consisted mainly of dark brown peaty material. In the 80

<i>Site</i>	<i>Depth (cm) and description</i>
RVM	0 – 20 Fine dark brown peat with many plant remains
	20 – 37 Dark black peat with few plant remains
	37 – 46 Sandy grey clay with little organic material
	46 – 71 Black material, decomposed organic matter
	71 – 80 Light-brown clay sediment
VP	0 – 30 Dark brown peat with plant remains
	30 – 44 Light grey sediment with little decomposed organic matter and fine sand
	44 – 60 Dark brown clayey sediments with organic material
	60 – 80 Grey clay with little organic matter

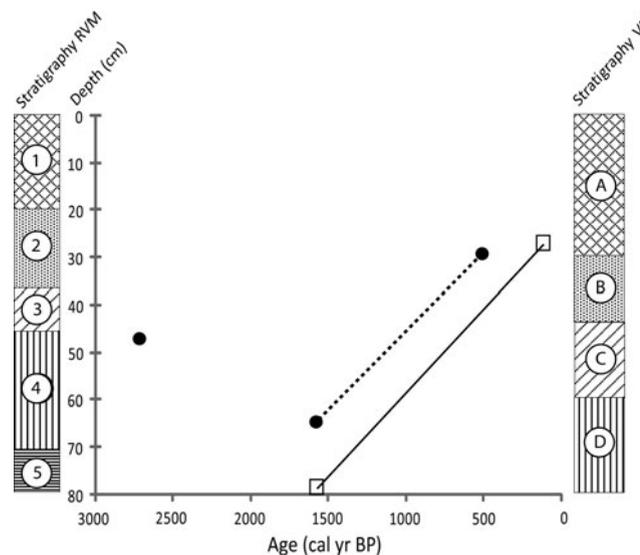
**Table 3.1** Stratigraphic description of the core Rabadilla de Vaca mire (RVM) and the core Valle Pequeño bog (VP).

cm long VP core, the sediment consisted mostly of clay. A detailed stratigraphic description of both cores is given in Table 3.1.

### 3.1.2 Chronology and pollen zonation

Five AMS radiocarbon dates provide the chronology of the two sediment cores. The ages indicate that both cores cover the late Holocene period (Table 3.2). The dates have been calibrated using CalPal Online (Weninger et al. 2004). All dates are given as cal yrs B.P.

For RVM, three AMS radiocarbon dates show that the mire contains deposits that cover the last 2100 cal yrs B.P. The age at 47 cm core depth,  $2796 \pm 63$  cal yr B.P. ( $2665 \pm 77$  uncal yr B.P.), is too old and has been excluded. According to the vegetation development (see below), a disturbance of the sediments seems to be unlikely. The very low sedimentation rate of 0.075 mm/yr, calculated using the age of  $2796 \pm 63$  cal yr B.P. at 47 cm depth seems to be unlikely. The date must be too old as is also indicated in the age-depth graph (Fig. 3.7). Disturbance of the deposits cannot be completely excluded, but it is not suggested by the pollen record. Additional dating would be



**Fig. 3.7** Age–depth model and stratigraphy of the core of Rabadilla de Vaca mire (black circles) and Valle Pequeño bog (white squares) based on three and two calibrated radiocarbon dates, respectively. Stratigraphic description: 1, fine dark brown peat, many plant remains; 2, dark black peat, few plant remains; 3, sandy grey clay with little organic material; 4, black material, decomposed organic matter; 5, light-brown clay sediment; A, dark brown peat with plant remains; B, light grey sediment with little decomposed organic matter and fine sand; C, dark brown clayey sediments with organic material; D, grey clay with little organic matter

appropriate in order to solve these uncertainties. Based on the two calibrated radiocarbon dates used, the sedimentation rate is 0.36 mm/yr for the lower part of the core and for the upper part 1.34 mm/yr. The rate of deposition in the lower part of the core is 31.8 yr/cm and in the upper part 19.4 yr/cm (Fig. 3.4).

**Table 3. 2** List of AMS radiocarbon dates from Rabadilla de Vaca mire (RVM) and Valle Pequeño bog (VP)

Core	Lab. number	Depth (cm)	<sup>14</sup> C-age (yrs B.P.)	Calendar age <sup>a</sup> (cal yrs B.P.)	1- $\sigma$ range (cal yrs B.P.)
RVM	Erl-11391	30	486 $\pm$ 42	530	512–544
	Erl-11033	47	2665 $\pm$ 77	2800	2733–2859
	Erl-11034	65	1727 $\pm$ 45	1640	1596–1684
VP	Erl-11027	27	156 $\pm$ 44	150	37–253
	Erl-11028	80	1717 $\pm$ 47	1640	1576–1690

<sup>a</sup> Calibration of <sup>14</sup>C ages is based on CalPal Online (CalPal 2007 HULU curve). The calibrated ages stand for the mean probability of the 1- $\sigma$  upper and lower age ranges.

For the VP core, two AMS radiocarbon dates (Fig. 3.7) show that its base has an age of 1633  $\pm$  57 cal yrs B.P. (1717  $\pm$  47 uncal yrs B.P.). Based on the two calibrated radiocarbon dates, the sedimentation rate for the lower part of the core is 0.36 mm/yr and for the upper part 1.34 mm/yr. (Fig. 3.7). The rate of deposition in the lower part of the core is 28.1 yr/cm and in the upper part 7.5 yr/cm (Fig. 3.6).

The CONISS cluster analyses and important changes in the pollen assemblages suggest four different pollen zones for RVM (RVM-I to IV) and three zones for VP (VP-I to III). The ages of each zone have been calculated by linear inter and extrapolation.

### 3.1.3 Description of the Rabadilla de Vaca mire (RVM) pollen diagram

The percentage pollen diagram displays 27 of the most frequent and important taxa out of 123 pollen and 35 spore types recognised (Fig. 3.3). The identified pollen taxa are grouped into four different vegetation types and are illustrated as summary pollen diagrams (Fig. 3.4).

Pollen concentration of 18,300–946,000 grains/cm<sup>3</sup> as well as pollen influx of 1,000–30,000 rains/cm<sup>2</sup> yr reach the highest values in Zone RVM-I and decrease upwards along the subsequent zones.

Charcoal concentrations of 140,500–4,155,000 grains/cm<sup>3</sup> and charcoal influx of 5,000– 1,300,000 particles/cm<sup>2</sup> yr vary markedly throughout the core, with significantly higher values at the end of Zone RVM-I and the beginning of Zone RVM-II and in RVM-III (Fig. 3.4).

**Zone RVM-I (80–67 cm, ca. 2100–1720 B.P., six samples)**

This zone is represented by low percentages of lower montane forest (LMF) taxa (6–8%), mostly Moraceae/Urticaceae (2–4%) and *Alchornea* (1–4%). The percentages of upper montane forest taxa (UMF) are markedly higher (9–19%), mainly *Hedyosmum* (6–12%) and low values of *Myrsine* (0–4%), *Weinmannia* and Podocarpaceae (0–2%). Pollen of subpáramo vegetation ranges between 23 and 34%, and is dominated by pollen of Melastomataceae (13–20%) and Asteraceae subfamily Asteroideae (6–9%). Páramo vegetation is represented by a large proportion of pollen (33–46%), of which Poaceae is the most frequent (32–42%). Cyperaceae and *Valeriana* (1–2%) occur in very low values. Spores of Pteridophyta are present in proportions between 8–15%. At the end of this zone, *Sphagnum* is represented with a value of 4%.

**Zone RVM-II (67–41 cm, ca. 1720–880 B.P., 13 samples)**

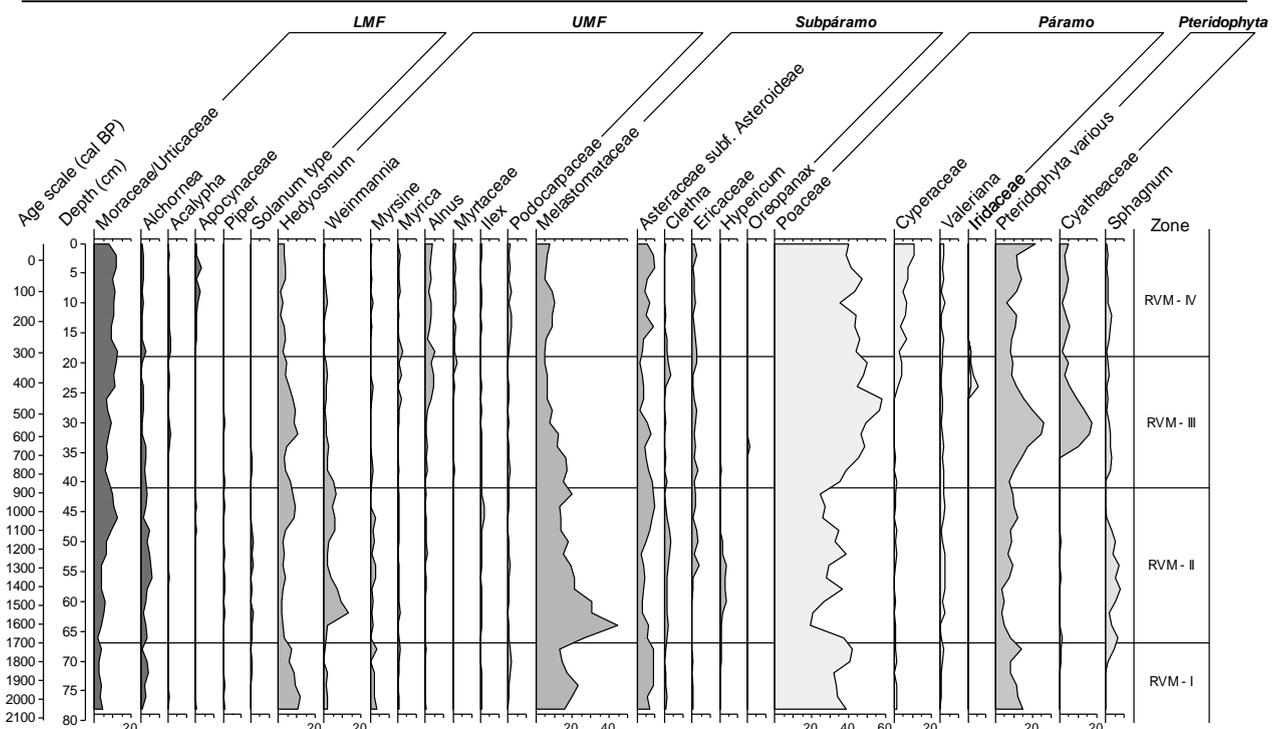
Compared with RVM-I, LMF pollen is still represented in low percentages, but increases markedly at the middle of the zone (6–15%) due to the increase of Moraceae/Urticaceae (2–12%) and *Alchornea* (1–7%). Pollen from UMF continues to be frequent (6–22%). Pollen of *Hedyosmum* decreases compared with the previous zone, but increases at the end of the zone from 1 to 9%. *Weinmannia* pollen (1–13%) increases significantly at the beginning and increases at the end of this zone. *Myrsine* pollen (0–3%) remains continuously low. The subpáramo vegetation group is represented by the highest values (23–55%), especially at the beginning of the zone, mostly by the marked increase of Melastomataceae (13–44%). Asteraceae subf. Asteroideae decreases slightly and increases again at the end of the zone (2–10%). Pollen of *Clethra* (0–3%), and later Ericaceae and *Hypericum* (both between 0 and 4%), are more frequent in this zone than in Zone RVM-I. The proportion of páramo taxa (21–43%) is lower, due to the decrease of Poaceae pollen (38–19%). Spores of Pteridophyta remain with no significant changes (3–12%). *Sphagnum* spores increase and are well represented (0–8%) in this zone.

**Zone RVM-III (41–19 cm, ca. 880–310 B.P., 11 samples)**

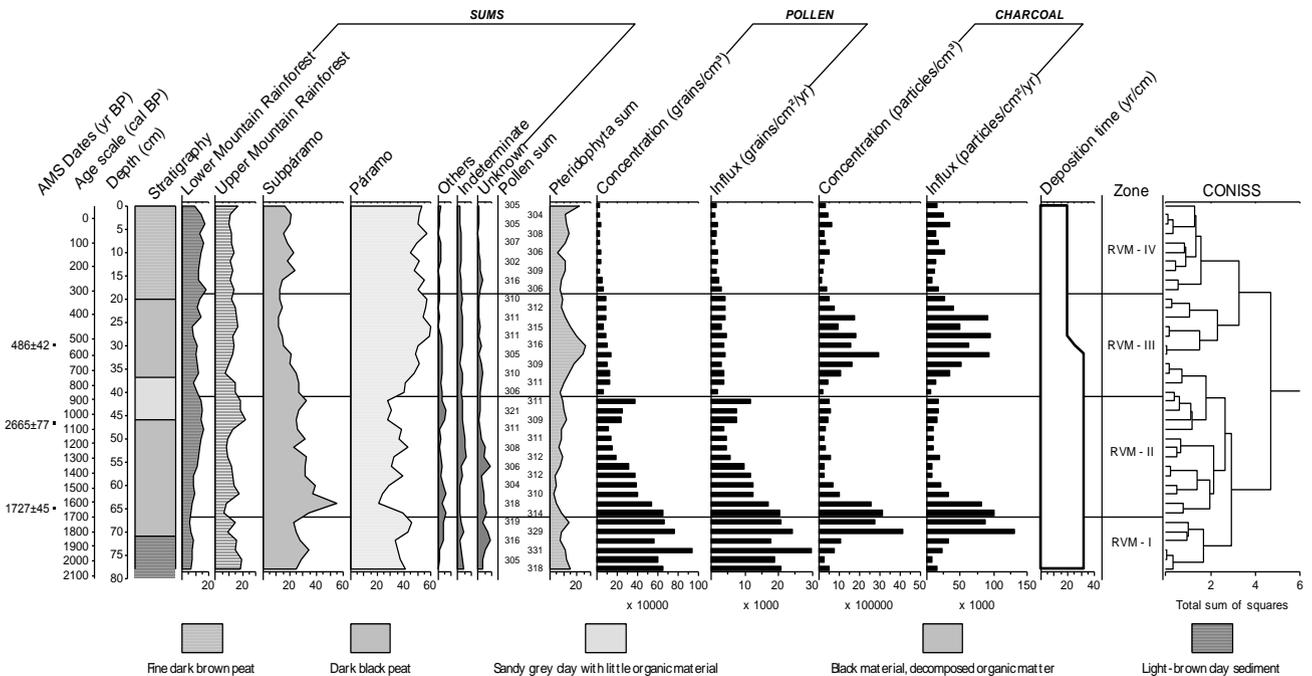
The LMF pollen representation is similar to that in the previous zone (8–14%). Moraceae/Urticaceae pollen remains relatively stable during this period (5–12%), while *Alchornea* pollen decreases slightly (0–3%). The UMF group decreases from 7 to 16%, *Hedyosmum* pollen increases (3–10%). *Weinmannia* pollen decreases at the beginning and *Myrica* (0–2%) as well as *Alnus* (0–5%) increase at the end of the zone. Pollen of subpáramo vegetation decreases markedly from 27 to 12% at the end of this zone, mainly in Melastomataceae (17–5%) and Asteraceae subf. Asteroideae (8–2%), while *Clethra* pollen (0–5%) is now rare, but increases at the end of the zone. Ericaceae pollen continues to be relatively stable with low values (1–3%). Páramo taxa increase markedly at the beginning of the zone (40–59%), dominated by Poaceae pollen (36–58%), which has the highest values in this period. Cyperaceae (0–4%) and Iridaceae pollen (0–2%) increase at the end of the zone. Pteridophyta spores reach the highest proportion (7–27%) in the middle of this zone. *Sphagnum* spores (0–3%) are less frequent.

