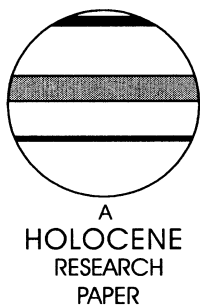


# A high mountain pollen–altitude calibration set for palaeoclimatic use in the tropical Andes

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**Abstract:** The numerical relationship between modern pollen assemblages and altitude in high mountain environments from the northern Andes is analysed, in order to find inference models that allow estimating palaeoaltitudes and palaeotemperatures from past pollen records. The calibration set (DM) consists of a 50-sample altitudinal transect between ~2300 and ~4600 m altitude. The overall and individual pollen responses to altitude were tested by correspondence analysis (CA), generalized linear regression (HOF) and weighted averaging (WA). Transfer functions were derived by weighted averaging-partial least squares (WA-PLS) regression. Overall, altitude is the main controlling factor for the composition of pollen assemblages, as shown by the high correlation between altitude and the first CA component ( $r = -0.88$ ). Individually, around 35% of the 82 pollen taxa show a significant response to altitude through monotonic or unimodal functions. The best transfer function obtained has a good statistical performance, as shown by the determination coefficient ( $r_{\text{jack}}^2 = 0.78$ ). The prediction power, as measured by the root mean square error of prediction (RMSEP), is of 256 m (12% of the total altitudinal gradient), which is equivalent to ~1.5°C. These parameters fall within the performance range of the inference models developed elsewhere using pollen and other biological proxies. It is concluded that the DM training set is useful to reconstruct Pleistocene and major Holocene palaeoclimatic trends. This study demonstrates the suitability of establishing reliable transfer functions for palaeoclimatic estimation in the highest altitudes of the tropical Andes, and encourages their continued improvement.

**Key words:** Modern analogues, calibration, transfer functions, pollen, palaeoclimatology, Neotropics, Andes, Holocene.

## Introduction

Modern pollen analogues are essential tools for palaeoecological reconstruction (Birks and Birks, 1980; Huntley, 2001). A variety of approaches have been developed to establish pollen–vegetation–climate relationships, in order to infer past environmental and biotic trends from sedimentary pollen records (Jackson and Williams, 2004). In the last decades, several numerical methods have been designed to quantitatively estimate climatic parameters – mainly temperature and precipitation – from modern pollen spectra. Among them, multivariate statistical methods and robust calibration techniques have been successfully used to obtain modern analogue-based transfer functions for quantitative palaeoclimatic estimation (Birks, 1998).

In tropical and subtropical areas, examples of different modern analogue surveys are available for Africa (Burney, 1988; Marchant and Taylor, 2000; Elenga *et al.*, 2000;

Gajewski *et al.*, 2002), Asia (Caratini *et al.*, 1973; Anupama *et al.*, 2000), Australia (Kershaw, 1973; Dodson, 1977, 1982, 1982/1983; Walker, 2000) and the Neotropics (Muller, 1959; Salgado-Labouriau, 1979; Grabandt, 1980; Jacobs, 1982; Rodgers and Horn, 1996; Bush and Rivera, 1998; Rull and Vegas-Vilarrúbia, 1999; Bush, 2000; Bush *et al.*, 2001; Hofmann, 2002; Markgraf *et al.*, 2002; Gosling *et al.*, 2003; Weng *et al.*, 2004). The northern and central Andes have been key areas for Neotropical palaeoecology and palaeoclimatology (Markgraf, 2000). Several modern analogue studies have been conducted in these mountains, most of them being qualitative and oriented to unravel pollen–vegetation relationships (eg. Salgado-Labouriau, 1979; Grabandt, 1980, 1985; Melief, 1985; Grabandt and Nieuwland, 1985; Hansen and Rodbell, 1995; Hansen *et al.*, 2003). Among the few quantitative/semi-quantitative surveys, the biomization approach has been used in the Colombian Andes to calibrate present pollen assemblages from an altitudinal transect in terms of vegetation (Marchant *et al.*, 2001a). The resulting model has been applied to several Holocene time slices to perform palaeovegetation

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reconstructions (Marchant *et al.*, 2001b, 2002a, 2004). In the Peruvian Andes, Weng *et al.* (2004) studied the pollen–altitude relationship in a forest transect using correspondence analysis regression. The good statistical correlation between altitude and the first component has been the basis for a transfer function with reliable statistical performance to infer altitude from pollen data.

