Vegetation/modern pollen rain relationship along an altitudinal transect between 1920 and 3185 m a.s.l. in the Podocarpus National Park region, southeastern Ecuadorian Andes

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ABSTRACT

To study vegetation/modern pollen rain relationship a total of 41 pollen traps have been installed for one year on an altitudinal transect between 1800 and 3185 m a.s.l. elevation in the montane forest and páramo vegetation type of the ECSF research area, located between Loja and Zamora in the southeastern Ecuadorian Andes.

Results revealed that the altitudinal vegetation gradient of lower montane forest, upper montane forest, subpáramo and páramo is well reflected in the modern pollen rain data.

Principal component analysis (PCA) on the pollen rain data indicate that a high number of pollen and spore taxa are characteristic for one vegetation type or reflect the altitudinal distribution of genera and families of modern vegetation. However, a considerable number of pollen and spore taxa not representing modern vegetation types were identified as well. Wind dispersal is supposed to be responsible for differences found between plant and pollen distribution patterns. Characteristic pollen and spore taxa for the lower montane forest are *Alchornea*, *Heliocarpus* and *Hyeronima*; for the upper montane forest *Cyathea* spp., *Elaphoglossum ciliatum* and *Purdiaea nutans*; and for the subpáramo Cyperaceae, Ericaceae, *Jamesonia* and *Valeriana*.

The position of the modern upper timberline in the research area is reflected in the pollen rain by an increase of subpáramo taxa and a decrease of montane forest taxa.

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1. Introduction

The Ecuadorian Andes harbour one of the most species rich ecosystems on earth (Barthlott et al., 2005). Despite this high biodiversity, habitat loss is a concern for conservation efforts. Huge areas in this region have been strongly affected by humans during the past in particular during the last decades. Conservation of natural vegetation, and less degraded areas as well as sustainable management in areas under land use are urgently needed. To study the highly diverse montane forest and páramo ecosystems in southeastern Ecuador, extended research has been carried out in the framework of the "Deutsche Forschungsgemeinschaft" (DFG) research unit "Tropical Mountain Ecosystems" focusing on the Podocarpus National Park (Beck et al., 2008a).

Studies on modern vegetation and pollen rain provide important background information for the interpretation of fossil pollen records to reconstruct past vegetation changes. Recent studies on vegetation and climate history of the Podocarpus National Park region (Niemann and Behling, 2008; Niemann and Behling, 2009a,b; Niemann et al., 2009; Brunschön and Behling, 2009) demand additional evidence of modern pollen rain data in relation to modern vegetation.

Few pollen rain studies are available from the northern Andes and western Amazonia (Fig. 1): The Sumapaz area, eastern Cordillera of Colombia between 1120 and 4250 m a.s.l. (Melief, 1985), the High Plain of Bogota (Colombia) between 2600 and 3800 m a.s.l. (Hooghiemstra and Cleef, 1984), the Mera site between 300 and 3400 m a.s.l. in Ecuadorian Amazonia (Bush et al., 1990), the Cuyabeno Faunal Reserve in Ecuadorian Amazonia (Bush et al., 2001), Laguna Baja between 2800 and 3800 m a.s.l. in northern Peru (Hansen and Rodbell, 1995), Junin area between 900 and 4600 m a.s.l. in central Peru (Hansen et al., 1984) and Madre de Dios River between 340 and 3530 m a.s.l. in southeastern Peru (Weng et al., 2004). From the southern Ecuadorian Andes, within the so-called Andean depression region (see below), no studies on vegetation/pollen rain relationships are available so far. Therefore, this work is very important for improving the interpretation of the fossil pollen records from this region.

In this study we present modern pollen rain data from tropical Andean habitats to test the hypothesis that pollen rain data can be quantified statistically and we address the following main questions: How is the modern vegetation reflected in the modern pollen rain spectra and are there any key taxa of pollen and spores representing different vegetation types? Is it possible to distinguish between

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Fig. 1. Map of northwestern tropical South America, showing the study site (star) and other locations of greater interest for this study (circles).
OMC (www.aquarius.geomar.de).

different vegetation types to identify the upper timberline position in the study area by modern pollen rain data? How do prevailing pollination systems influence the distribution pattern of modern pollen rain? And finally, what can we learn from modern pollen data for the interpretation of fossil pollen records?

2. Site description

2.1. Location

The Andes of southern Ecuador and northern Peru are part of the Andean depression region (Depression of Giron-Cuenca in Ecuador and of Huancabamba in Peru). The highest peaks of the mountains in this region reach up to about 4000 m a.s.l. Active volcanoes are absent (Richter and Moreira-Muñoz, 2005).

The study area is located within this Andean depression at the eastern escarpment of the eastern Cordillera (Cordillera Real) in the upper Rio San Francisco valley. The study was carried out in the northern part of the Podocarpus National Park inside the Estación Científica San Francisco (ECSF) research area (3° 58′ 30″ S, 79° 4′ 25″ W) between 1800 and 3185 m a.s.l. (Fig. 2). The studied mountain ridge is called Cerro del Consuelo. The ECSF area is adjacent to the main road between Loja (2200 m a.s.l.) in the inter-Andean valley and Zamora (1000 m a.s.l.) at the Amazonian flank. The whole area covers about 1100 ha along a ca. 5 km mountain ridge system orientated north-southwards (Fig. 2).

2.2. Climate

The climate of Ecuador is dominated by the tropical trade wind regime, which is well established in the mid- and higher troposphere,

with strong easterly winds throughout the year. The surface wind field is locally and regionally modified by the complex topography of the Andes and the thermal land–sea contrast at the Pacific coast. The southeastern part of the country, encompassing the ECSF research area, is mainly influenced by easterly winds. Westerly winds occur occasionally in austral summer. The main rainy season lasts from April to August, but rainfall is high throughout the whole year (Beck et al., 2008b). As part of the so-called Andean depression, all summits in the southern Ecuadorian Andes are below the snowline.

The Cordillera Real forms a division that separates the moist eastern Andean slopes facing the Amazon basin from the dry inter-Andean basins (e.g., the Loja- and Catamayo Basin). Between the eastern slopes of the Cordillera Real and the dry valley of Catamayo, which is less than 70 km apart, annual rainfalls drop from over 4000 to 300 mm (Bendix et al., 2004). Studies from Bendix et al. (2008) showed that precipitation and wind speed are strongly positive related to elevation in the ECSF research area (Table 1).

2.3. Vegetation

The description of modern vegetation types and their characteristic vascular plant species of the ECSF research area (Table 2) is based on the fieldwork data of Homeier et al. (2008).

The lower montane forest (LMF) occurs between ca. 1300 and 2100 m a.s.l. with an extremely diverse, two-storied tree stratum and a canopy height up to 30 m. Undisturbed communities of this type can be found particularly on steep slopes with 30° to 50° inclination, as well as up to ca. 2300 m at the bottom of wind-protected river valleys. The upper montane forest (UMF) occurs between ca. 2100 and 2700 m a.s.l., showing a monotypic formation with only one tree stratum. The canopy heights attain up to 25 m. Between ca. 2700 and 3100 m a.s.l. the elfin-forest or subpáramo (SUB) vegetation occurs. This vegetation type forms the upper timberline ecotone with a canopy height of 6–8 m. The páramo (PAR) occurs in the crest regions of the Cordillera Real above the upper timberline between ca. 3100 and 3700 m a.s.l. and attains heights of up to 2 m.

For describing the upper boundary of closed forest different terms exist. We will use here exclusively the term of upper timberline (UTL) as it is generally used within the "Tropical Mountain Ecosystems" research unit (Richter et al., 2008).