**Zone RVM-IV (19–0 cm, ca. 310 B.P.—present-day, 10 samples)**

The representation of LMF pollen (10–18%) increases slightly with higher values of Moraceae/Urticaceae (9–13%) and Apocynaceae (0–3%). The proportion of UMF taxa (10–16%) remains stable. However, pollen of *Hedyosmum* decreases (4–1%). Myrtaceae and Podocarpaceae remain low (0–2%), *Alnus* decreases slightly compared to the upper part of the previous zone from 5 to 2%, but is still high compared to other zones in the record. Pollen of subpáramo vegetation (13–24%) increases slightly through the higher representation of Melastomataceae (5–10%) and Asteraceae subf. Asteroideae pollen (3–10%). Páramo taxa are well represented, but decrease slightly in this zone (55–45%) by the slight decrease of Poaceae (47–40%), while Cyperaceae pollen increases from 3 to 11%. *Valeriana* pollen shows values between 1 and 3%. Representation of Pteridophyta spores remains stable (6–27%). *Sphagnum* spores still occur in low frequencies (1–3%).



**Fig. 3.3** Pollen percentage diagram of Rabadilla de Vaca mire (3,200 m a.s.l.) showing selected pollen and spore taxa grouped into vegetation of lower mountain forest (LMF), upper mountain forest (UMF), subpáramo, páramo and Pteridophyta



**Fig. 3.4** Summary pollen diagram of Rabadilla de Vaca mire (3,200 m a.s.l.) showing radiocarbon dates, age scale, stratigraphy, ecological groups, pollen sum, values of pollen and charcoal concentration, pollen and charcoal influx values, deposition time, zones and the CONISS dendrogram.

### 3.1.4 Description of the Valle Pequeño (VP) pollen diagram

The percentage pollen diagram displays 25 of the most frequent and important taxa out of 128 pollen and 29 spore types recognised (Fig. 3.5). The identified pollen taxa are grouped into four different vegetation types as illustrated in the summary pollen diagram (Fig. 3.6).

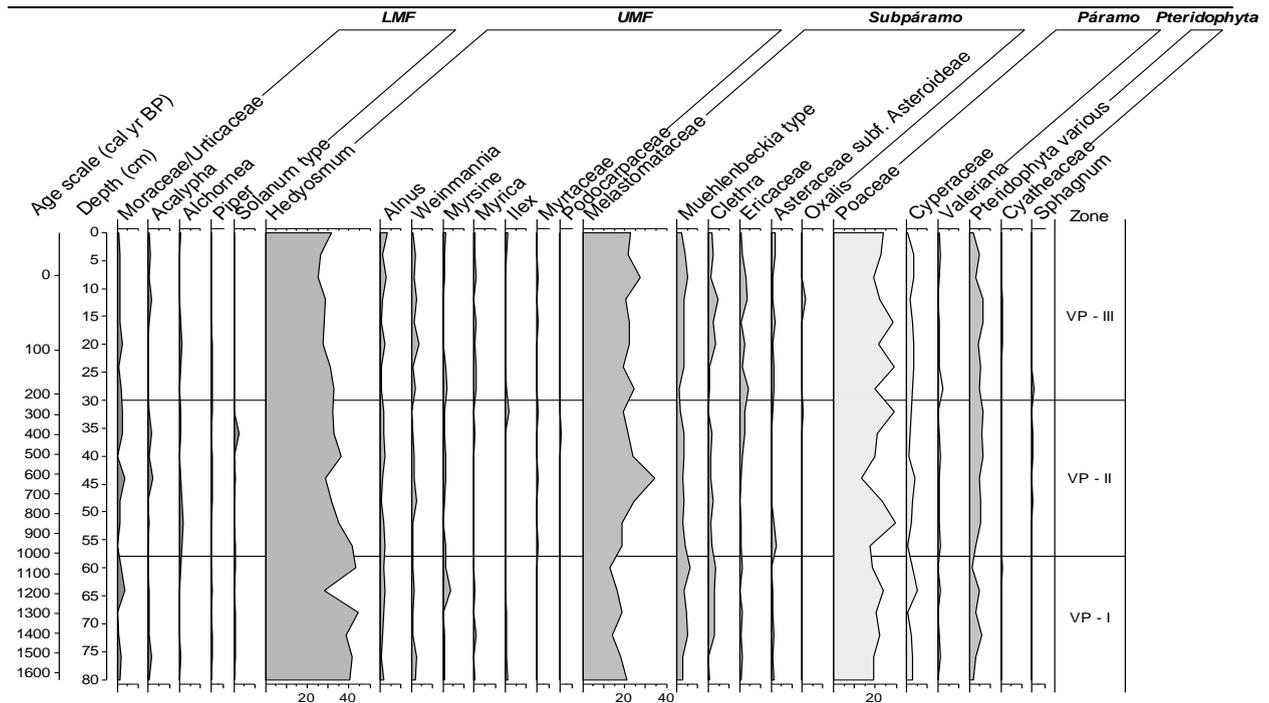
Pollen concentrations of 280,000–4,850,000 grains/cm<sup>3</sup> reach the highest values in Zone VP-I and pollen influx of 10,000–1,720,000 grains/cm<sup>2</sup> yr has high values in VP-I and VP-III. Charcoal concentration of 208,000–1,490,000 particles/cm<sup>3</sup> show the highest values in VP-I and VP-III, and charcoal influx of 7,400–181,700 particles/cm<sup>2</sup> yr with markedly higher values in Zone VP-III (Fig. 3.6).

#### **Zone VP-I (80–58 cm, ca. 1630–1020 B.P., six samples)**

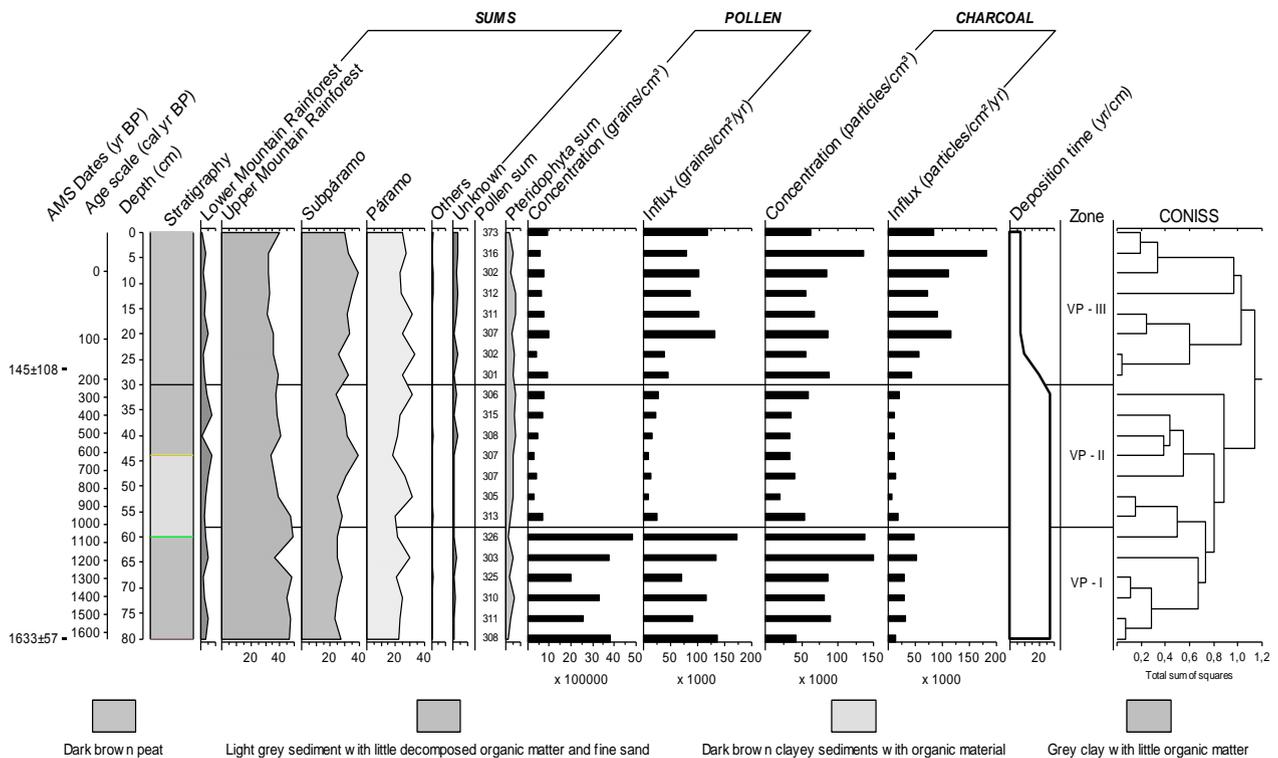
Pollen from lower montane forest (LMF) taxa is poorly represented (2–5%). The most frequent pollen is from Moraceae/Urticaceae (0–4%). Proportions of upper montane forest (UMF) taxa are notably higher (36–49%) with pollen of *Hedyosmum* (28–44%) and low values of *Myrsine* (1–4%), *Alnus* and *Weinmannia* (1–2%). Pollen of subpáramo vegetation ranges between 23 and 28%, dominated by Melastomataceae (13–21%). Much less frequent is pollen of the *Muehlenbeckia* type (3–6%), *Clethra* (0–4%), Ericaceae and Asteraceae subf. Asteroideae (both between 0 and 2%). Páramo vegetation is represented in markedly higher proportion (21–30%), dominated by Poaceae (19–24%) and Cyperaceae (0–5%). Spores of Pteridophyta are represented in low proportions (1–6%).

#### **Zone VP-II (58–30 cm, ca. 1020–230 B.P., seven samples)**

LMF pollen increases from 1 to 8%, due to the increase of Moraceae/Urticaceae (0–4%) and pollen of *Acalypha*, *Alchornea* and *Solanum* type (0–2%). UMF pollen (34–48%) continues to be dominant, but decreases at the end of this zone, primarily due to changes in *Hedyosmum* pollen (42–29%). Values of *Weinmannia* (0–3%), *Alnus*, *Myrsine* and *Ilex* pollen (0–2%) remain low. The subpáramo group is well represented (24–39%) compared to the previous zone, mainly through the increase of Melastomataceae pollen (19–34%). The values of the páramo group remain relatively stable (19–32%), but the variation of Poaceae pollen is stronger (13–30%). Representation of Pteridophyta spores remains stable (3–7%).



**Fig. 3.5** Pollen percentage diagram of Valle Pequeño bog (3,244 m a.s.l.) showing selected pollen and spore taxa grouped into vegetation of lower mountain forest (LMF), upper mountain forest (UMF), subpáramo, páramo and Pteridophyta



**Fig. 3.6** Summary pollen diagram of Valle Pequeño bog (3,244 m a.s.l.) showing radiocarbon dates, age scale, stratigraphy, ecological groups, pollen sum, pollen values and charcoal concentrations, pollen and charcoal influx values, deposition time, zones and the CONISS dendrogram

**Zone VP-III (30–0 cm, ca. 230–60 B.P., eight samples)**

Representation of LMF pollen decreases slightly (1–5%) compared to VP-II from the slightly lower frequency of Moraceae/Urticaceae pollen (1–3%) and other taxa. The sum of UMF pollen decreases (39–32%), due to a lower representation of *Hedyosmum* (33–25%). Subpáramo taxa are well represented (26–39%) and increase slightly compared to Zone VP-II. Pollen of páramo taxa increases slightly (23–34%) primarily from Poaceae (19–29%). Spores of Pteridophyta do not show marked changes compared to Zone VP-II (3–7%).

**3.5. Interpretation and discussion****3.1.5 Vegetation changes during the late Holocene**

The records from the Rabadilla de Vaca mire (RVM) and Valle Pequeño (VP) cores reflect the vegetation changes on the drier western slopes of the Podocarpus National Park from 2100 B.P. and 1630 B.P., respectively. The composition of the pollen assemblages on both sites was similar, but representation of the taxa differed due to different local topographic conditions, since the RVM site lies on a slope and VP is in a small valley. In spite of the slightly higher elevation of the VP site (44 m), upper montane forest (UMF) was strongly represented, in particular by *Hedyosmum*, compared to the RVM site. This was probably due to the valley conditions around VP, which might be locally favourable for *Hedyosmum*.

The results of the RVM record show that from ca. 2100 to 1720 B.P. (Zone RVM-I), lower montane forest (LMF) was less represented due to the lower frequency of Moraceae/Urticaceae, and UMF was most abundant due to the higher occurrence of *Hedyosmum*. Lower values of Poaceae and Cyperaceae than at present show that there was less páramo vegetation in the area, while subpáramo was more strongly represented, as indicated by increased Melastomataceae.

The period from ca. 1720 to 880 B.P. is included in both records, Zone RVM-II and Zone VP-I and the lower part of Zone VP-II. The RVM record shows no marked changes in the proportion of the LMF; however, in the second part of this period, from 1200 B.P. to the present day, Moraceae/ Urticaceae became more abundant. This period also shows a stronger occurrence of *Weinmannia* in the UMF compared to the previous and subsequent periods.

At the beginning of this period, a marked increase of subpáramo taxa in the RVM area is indicated by increased Melastomataceae. Páramo was partly replaced by subpáramo and UMF taxa, and as a consequence, there were fewer Poaceae in the study area. In the VP record, no marked vegetational changes can be detected during this period.

From ca. 880 to 310 B.P., in Zone RVM-III the proportion of the LMF and UMF remained relatively stable as in VP. Páramo vegetation expanded continuously due to the spread of Poaceae, while subpáramo vegetation decreased, as indicated by the continuously lower occurrence of Melastomataceae in this area. In Zone VP-II upper part, first a slight increase and then a slight decrease of subpáramo, is indicated especially by the increasing and decreasing representation of Melastomataceae.

From ca. 310 B.P. until present, in the RVM and VP areas the proportion of the LMF and UMF still remained relatively stable. One important difference between the two pollen records is that *Alnus*, which was so far rare, became quite frequent in the UMF of the RVM area. The páramo ecosystem was dominant in the RVM area, reflected by the still frequent occurrence of Poaceae and a stronger distribution of Cyperaceae. The area of subpáramo was relatively small. In the Valle Pequeño, the different vegetation types remained relatively stable during this period (Zone VP-III).

Summarising, both records reflect relatively stable vegetation over the past 2100 and 1660 years, respectively, compared to the modern vegetational conditions as indicated by the pollen assemblages of the top samples of the sediment cores. With the exception of some minor fluctuations, the composition and the proportion of the LMF and the UMF remained stable. However, some noticeable vegetational changes occurred in the extent of subpáramo and páramo vegetation, in particular in the RVM record, where subpáramo had a stronger representation between 2100 and 880 B.P., followed by a period of marked páramo vegetation expansion between 880 and 310 B.P., and a period of stronger páramo representation during the last 310 yrs B.P. In the VP record the proportion of different ecosystems was relatively stable, with the exception of a slight decrease of the UMF and a slight increase of the subpáramo taxa, suggesting a lowering of the upper forest limit (UFL).

### 3.1.6 Fire and human impact during the late Holocene

The charcoal records of the RVM and VP sites indicate that fires occurred in the region throughout the late Holocene. In the RVM core two periods of higher fire frequency, best reflected in the charcoal influx data, are indicated between 1800 and 1600 B.P. in the upper part of Zone RVM-II and between 600 and 400 B.P. in Zone RVM-III. In the VP core only one period with increasing higher fire frequency is found from 310 to 60 B.P. in Zone VP-III. The charcoal records from both sites, located on the western slopes of the Podocarpus National Park about 16.5 km apart, indicate that frequent fires did not occur synchronously at both sites. This might suggest that frequent fires have been caused by human activities rather than naturally, due to drier conditions and lightning. However, the different settings of the sites may also play a certain role.

Further evidence of human activity in the region might be reflected by the higher values of *Alnus* in RVM from ca. 480 B.P. and in VP since ca. 50 yrs. *Alnus* is a pioneer tree which colonises wet bare ground following landslides (Marchant et al. 2002) and also occurs on wet soils along drainage systems (Weng et al. 2004).