Most palaeoecological and palaeoclimatic reconstructions from the northern Andes have been conducted on the páramo, the biome situated between the upper forest line (*sensu* Wille *et al.*, 2002) and the snowline, which has shown to be especially useful for such purpose (Luteyn, 1999). However, calibration studies quantitatively relating pollen with altitude or climatic parameters are still lacking. Here, the relationship between surface pollen spectra and altitude is studied in the high mountain environments from the Venezuelan Andes, to obtain transfer functions that allow estimating altitude from pollen assemblage composition. Since altitude and annual average temperatures follow a known, fairly constant inverse relationship, further indirect temperature estimates will be possible. Furthermore, it will also be possible to estimate variations in the vertical distance from a given coring site to the palaeoaltitude of the upper forest line (UFL) or the snowline, which are very useful parameters for palaeoclimatic reconstruction. It is hoped that the application of such calibration functions to past pollen records will provide more detailed and accurate quantitative palaeoenvironmental reconstructions. It should be stressed that this paper is strictly a pollen–altitude calibration attempt, and the relationship between pollen and vegetation is beyond the scope of the study. Issues such as, for example, pollen representivity or pollen/vegetation indices are not considered here.

## Study area: climate and vegetation

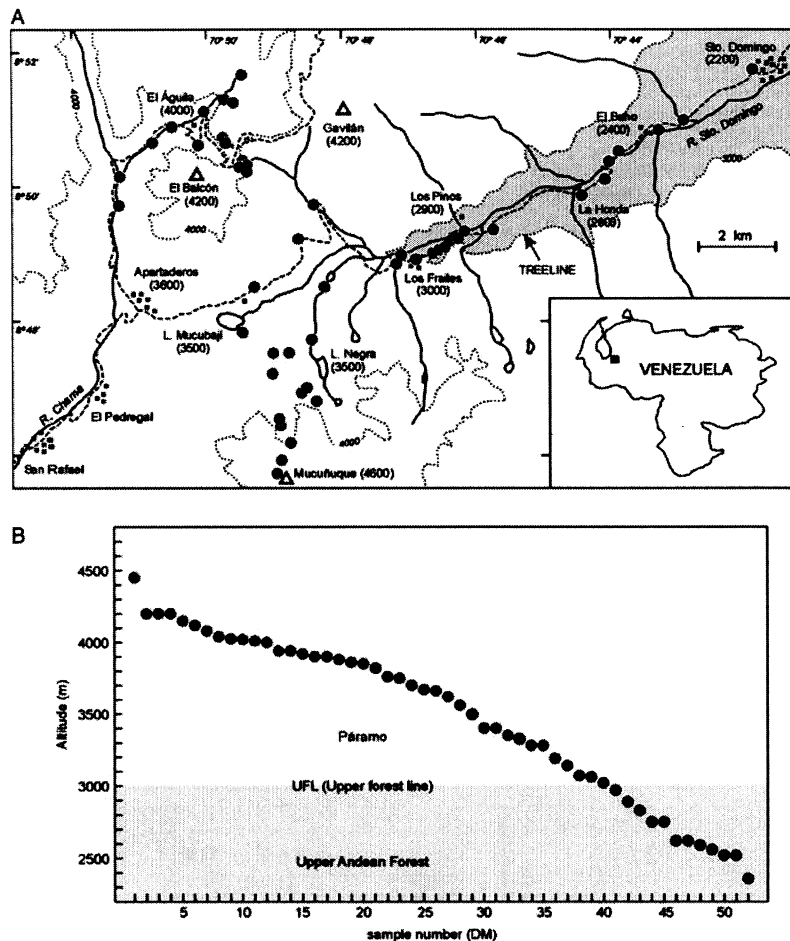
The study area belongs to the Sierra de Santo Domingo, and is among the highest mountain environments of the northern Andes, covered by upper montane forests and páramo biomes (Figure 1). In the Venezuelan Andes, the altitude of the upper forest limit (UFL) varies between about 3000 and 3300 m altitude, depending on local physiographical and climatic features, as well as human disturbance (Monasterio and Reyes, 1980). In the region under study, the UFL is around 3000 m, although human practices have lowered it by 100–200 m in some areas. The upper forest layer, with which this study is concerned, is a characteristic montane cloud forest, extending downward until some 1700 m altitude. Among the dominant trees, *Podocarpus* (Podocarpaceae), *Weinmannia* (Cunoniaceae), *Hedyosmum* (Chloranthaceae), *Alnus* (Betulaceae) and several genera of Lauraceae and Guttiferae (including *Clusia*) are noteworthy (Salgado-Labouriau, 1979). The alder (*Alnus jorullensis*) is especially abundant in gallery forests along the drainage systems and can penetrate upslope into the páramos, following water courses. The transition between cloud forests and páramos is not sudden but is characterized by an ecotone dominated by shrubs. It is called páramo shrubland (Monasterio and Reyes, 1980) or subpáramo (Cuatrecasas, 1968).