The position of the UTL varies considerably along the neotropical cordilleras. High neotropical timberlines are found between 1° N and 17° S where the UTL is located between 4000 and 4800 m a.s.l. and often represented by *Polylepis* woodlands. Open *Polylepis* stands even can occur up to 5100 m a.s.l. (Richter et al., 2008). Bakker et al. (2008) show that the modern UTL in the Guandera Biological Reserve (0°36′ N), near the Ecuadorian–Colombian border, is at ca. 3600 m a.s. l. In contrast to the high neotropical timberline, the Andean depression region (3°–7° S) holds an especially low neotropical timberline between 2600 and 3360 m a.s.l. (Weigend, 2002). At the El Tiro-Pass, which is only 10 km west of ECSF research area, the UTL is between 2790 and 2820 m a.s.l. In the upper part of the ECSF research area, the UTL is between 2730 and 3040 m a.s.l. (Richter et al., 2008).

3. Materials and methods

3.1. Vegetation

A detailed vegetation survey within the ECSF research area along the altitudinal gradient of the Cerro del Consuelo (Table 3a) is recently available (Diertl, personal communication, 2009) and is used for the ecological grouping of pollen taxa. A set of 24 plots (2×50 m), following the same trail system as used for the pollen traps, gives detailed information about the surface cover of all terrestrial plants recorded (method after Gentry, 1995). The plots cover an altitudinal range between 2029 and 3011 m a.s.l. and represent all described
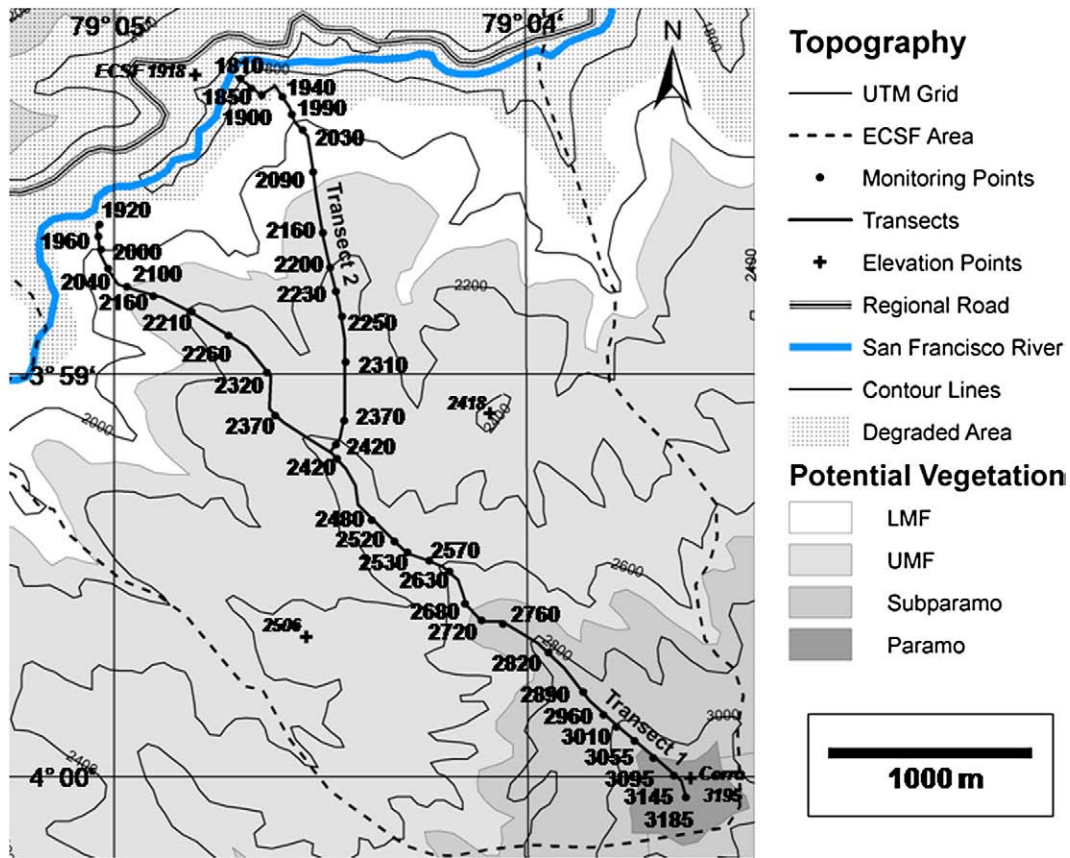
Fig. 2. Map of the ECSF research area, showing the potential vegetation and the sampling sites of the modern pollen rain, including the elevation.
Mapa Topográfico del Ecuador 1:50.000, Hoja Loja Sur 3781-I.

vegetation types (LMF, UMF, SUB and PAR). Within the LMF only one plot is available, what has to be considered for comparing data between the vegetation types. Important pollen taxa without an appropriate plant record in the vegetation study of Diertl (personal communication, 2009) were grouped (Table 3b) using available data from Homeier and Werner (2005), Lehnert et al. (2008) and Marchant et al. (2002).

3.2. Modern pollen rain spectra

In the ECSF research area a total of 41 pollen traps (11.5 cm long plastic tubes with 2.7 cm in diameter, Fig. 3) were installed ca. 20–30 cm above the ground. The pollen traps were filled with ca. 5 ml glycerine and covered with a synthetic net. The glycerine assures that the pollen remains in the trap during times of high rainfall, which might cause overflows of the traps. Elevation distance between the traps is ca. 50 m in the range of 1800 to 3185 m a.s.l. along an existing trail system. After one year, (March 2005 to March 2006) the pollen traps were recollected. The ca. 5000 m long transect 1 starts ca. 70 m above the valley bottom of the San Francisco river (1920 m a.s.l.) and reaches the crest region of the Cerro del Consuelo at 3185 m a.s.l. Transect 2 starts at the valley bottom of San Francisco river (1810 m a.s.l.) and is connect to Transect 1

at 2420 m a.s.l. (Fig. 2, Table 4). The lowermost samples of transect 2 are located in a disturbed area, therefore this pollen traps have to be excluded from further analysis. Transect 2 in general represents replicated pollen data for the lower part of transect 1. Hence, for the analysis only data derived from transect 1 were used to avoid any disequilibrium in the dataset. Consequently, we present in this study exclusively pollen data of transect 1 with 27 pollen traps installed. The pollen rain data of transect 2 will be used in further studies, focusing on the comparison between pollen rain data within same vegetation types.

The contents of the pollen traps were concentrated in a centrifuge and treated by acetolysis. Before treatment, exotic *Lycopodium* spores were added to each sample for calculation of pollen accumulation (pollen/cm^2/year). About 300 pollen grains were counted for each sample. The pollen sum includes trees, shrubs, and herbs and excludes fern spores. Pollen identification relied on the reference collection from the third author with about 3000 neotropical species (Behling, 1993), an Ecuadorian reference collection with about 300 species (collected during fieldwork and from the herbarium of the ECSF research station) and literature (Hooghiemstra, 1984).

The ecological grouping of the identified pollen taxa into LMF, UMF, SUB and PAR follows available data after Diertl (personal

Table 1
Meteorological data of four sites of the ECSF research area, after Bendix et al. (2008).

Site name	Elevation (m a.s.l.)	Rain (mm yr^{-1})	Horizontal dep. (mm yr^{-1})	Sum (mm yr^{-1})	Temperature (min. °C)	Temperature (max. °C)	Aver. wind speed (m s^{-1})
ECSF research station	1960	2176	121	2297	5.0	29.1	1.0–2.0
Plataforma	2270	2193	210	2403	–	–	–
TS1	2660	4779	527	5306	4.7	25.5	0.5–1.5
Cerro de Consuelo	3180	4743	1958	6701	2.6	20.7	4.5–7.5

Table 2
Characteristic vascular plant species for the different vegetation types in the ECSF research area, after Homeier et al. (2008).