### 3.1.7 Upper forest line changes and the role of fire and climate during the late Holocene

Upper Forest Line dynamics should be mainly reflected by fluctuations in the proportion of upper montane forest (UMF) and subpáramo vegetation. The vegetation reconstruction of both sites indicates that the proportions of the UMF and subpáramo were relatively stable during the recorded period. However, the VP record indicates a trend of decreasing UMF and increasing subpáramo, pronounced since about 230 B.P., at the end of Zone VP-II. This might reflect a slight lowering of the upper forest limit. In the RVM record a relatively stable proportion of UMF can be observed with some fluctuations, but there are some more distinct changes to higher proportions of the subpáramo, particularly between 880 to 310 B.P. in Zone RVM-II. This dominant representation of subpáramo was mainly related to the decrease of páramo vegetation. However, the expansion of *Weinmannia* during the period between 1720 and 880 B.P. may indicate an expansion of the UMF and therefore a raising of the upper forest limit during that time.

Important questions are what controlled the UFL dynamics during the late Holocene period, whether fires were natural or anthropogenic and if climate was an important factor.

Comparing vegetation and fire records of the two sites, it is evident that frequent fires favoured the expansion of grass páramo at the expense of the subpáramo. This is best indicated in the RVM record, where the decrease of fire frequency in RVM-II favoured the expansion of subpáramo and *Weinmannia* in the UMF, and the increase of fire in Zone RVM-III favoured the expansion of grass páramo and a decrease of *Weinmannia*. In the VP record, the minor decrease of the UMF and the increase of subpáramo since about 230 yrs B.P. at the end of Zone VP-II is also a period with a higher fire frequency. This also suggests that the increase of fire frequency played an important role in the lowering of the upper forest limit. Consequently, climate change and its role in controlling the UFL cannot be disclosed through these two late Holocene records, due to the relatively strong correlation between vegetation and fire dynamics.

Overall, it is necessary to consider that charcoal influx based frequency of fires in the two records is relatively low compared to other records from the region. In the El Tiro record, Niemann and Behling (2008a) show that charcoal influx increased during the mid Holocene and in particular during the late Holocene, before decreasing significantly after 500 B.P. The increase of fire frequency, even during the wet late Holocene period, probably indicates that the fires were of human origin. Both sites differ slightly and fires may have had different local effects, but a markedly different fire frequency may also suggest changes in human activity. Vegetational changes, such as the increase of Moraceae/Urticaceae in the RVM record since ca. 1200 B.P. and the replacement of some areas of grass páramo by subpáramo and UMF with *Weinmannia* between ca. 1600 and 880 B.P. might reflect an increase in temperature. However, due to the strong correlation between vegetation changes and fire it is difficult to address the role of climate in changes to the upper forest limit. Additional studies of pollen records at the UFL in places far from human settlements are needed to clarify this issue.

### **3.6. Comparison with other records from the Parque Nacional Podocarpus and from other sites in the Andes**

Four other records from the Parque Nacional Podocarpus (PNP) region are important for comparison of the upper forest limit (UFL) (Fig. 3.1). The first site, Laguna Rabadilla de Vaca (RV) at 3,312 m and about 1 km from RVM and about 110 m higher up, is located in the páramo vegetation zone (Niemann et al. 2009). Since ca. 3700 yrs, the dominance of herbaceous páramo at this site reflects cooler climatic conditions than during the previous mid and early Holocene from 3700 to 11700 B.P.

Sediment analysis by XRF scanning indicates a decrease of Si and Ti suggesting drier conditions during the whole late Holocene, compared to the late middle Holocene period. The new results for RVM show an expansion of páramo vegetation from 880 B.P. until the present day, which coincides with the Laguna RVM findings. In the RVM record, two periods of high fire frequency are recorded between 1800–1600 and 600–400 B.P., which show that burning associated with humans controlled the UMF vegetation and favoured expansion of páramo vegetation; meanwhile, in the record from Laguna RVM the very high charcoal influx may suggest uncontrolled burning caused by humans near the study site at ca. 3600 B.P.

The second record comes from El Tiro at 2,810 m, located about 14 km north of VP (Niemann and Behling 2008a). Pollen data show that UMF decreased and the modern subpáramo vegetation with high Melastomataceae became established and was relatively stable since ca. 3300 yrs. This shows vegetation change because of wetter and probably cooler conditions than those of the early-mid Holocene from 11200 to 8900 B.P. Fires increased after 8000 B.P., and became even more frequent after 3500 B.P., suggesting that they were caused by humans even during this wetter period. During the last 500 yrs, fire frequency decreased, probably due to the decrease of the human population (Niemann and Behling 2008b). The upper forest limit at Paso El Tiro is at ca. 2,800 m, thus ca. 400 m lower than at RVM and VP.

The third record is Cerro Toledo at 3,150 m, located 13 km south of RVM, where since ca. 1800 B.P. a slight decrease in páramo could indicate a change to somewhat warmer temperatures. The highest temperatures probably occurred between 9300 and 8500 B.P. changing to somewhat cooler conditions after 1800 B.P. (Brunschön and Behling 2009).

The fourth record is Laguna Zurita at 2,590 m, ca. 10 km north of Loja, where XRF data of a sediment core show wet climatic conditions before ca. 790 cal yrs B.P. and drier conditions between ca. 790 and 480 B.P. (Niemann and Behling 2010).

In Pantano de Pecho (Fig. 3.1) at 3,870 m, a Poaceae dominated herbaceous páramo occurred from ca. 3700 B.P. until modern times, reflecting cooler climatic conditions compared to the mid Holocene between 8990 and 3680 B.P. (Wille et al. 2002). However, after ca. A.D. 1595 (A.D. 1640), increasing amounts of charcoal particles suggest an intensification of human impact related to the Spanish conquest in this area around A.D. 1540 (Wille et al. 2002).

Based on the results from Lago Surucucho at 3,180 m, 165 km north of VP, Colinvaux (1997) stated that forest could be established at 3,180 m and that the UFL was at a similar altitude as in the Parque Nacional Podocarpus area (Fig. 3.1). Fires were very frequent at Lago Surucucho between 2000 and 600 B.P., suggesting a continuous change of UFL during the past. According to the pollen diagram in VP, the signal of upper forest limit changes is much less obvious, suggesting that the UFL was much more stable in the so-called Andean depression compared to areas to the north of the Andean regions.

Di Pasquale et al. (2008) showed that in Guandera, northern Ecuador, the UFL had moved up to its present position at 3,600 m only during the late Holocene, after ca. 5850 B.P., and that the UFL may have been situated between 3,600 m and 3,800 m at some time after ca. 4900 B.P., or it may never have been higher than it is today (Fig. 3.1). These results differ from palaeoecological reconstructions of Llanos Orientales in Colombia and Rupununi savanna in Guyana, which suggest a rapid UFL rise during the Pleistocene–Holocene transition (Van der Hammen 1974; Flenley 1979; Di Pasquale et al. 2008). They also contradict the hypothesis that fires caused by humans have destroyed large areas of forest which had grown above the modern UFL. Instead, páramo fires have probably contributed to the slow rates of UFL rise during the Holocene (Di Pasquale et al. 2008). Bakker et al. (2008) also demonstrated that in Guandera at 3,400 m fires became more frequent in the region from 2160 to ca. 910 B.P. From ca. 910 to ca. 520 B.P., the UFL moved to 3,250–3,300 m, and fire became increasingly frequent but the particles were mostly small. From 520 B.P. to the present day, the UFL moved up some 200–3,600 m. The abundance of charcoal particles further increased during this period, indicating that fires became more frequent. This supports the interpretation that human impact became an important factor during the last six centuries. During recent decades, values of arboreal taxa have remained constant. However, shrubs in particular decreased, while grassy vegetation increased. This change in composition suggests that the subalpine rainforest (SARF) is disappearing, possibly as a result of burning, as charcoal remains abundant.

Results from Pantano de Pecho in the central Ecuadorian páramo at 3,870 m, show that during the past six centuries the UFL has moved to between 3,400 and 3,650 m (Wille et al. 2002). The results from the Ecuadorian records of Guandera and Pantano de Pecho and the Colombian pollen record of Llano Grande-II show that the UFL could have had its highest position at 3,700 m from 4000 to 3000

uncal yrs B.P. The UFL subsequently descended and reached its lowermost position between 1100 and 600 uncal yrs B.P. (Bakker et al. 2008).

### **3.7. Conclusions**

Pollen and charcoal records from Rabadilla de Vaca Mire and Valle Pequeño have allowed the reconstruction of vegetation, fire and upper forest limit changes in the Parque Nacional Podocarpus during the last ca. 2100 yrs and 1630 B.P., respectively. The RVM record shows that the upper forest limit has been relatively stable in the study areas during the late Holocene. Changes between the proportion of upper montane forest and subpáramo vegetation probably reflect changes in the upper forest limit from 2100 B.P., indicating that the limit dividing forest from páramo was higher during the period between 1600 to 880 B.P. and became lower after about 880 B.P., becoming more stabilized after about 310 B.P.

The marked increase of fire frequency at RVM between 1800 and 1600 B.P. and 600 and 400 B.P. suggests that ecosystems in the study area were affected by human activity even under wetter conditions. For VP, the stability of the upper montane forest suggests no clear evidence of changes to the upper forest limit, although a slight change during recent decades has been detected. The higher fire frequency from ca. 230 B.P. suggests that human activities have had some impact on this area.

Comparing the vegetation and fire records of the two sites, it is evident that frequent fires favoured the expansion of grass páramo vegetation and curtailed the expansion of subpáramo vegetation and upper montane forest. Because fire probably played an important role in controlling changes to the upper forest limit since ca. 1800 B.P., it is difficult to detect whether climate change played an important role in these changes during this period.

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## Chapter IV

### 4. Late Quaternary vegetation, climate and fire dynamics, and evidence of early to mid-Holocene *Polylepis* forests in the Jimbura region of the southernmost Ecuadorian Andes

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**Abstract:** The vegetation, climate and fire history of high mountain ecosystems in the southern Ecuadorian Andes are documented in a continuous pollen and charcoal record, from Lagunas Natasas Forest bog, at 3495 m a.s.l. spanning the late Pleistocene and Holocene period since 15,930 cal yr BP. The chronology of this record is based on four radiocarbon dates. Páramo vegetation with abundant Poaceae and *Plantago rigida* characterized the Late Glacial (LG) period, implying cold and wet conditions. Slight expansions of mountain forests suggest warming during the LG. The upper forest line was lower than today and fire events were rare during the Pleistocene. During the early and mid-Holocene until 4300 cal yr BP, the area of páramo was markedly smaller and the subpáramo with woody vegetation (Melastomataceae) was larger. The upper mountain forest dominated and the upper forest line shifted to higher elevations. The pollen record provides the first evidence of the development of *Polylepis* forests in the southern part of the so-called Andean Depression reflecting warmer and drier climatic conditions during early and mid-Holocene. The late Holocene after about 4300 cal yr BP is characterized by larger areas of páramo and subpáramo promoted by moister conditions. These moister conditions and frequent fires may have been the cause of the very rare occurrence or even extinction of *Polylepis* populations in the Jimbura region. Since ca. 1000 cal yr BP human occupation has altered the landscape by frequent burning, wood cutting, grazing and cultivation.

**Keywords:** Ecuador, Andes, Mountain Forest, Páramo, Palynology, *Polylepis*, Fire History, Forest Line, Late Glacial, Holocene.

## 4.1. Introduction

The tropical eastern Andes and the northern parts of western Amazonia are among the global hot spots of vascular plant diversity related to their high diversity in relief and geo-diverse areas (Mutke and Barthlott, 2005). Although the Ecuadorian Andes harbor ecosystems with one of the highest biodiversity on earth, the role which history has played to produce and maintain this species richness is not well-known. This knowledge, however, is needed as background information to conserve and manage the remaining ecosystems and their biodiversity.

The present position of the Andean forest line is largely due to past ecological processes, influenced by past environmental changes including climate, fire and land use. Vegetation history is therefore essential for understanding ecosystem dynamics. The actual position of this forest line is interpreted as remnants of high altitude forests now destroyed by human-made fires and forest clearing (Ellenberg, 1958; Laegaard, 1992; Sarmiento and Frolich, 2002).

The Andean forest limit ecotone extends between 2800 m and – on rocky outcrops – 3300 m a.s.l. and thus is much lower than in most other regions in Ecuador. About 20 tree species constitute this forest limit ecotone – an astonishing number taking into account that commonly only two or three tree species (e.g. *Polylepis*, *Gynoxys*) form the forest limit in the Neotropics. The genus *Polylepis* (Rosaceae) is represented by several species distributed throughout the Andes (Schmidt-Lebuhn et al., 2006). Due to their patchy distribution and location at the highest elevations of the forest limit, this genus has become the focus of many ecological and physiological studies (Rada et al., 1996; Enrico et al., 2004; Cierjacks et al., 2007; Jameson and Ramsay, 2007; Kessler et al., 2007; Seltsmann et al., 2007;). Bakker et al. (2008) demonstrated in Guandera at 3400 m that increases in fires in the region restricted the expansion of forest taxa. Rodríguez and Behling (2010) documented in pollen records from the Rabadilla de Vaca Mire and Valle Pequeño in the Podocarpus National Park that frequent fires favoured the expansion of grass páramo vegetation and curtailed the expansion of subpáramo vegetation and upper mountain forest.

In the Andean Depression region the forest limit is highly variable and still poorly defined. While North and South of the depression the forest limit is located at 4000 m a.s.l. or even higher, the South Ecuadorian forest limit is found at 2800-3300 m a.s.l. In Northern Ecuador, e.g. at the Guandera Biological Station where annual precipitation amounts to 1700 mm, the modern forest

limit is at ca. 3600 m a.s.l. (Di Pasquale et al., 2008).

Where the forest limit is depressed *Polylepis* is absent. Ecological conditions of *Polylepis* forests can be characterized primarily in relation to temperature and soil moisture conditions. Due to its location at high elevations in the Andes, *Polylepis* forests are subject to wide diurnal temperature fluctuations, usually with a 20-30° C difference between day and night and frequent freezing temperatures. These fluctuations represent enormous stress for plants (Gosling et al., 2009). In Ecuador, which has no extensive arid zones in the high Andes (Luteyn, 1999), the only species of *Polylepis* adapted to these habitats is *P. microphylla* on the slopes of Volcán Chimborazo (Romoleroux, 1996). Particularly at altitudes above 4000 m a.s.l., the vast majority of species show morphological adaptations to low temperature like thick bark and cushion growth (e.g. *Azorella*) or physiological adaptations like freezing resistance (Goldstein et al., 1994; Körner, 1999; Hoch and Körner, 2005). *P. sericea* shows super cooling of all its tissues (Goldstein et al., 1994; Rada et al., 1996).

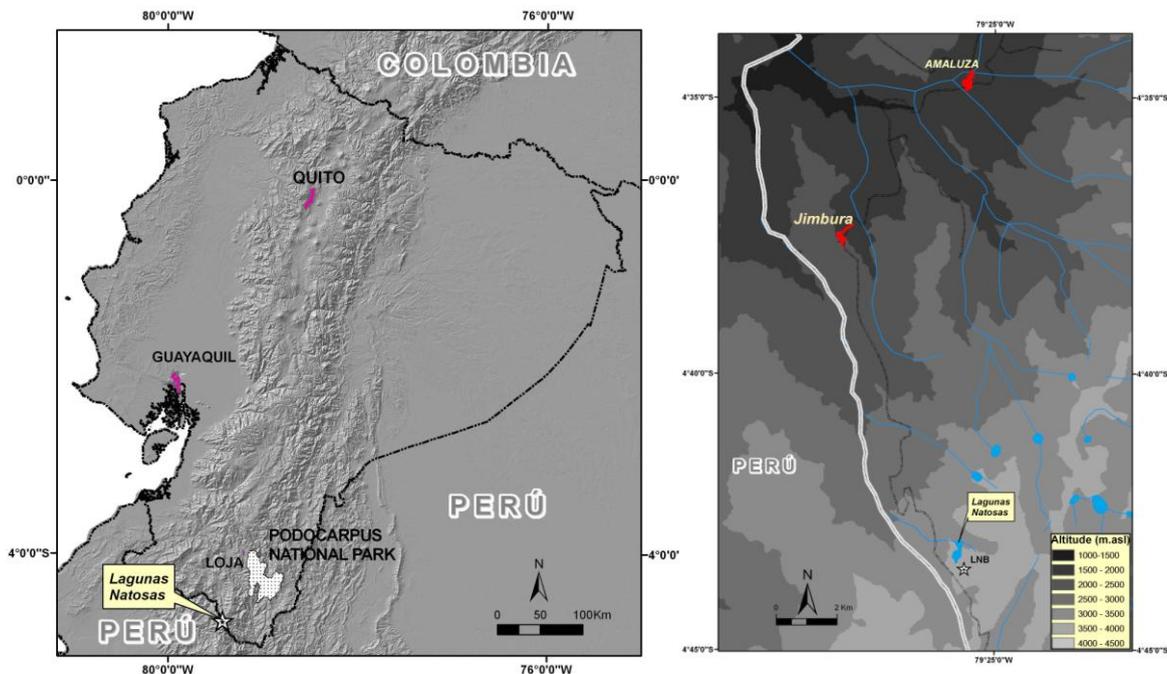
The vegetation dynamics for the northern tropical Andes has been addressed by a number of palynological studies since the 1960s (e.g. Van der Hammen and González, 1960; Van Geel and Van der Hammen, 1973; Hooghiemstra, 1984; Colinvaux et al., 1997; Hansen et al., 2003). However, there is no general consensus about what happened during the late Quaternary, as different pollen studies and their interpretations are often contradictory, and the timing of events somewhat uncertain (Markgraf, 1989; Van't Veer et al., 2000; Marchant et al., 2001). Prior investigations from the Andes of Ecuador are restricted to northern locations on the Inter-Andean Plateau (Colinvaux et al., 1988) and to two southern locations in the western Cordillera (Colinvaux et al., 1997; Hansen et al., 2003). The only available pollen records for the south-eastern Andes were provided by recent studies within a research project focusing on the Podocarpus National Park area and its highly diverse mountain ecosystems (Beck et al., 2008). Several sediment cores from sites between 2000 and 3300 m a.s.l. provide reconstructions of the environmental history mostly of the northern Podocarpus National Park (Niemann and Behling, 2008, 2009; Niemann et al., 2009). Pollen rain studies of recent vegetation provide important background information for the interpretation of late Quaternary pollen records (Brunschön and Behling, 2009; Brunschön et al., 2010; Niemann and Behling, 2010; Rodríguez and Behling, 2010). Palaeoecological studies from the southernmost region of Ecuador, which is the Southern part of the Andean Depression, are not available so far.

In this study we will focus on the following research questions: 1) what were vegetation, climate and fire dynamics in the southernmost region of Ecuador during the late Quaternary? 2) how widespread was *Polylepis* in the southernmost region of Ecuador during late Quaternary? 3) how did anthropogenic or climatic conditions influence the occurrence of *Polylepis* in the study area? and 4) how stable was the forest limit since the late Pleistocene in the southern part of the Andean Depression?

## 4.2. Study area

### *Location*

The study region is located in the southernmost region of the southeastern Ecuadorian Andes at the Peruvian border, approximately 125 km south of the city of Loja and about 12 km south of the town of Jimbura (Fig. 4.1). The investigated peat bog of the study site Lagunas Natosas Forest (LNB) is situated in the base of a small valley, about 1 km long and 400 m wide with an opening to the south, partly formed by glaciers. Today the vegetation in this valley is páramo, but a small patch of upper



**Fig. 4.1:** Map of Ecuador showing the location of Parque Nacional Podocarpus (Podocarpus National Park) and detailed site location of the Lagunas Natosas Forest core (LNB) at 3495 m a.s.l. in the southern Andes of Ecuador

mountain rainforest (c. 100 x 50 m) is found in the northwestern part of the valley. The studied peat bog is next to the forest patch, situated 04°43'49.5" S and 79°25'26.63" W at 3495 m a.s.l. This area is also part of the Colambo Yacuri National Park with an altitudinal range from 1640 m in Sanambay up to 3880 m at Sabanilla Cordillera.

### ***Geomorphology and Geology***

The Andes of southern Ecuador and northern Peru include the so-called Andean Depression (Girón-Cuenca Depression in Ecuador and Huancabamba Depression in Peru). The main peaks of the mountains in this region reach about 4000 m a.s.l. in the Nudo de Loja from which the Inter-Andean Sierras stretch towards SW, S and SE, dissected by valleys and basins. Active volcanoes are absent (Richter and Moreira-Muñoz, 2005). The southern Cordillera Real is mainly composed by the Zamora series, consisting of Palaeozoic metamorphic rocks of widely varying metamorphic grade. Local bedrock is dominated by semi-pelites, quartzites and black phyllites with some granitic intrusions (Litherland et al., 1994).

Little is known about the extent of late Quaternary glaciations. The period of greatest glaciations in Southern Ecuador occurred between 35,000 and 27,000 yr BP (Bush, 2004). The lakes and lagoons in the eastern Andes Cordillera, located about 2800 m a.s.l, indicate that glaciers in northern Ecuador did not extend to those low elevations (Rozsypal, 2000). Around the El Compadre lakes within the Podocarpus National Park, peaks have a maximum height of 3694 m a.s.l., which is much lower than in northern Ecuador and Peru. Below the small lagoons of El Compadre are lateral and terminal moraines that give evidence of a glacial minimum level between 2750 and 2800 m elevation (Rozsypal, 2000). Glacial erosion in the upper parts of the valley has formed typical U-shaped valleys.

### ***Climate***

The climate in the southeastern Ecuadorian Andes is influenced by warm, moisture-laden air rising from the Amazonian lowland, which collides with cold mountain air masses. This produces much of the rainfall in the eastern Andean mountains. The climate of the páramo is of the humid tropical diurnal type with cold nights and cool days. There is a drier period lasting from December to 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 (e.g., 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 and Rollenbeck, 2004).

According to Robles et al. (2008), the lowland area of the Jimbura region has a sub-humid climate, temperate meso-thermic, characterized by temperature variations from 18 to 22 °C and rainfall from 1500 to 2000 mm. On the other hand, the highland zone presents a sub-humid climate with small deficit of water, defined as cold temperate meso-thermic and characterized by thermal variations between 6 and 8 °C and rainfall between 1000 and 1500 mm (INAMHI, 2005).

### **Modern vegetation**

The study area is located in a small glacial valley. The vegetation type mainly corresponds to páramo and subpáramo, with isolated upper mountain forest (UMF) forest patches on the slopes.

According to Baquero et al. (2004), four vegetation types occur in the study area: subpáramo, montane cloud forest, montane wet scrub and montane dry scrubland, but the anthropogenic influence in this region by grazing and agricultural activities has transformed the landscape. The remaining natural vegetation consists of páramo and forest patches. Páramo is a tropical Andean ecosystem between the actual or potential upper limit of the closed Andean forest and the line of perpetual snow between 2200 to 3880 m a.s.l., and is characterized by grasslands (Medina et al., 2000). Grasses include *Calamagrostis macrophylla*, *Stipa ichu* and *S. rose*, and the bamboos *Neurolepis elata*, *N. laegaardii* and *Chusquea neurophylla*. Other taxa are *Baccharis genistelloides*, *Chuquiraga jussieui*, *Diplostephium empetrifolium*, *Hieracium frigidum* (Asteraceae), *Blechnum aurantium* (Blechnaceae), *Brachyotum andreanum* (Melastomataceae), *Escallonia myrtilloides* (Escalloniaceae), *Huperzia reflexa* (Lycopodiaceae), *Hypericum decandrum* (Hypericaceae), *Gaultheria amoena*, *Macleania rupestris*, *Pernettya prostrata*, *Vaccinium floribundum* (Ericaceae), *Puya eryngioides*, *Puya nitida* (Bromeliaceae), *Rhynchospora vulcani* (Cyperaceae) and *Valeriana plantaginea* (Valerianaceae) (Richter and Moreira-Muñoz, 2005; APG III, 2009).

The UMF is confined to small ravines, along the surrounding slopes and in isolated forest patches. The most frequent arboreal species present in the area are: *Miconia ligustrina* (Melastomataceae),

*Weinmannia auriculata* (Cunoniaceae), *Hedyosmum cumbalense* (Chloranthaceae), *Myrsine dependens* (Myrsinaceae), *Oreopanax andreanus* (Araliaceae), *Axinea*, *Clethra sp.* (Clethraceae), *Polylepis reticulata* (Rosaceae) and *Gaiadendron punctatum* (Loranthaceae) (Peters, 2009).

### ***Human occupation***

Despite limited research on pre-historic settlements in the study region it is certain that there was a large political complex in the area during the period between Inca rule and Spanish conquest. The time interval for human settlements south of the town of Catamayo, 80 km north of the study area, is from the Formative period (6000 BC - 500 BC) and includes three ceramic phases (Catamayo I, II, III) (Robles et al., 2008). Afterwards, during the period of regional development and integration (500 BC–1500 AC) the dominant cultures were Catacocha, Macará and Catamayo. Today, the Jimbura region is one of the most important economic zones in the production of organic coffee. However, it is an area where the degradation of natural ecosystems due to forest fires and grazing is significant, which greatly affects the high degree of endemism that is restricted to the south of the country. Predominant activities of the inhabitants of the zone are agriculture, livestock and trade (Flachier et al., 2009).

## **4.3. Materials and methods**

### ***Coring***

The sediment core was taken using a Russian corer from a peat bog located at the base of the U-shaped valley in páramo vegetation next to a UMF patch. The total length of the recovered core is 182 cm. For transportation, sections of 50 cm length were extruded on site, covered with plastic film and placed in split PVC tubes. Core was stored under cold (+4 °C) and dark conditions.

### ***Sample processing and analysis***

For accelerator mass spectrometer (AMS) radiocarbon dating four 0.5 cm thick samples were taken. Radiocarbon ages were calibrated using CalPal (Weninger et al., 2004).

For pollen and charcoal analyses 48 subsamples of 0.25 cm<sup>3</sup> volume were taken at 4 cm intervals along the core. Standard analytical methods were used to process the samples (Faegri and Iversen,

1989). Exotic *Lycopodium* spores were added to each sample before treatment for calculation of pollen and charcoal concentration (grains or particles/cm<sup>3</sup>) and influx rates (grains or particles/cm<sup>2</sup>/yr). A minimum of 300 pollen grains was counted for each sample. Tree, shrub and herb pollen were included in the pollen sum. Spores and aquatic taxa were excluded from the sum. For pollen identification, we used the Department of Palynology and Climate Dynamics in Göttingen reference collection for Neotropical species and related literature (Hooghiemstra, 1984; Behling, 1993). Charcoal particles of 5-150 µm size were counted for each sample on the pollen slides.

Pollen types were grouped according to ecosystem or habitat type for which they are most characteristic. Four main vegetation types were defined: Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo and Páramo. Pollen and spore data were presented as percentage diagram based on the pollen sum using the programs TILIA and TILIAGRAPH for calculation, illustration and zonation (Grimm, 1987). Two pollen diagrams were generated. First, a percentage diagram with the most important or representative taxa for each ecosystem (Fig. 4.2), and second, a summary diagram of the pollen taxa expressed in percent and grouped according to ecosystem or habitat type (Fig. 4.3). The zonation of the pollen record is based on major changes in the pollen assemblages reflected by cluster analysis using CONISS (Grimm, 1987) and visual inspection.

## **4.4. Results**

### **4.4.1. Stratigraphy**

Visual inspection of the 182 cm long sediment core (LNB) showed the following stratigraphic sequence:

From the base of the core at 182 to 166 cm a light brown to beige-grey layer consists of deposited fine sand with clay and mica. Between 177 and 172 cm mixed colour light to dark brownish sediments are characterized by silty clay with some sand and mica particles with very little organic material. From 166 to 96 cm a black to brownish, decomposed and compact peaty material is present without macro plant remains; between 147 and 143 cm some wood remains were found. From 96 to 12 cm the sediment is black-brown, decomposed, compact peaty material with some plant remains. From

12 cm to the top of the core the material is dark brown and contains very moist fine peat with many plant remains (Table 4.1).

**Table 4.1** Stratigraphic description of Lagunas Natosas Forest core

Depth (cm)	Description
0 – 2,5	Not decomposed plant material, some fresh green remains (moss and grass) – humus layer
2,5 - 12	Peaty material with high proportion of plant remains, dark brownish,
12- 48	Decomposed but less compact peaty material with high proportion of plant remains, dark brownish
48-62,5	Compact decomposed peaty material with plant remains, black-brownish,
62,5-96	Compact decomposed peaty material with some plant remains, black-brownish
96-128	Highly decomposed and compact peaty material, with few plant remains, black-brownish
128 – 151, 5	Highly decomposed and compact peaty material with few plant remains, black-brownish, between 143-147cm wood remains
151,5 - 166	Highly decomposed and compact peaty material, without plant remains, black-brownish coloured
166- 180	Deposited fine sand with clay, light brown to beige-grey, with mica, between 177-172 cm is characterized by silty clay with some sand and mica particles, mixed coloured light to dark brownish, very few organic material

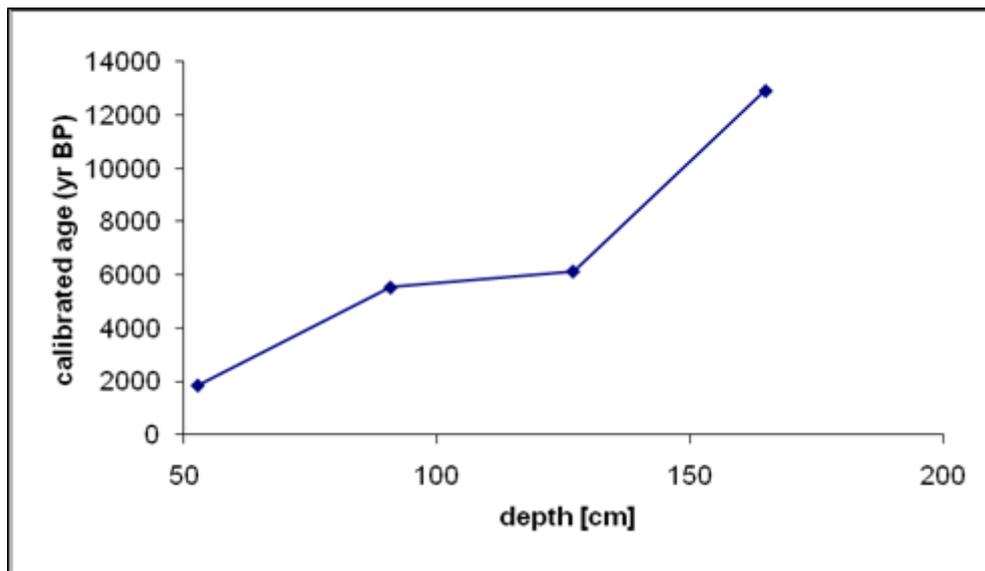
#### 4.4.2. Chronology and pollen zonation

Four AMS radiocarbon dates provide the chronological control of the sediment core. Ages indicate that the core covers the late Pleistocene and complete Holocene period (Fig. 4.4, Table 4.2). Extrapolation of the dates suggests that the base of the core has an age of 15,930 cal yr BP. Based on the four calibrated radiocarbon dates the sedimentation rate in the core range between 178 yr<sup>-1</sup>/cm for the lower part (182 to 134 cm) and 36 yr<sup>-1</sup>/cm for the upper part (48 to 0 cm) , (Fig. 4.3). The CONISS cluster analysis suggests four different pollen zones for LNB (LNB-I to IV). The ages for each zone have been calculated by linear inter and extrapolation.