Lower montane forest (1300–2100 m a.s.l.)	Upper montane forest (2100–2700 m a.s.l.)	Subpáramo (elfin forest) (2700–3100 m a.s.l.)	Páramo (3100–3700 m a.s.l.)
Alzatea verticillata (Alzateaceae)	*Ilex rimbachii* (Aquifoliaceae)	*Ilex* spp. (Aquifoliaceae)	*Gynoxis* spp. (Asteraceae)
Chamaedorea pinnatifrons	*Hedyosmum* spp. (Chloranthaceae)	*Puya eryngioides* (Bromeliaceae)	*Puya eryngioides*
Dictyocaryum lamarckianum	*Clethra revoluta*	*Hedyosmum cumbalense*	*Puya nitida* (Bromeliaceae)
Wettinia maynensis (Arecaceae)	*Purdiaea nutans* (Clethraceae)	*Hedyosmum scabrum* (Chloranthaceae)	*Hypericum decandrum* (Clusiaceae)
Piptocoma discolor	*Clusia ducu*	*Clethra ovalifolia* (Clethraceae)	*Rhynchospora vulcani* (Cyperaceae)
Mikania spp. (Asteraceae)	*Tovomita weddeliana* (Clusiaceae)	*Clusia elliptica* (Clusiaceae)	*Befaria resinosa*
Tabebuia chrysantha (Bignoniaceae)	*Weinmannia pinnata*	*Weinmannia cochensis*	*Disterigma pentandrum*
Vismia tomentosa (Clusiaceae)	*Weinmannia* spp. (Cunoniaceae)	*Weinmannia loxensis*	*Gaultheria erecta*
Cyathea caracasana (Cyatheaceae)	*Cyathea bipinnatifida* (Cyatheaceae)	*Weinmannia rollottii* (Cunoniaceae)	*Gaultheria reticulata*
Inga acreana	*Befaria aestuans* (Ericaceae)	*Gaultheria reticulata* (Ericaceae)	*Vaccinium floribundum* (Ericaceae)
Inga spp. (Fabaceae)	*Alchornea grandiflora* (Euphorbiaceae)	*Escallonia myrtilloides* (Grossulariaceae)	*Escallonia myrtilloides* (Grossulariaceae)
Nectandra lineatifolia	*Macrocarpaea revoluta* (Gentianaceae)	*Orthrosanthus chimborazensis* (Iridaceae)	*Brachyotum andreanum* (Melastomataceae)
Nectandra membranacea	*Eschweilera sessilis* (Lecythidaceae)	*Persea ferruginea*	*Neurolepis asymmetrica*
Ocotea aciphylla (Lauraceae)	*Licaria subsessilis*	*Ocotea infravoveolata* (Lauraceae)	*Neurolepis elata*
Miconia imitans	*Ocotea benthamiana*	*Gaiadendron punctatum* (Loranthaceae)	*Neurolepis laegaardii*
Miconia punctata (Melastomataceae)	*Persea ferruginea* (Lauraceae)	*Graffenrieda harlingii* (Melastomataceae)	*Chusquea neurophylla* (Poaceae)
Cedrela montana (Meliaceae)	*Graffenrieda emarginata*	*Myrteola phylicoides* (Mytraceae)	*Monnina arbuscula* (Polygalaceae)
Ficus spp.	*Graffenrieda harlingii*	*Chusquea falcata*	*Valeriana microphylla*
Morus insignis	*Tibouchina lepidota* (Melastomataceae)	*Chusquea scandens* (Poaceae)	*Valeriana plantaginea* (Valerianaceae)
Sorocea trophoides (Moraceae)	*Myrica pubescens* (Myricaceae)	*Hesperomeles ferruginea* (Rosaceae)	
Piper spp. (Piperaceae)	*Myrsine coriacea* (Myrsinaceae)	*Styrax foveolaria* (Styracaceae)	
Heliocarpus americanus (Tiliaceae)	*Calyptranthes pulchella*	*Symplocos sulcinervia* (Symplocaceae)	
	Myrcia spp. (Mytraceae)	*Gordonia fruticosa* (Theaceae)	
	Podocarpus oleifolius		
	Prumnopitys montana (Podocarpaceae)		
	Dioicodendron dioicum		
	Palicourea spp. (Rubiaceae)		
	Matayba inelegans (Sapindaceae)		
	Drimys granadensis (Winteraceae)		

communication, 2009), Homeier et al. (2008), Homeier and Werner (2005), Lehnert et al. (2008) and Marchant et al. (2002). Pollen and spore data are presented in pollen diagrams as percentages of the pollen sum. The software TILIA and TILIAGRAPH (Grimm, 1987) were used to plot the pollen and spore data. Cluster analysis (CONISS, Grimm, 1987) of pollen and spore taxa was used to identify the pollen zones (Fig. 4a and b).

3.3. Multivariate analysis

Principal component analysis (PCA) as an indirect ordination method was used for the statistical analysis of pollen and spore data and the relationship between modern pollen rain and vegetation. The applicability of PCA was verified by a prior detrended correspondence analysis (DCA), which revealed a relatively low gradient length of 1.7 SD. To reduce highly local influences and over-representation of pollen taxa PCA was based on pollen percentages of taxa occurring in at least two samples and with values >1% in at least one sample. This resulted in a set of 53 pollen and spore taxa included in the ordination. A log-transformation for the percentage data was chosen to reduce

the effect of generally over-represented taxa in the data set. Analysis was carried out by using the Canoco for Windows Version 4.54 software and ordination diagrams were prepared with CanoDraw for Windows 4.13 (ter Braak and Šmilauer, 2002). The same analytical method tested with accumulation rates revealed comparable results. Thus, percentage data were chosen for analysis and interpretation as the data are supposed to be more stable.

4. Results

4.1. Modern pollen rain transect

Percentage data of the most abundant and important 38 pollen and spore taxa out of 129 identified taxa are displayed in Fig. 4a. Additionally, a summary diagram (Fig. 4b) displays percentages of the vegetation types for every sample based on the ecological grouping of all pollen and spore taxa. The zonation of the diagrams supported by cluster analysis represents the distribution limits of the different vegetation types and the zone names were given accordingly.

Table 3a

Mean percentages of selected plant taxa over the altitudinal gradient and their ecological grouping. The grey shaded zones show the main distribution of the different taxa. Respectively, the ecological group given for each taxon is italicized if the taxa occur in more than one vegetation type.

Diertl (personal communication, 2009).