**Table 4.2** AMS radiocarbon dates and depths for Lagunas Natosas Forest core (3495 m a.s.l.)

<i>Core</i>	<i>Lab. - no.</i>	<i>Depth (cm)</i>	<i><sup>14</sup>C age (yr BP)</i>	<i>Calibrated age<sup>1</sup></i>	<i>1-σ range (cal yr BP)</i>	<i>Dated material</i>
LNB 53	Erl-12176	53-53,5	1913 ± 44	1864 ± 47	1817-1911	decomposed organic material
LNB 91	Erl-12177	91-91,5	4805 ± 56	5536 ± 56	5480-5592	decomposed organic material
LNB 127	Erl-13826	17-127,5	5355 ± 44	6137 ± 87	6050-6224	decomposed organic material, wood
LN-B 165	Erl-11390	165-165,5	10950 ± 132	12905 ± 126	12779-13031	decomposed organic material

<sup>1</sup> calibration of <sup>14</sup>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.



**Fig. 4.4** Age–depth model and stratigraphy of the sediment of Lagunas Natosas Forest core (3495 m a.s.l.) based on four calibrated radiocarbon dates

#### 4.4.3. Description of the Lagunas Natosas Forest bog (LNB) diagram

The percentage pollen diagram (Fig. 4.2) displays 38 of the most frequent and important taxa out of 105 pollen and 25 spore types recognized. The identified pollen taxa are grouped in four different vegetation types and are illustrated in the summary pollen diagram (Fig. 4.3).

Pollen concentration (17,400-434,600 grains/cm<sup>3</sup>) as well as pollen influx (98–19,400 grains/cm<sup>2</sup>/yr<sup>-1</sup>) vary markedly throughout the core, with significantly higher values at the end of zone LNB-I and LNB-II, respectively (Fig. 4.3).

Charcoal concentration varies along the core with very low values of 14,200 particles/cm<sup>3</sup> in zone LNB-I during late Pleistocene to very high values of >6,814,400 particles/cm<sup>3</sup> in zone LNB-II during the early Holocene. Except the very high values during the early Holocene charcoal concentrations are relatively high during mid and late Holocene. Charcoal influx also fluctuates markedly in the core with the lowest value of 8000 particles/cm<sup>2</sup>/yr<sup>-1</sup> in LNB-I at the base of the core during the late Glacial and the highest value of 5,086,600 particles/cm<sup>2</sup>/yr<sup>-1</sup> in LNB-IV at the end of the Holocene (Fig. 4.3).

##### **Zone LNB-I (182-156 cm, ca. 15,930-11,660 cal yr BP, 7 samples):**

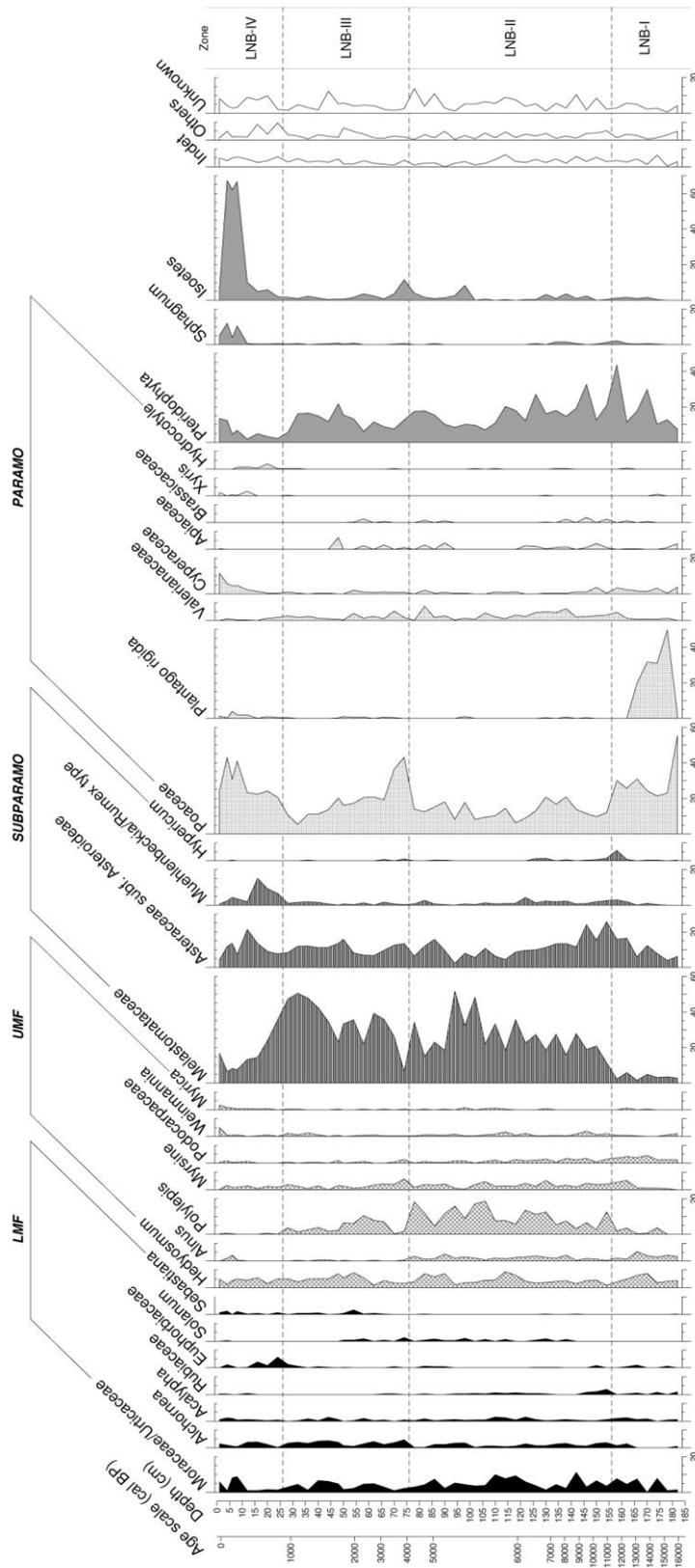
In this zone the páramo is well represented by high proportion of pollen (32-76%). The most frequent taxa are Poaceae (21-55%) and *Plantago rigida* (0-50%). With lower values occur pollen of Valerianaceae (0-5%), Cyperaceae, (0-4%), Apiaceae (0-3%). Percentages of the LMF group (1-12%) are low, represented mostly by pollen of Moraceae/Urticaceae (up to 8%), Flacourtiaceae (0-3%), Euphorbiaceae, Rubiaceae, *Alchornea*, *Acalypha* (0-2%). The values of the UMF pollen are relatively high (10-22%), represented by *Hedyosmum* (3-8%), *Myrsine* (0-5%), *Polylepis* (0-4%), *Alnus* (1-5%), Podocarpaceae (2-4%) and *Weinmannia* (0-2%). The sum of subpáramo taxa is between 8-25%, dominated by pollen of Asteraceae subf. Asteroideae (4-16%) and Melastomataceae (2-6%). Spores of pteridophyta group are present in proportions between 7-44%. At the end of this zone *Sphagnum* and *Isoetes* spores occur with low values (0-2%).

**Zone LNB-II (156-76 cm, ca. 11,660-4280 cal yr BP, 20 samples):**

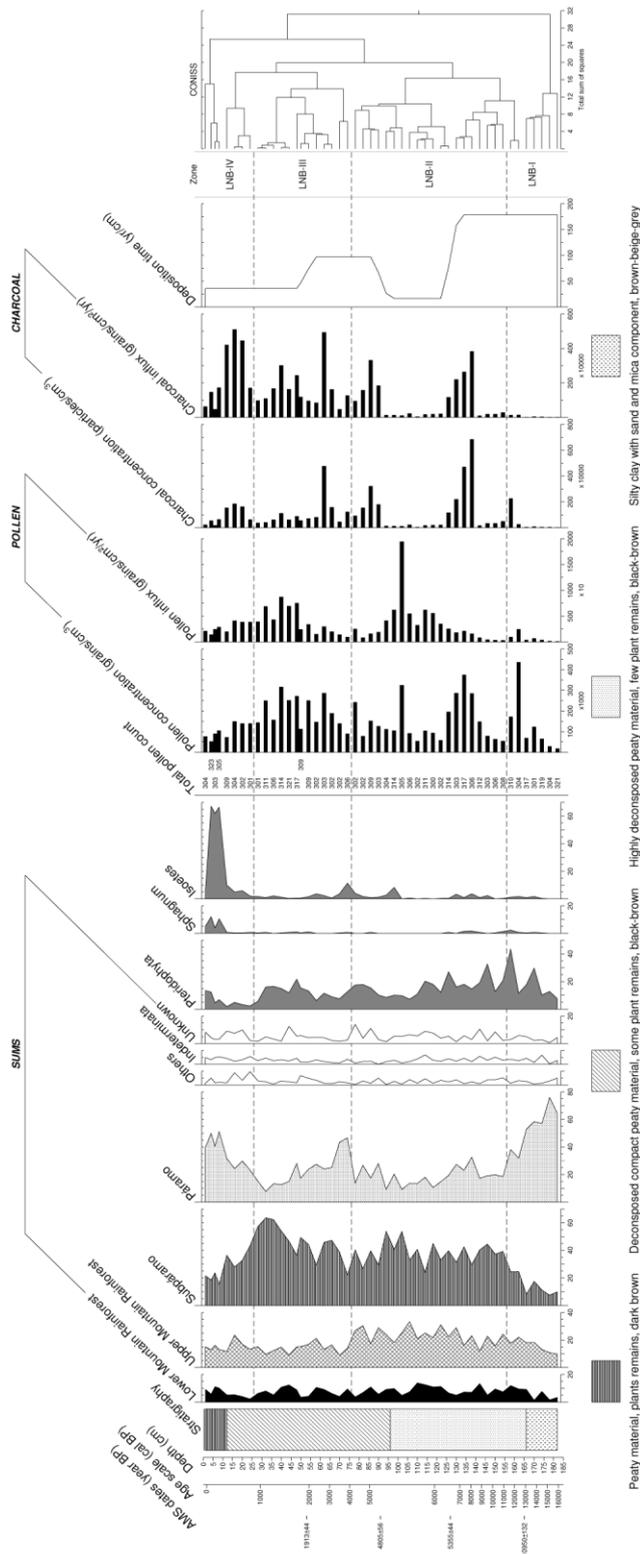
Compared with the former zone the proportion of páramo taxa decreases markedly (33-9%) due to the decrease in Poaceae pollen (21-6%). *Plantago rigida* decreases markedly (0-1%), while *Valeriana* pollen increases from 0 to 8%. LMF pollen is still present in low values (4-14%). The most frequent pollen found for this group is Moraceae/Urticaceae (1-11%), while *Alchornea* pollen remains low, but slightly higher (0-3%). Taxa that originate from the UMF reach the highest values (12-33%) in this zone. *Polylepis* is the most notable pollen which reaches the highest values (3-18%) in this zone. *Hedyosmum* remains stable regarding the previous zone, but increases at the end of the zone (2-8%). *Myrsine* (0-5%) and *Alnus* (0-4%) remain continuously low. Podocarpaceae and *Weinmannia* maintain relatively stable with low values (0-3%). The subpáramo group is represented by the highest values in this zone (24-54%), especially at the third part of the zone, mostly by the marked increase of Melastomataceae pollen (11-52%). Asteraceae subf. Asteroideae increases slightly and decreases again at the end of the zone (28-2%). Spores of pteridophyta decrease slightly (33-7%) compared with the former zone. *Sphagnum* spores remain stable with low percentages (0-2%), but spores of *Isoëtes* increase (0-8%) in this zone.

**Zone LNB-III (76-26 cm, ca. 4280 -960 cal yr BP, 13 samples):**

The LMF proportions remain similar as before (4-12%). Moraceae/Urticaceae pollen (1-7%) remains relatively stable during this period. *Alchornea* pollen increase slightly (1-5%). Pollen of the UMF group decrease (21-9%), *Hedyosmum* pollen increase slightly (1-8%). *Polylepis* pollen decrease compared with the former zone (0-11%). *Myrsine* pollen is still represented by low percentages (0-6%). Pollen of Podocarpaceae and *Weinmannia* decrease (0-2%), while *Myrica* and *Alnus* are represented with less than 1%. Subpáramo have highest values (22-64%) mainly at the end of this zone, basically by pollen of Melastomataceae (7-50%) and Asteraceae subf. Asteroideae (7-16%). Páramo decreases markedly at the end of this zone (47-8%), mainly due to the decrease of Poaceae pollen (43-5%), which has high values at the beginning of this period. *Valeriana* pollen (0-5%) is frequent in the first part of this zone. The proportion of pteridophyta spores decrease (22-6%) at the end of this zone and the frequency of *Isoëtes* decreases markedly (11-0%).



**Fig. 4.2** Pollen percentage diagram of Lagunas Natasas Forest core (3495 m a.s.l.) showing selected pollen and spore taxa grouped into vegetation of Lower Mountain Forest (LMF), Upper Mountain Forest (UMF), Subpáramo, Páramo and Pteridophyta



**Fig. 4.3** Summary pollen diagram of Lagunas Natasas Forest core (3495 m a.s.l.) showing radiocarbon dates, age scale, stratigraphy, ecological groups, pollen sum, values of pollen and charcoal concentration, pollen and charcoal influx values, deposition time, zones and the CONISS dendrogram

**Zone LNB-IV (26-0 cm, ca. 960 cal yr BP – present-day, 8 samples):**

The percentages of the LMF group (2-11%) increase slightly to higher values due to increase in Moraceae/Urticaceae (1-9%) and Euphorbiaceae (0-6%). The proportions of *Alchornea* (0-3%) and *Acalypha* (0-2%) increases from the middle of this zone. The proportion of UMF (12-24%) remains stable. However, *Alnus* and *Myrica* increase slightly (0-3%), as well as *Weinmannia* (0-5%) especially towards the end of the zone. Values of *Hedyosmum* (2-6%) and *Myrsine* (0-2%) remain stable. *Polylepis* is present with >1%. The sums of subpáramo taxa (44-15%) decrease markedly by lower representation of Melastomataceae (36-7%), Asteraceae subf. Asteroideae pollen (21-4%) and the *Muehlenbeckia/Rumex* type (15-1%). Páramo is very well represented, increasing at the end of this zone (23-51%), mainly through the increase of Poaceae (21-43%) and Cyperaceae pollen (0 to 12%). *Plantago rigida* shows a slight increase (0-4%). Spores of pteridophyta are represented by lower values (2-17%) going up at the end of the zone. *Sphagnum* (0-12%) and *Isoetes* spores (2-67%) get their highest values at the end of the zone.

## **4.5. Interpretation and discussion**

### **4.5.1. Late Glacial environment**

During the LGM, most Andean glaciers moved down slope and reached their lowermost positions at about 3000 m in the eastern Andes of Colombia, Ecuador and northern Peru (Rodbell, 1992; Clapperton, 1993). At the end of the Last Glacial Maximum (LGM) the volume of glaciers decreased creating moraines and small peri-glacial lakes and bogs, indicating that temperatures must have gradually increased (Heine, 2004; Mark et al., 2004). At the Lagunas Natosas Forest area this environmental condition allowed the accumulation of sediments and pollen deposition. Low values in pollen concentration and influx (Fig. 4.3) may suggest that the páramo vegetation was sparse in the area during this period.

The record of Lagunas Natosas Forest bog at 3495 m a.s.l. shows between 15,930 and 11,660 cal yr BP (zone LNB-I) dominance of páramo taxa with high proportions of Poaceae. *Plantago rigida*, present in high values, probably reflects presence of cushion mires in depressions. *P. rigida*, along with the high occurrence of pteridophytes indicates locally cold and humid conditions that likely prevailed during this late Glacial (LG) period (Cleef, 1978; Bosman et al., 1994). The marked decrease

of *P. rigida* towards the end of this zone may be related to local environmental change to denser vegetation reflected by a change in stratigraphy from clayey/sandy to more organic sediments. The marked increases of pteridophytes at the end of the LG suggests a change to markedly wetter conditions.

The low presence of mountain forest taxa is probably related to low temperatures at that time which did not allow the development of mountain forest near the study site. The presence of clayey sediment and low organic matter could also reflect the lack of forest vegetation near the coring site. In this context, it is assumed that the forest limit was at a lower elevation compared with the present.

The occurrence of *Hedyosmum* indicates also relatively wet conditions during the LG period. Small populations of *Polylepis* became established during the LG period in the region. Moraceae/Urticaceae pollen is easily wind transported over longer distances and its high representation may be related to this factor (Bush et al., 1990; Niemann and Behling, 2009). At Laguna Baja in northern Peru over representation of forest taxa (e.g., *Hedyosmum*) in páramo samples is attributed to low pollen productivity of local plants at high elevations resulting in higher values of long distance wind transported pollen (Hansen and Rodbell, 1995). High representation of *Alnus* pollen in páramo was observed also in the superpuna of the Junín area in central Peru between 4400 and 4900 m a.s.l., and was assumed due to long distance transport (Hansen et al., 1984). The presence of *Alchornea* and other LMF and UMF taxa may indicate instead local expansion of the mountain forest.

The near absence of carbonized particles suggests absence of fires suggesting absence of anthropogenic influence during this period. Also spontaneous fires are discarded due to wet and cold environmental conditions.

#### **4.5.2. Early to mid-Holocene environment**

A marked decrease of páramo vegetation, primarily grasses, occurred between 11,660 and 4280 cal yr BP (Zone LNB III) and *Plantago rigida* almost disappeared. Instead, woody vegetation increased with high values of Melastomataceae, *Polylepis* and Asteraceae. Dwarf shrubs can survive and reproduce well above forest line. Their success in cold environments can be explained by specific microclimatic conditions above and within the dwarf vegetation. The temperatures of dwarf plants

are decoupled from air temperature, being considerably higher during the day compared to those of the air above, because of transfer of heat between vegetation and atmosphere (Wilson et al., 1987; Grace et al., 1989). Furthermore, the shift of the upper forest limit (UFL) is less evident in southern Ecuador than in other sites where the tree *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 up-slope shift (Hansen et al., 2003). This is confirmed by the findings in this study; *Polylepis* was well represented and most likely widespread in this area, indicating marked changes not only in vegetation structure but also in ecosystem composition. The dominance of this vegetation type represents the upslope shift of UFL which most likely is the result of warmer and drier conditions characteristic of the transition from Pleistocene to Holocene. According to Thompson et al. (2000) the climate was 1.5 to 2° C warmer than today, favouring the development of forest vegetation.

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. This change to cooler conditions is evident between 5000 and 4000 around 4300 cal yr BP in LNB area, with an increase of páramo vegetation, primarily in Poaceae.

#### **4.5.3. Late Holocene environment**

The palynological data show after about 4300 cal yr BP until ca. 1000 cal yr BP (Zone LNB III) at first and increase of páramo (Poaceae) and then a decrease while subpáramo (Melastomataceae and Asteraceae) increased. The representation of the UMF is markedly lower than during the early to mid-Holocene period. These vegetation changes suggest slightly cooler and wetter environmental condition than during the former period. Frequent fires, probably caused by humans, favoured the expansion of páramo and subpáramo taxa. *Polylepis* populations decreased markedly and became very rare due to the change in the climatic conditions and frequent fires, indicating wetter climatic conditions during the late Holocene than during earlier periods. Similar times for major environmental changes have been identified in the Amazonian lowland, illustrated by the expansion of the Amazon rainforest north and south of the Equator (Behling and Hooghiemstra, 1998, 2000; Mayle et al., 2000).

Since about 1000 cal yr BP the evidence of an increase in páramo taxa, primarily by Poaceae and a decrease of Melastomataceae is probably related to frequent fires. The increase in fire activity during this period most likely was related to human activities, to clear the forest for hunting, grazing, cultivation and wood gathering, comparable to the present situation found at lower elevations in the Jimbura region. The higher occurrence of Cyperaceae, *Isoëtes* and *Sphagnum* suggest moister conditions than during the preceding period.

#### 4.5.4. Comparison with other regions of Ecuador

Studies from central southern Ecuador in the El Cajas National Park of the western Cordillera (3700 m a.s.l. 230 km to the north) indicate for the late Glacial period (17,000-11,000 cal yr BP) presence of herbaceous vegetation, reflecting colder and moister climatic conditions than those of today (Hansen et al., 2003). These environmental conditions are also inferred in the present study site in southernmost Ecuador based on the dominance of páramo vegetation. Both records, Laguna Junín and Río Blanco pond in Peru have earlier intervals of lower temperatures around 12,000 years and ending, at least at Junín, about 11,000 cal yr BP. This period was dominated by grasslands characteristic of puna ecosystems (Hansen et al., 1984). At Laguna Baja a pronounced change from a mixed páramo/mountain forest to páramo (>60% Poaceae), and back to mountain forest seems to signal a climatic reversal in the northern Peruvian Andes between 14,000 and 11,500 cal yr BP (Hansen, 1995).

In the Lagunas Natosas Forest site, the evidence of abundant páramo taxa (Poaceae, *P. rigida* and pteridophyta) between 15,930 and 11,660 cal yr BP demonstrates cold and moist climates, which probably restricted the establishment of forest taxa. Low amounts of Asteraceae, Melastomataceae, Moraceae/Urticaceae, *Polylepis*, *Hedyosmum*, and *Alnus*, among others, suggest presence of isolated patches of woody vegetation maybe restricted to small valleys or ravines at lower located areas where the local and specific climatic conditions allowed establishing this vegetation type.

At the transition between Pleistocene and Holocene (11,500 cal yr BP) the spread of woody taxa like Melastomataceae and Asteraceae and the decrease of Poaceae and absence of *Plantago rigida* suggesting locally drier and warmer conditions.

During the Holocene in El Cajas National Park, *Polylepis* became more frequent and reached its maximum during the mid-Holocene period. The climate was warmer with a moderate seasonality during the early Holocene than nowadays (Hansen et al., 2003). In LNB study area between 11,660 and 4300 cal yr BP *Polylepis* was abundant reflecting warmer and drier conditions. This climatic condition coincides with the result obtained from Cerro Toledo (Brunschön and Behling, 2009) as well as El Tiro (Niemann and Behling, 2008) in the central part of the Andean Depression.

In the Papallacta páramo located in the eastern cordillera of Ecuador between the Cayambe and Antisana volcanoes, about 30 km east of Quito, *P. incana* occupies an altitudinal belt between 3500 m and 4100 m a.s.l. and forms monospecific forests between 3600 m a.s.l. and 3800 m a.s.l. The general weaker signal of a forest limit shift at Cerro Toledo (3150 m a.s.l. ca., 50 km northeast from LNB) and in the south-western Ecuadorian Andes could be due to the absence of *Polylepis* related to high precipitation and strong winds in that region or could indicate that the fluctuations of past forest limit shifts in this area were minor (Brunschön and Behling, 2009).

At Rabadilla de Vaca mire (3200 m a.s.l.), 60 km northeast in the Podocarpus National Park, pollen record showed that from ca. 2100 to 1720 cal yr BP subpáramo vegetation was most abundant illustrated by the high values for Melastomataceae and low values of Poaceae and Cyperaceae, which suggests warmer and drier conditions (Rodríguez and Behling, 2010). During the same period in LNB Melastomataceae started to be common maintaining its dominance until about 900 cal yr BP. Since then until the present forest taxa remained relatively stable. Páramo vegetation expanded continuously due to the spread of Poaceae and *Isoëtes*, while subpáramo vegetation decreased, as indicated by the continuously lower occurrence of Melastomataceae in this area.

#### **4.5.5. Drivers of past changes in *Polylepis* populations from southern Ecuador**

Ecuador is considered a centre of diversification of *Polylepis* after Peru and Bolivia. The genus *Polylepis* is represented by eight species in the Ecuadorian Andes: *P. pauta*, *lanuginosa*, *sericea*, *weberbaueri*, *microphylla*, *reticulata*, *incana* and *racemosa* (Simpson, 1979), many of them ending their distribution in southern Ecuador, an interesting fact from a biogeographic point of view.

*Polylepis* is a tree-forming genus that occurs naturally at higher elevations than any other angiosperm tree and grows near massive rock outcroppings and slopes (Simpson, 1979, 1986; Romoleroux, 1992).

Some studies found a lack of correlation between air temperature and elevation in *Polylepis* forest (Cabrera et al., 1998). These data suggest the presence of special microclimatic conditions (thermal refuges) that moderate freezing temperatures in relation to surrounding páramos. In addition, warm air present in these thermal refuges is enhanced by the rock outcrops and better soil conditions than in surroundings areas. Consequently, warmer soils improve the establishment and growth of tree seedlings. These forests represent one of the world's most threatened ecosystems, and play a central role in Andean ecology as habitats for many species of plants and animals as well as being an important resource for local people (Kessler, 2006).

Studies show that the present distribution of *Polylepis* is primarily the result of thousands of years of human activities on the high Andes (Kessler, 2002). Anthropogenic practices like fires for hunting and to improve agricultural yield have reduced the coverage of forest (Kessler and Driesch, 1993). Because of this process, which probably started during the Holocene, but certainly intensified since the Spanish Conquest, it is estimated that 98% of *Polylepis* forests have disappeared in Peru (Fjeldså and Kessler, 1996). In Bolivia, the eastern Andes have lost more than 99% of *Polylepis* forests; while in the western Cordillera remain around 50% of *Polylepis* forests. Transplant experiments suggest that trees are very susceptible to salty soil conditions or standing water (Kessler, 1995). As a result, it is expected that large high Andean plains often flooded at least in the rainy season forests have always been free of *Polylepis*.

In the LNB area (3495 m a.s.l.) *Polylepis* was abundant during early and mid-Holocene times when subpáramo taxa like Melastomataceae and Asteraceae dominated while páramo vegetation declined. These data may suggest the dominance of *Polylepis* as part of complex forest vegetation, which could be part of the upper forest limit favoured by ideal environmental conditions for the developing of woody vegetation.

During the late Holocene humid and cooler conditions and frequent fires could be considered the factors that most likely influenced the almost absence of *Polylepis*. This genus also has inconspicuous wind-pollinated flowers (Simpson, 1986) and is regarded a poor disperser of pollen (generally within 1 km), a constraining factor under adverse climates (Kuentz et al., 2007).

In Cerro Toledo, south of the Podocarpus National Park ca. 50 km northeast from LNB, the absence of *Polylepis* could be due to high precipitation and strong winds mainly in open areas and top hills, or could reflect minor fluctuations of past forest limit shifts as well (Hansen et al., 2003).

The presence of charcoal in the Lago Grande record in Peru reveals that fire is a natural component of Andean ecosystems through glacial-interglacial cycles; albeit at an intermittent and low level for much of this time. The major peaks in charcoal occur in association with warm, interglacial, conditions and/or high proportions of *Polylepis* (Gosling et al., 2009). At Laguna de Chochos in Perú, *Polylepis* has its maximal abundance between 10,000 cal yr BP and 7300 cal yr BP with an absolute maximum occurrence at ca. 9200 cal yr BP. The inferred drier and warmer climate of this interval is consistent with the presence of forests with *Polylepis* and Podocarpaceae. Pollen records from Junín in Peru, suggest that the major destruction of the *Polylepis* forest took place about 10,000 years ago, but it is still not clear whether this loss was mostly a consequence of climate changes or human activity (Hansen et al., 1994). Later on, camelids domestication by pre-Inca cultures led to widespread overgrazing and soil erosion (Bowman, 1974). It is therefore possible that through the use of fire early human inhabitants could have destroyed *Polylepis* forests.

Records from the LNB core reveal high fire frequencies for late Holocene; it is assumed that fires were produced by anthropogenic activities that limited the *Polylepis* expansion, which seems likely because the genus tends to avoid per-humid regions (Kessler, 1995; Richter and Moreira-Muñoz, 2005). This could also be the reason for the expansion of páramo vegetation that did not allow the advance of the forest line upslope. The value of the *Polylepis* timber is clear and there is increasing evidence of the detrimental effect of modern human activity on sustaining and re-establishing *Polylepis* by grazing (Teich et al., 2005), soil degradation (Renison et al., 2004, 2005) and fires (Renison et al., 2002).

General consensus is that fires reduce *Polylepis* adult survival and inhibit its regeneration (Renison et al., 2002; Cierjacks et al., 2008). The findings of a reduced *Polylepis* niche during warmer and drier than modern conditions conform to predictions that high Andean woodlands could be particularly vulnerable to predicted future climate change (Bush, 2002; Malcolm et al., 2006).

## 4.6. Summary and conclusions

The pollen record from Lagunas Natasas Forest bog (3495 m a.s.l) reveals that, in this glacial valley during late Pleistocene (15,930-11,660 cal yr BP) páramo vegetation expanded, dominated by Poaceae and *P. rigida*, most likely in the form of cushion mires. This indicates cold and humid conditions which constrained the expansion of mountain forest. A slight warming during the Late Glacial (LG) favoured the slight expansion of forest taxa like *Hedyosmum* and Moraceae/Urticaceae. First small *Polylepis* populations became established during the LG period. The UFL was lower than at the present time. Fires were very rare during the LG comparable to several other records from the Andean Depression. During early and mid-Holocene (11,660 - 4300 cal yr BP), the climate was warmer and drier than today, as suggested by the low proportion of páramo, high proportion of subpáramo (Melastomataceae and Asteraceae) and the dominance of forest taxa. This indicates also the upslope shifting of the UFL. The high proportion of *Polylepis* documents the first evidence of *Polylepis* forest in the southernmost region of the Andean Depression under different climatic conditions. This is not evident so far from other regions of the Andean Depression. During the late Holocene after 4300 cal yr BP, the UMF became reduced and the area of subpáramo and páramo increased suggesting that the UFL shifted to lower elevations.

*Polylepis* became rare during the late Holocene and almost absent during the last about 1000 years, probably due to increased fire frequency and wetter conditions. During the last about 1000 years páramo was dominant in the study area due to frequent fires most likely by anthropogenic activities.

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## Chapter V

### 5. Current Cultural Services: Landscape History

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#### Abstract

Three pollen profiles reveal vegetation changes during the past 16,500 years of the Podocarpus National Park (PNP) in the Southern Ecuadorian Andes. Andean glaciers retreated after the Last Glacial Maximum and the Younger Dryas cold interval, accompanied by a marked decline of páramo vegetation between 11,660 and 4280 years B.P., and the expansion of subpáramo vegetation. *Polylepis* was widespread during the warm early Holocene, whereupon páramo vegetation increased after 4200 B.P. The upper montane forest became abundant after 4200 B.P., and an increase of páramo taxa since 500 B.P. indicates moister climate since then. Charcoal particle concentration maxima are evident between 1800 to 1600 B.P. and 600 to 400 B.P. The mountain region became permanently settled at the end of the 19th century when the exploitation of natural resources was initiated. Decadal variations in ring-width chronology from *Cedrela montana* are possibly related to large-scale atmospheric pressure variations in the tropical Pacific Ocean.

**Key words:** Late Holocene, Podocarpus National Park, Ecuadorian Andes, pollen, tree- ring chronology, land use history.

## 5.1. Introduction

The ecosystem of the Podocarpus National Park (PNP, see Figure 5.1) in the Southern Ecuadorian Andes is well recognized worldwide as a “hotspot” of biodiversity (Richter et al. 2009). The altitudinal range in effect here has allowed the development of highly diverse habitats which contribute to the extraordinarily high degree of biodiversity (Richter et al. 2009). Other ecosystems present in the area are evergreen tropical mountain forests (montane rainforests) and elfin forests in the transition zone to the páramo ecosystem (see Figure 1.6 in Beck et al. 2008). However, natural and anthropogenic impact has influenced the transformation of ecosystem areas concomitant with the loss of original ecological integrity. The present landscape of the PNP is the result of human impact and climate change that have been taking place for thousands of years. Some valleys that were formed during the cold Pleistocene (from around 2,6 million years ago till 10,000 B.P.) are witness to ancient glaciations in the Podocarpus plateau. The landscape has been transformed during recent centuries upon human colonization to satisfy the population needs. Deforestation caused by timber, agriculture and grazing activities has changed the original ecosystem vegetation to the point where it has been replaced by other opportunistic and pioneer plant communities that were able to develop in the transformed areas. Today only small patches of natural forests remain due to the long history of occupation and, in particular, to increasing human impact during recent decades (Dodson and Gentry 1991; Pohle 2008).