| | Elevation (m a.s.l.) Vegetation type | 2029 LMF | 2111 | 2256 | 2225 | 2334 | 2336 | 2411 | 2425 | 2415 | 2517 | 2515 | 2518 | 2595 | 2594 | 2599 | 2748 | 2758 | 2816 | 2837 | 2904 | 3008 | 3106 | 3142 | 3111 |
								UMF											SUB				PAR		
Taxa	**Ecol. group**																								
Alchornea (2 sp.)	*LMF*, lower UMF	3.4	2.4	2.7	3.3	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asteraceae (50 sp.)	UMF, *SUB*	3.5	3.1	2.8	5.5	3.1	2.8	2.5	2	3.1	1.5	2.9	3.5	1.6	2	2	7.3	12.7	3.8	10.3	1.1	1.1	2.2	0.3	1.9
Calceolaria (*fusca*)	PAR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
Clusia (8 sp.)	*UMF*, SUB	0.6	16.3	8	6.7	6.6	5.2	5.8	4.5	4.7	7.1	7.2	5.6	2.5	3.1	4	1.9	1.7	6.4	2.8	5.9	6.9	0.2	1.1	0.9
Cyathea (7 sp.)	LMF, *UMF*	10.9	0	11.9	1.3	5	7.9	11.7	3.3	7.3	1	1.2	1.9	0.3	3.8	1.9	0	0.7	0.5	0	0.6	0	0	0	0
Cyperaceae (2 sp.)	SUB	0	0	0	2.9	0.9	1.1	2.1	0	0	0.2	0.3	0.3	0.8	0.4	1.1	1.9	11.1	0.2	5.2	0.4	1.2	0.8	2.3	0
Elaphoglossum ciliatum	Lower UMF	0	3.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ericaceae (30 sp.)	UMF, *SUB*, PAR	3	14.7	10.9	9.1	9.3	11.8	7.1	8.2	6.6	8.1	13.7	11	10.9	8.1	9.3	7.1	20.7	12.9	21.7	12	18.8	9.2	14.1	13.6
Eschweilera (*sessilis*)	UMF	0	0	0	0.8	0	0.5	0.4	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hedyosmum (5 sp.)	LMF, *UMF*, SUB	5.3	0.1	2.5	2.2	1.3	1.4	1.4	0.7	1	0.7	2.6	0.1	0.2	0.6	0.5	0.8	1.3	2.4	2.3	0.5	1	0	0	0
Hyeronima (2 sp.)	LMF, lower UMF	3.4	8.1	0	0	0	0.4	0.6	0	0.7	0	0	0.2	0.2	0.2	0.2	1	4.2	0.2	0	0	0	0	0	0
Ilex (15 sp.)	UMF, *SUB*	0.7	0	0.6	1.2	2.9	2.4	0	3.2	0.9	2.6	2.7	4	2.1	0.6	0.2	1	3.4	3.3	4.9	1.7	2.6	0	0.7	1.7
Lycopodium (3 sp.)	UMF, SUB, PAR	0	0	0.7	0.2	1.2	1.3	0	0	0	0	0.2	0	1	0.3	0.3	1.5	3.2	0.9	1.3	0.1	0.4	0.7	1.1	1.4
Melastomataceae (54 sp.)	LMF, *UMF*	29.2	15.4	25.9	8.2	17.7	20.5	14.2	17.1	24.8	16.2	15.3	19.4	9.5	11.6	10.1	5.9	9.7	4.3	4.9	8.2	10.1	6.1	7.4	9.7
Mikania (17 sp.)	LMF	2.1	0.6	0.5	0	1.4	0	0.6	0.9	0.6	0.1	0.4	0.8	0.1	0.7	0.3	0.1	0.3	0.4	0.7	0	0.1	1.2	0.1	0.1
Moraceae (3 sp.)	*LMF*, lower UMF	0.2	0.9	1.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrica (*pubescens*)	SUB	0	0	0	0	0	0.2	0	0	0	0.1	0	0	0	0	0	0	4.8	0	1.9	0	0	0	0	0
Myrsine (3 sp.)	*UMF*, SUB, PAR	0	1.2	0.8	1.1	3.6	4.8	0.3	0.4	0.6	1.8	1.4	0.8	0.8	0.8	0.6	2.8	0.1	0.5	0.2	0	0.1	1	1.1	3.2
Poaceae (11 sp.)	Upper UMF, SUB, *PAR*	1.9	3.7	3.6	0	0.6	0.1	2.9	1.6	2.2	6.1	5.8	3.4	11.8	4.6	12	9.9	13.9	15.7	6.8	7.3	6.3	20.8	16.3	14.9
Podocarpus (*oleifolius*)	*UMF*, SUB	0.3	2.8	3.6	3	0.8	0.7	0	1	0	0	0	0	0.3	2.4	0	0	0	4.1	0.9	3.7	3.4	0	0	0
Purdiaea nutans	UMF	0	0	13.3	15.1	8.4	15.6	9	8	5.4	10.8	7.6	6.1	9.8	11.2	3.8	0	1.6	0.4	0	0	0	0	0	0
Symplocaceae (10 sp.)	*UMF*, SUB	0	0	0.7	0	0.3	1.2	0	0.4	2.4	0.6	0.6	0.4	0.9	0.7	1.3	0.2	0.3	0.4	0	1.3	0.8	0.3	0	0
Valeriana (2 sp.)	*SUB*, PAR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0.3	0.2	0	0.5	0
Viburnum (2 sp.)	UMF	0	0	0.6	0	0.3	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Weinmannia (11 sp.)	*UMF*, SUB, PAR	0.5	0.8	2	0.7	2.6	4.7	0.9	5.9	1.4	2.3	3.7	3.6	3.3	2.1	4.1	1.7	0.2	1.9	2.5	3.6	6.8	2.9	2.5	3.1
Xyris (*subulata*)	SUB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.4	0.8	0	18	0.4	0.6	0.8	0.7	0

Table 3b
Additional plant taxa and their ecological grouping.
Homeier and Werner (2005), Lehnert et al. (2008) and Marchant et al. (2002).

Taxa	Vegetation type	Distribution (m a.s.l.)	Reference
Acalypha (2 sp.)	LMF	1800–2000	Homeier and Werner (2005)
Alnus	Upper montane rainforests	–	Marchant et al. (2002)
Cecropia (4 sp.)	*LMF*, UMF	1800–2700	Homeier and Werner (2005)
Celtis (1 sp.)	LMF	1850	Homeier and Werner (2005)
Clethra (3 sp.)	LMF, *UMF*	1800–2700	Homeier and Werner (2005)
Croton (1 sp.)	LMF	1900	Homeier and Werner (2005)
Heliocarpus (1 sp.)	LMF	1800–2000	Homeier and Werner (2005)
Jamesonia (1 sp.)	SUB	2900	Lehnert et al. (2008)
Piper (30 sp.)	LMF, lower UMF	1800–2300	Homeier and Werner (2005)
Polystichum (4 sp.)	LMF, UMF	1800–1900, 2500–2600	Lehnert et al. (2008)
Styrax (3 sp.)	*UMF*, SUB	2100–2500, 2900–3100	Homeier and Werner (2005)

Table 4
Site specific data of transects 1 and 2 of modern pollen rain.

Site name	Elevation (m a.s.l.)	Length (m)	Number of ident. taxa	Number of pollen traps	Vegetation type
Transect 1	1920–3185	ca. 5000	129	27	LMF, UMF, Subpáramo, páramo
Transect 2	1810–2420	ca. 2300	128	14	LMF, UMF

Pollen taxa from different vegetation types (Fig. 4a and b) show a relatively stable representation in zone LMF (ca. 1920–2100 m a.s.l.) and UMF (ca. 2100–2700 m a.s.l.). While in zone SUB (ca. 2700–3100 m a.s.l.) and PAR (>3100 m a.s.l.) pollen taxa from the UMF decreased and SUB/PAR pollen taxa strongly increased. Pteridophyta spores show their highest amounts in zone LMF and UMF, below ca. 2500 m a.s.l., and decrease with altitude. Pollen and spore accumulation is highest in Zone LMF (Fig. 4b).

4.2. Multivariate analysis

PCA displays the pollen traps along the first axis, which strongly correlates (98.5%) with the altitudinal gradient, revealed by a secondary analysis including elevation as environmental variable (Fig. 5a). The first two axes explain 36.2% of the total variance in the dataset (axis eigenvalue 0.23, axis 2 eigenvalue 0.12). The ordination diagram of the pollen traps indicates according to the elevation gradient the different vegetation types. Pollen traps situated closed

together along the first axis represent the same vegetation type as illustrated in Fig. 5a. Based on the results of the PCA (Fig. 5b) 10 key taxa (capital letters) out of the complex pollen assemblage were identified to characterize the vegetation types. Another 11 taxa (lower case letters) show a good correlation with the present vegetation over the altitudinal distribution. A set of 16 important pollen taxa (italics) displayed in the diagram show no statistical relation with the vegetation distribution or a very low influence within the total dataset. Among the remaining 16 taxa, which were included in the analysis but not shown in the ordination diagrams, are taxa of very low influence. These less important pollen and spore taxa might correspond to plants with a wide altitudinal distribution and do not represent a particular vegetation type. For a better understanding how the pollen rain reflects the actual vegetation, PCA results were shown in an additional ordination diagram (Fig. 5c), displaying the position of the pollen taxa relative to the vegetation types.

5. Interpretation and discussion

5.1. Vegetation/modern pollen rain relationship in the ECSF research area

The comparison of plant genera and families distribution (Tables 3a and 3b) with the respective modern pollen rain taxa (Fig. 4a and b) allows to understand the vegetation/modern pollen rain relationship. Multivariate analysis results (Fig. 5a–c) classified pollen and spore taxa (Table 5) according to their correlation with the modern vegetation and environmental conditions.

The first group holds pollen taxa representing a single vegetation type. Therefore, these taxa were defined to be key taxa ("++" in Table 5). The second group contains important pollen and spore taxa ("+" in Table 5) following the altitudinal distribution of plant genera and families of modern vegetation. This means that pollen and spore taxa of this group represent plant distribution patterns but do not reflect single vegetation types. The third group of pollen and spore taxa ("−" in Table 5) does not reflect the modern vegetation pattern or are taxa of minor influence for the differentiation between the vegetation types. This is either caused by very low pollen frequencies of the different taxa (Figs. 4a and 5b) or by a different pollen distribution compared to the respective plants (Fig. 5c). For the interpretation of the modern pollen rain data it has to be considered that some pollen traps were located beneath individual plants contributing substantially to the pollen accumulation. This causes under-representation of other taxa in the percentage diagram. Examples for high values of a single pollen taxon in one pollen trap (Fig. 4a) are found for Symplocaceae (38% at 2630 m a.s.l.), Cyperaceae (65% at 3145 m a.s.l.), Melastomataceae (60% at 3185 m a.s.l.) and *Lycopodium cernuum* type (75% at 2480 m a.s.l.). These local effects should be neglected when inferring general trends.

Important key taxa for the LMF are *Alchornea*, *Heliocarpus* and *Hyeronima*; for the UMF *Cyathea* spp., *Elaphoglossum ciliatum* and *Purdiaea*; and for SUB Cyperaceae, Ericaceae, *Jamesonia* and *Valeriana*. Key taxa for PAR could not be defined, which might be due to the low number of recorded pollen and spore taxa (in total 7 taxa) representative for PAR vegetation. Additionally, this few taxa are represented by low percentages. Therefore, PAR taxa which are
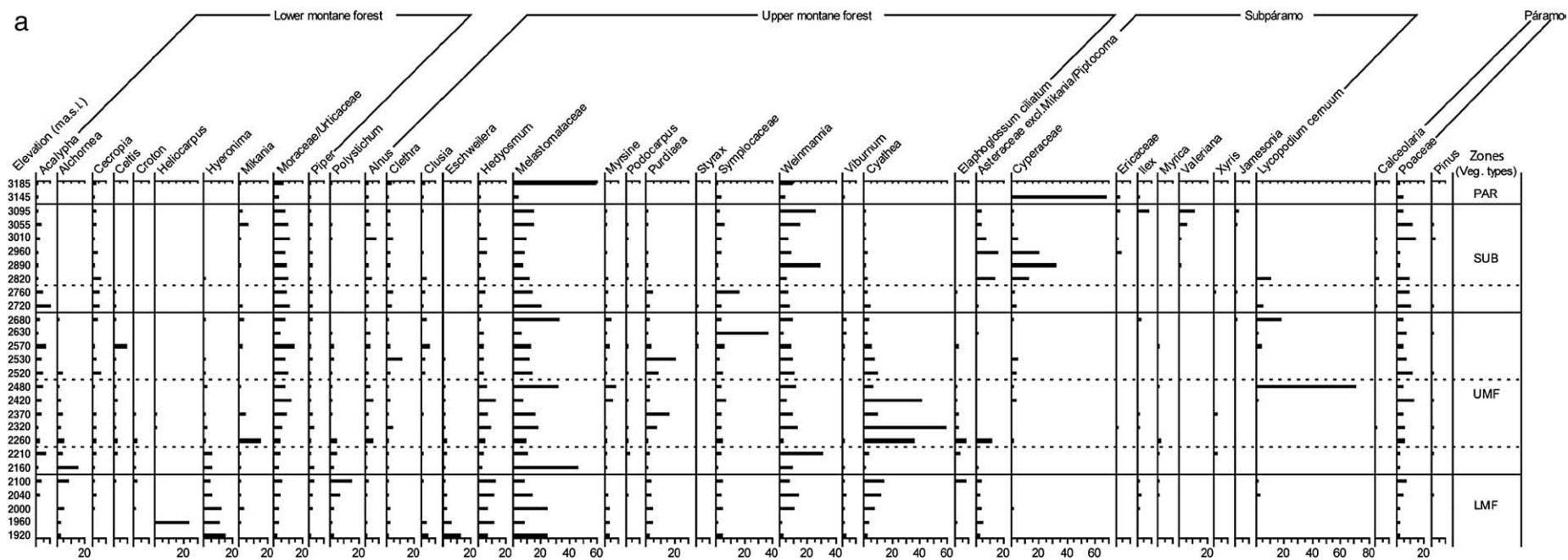

Fig. 3. Photograph of a pollen trap.

Fig. 4. a: Pollen percentage diagram of modern pollen rain (transect 1 (1920–3185 m a.s.l.)), showing selected pollen taxa grouped into lower montane forest (LMF), upper montane forest (UMF), subpáramo (SUB) and páramo (PAR).
b: Summary diagram of modern pollen rain (transect 1 (1920–3185 m a.s.l.)), showing sums of ecological groups, the pollen sum, the pollen and spore accumulation and the CONISS cluster dendrogram.
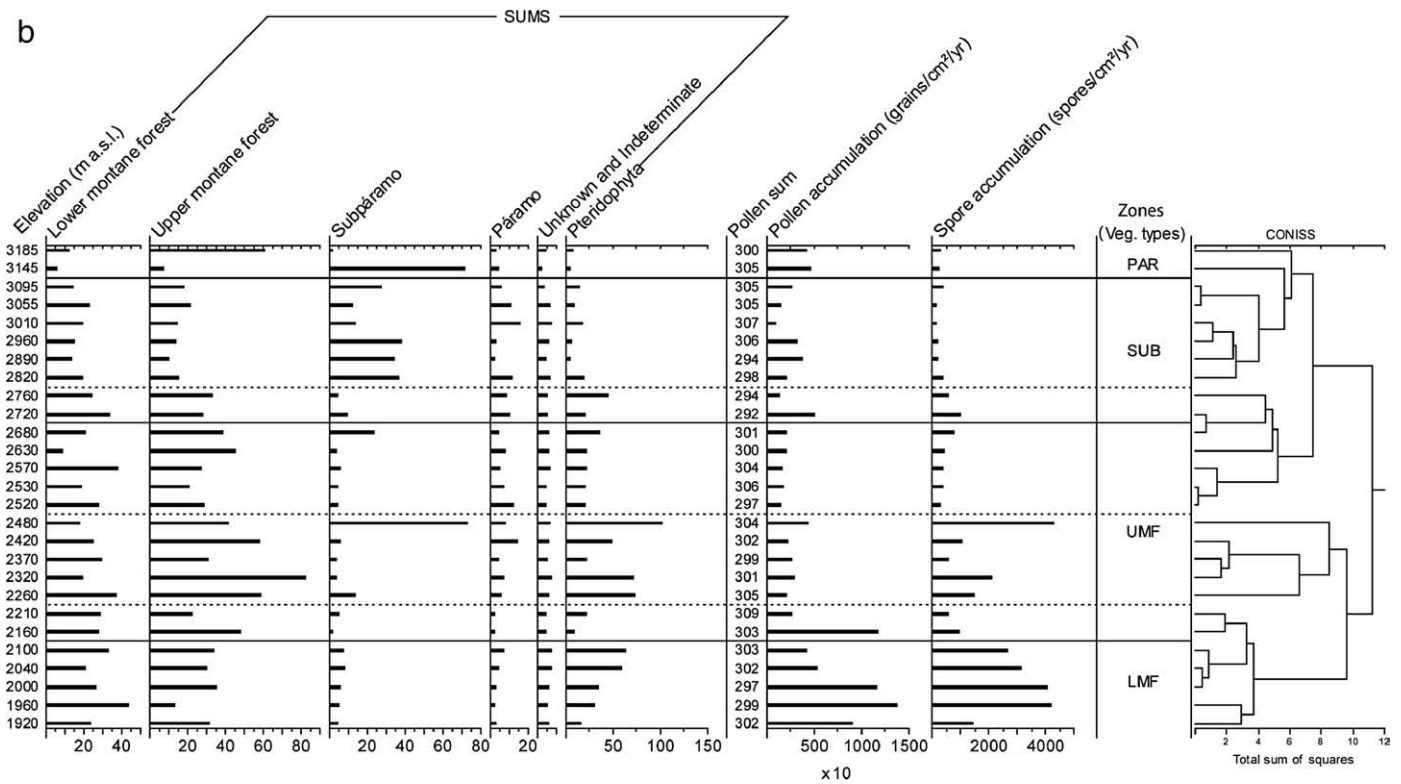
Fig. 4 (*continued*).