The reconstruction and understanding of past vegetation and climate changes, as well as of human impact, can enhance our knowledge as to how past processes have influenced ecosystem dynamics and led to the development of the outstanding diversity in the study region. This will also further improve our understanding of the reactions of the tropical mountain ecosystems to environmental changes on local and regional scales. Such information is crucial for developing management and conservation strategies within the context of changing climatic conditions. In this chapter we consider the landscape dynamics having taken place during the last 16,000 years (Late Quaternary) in the wider area of the PNP region. These include changes in vegetation, biodiversity, climate, tree growth, fire and land use.

## 5.2. Methods and Analysis

Pollen analysis was carried out on three soil cores taken in the transition zone between the forest and the páramo ecosystems (Fig. 5.1). Two cores originate from north of the PNP (Ravadilla de Vaca, RVM, and Valle Pequeño, VP), the third being taken in a glacial valley (Lagunas Natasas Forest, LNB) close to the Peruvian border, 12 km to the south of the town of Jimbura. Radiocarbon ages were determined for each sample using CalPal (Weninger et al. 2004). For pollen and charcoal analyses, subsamples (0.25 cm<sup>3</sup>) were taken at 4 cm intervals along the cores. Standard analytical methods were used to process the samples (Faegri and Iversen 1989). Known amounts of exotic *Lycopodium* spores were added to each sample before treatment as internal controls of charcoal concentrations (grains or particles/cm<sup>3</sup>) and influx rates (grains or particles cm<sup>-2</sup> yr<sup>-1</sup>). A minimum of 300 pollen grains were counted for each sample. Tree, shrub and herb pollen grains were included in the pollen sum, whereas spores and aquatic taxa were excluded. Pollen types were grouped according to the ecosystem or habitat type for which they are most characteristic. Four main vegetation types were defined: Lower Mountain Rainforest (LMF), Upper Mountain Rainforest (UMF), Subpáramo and Páramo. Pollen and spore data are presented as percentage diagrams based on the pollen sum using the programs TILIA and TILIAGRAPH for calculation, illustration and zonation (Grimm 1987). The zonation of the pollen record is based on important changes in the pollen assemblages cluster analysis by CONISS (Grimm 1987).

Tree-ring widths of 70 increment cores taken from 32 *Cedrela montana* (Meliaceae) individuals from the Reserva Biológica San Francisco (RBSF; Fig. 5.1) were measured at a precision of 0.01 mm. To remove the biological age trend inherent in ring-width series, the measured raw values were standardized with a cubic smoothing spline removing 50% of the tree-growth variance at 2/3 of the original series length (Cook and Kairiukstis 1990). Climate-growth relationships were calculated as correlation functions with local climate station data and variations of the Southern Oscillation Index (SOI) taken from the 'Global Change Master Directory' (GCMD, 2012).

### 5.3. Results and Discussion

#### 5.3.1. Vegetation of Southern Ecuador

The páramo areas of southern Ecuador are characterized by irregular topography (Maldonado 2002). The vegetation of the herbaceous páramo (Paramo herbáceo) found at about 3100–3400 m a.s.l. is rich in *Neurolepis nana*, *Calamagrostis macrophylla* and *Niphogeton dissecta*. This vegetation unit is 0.2 -1 m in height and covers flat slopes and concave terrains, as well as ridge areas. The shrub paramo (Páramo arbustivo bajo) occurring at about 2900-3400 m a.s.l. is rich in *Weinmannia rollottii*, *Oxalis spiralis* and *Ilex andicola*. This páramo type is found mainly on steep slopes (Lozano et al. 2003) and exhibits shrubs and herbs of from 0.5 to 1.2 m height. The subpáramo (approx. 2800-3100 m a.s.l.) is characterized by *Puya nitida*, *Brachyotum rotundifolium* and *Oritrophium peruvianum*. Shrubs and herbs grow up to 1 m in height, while individual shrubs can be 2 - 3 m tall. The upper montane rainforest (UMF) is present between about 2100 - 2750 m a.s.l. and is represented by a low, single-tree stratum of between 5 and 10 m in height, occasionally up to 15 m. Characteristic trees are *Morella pubescens* (Myricaceae) and *Myrsine andina* (Myrsinaceae) (Bussmann 2005; Lozano et al. 2003).

#### 5.3.2. Past Climate, Vegetation and Fire Dynamic in the PNP

A few palynological records for the Ecuadorian Andes (Colinvaux et al. 1997; Hansen et al., 2003; Fig. 5.1) and some more recent studies on upper forest line (UFL) changes in northern Ecuador (Bakker et al. 2008; Di Pasquale et al. 2008; Wille et al. 2002; Fig. 5.1) have contributed to the environmental history of the northern Ecuadorian Andes and thus to our understanding of the present vegetation distribution in the PNP area,. However, palaeoecological research in Ecuador has concentrated mainly on the Amazon basin (e.g. Bush and Colinvaux 1988; Bush et al. 1990; Colinvaux et al. 1988a; Liu and Colinvaux 1985), and only one study is available as to the inter-Andean Plateau (Colinvaux et al. 1988b; Fig. 5.1).

#### 5.3.3. The Late Glacial Environment

The area's outstanding biodiversity has evolved from the interplay of several regional and local scale environmental factors (e.g. climatic, geologic, orographic and edaphic conditions as well as natural

and anthropogenic disturbance regimes, see Chap. 1) and the environmental history that has figured importantly in the development of the current plant diversity pattern (Broecker 1997; Churchill et al. 1995; Richter et al. 2009). Since the onset of the Pleistocene around 2.6 million years ago, recurrent climate alterations between cold and warm periods have resulted in changes in the number and distribution of ecosystems in the area.

During the Last Glacial Maximum (LGM, 18,000 years ago), most Andean glaciers advanced and reached their lowermost positions at about 3000 m a.s.l. in the eastern Andes of Colombia, Ecuador and northern Peru (Clapperton 1993; Rodbell 1992; Heine 2011). Temperatures in the area gradually increased at the end of the LGM. As the retreating glaciers shrunk, they left behind them moraines and small glacial lakes (Heine 2011; Mark et al. 2004). Data for the Lagunas Natosas forest bog at 3495 m a.s.l. (Fig. 5.2) respective of the late Pleistocene and Holocene periods (the last approximately 10,000 years) shows that páramo vegetation (Poaceae) was dominant during the period of 15,930-11,660 B.P. (zone LNB-I, Fig. 5.2). The pronounced abundance of *Plantago rigida* and pteridophytes indicate that cold and humid conditions prevailed locally during the Late Glacial period (Cleef 1978; Bosman et al. 1994) and formed cushion mires in depressions. The limited number of mountain forest taxa reflects the prevalence of low temperatures during the Last Glacial period. The presence of clayey sediment poor in organic matter may also reflect the lack of forest vegetation near the coring site. In this context, it is assumed that the forest line was at a markedly lower elevation than it is at present.

The Bølling-Allerød interstadial during the period of from 14,700 to 12,700 B.P. was characterized by relatively warm and moist conditions (Cronin 1999), which favored an abundant presence of *Hedyosmum* and pteridophytes. Small populations of *Polylepis* also became established during the Last Glacial period in the region. Moraceae/Urticaceae can easily be transported by wind over longer distances, and their ample representation may thus be related to this factor (Bush et al. 1990; Niemann and Behling 2009).

The Younger Dryas period was a cold climate period at the end of the Pleistocene between 12,800 and 11,500 years ago. Rapid climatic fluctuations during the last deglaciation phase of this period are documented by glacier advances in the Ecuadorian Andes before 12,500 B.P. and between 10,500 and 9000 years ago. (Heine 2011). The local absence of *P. rigida* in the study area at approx. 12,600

years ago, whereas it had previously represented the most abundant taxon, suggests a drying of the climate at this time.

The incidence of fires during this period can be disregarded due to the wet and cold environmental conditions. This notion is supported by the almost complete absence of carbonized particles, which suggests that anthropogenic influences played no role during this period.

#### **5.3.4. Early to Mid-Holocene Environment**

The LNB core points a marked decrease of páramo vegetation between 11,660 and 4280 B.P. (Zone LNB III, Fig.5.2). The expansion of woody dwarf shrub vegetation (Melastomataceae and Asteraceae) is mostly associated with the subpáramo ecosystem. Dwarf shrubs can survive and reproduce well above the forest line. Furthermore, an indication of upper forest line (UFL) shift is less evident in southern Ecuador than on other sites where the typical treeline genus *Polylepis* dominates the UFL. *Polylepis* was well represented and most likely widespread in southern Ecuador, as evidenced by marked changes in not only vegetation structure but also ecosystem composition. Warmer and drier conditions characterized the transition from the Pleistocene to the Holocene, allowing an upslope shift of the UFL. According to Thompson et al. (2000), the early Holocene climate was 1.5 to 2° C warmer than that today, favoring the development of forest vegetation. The period was 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 B.P. This phenomenon is evident in soil core data for approx. 4200 B.P. in the LNB area, and corresponds to an increase in páramo vegetation.

#### **5.3.5. Late Holocene Environment and Human Settlement History**

According to Guffroy (2004), signs of human activity in the Loja region are evident for times as early as about 4500 years ago. However, human activities may have occurred much earlier in the dry inter-Andean valley. At Paso El Tiro, located 10 km east of Loja, Niemann and Behling (2008) found evidence of increased fire intensity during the wetter late Holocene. This suggests the occurrence of frequent fires of anthropogenic origin used for hunting purposes and slash-and-burn activities in the drier lower valleys. The palynological data show a dynamic transition between subpáramo and páramo from 4280 years ago until the present (Zone LNB III and IV). Poaceae were dominant around 4200 B.P., but suffered a critical decline in the vicinity of 3100 years ago. An important increase in the

abundance of Melastomataceae and Asteraceae at the same time has been registered. The results of the RVM record (Fig. 5.3) from 125 km north of the LNB (Zone RVM-I) show that the UMF was most abundant from about 2100-1720 B.P. as evidenced by the greater abundance of *Hedyosmum*, while the subpáramo was more strongly represented as indicated by an increased abundance of Melastomataceae. Pollen data in the RVM core show that Moraceae/ Urticaceae became more abundant after 1200 B.P. This period also shows a greater abundance of *Weinmannia* in the UMF compared to the previous and subsequent periods. Melastomataceae were abundant at the LNB around 1200 years ago, while Poaceae declined radically.

This vegetation composition reveals that somewhat warmer and drier environmental conditions most likely prevailed during this period. In the VP record no marked vegetation changes can be detected (Fig. 5.4).

After the 15<sup>th</sup> century the area around the upper range of the Cordillera Oriental close to the present city of Loja was the Eastern border of the Inca Empire and the Shuar territories (cf. Hocquenghem et al. 2009). The Shuar had triumphantly defended themselves against the Inca armies of Túpac Yupanqui, who finally considered the Shuar to be indomitable (González-Suarez 1890). After 60 years of coexistence the Shuar successfully revolted in 1599 against the Spaniards (Conde 1988), who then had to abandon the gold mines and settlements on the eastern part of the Cordillera. The region was probably sparsely inhabited between the 15<sup>th</sup> century and the end of the 19<sup>th</sup> century. It was not until the end of the 19<sup>th</sup> century that missionaries, soldiers and gold miners successfully installed permanent settlements in the mountain area, initiating the current processes of forest exploitation and agricultural expansion (Gerique 2010). The evidence of a very strong increase in páramo taxa (Poaceae and Cyperaceae), *Isoëtes* and *Sphagnum* during the last 500 years in the LNB core shows the area to be a moister ecosystem than it was during the previous period. This is corroborated by the fact that the oldest trees of the PNP as dated by radiocarbon are *Prumnopitys montana* (Podocarpaceae) growing in a valley north of the RVM pollen site at an elevation of about 2100 m a.s.l. at the lower limit of the UMF. After calibration with the Southern Hemisphere Calibration dataset (McCormac et al. 2004), <sup>14</sup>C dates collected from the inner parts of a *P. montana* stem (lab code Erl-12870) showed the tree to be 418 ± 35 years old, corresponding to A.D. 1453-1504. Since there are even taller trees than the tested one in the forest, it can be inferred that the lower (dry) altitudinal limit of the UMF has not decreased during the past ca. 500 years.

The strong decline of Melastomataceae up to the present day suggests that the UFL has shifted slightly downslope. This situation is similar to that inferred from the RVM and VP cores, which show that the proportions of the LMF and the UMF remained relatively stable during the period between 880 and 310 B.P. In contrast, the páramo vegetation expanded continuously due to the spread of Poaceae, while the subpáramo vegetation declined as indicated by the progressively more infrequent occurrence of Melastomataceae. The proportions of the LMF and the UMF have remained relatively stable in the RVM and VP areas during the last approximately 300 years. One important difference between these two areas as shown by the pollen records is that *Alnus*, which used to be rare, has become quite frequent in the RVM area. The páramo ecosystem was dominant in the RVM and LNB areas, as shown by the frequent occurrence of Poaceae. The different vegetation types remained relatively stable in the VP area during this period.

The carbon particle concentration has increased in the LNB during the last 900 years. In spite of the very wet local conditions, human activities to promote hunting or grazing could have led to frequent fires. Other activities such as deforestation to provide for a supply of wood, grazing and cultivation may have taken place during this period. Charcoal records indicate that fires occurred at the RVM and VP sites throughout the late Holocene. Two periods of enhanced fire frequency (during 1800 to 1600 and 600 to 400 B.P.) are evident from the RVM core.

The oldest tree-ring record presently available for the PNP dates back to 1840 A.D. It originates from the deciduous species *Cedrela montana* (Meliaceae), the wood of which forms clearly visible annual rings and exhibits cambial activity mainly between January and April (Bräuning et al. 2009). However, *Cedrela* ceases growth activity during dry periods and is thus sensitive to drought (Bräuning 2009). Although the oldest individuals having been found are up to 140 years of age, most trees are not older than 60 years. Since the average correlation between all individual ring-width series averaged in the final chronology is rather low (mean  $r = 0.19$ ), the present dating of *Cedrela* has attained a sufficient level of confidence only for growth having commenced after 1950, when more than 20 series became available for the chronology analysis. The growth of *Cedrela* at the local level is promoted by lower temperatures having occurred during previous year's growing season. This relationship is reversed during April-September of the current growth year (Fig. 5.5c). Since local climate data from the RBSF are only available for the short time period since 1998, we also tested correlations between the tree-ring chronology and regional climatic data and found significantly

negative correlations ( $r = -0.52$ ) with the Southern Oscillation Index (SOI, Fig. 5.5b). Decadal ring-width variations (Fig. 5.5a) may accordingly be related to large-scale atmospheric pressure variations in the tropical Pacific Ocean. A larger quantity of older tree-ring data is nevertheless required to improve the chronology quality for time periods having occurred prior to the 20<sup>th</sup> century.

#### 5.4. Conclusions

During the Late Pleistocene (15,930-11,660 B.P.) grass páramo vegetation dominated the PNP and its surroundings, and the presence of *Plantago rigida* suggests that the area was cold and wet. The minor warming of the climate during the Bølling-Allerød interstadial allowed the expansion of forest taxa (*Hedyosmum* and Moraceae\Urticaceae), and *Polylepis* appeared in the south of Ecuador. A short cold period comprised by the Younger Dryas event (12,800 to 11,500 B.P.) exercised constraints on the *P. rigida* population and promoted the expansion of grass páramo (Poaceae). It is assumed that the UFL was lower at that time than it is nowadays. The climate was warmer and drier than it is today during the early and mid-Holocene (11,660-4280 B.P.), promoting the dominance of forest taxa (Melastomataceae and Asteraceae) and the decline of páramo vegetation, the latter being adversely influenced by frequent fires. An upslope shift in the UFL is suggested by an increase in the proportion of *Polylepis*. The late Holocene was marked by the expansion of subpáramo vegetation which could have led to the UFL upslope shifting. *Polylepis* became rare and almost absent during the Late Holocene due to wetter conditions and frequent fires. The vegetation and fire records of the investigation sites make it evident that fires favored the expansion of grass páramo vegetation and curtailed the expansion of subpáramo vegetation and the upper montane forest. Because fire probably played an important role in determining the upper forest limit during the Late Holocene, it is difficult to conclude whether climate change played an important role in changes in the UFL taking place during this period. The fire events occurred diachronously between sites, suggesting strong anthropogenic influence. Although regional vegetation is influenced by large-scale climate variability, local conditions of temperature, precipitation, wind regimes, radiation, geomorphological features and human land-use history also have a strong impact on vegetation patterns and are important in determining the structure, heterogeneity and distribution of ecosystems.