expected to be common in the uppermost two samples within the PAR vegetation are under-represented in the pollen rain. Key taxa of the study site are plants with a narrow distribution within only one vegetation type. This is represented for the key taxa in the modern vegetation as well as in the pollen rain. Accordingly, the pollen dispersal of these taxa seems to be restricted to the local occurrences of the plants. For *Purdiaea* this can be explained by the pollination system, as the plant is animal pollinated.

Important taxa not representing a single vegetation type, but following the altitudinal distribution of genera and families of modern vegetation are Asteraceae, *Clusia*, *Hedyosmum*, *Ilex*, Melastomataceae, *Myrsine*, Poaceae, *Styrax*, Symplocaceae, *Weinmannia* and *Lycopodium cernuum*.

Poaceae are mostly common in PAR vegetation. Pollen of Poaceae generally occurs more frequently in higher elevations, shown by the position in the ordination diagram between SUB and UMF, but highest values were not found in PAR, as expected. A relatively high pollen proportion of Poaceae (5–10%) in the UMF vegetation type relates either to the occurrence of forest grasses, with high pollen production, or to wind transport from disturbed areas around the ECSF research area, where Poaceae prefer to grow. Comparable results were found in other studies, e.g. pollen rain data from the Mera site in Ecuadorian Amazonia show a high representation of Poaceae (up to 70%) between 2100 and 2800 m a.s.l., which may be a result of local pollen input to moss cushions and presumably represents forest grass (Bush et al., 1990). Surface samples from the Junin area in central Peru show higher pollen representation of Poaceae (40–60%) in the forest zones (up to 3200 m a.s.l.) than in the shrub land above, which may be attributed to agricultural disturbance (Hansen et al., 1984).

Pollen of Melastomataceae is found in almost same frequencies all over the altitudinal transect. This is also shown for modern vegetation (Table 3a). Melastomataceae represents one of the most species rich families (55 species, 10 genera) in the study area (Homeier and Werner, 2005), what might explain the wide distribution range. *Weinmannia* and *Hedyosmum* are also examples of plants/pollen with

a wide distribution range (Table 3a, Fig. 4a), which results to a low influence of these taxa for determining vegetation type limits.

Important pollen taxa not representing a certain vegetation type and not following the altitudinal distribution of modern vegetation are *Acalypha*, *Alnus*, *Calceolaria*, *Cecropia*, *Celtis*, *Clethra*, *Croton*, *Eschweilera*, *Mikania*, Moraceae/Urticaceae, *Myrica*, *Piper*, Podocarpus, *Viburnum*, *Xyris* and *Polystichum*.

Multivariate analysis showed the highest pollen occurrence of LMF taxa *Acalypha*, *Celtis*, *Cecropia*, *Croton*, *Mikania*, Moraceae/Urticaceae and *Piper* in the UMF and in the SUB/PAR vegetation type. This indicates that pollen rain and pollen distribution of these taxa does not reflect the local vegetation pattern. Pollen of the UMF taxa *Clethra* shows highest occurrence in the SUB/PAR vegetation type (Fig. 5c). The comparison of modern vegetation distribution in the ECSF research area and its pollen rain suggests a transport of pollen to higher elevations, leading to an over-representation of lowland taxa in the UMF and SUB/PAR vegetation types. Strong easterly winds, which blow up the Rio San Francisco valley most likely transport pollen to high elevations. This upslope transport is evident in the statistical analysis as described.

Bush (1991) showed that different types of tropical lowland vegetation produce characteristic and identifiable pollen rains, separating igapo, varzea, terra firme, semi-deciduous and cerrado sites. Data from Cuyabeno in Ecuador and Manaus in Brazil (Bush et al., 2001) also provide a caution by ecological factors such as climate or soil type. In contrast, tropical highland vegetation offers one more complex dimension — the altitudinal gradient, influenced by local wind regimes. Due to the extraordinary high wind speed and prevailing eastern wind direction within the study area a relatively high number of different pollen taxa seems to be widely wind dispersed to higher elevations. This effect might be extremely significant for the pollen rain distribution pattern in the ECSF area compared to other pollen rain studies.

Studies from tropical Andes over an altitudinal gradient show that wind transport over longer distances have to be taken into account.
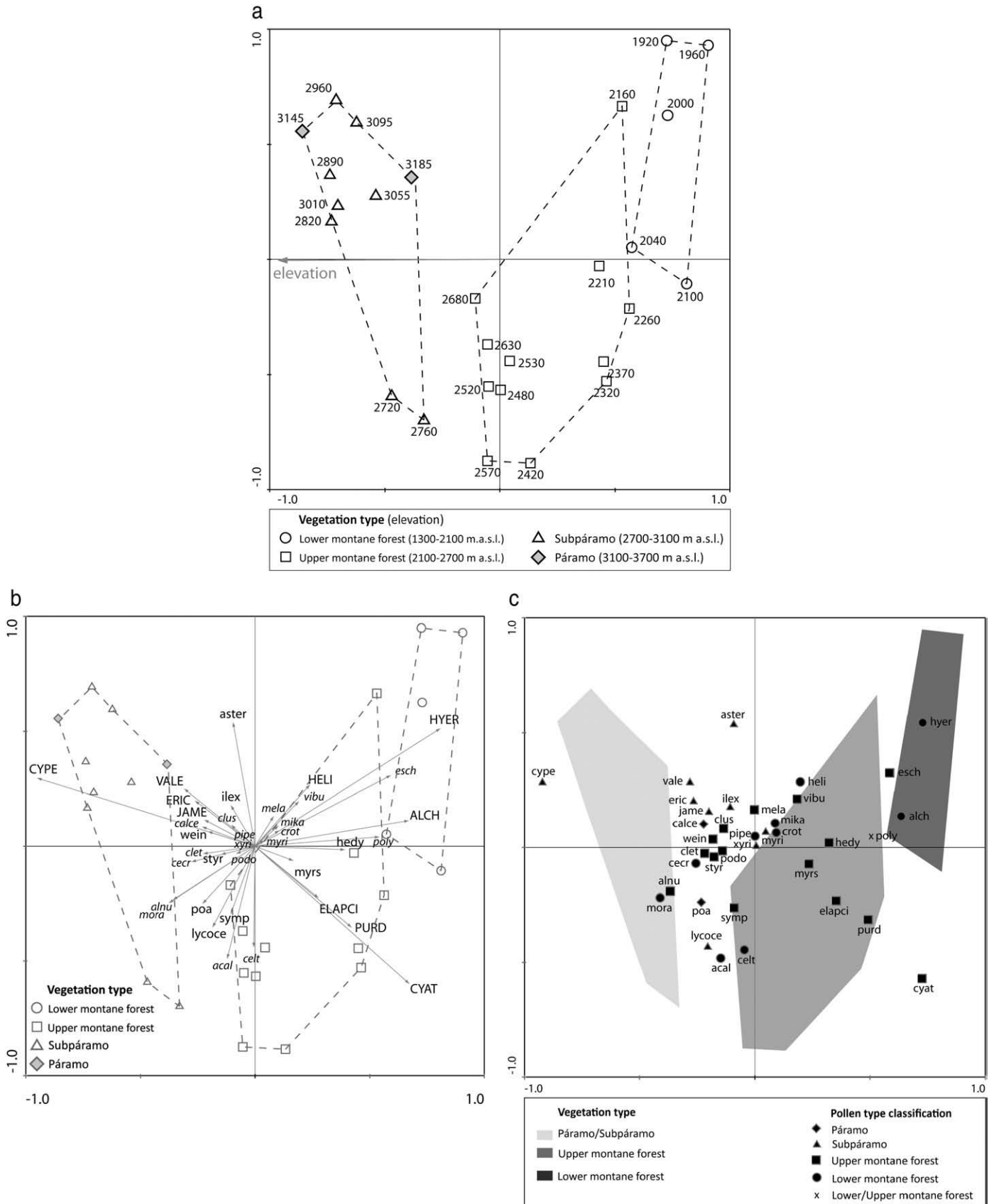
Fig. 5. a: Ordination diagram (PCA) showing the elevation for all pollen traps and the respective vegetation type after Homeier et al. (2008). The first axis is positive correlated with the altitudinal gradient (elevation). b: Ordination diagram (PCA) showing the 37 pollen taxa and their varying importance (arrow length) for the differentiation of vegetation types along the altitudinal gradient (correlated with axis 1). Key taxa are displayed in capital letters, taxa corresponding to the vegetation patterns are displayed in lower case letters and taxa without any correlation to modern vegetation and/or of low influence are shown in italics. c: Ordination diagram (PCA) showing the 37 taxa (see b) and their ecological grouping. The different vegetation type distribution is displayed as shaded plot in the background.

Table 5
List of abbreviations of pollen taxa in the ordination diagrams (Fig. 5a–c) and classification of pollen taxa: Representing a vegetation type (key taxa, "++"), following the altitudinal distribution of genera and families of modern vegetation (important taxa, "+") and not reflecting modern vegetation structures (−).

Abbreviation	Taxa	Class	Abbreviation	Taxa	Class
acal	*Acalypha*	−	mora	Moraceae/Urticaceae	−
alch	*Alchornea*	++	myri	*Myrica*	−
alnu	*Alnus*	−	myrs	*Myrsine*	+
aster	Asteraceae	+	pipe	*Piper*	−
calce	*Calceolaria*	−	poa	Poaceae	+
cecr	*Cecopia*	−	podo	*Podocarpus*	−
celt	*Celtis*	−	purd	*Purdiaea*	++
clet	*Clethra*	−	styr	*Styrax*	+
clus	*Clusia*	+	symp	Symplocaceae	+
crot	*Croton*	−	vibu	*Viburnum*	−
cype	Cyperaceae	++	vale	*Valeriana*	++
eric	Ericaceae	++	wein	*Weinmannia*	+
esch	*Eschweilera*	−	xyri	*Xyris*	−
hedy	*Hedyosmum*	+			
heli	*Heliocarpus*	++	cyat	*Cyathea*	++
hyer	*Hyeronima*	++	elapci	*Elaphoglossum ciliatum*	++
ilex	*Ilex*	+	jame	*Jamesonia*	++
mela	Melastomataceae	+	lycoce	*Lycopodium cernuum*	+
mika	*Mikania*	−	poly	*Polystichum*	−

Results from the Mera site in the Ecuadorian Amazonia (Bush et al., 1990) show that between 2100 and 3400 m a.s.l. Moraceae/Urticaceae pollen is well represented (up to 12%). Gosling et al. (2009) confirmed recently the assumption that Moraceae/Urticaceae and *Cecropia* are over-represented in ecosystems beyond their distribution range. Surface samples along an elevation gradient between 2800 and 3800 m a.s.l. at Laguna Baja in northern Peru show an over-representation of forest pollen (e.g., *Hedyosmum*), which was attributed to low pollen productivity of local plants at high elevations and by long distance wind transport (Hansen and Rodbell, 1995). High proportions of *Alnus* pollen in the superpuna of the Junin area in central Peru between 4400 and 4900 m a.s.l. is also related to wind transport (Hansen et al., 1984). Pollen rain data from the High Plains of Bogota in Colombia show low percentages of subandean taxa nearly everywhere between 2600 and 3800 m a.s.l. (Hooghiemstra and Cleef, 1984).

In contrast, other studies show good correlations between local vegetations and their pollen rain. Data of the Madre de Dios River in southeastern Peru (240 to 3500 m a.s.l.) show that modern pollen assemblages reflect local floras and provide a characteristic pollen spectrum for each elevation. Forest turnover along an altitudinal gradient provided a strong correlation with changing pollen spectra (Weng et al., 2004). Pollen of *Alnus*, *Hedyosmum*, Combretaceae/ Melastomataceae and Poaceae are abundant between 1600 and 2000 m a.s.l. *Alnus* pollen is most abundant between 2000 and 2700 m a.s.l., and Poaceae is rare. Above 2700 m a.s.l., Asteraceae, the *Muehlenbeckia* type, *Myrsine*, Poaceae and *Polylepis* pollen are dominant (Weng et al., 2004). Vegetation types (Subandean forest, Andean forest, páramo and super páramo) are also reflected in the pollen rain data, from the Sumapaz area, eastern slope of the Central Cordillera, Colombia (1120 and 4250 m a.s.l.), but with a high input of extraneous pollen (Melief, 1985). But it has to be considered that such comparisons between different pollen rain studies might be difficult due to different distributions of vegetation zones and taxa. And moreover comparing other Andean studies with our study located in the Andean depression is vague and hardly appropriate because of the special environmental conditions in the depression region.

Most modern and fossil pollen diagrams contain primarily wind pollinated taxa. During our palynological study a total of 129 different pollen and spore taxa have been identified for an area which is known to hold more than 130 families, 420 genera and 1200 species of spermatophytes (Homeier and Werner, 2005). Hence, pollen identification demonstrates that most species in the ECSF research area are animal pollinated and often lack in the pollen record. The majority of identified spermatophytes in the ECSF area are Orchidaceae (338 species) and Bromeliaceae (56 species), which produces low numbers of pollen missing in most pollen records. An example of pollen found from animal pollinated taxa is *Purdiaea*, which shows main pollen proportions between ca. 2300 and 2550 m a.s.l. (Fig 4a). *Purdiaea nutans* (Clethraceae) is a small evergreen tree with local abundances in montane forests in northern South America. In the Rio San Francisco valley of southeastern Ecuador, *P. nutans* is dominant between 2150 and 2650 m a.s.l., where the trees form large stands. Here *Purdiaea* accounts for up to about 80 % of the individuals, mixed with e.g. *Hedyosmum*, Melastomataceae, *Myrsine* and (tree)-ferns (Mandl et al., 2008). The dominance of *Purdiaea* pollen found between 2300 and 2550 m a.s.l., shows no shift in pollen distribution according to the vegetation data. Therefore, pollen from animal pollinated species represents the vegetation in our area more accurate. Unfortunately, animal pollinated taxa are rare in the pollen record. The low pollen accumulation rate at altitudes with *P. nutans* dominance reflects this. In a forest with a closed canopy a higher pollen accumulation has to be assumed.

Alnus and *Pinus* do not occur in the ECSF research area (Homeier and Werner, 2005). The relatively high representation of *Alnus* (1– 7 %) and *Pinus* (0–3 %) pollen (Fig. 4a) indicates long distance pollen transport from outside the ECSF research area. *Pinus* plantations exist on the opposite slope of the Rio San Francisco valley at about 2 km distance from the ECSF research area. *Alnus* trees are also observed at the slopes of the Rio San Francisco valley growing as pioneers in disturbed areas. Comparing the accumulation rates of *Alnus* and *Pinus* pollen (not shown in the pollen diagram) it can be outlined, that even if both plants occur at same distances from the study site, the influence of *Alnus* is much higher than from *Pinus*. While *Pinus* pollen is found with max. 40 grains/cm²/year, *Alnus* pollen reaches high accumulations of 120 grains/cm²/year in some pollen traps.