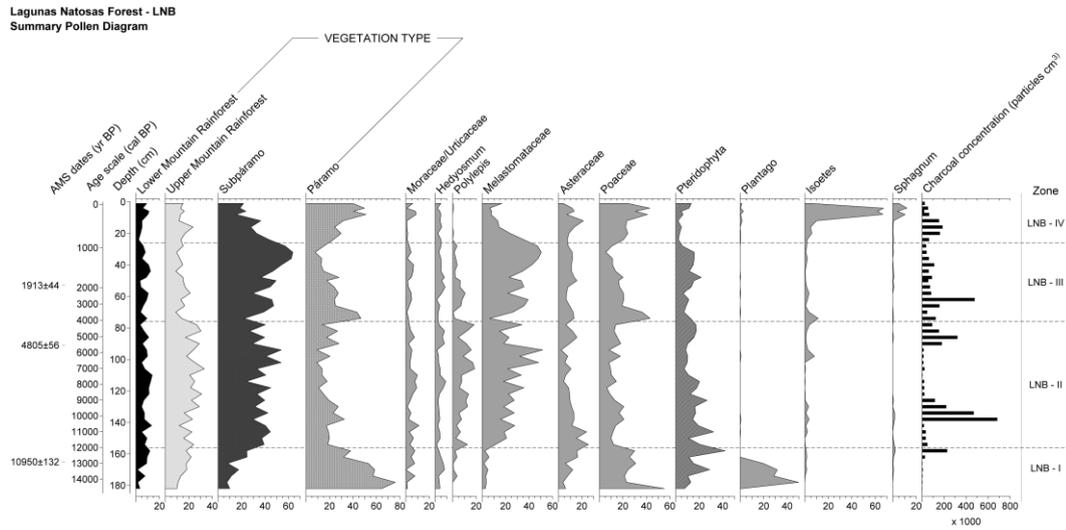
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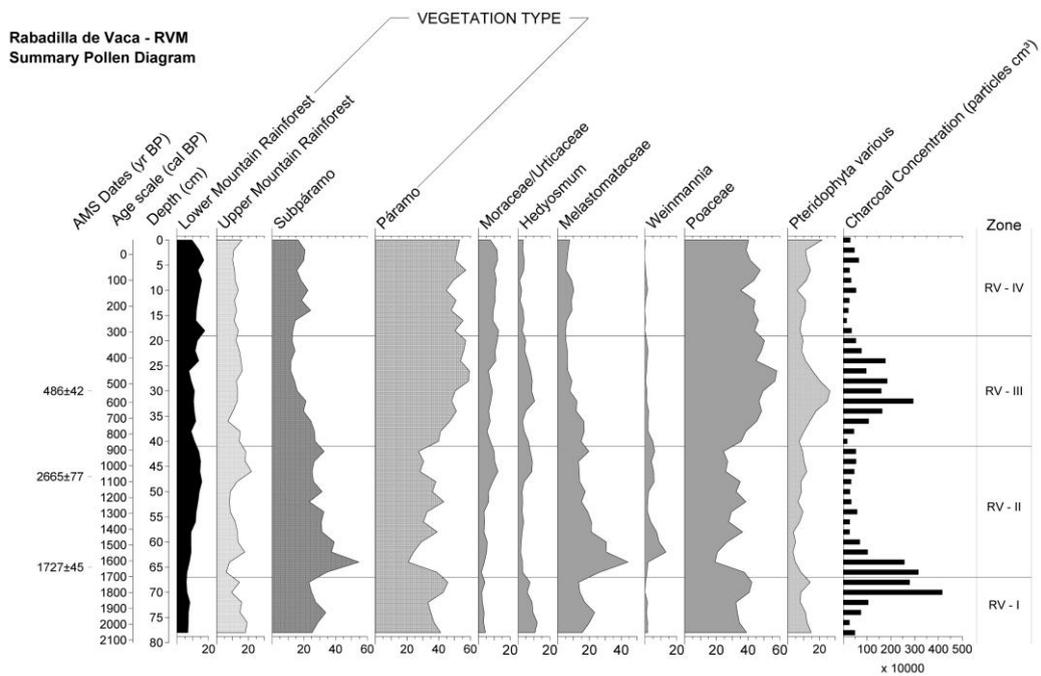
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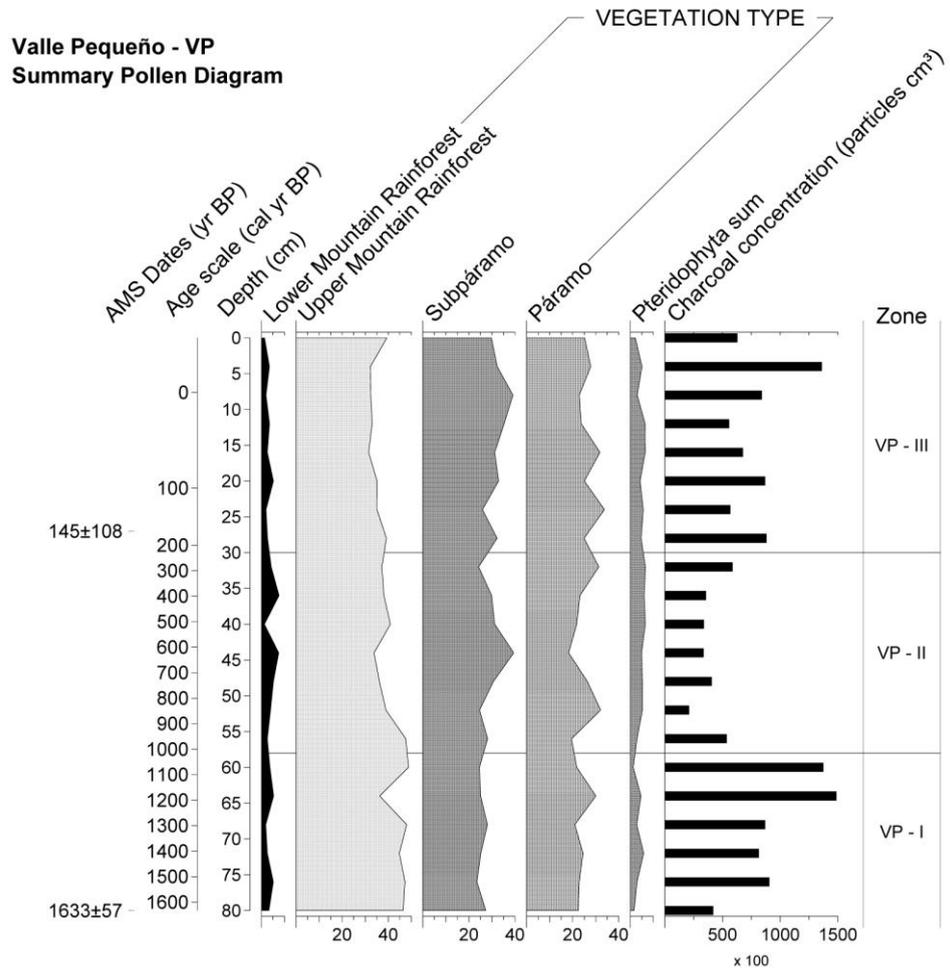


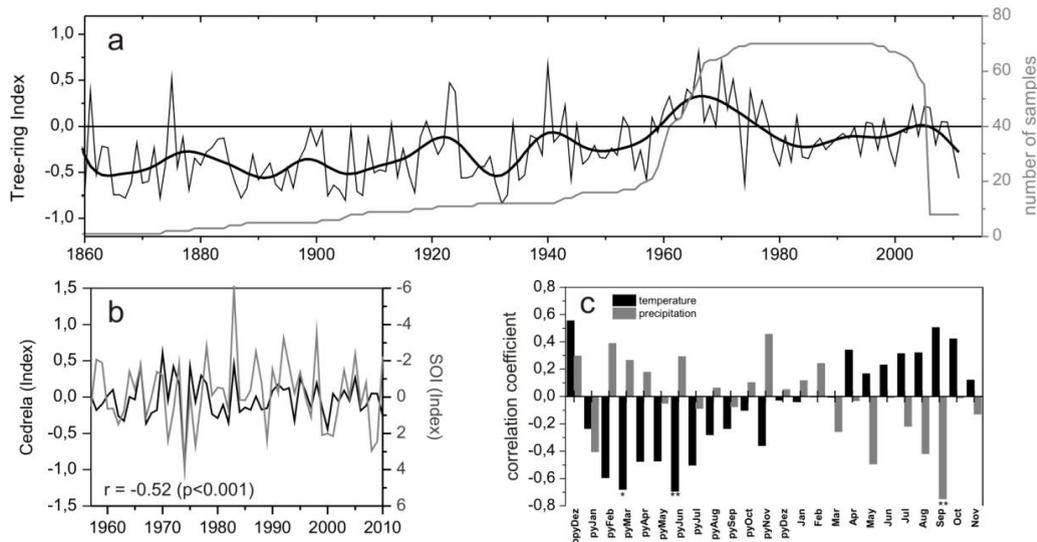


**Fig. 5.2** Analysis of the Lagunas Natosas Forest core (3495 m a.s.l.) showing radiocarbon dates, age scale, ecological groups, values of charcoal concentration and zones.



**Fig. 5.3** Analysis of the Rabadilla de Vaca Mire core (3,200 m a.s.l.), showing radiocarbon dates, sums of ecological groups, records of charcoal concentration and zones.





**Fig. 5.5 a)** Ring-width index chronology of *Cedrelel montana* (thin black line) with 5-year smoothing (thick black line) and number of samples included in the chronology (grey line); **b)** Comparison between the *Cedrelel* ring-width index (black) and variations of the November-February Southern Oscillation Index (SOI; grey); **c)** correlation function diagram between the *Cedrelel* ring-width index and monthly means of temperature and monthly sums of precipitation of local climate station data at the Reserva Biologica San Francisco (RBSF; 1998-2011). Correlations significant at  $p < 0.05$  and  $p < 0.01$  (t-test) are marked with one and two asterisks, respectively. py and ppy correspond to respective months in the year prior to growth or two years prior to growth.

## Chapter VI

### 6. Synthesis

The PNP contributes substantially to the biodiversity hotspot in Ecuador, especially with regards to the divergence zone of the ranges south of the “Nudo de Loja” with its highly complex structures from xeric to hygric vegetation types within a short distance, where a rapid genetic interchange is guaranteed.

For a better understanding of ecosystem dynamics in southern Ecuador since the late Quaternary, palynological studies have been carried out in the PNP region. The records and results from the three cores are presented in this study (Lagunas Natosas, ca. 16,000 cal yr BP; Rabadilla de Vaca, 2100 cal yr BP; and Valle Pequeño, ca. 1600 cal yr BP). Several questions were addressed with the intention to clarify the driving factors influencing the ecosystem dynamics of the Andean Depression: What determined the dynamic of the ecosystem in the past? Which environmental factors have driven possible changes in vegetation and upper forest line (UFL) dynamics? Do natural or anthropogenic factors (fire) play a role in the dynamics of the UFL in the PNP during the late Quaternary?

Additional palaeoecological information provides important new insights and addresses the main research goals introduced in Chapter 1.

#### **Vegetation and Climate Dynamics in the Podocarpus National Park Region during the Late Quaternary**

Most of the areas of the PNP were covered by glaciers during the LGM, which reached areas down to 3000 m elevation. The retreat of glaciers formed U shapes valleys often spotted with small water bodies (ponds, lagoons or lakes) and leaving the bed rocks exposed. During the recorded late Glacial period from ca. 16,000 cal yr BP, in the Lagunas Natosas Forest area (3495 m a.s.l) low values in pollen concentration and influx registered in the studied sediment core suggest a sparse páramo vegetation dominated by Poaceae. Mountain rainforest was probably restricted to small ravines and valleys. The frequent occurrence of pteridophytes and *Plantago rigida* indicate cold and humid conditions during late Glacial period. During the Bølling-Allerød interstadial from 14,700 to 12,700 cal yr BP forest taxa became frequent favoured by a moister and somewhat warmer climate which

allowed also the first establishment of *Polylepis* forest, and a marked decrease of *P. rigida* and Poaceae. However, the influence of the Younger Dryas, a short colder period between 12,800 to 11,500 yr, limited the advance of forest vegetation. Also the presence of clayey sediments with poor organic matter suggests the lack of forest taxa. Under these conditions the UFL was expected to be much lower than today. However, at the end of the late Glacial period, forest taxa population became established in the area with important taxa being *Hedyosmum*, Moraceae-Urticaceae and *Polylepis*.

Since the beginning of the Holocene at 11,500 yr BP until 4280 cal yr BP, the subpáramo vegetation became more frequent (Melastomataceae, *Polylepis* and Asteraceae) and a marked decrease of páramo took place. For the first time relatively large *Polylepis* populations were well represented in this area, allowing an upslope shifting of the UFL. During the early to mid Holocene conditions of between 1.5 to 2° C warmer than today also favoured the development of forest vegetation. But, around 4200 cal yr BP, climate in the Lagunas Natasas Forest area returned to cooler conditions and favoured the expansion of páramo vegetation dominated by Poaceae.

The late Holocene (4300 cal yr BP) until present-day is characterized by a continuous fluctuation between páramo (Poaceae) and subpáramo (Melastomataceae and Asteraceae, dwarf shrubs) vegetation. Around 1200 cal yr BP subpáramo (dwarf shrubs) was frequent; suggesting a moderate increase in temperature and moisture, and *Polylepis* was poorly represented.

The Rabadilla de Vaca Mire record, 60 km north of LNB at the western slope of the PNP, spans the last 2100 cal yr BP. Here, subpáramo was strongly represented by high occurrence of Melastomataceae until 1720 cal yr BP, thereby confirming the indication of wetter and warmer conditions found in LNB. The UFL shift is not evident at this period, since there are no strong changes in forest vegetation in the study area which is even less dominant than in former periods. However, since last 1000 cal yr BP and more intense since 500 cal yr BP, the widespread distribution of páramo vegetation implies moister conditions than during previous times, also corroborated by the occurrence of Cyperaceae, *Isoetes* and *Sphagnum*. The UFL was possibly situated at lower elevations, influenced by the continuous decline of subpáramo vegetation. RVM and VP (16.5 km north of RVM) cores between 880 to 310 cal yr BP, forest taxa remained stable, whereas páramo (Poaceae)

expanded continuously. These environmental conditions, with the dominance of páramo ecosystem and the stable distribution of other vegetation types, remain prevalent until present-day.

### **Fire and Human Impact on Vegetation in the Podocarpus National Park Region**

As can be seen in the RVM records, the presence of carbonized particles in the sediment archives is evident during late Holocene between 1800 and 1600 cal yr BP and 600 to 400 cal yr BP. In VP increased fire frequency occurred during the last 300 years. In the LNB area 60 km south of RVM, evidence of frequent fire activities has been recorded for the last 900 cal yr BP and a marked decrease in *Polylepis* populations is observed. Evidence of human activity is reflected by the high occurrences of *Alnus* in RVM (since ca. 480 cal yr BP) as well as in VP (since ca. 50 cal yr BP). *Alnus* is considered as a pioneer species that colonizes areas after land slide events. Considering the moister and cold conditions of the area during this period, it is assumed that fires were produced by human activities – which include not only hunting, slash and burning, but also logging for fuel supply and infrastructure. This indicates that fires did not occur simultaneously in the whole study area. Nowadays, the study area itself is not inhabited; however, the ecosystem is still used by humans, mainly for grazing and timber extraction.