Cluster analysis of terrestrial pollen and spore taxa shows a floristic change within the UMF vegetation type at ca. 2500 m a.s.l. (Fig. 4b, dotted line between 2480 and 2520 m a.s.l.). This may reflect a topographical aspect given that between 2480 and 2520 m a.s.l. the mountain ridge becomes flat and moist. Otherwise this might reflect the limit of *Purdiaea* dominance.

The diversity of pteridophyta decreases more or less directly with increasing elevation (1920–3185 m a.s.l.) in the ECSF research area (Fig. 4b). The highest spore proportion at ca. 2480 m a.s.l. coincides with the distribution of modern fern individuals which show a maximum at ca. 2400 m a.s.l. (Kessler, personal communication). Pteridophyta spores (e.g. *Cyathea* and *Lycopodium cernuum* type) strongly increase in the UMF vegetation type (Fig. 4a) and modern fern individuals show the highest number of species in the UMF vegetation type, related to a high level of moisture. Data of horizontal rain and cloud/fog water deposition along an altitudinal gradient show the strongest increase of precipitation between 2270 m a.s.l. (2403 mm) and 2660 m a.s.l. (5306 mm) (Bendix et al., 2008). This pattern conforms to the spore accumulation rates over the altitudinal gradient of our study (Fig. 4b). Hence, spore data reflect well the occurrence of Pteridopyta at humid locations. The total pollen accumulation decreases in higher elevations as expected. This shows that pollen accumulation is less in open vegetation, compared to forest sites with closed canopies.

Finally, the circumstance that the studied pollen rain presents only data of one year has to be addressed. Pollen rain composition most likely varies over two or three years as the pollen production vary according to plant specific systems and changing climatic conditions over the years. Consequently, results of this study provide a first insight of the pollen rain in the ECSF area and have to be enhanced by additional pollen rain studies in this area.

5.2. The reliability of modern pollen rain representing vegetation types

The distribution of LMF, UMF, SUB and PAR of the ECSF research area is generally well reflected in the modern pollen rain data. A high number of modern pollen taxa represent the altitudinal distribution of plant genera or families of the modern vegetation. The dendrogram provided by cluster analysis verifies the same zonation for the modern pollen rain taxa as described for the vegetation types. Minor changes in elevational limits by analysing the pollen data might reflect the difficulties to define exact distribution limits between vegetation types, as they do not show sharp borders.

The discrepancy between floral limits and pollen compositional changes can be observed using the dendrogram (Fig. 4b, dotted lines between 2210 and 2260 m a.s.l and between 2760 and 2820 m a.s.l.). According to Homeier et al. (2008) the LMF vegetation type extends up to 2100 m a.s.l. and the following UMF vegetation type to 2700 m a.s.l. Cluster analysis of pollen rain data reflects an uplift of ca. 100 m for the upper limits of LMF and UMF. This upslope shift of the vegetation type limits reflected by the pollen data probably is related to the uphill pollen transport by wind, as discussed above.

A change of floristic composition at ca. 2790 m a.s.l. is reflected by an increase of SUB pollen and a decrease of LMF and UMF pollen (Fig. 4b, dotted line between 2760 and 2820 m a.s.l). This changeover is in the same altitudinal range of the present day UTL in the research area, which is between 2730 and 3040 m a.s.l. (Richter et al., 2008). Pollen proportion of all LMF and respectively UMF taxa are <25% above ca. 2800 m a.s.l. (Fig. 4b), not considering the exception of a probably local occurrence of Melastomataceae in the uppermost pollen trap. Hence, the UTL seems to be reflected in the pollen composition by the decrease of forest pollen taxa below 25%. The increase of PAR taxa may be not as important as the decreases of forest taxa, because of the under-representation of PAR taxa in the pollen rain. In regions outside the Andean depression not only the UTL is located at higher elevations (see chapter 2.3) but also vegetation types in general have higher distribution limits. The vegetation zonation after Van der Hammen (1974) for the tropical Cordillera Oriental locate the Subandean forest at elevations between ca. 1000 and 2500 m a.s.l., the Andean forest from ca. 2500 to 3500 m a.s.l. and the (sub)-páramo from ca. 3500 to 4200 m a.s.l. At Laguna Baja in the Cordillera Oriental of Peru the border between wet montane forest and páramo vegetation is at about 3400 m a.s.l. (Hansen and Rodbell, 1995).The comparable low position of vegetation types and UTL in the ECSF research area might be a result of the Andean depression and the unique climatic conditions (Richter et al., 2008). The zone of "low Neotropical UTL" is between 3° and 7° S, within the so-called Amotape–Huancabamba Floristic Zone (Weigend, 2002). The UTL depression results from the absence of the high elevation genus Polylepis, which probably is caused by the extremely high precipitation in the eastern Andean chain in northern Peru and southern Ecuador. Polylepis tends to avoid perhumid mountain regions (Kessler, 1995).

The change of the floristic composition between ca. 3070 and 3120 m a.s.l. (Fig. 4b) might reflect the border between SUB and PAR. However, this remains speculative as the compositional change in the pollen record is not that obvious. Additionally, the two locally high occurrences from Melastomataceae and Cyperaceae in the uppermost pollen traps might have overprinted the general pattern of the pollen rain. Due to the last transect sample at 3185 m a.s.l., further studies in elevations higher than 3185 m a.s.l. are needed to study the transition between SUB and PAR in detail.

6. Summary and conclusions

Statistical analysis (PCA) on the pollen rain data revealed a high number of pollen and spore taxa representing a vegetation type or following the altitudinal distribution of genera and families of modern vegetation.

Characteristic pollen and spore taxa (key taxa) for the LMF are Alchornea, Heliocarpus and Hyeronima, for the UMF Cyathea spp., Elaphoglossum ciliatum and Purdiaea and for the SUB Cyperaceae, Ericaceae, Jamesonia and Valeriana. However, there are also a considerable number of pollen taxa not reflecting the modern vegetation structure. This is mostly due to a wide distribution pattern of pollen and plant taxa. But over-representation in higher elevations of pollen taxa originating from lower locations plays a significant role, too.

Wind dispersal is supposed to be responsible for the high occurrences of the LMF pollen taxa in the UMF and SUB/PAR vegetation types and a high proportion of UMF pollen taxa in the SUB/PAR vegetation type. Wind dispersal is rarely discussed posing a problem in fossil pollen records. The results of this study clearly point out the importance of this discussion. This is especially important for the ECSF study area, where strong easterly winds occur.

Cluster analysis verified the different altitudinal limits of the vegetation types LMF, UMF, SUB and PAR reflected by the modern pollen rain. Only minor differences were observed. Therefore, palynological studies on modern and fossil pollen data can be used to reconstruct the vegetation in the study area and the dynamics of the altitudinal distribution. The modern UTL in the research area, indicated by the pollen record between ca. 2760 and 2820 m a.s.l., is mainly reflected by low amounts <25% of montane forest taxa above the UTL.

The strong influence of upslope wind dispersal of different pollen taxa, e.g. of Moraceae/Urticaceae and Alnus, have to be taken into account for the interpretation of fossil pollen records in this region. It is also important to know, that PAR taxa seems to be under-represented in the pollen rain. Poaceae is one of the most characteristic plant families occurring in PAR vegetation, but the family shows highly homogenous pollen dispersion in all vegetation types. Hence, frequently recorded Poaceae pollen in fossil pollen records have to be interpreted with caution, as Poaceae generally are associated with PAR vegetation. To sum up, the compositional change of different pollen taxa gives more reliable information on vegetation changes than single taxa may do.

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