The páramos range from about 2800–3000 m to 4700 m altitude, where bare rock and glaciers begin. Climatically, the upper and lower páramo boundaries are characterized respectively by the 0°C and 10°C isotherms of annual average temperature (Monasterio and Reyes, 1980), and there is a fairly constant decrease of  $-0.6^{\circ}\text{C}/100\text{ m}$  altitude (Salgado-Labouriau, 1979). On the contrary, variations in total annual precipitation are mostly related to slope orientation. Indeed,

‘humid’ SE slopes (1600–2300 mm/yr) contrast with ‘dry’ NW slopes, in which total annual precipitation ranges from about 700 to 900 mm (Monasterio, 1980a). Páramo vegetation is open and characterized by three strata. The upper stratum (up to 1.5 m high) is dominated by typical shrubby stem rosettes of several *Espeletia/Espeletiopsis* (Asteraceae) species, which determine the general physiognomy of this biome, accompanied by shrubs of *Hypericum* (Guttiferae), *Hesperomeles* (Rosaceae), *Pernetia* (Ericaceae) and *Arcytophyllum* (Rubiaceae), among others. The intermediate stratum (up to 0.5 m) is dense and composed mainly of Poaceae (*Poa*, *Calamagrostis*, etc.) and other herbs, as well as low shrubs. The lower stratum (up to 10 cm) is made of small cushion and rosette plants such as *Agrostis*, *Aciachne* (Poaceae), *Carex* (Cyperaceae), *Arenaria* (Caryophyllaceae), *Geranium* (Geraniaceae), *Acaena* (Rosaceae), etc. Altogether, these three plant layers entirely cover the substrate, and no bare soil is commonly observed (Monasterio, 1980a). The uppermost páramo levels, from about 3800–4000 m upwards, show a progressive vegetation impoverishment owing to an intensification of periglacial phenomena. There is a decrease in plant cover and diversity, as well as a different taxonomic composition. This so-called superpáramo (Cuatrecasas, 1968) is characterized mainly by two vegetation types, namely the desert páramo and the periglacial desert (Monasterio, 1980a). The desert páramo is dominated by tall columnar rosettes of *Espeletia/Espeletiopsis* up to 3 m high, and a lower discontinuous stratum of flat plants attached to the soil. The total soil cover of this formation ranges from 10% to 50%. The periglacial desert is the uppermost life zone of the páramos, with few cushion and acaulescent rosette life forms on an almost bare soil, which is around 95–99% uncovered. The more conspicuous superpáramo cushion forms belong to the genera *Arenaria*, *Azorella* (Apiaceae), *Aciachne* and *Montia* (Portulacaceae), while the more common acaulescent rosettes are *Draba* (Brassicaceae), *Hypochoeris* (Asteraceae), *Cerastium* (Caryophyllaceae) and *Calandrinia* (Portulacaceae) species.

Glacial lakes and peat bogs are common in the páramos. In the lake shores, aquatic and semi-aquatic plants such as for example several Cyperaceae species and *Isoetes* (Isoëtaceae) are common. In the peat bogs, many cushion and rosette plants of the genera already mentioned and others are typical. Another vegetation type locally important in the páramos is the *Polylepis* forest, the only arborescent formation above the UFL. Ranging from 3500 to 4500 m altitude and dominated by *Polylepis sericea* (Rosaceae), this dwarf forest forms isolated patches that grow directly on rocky substrates, where temperatures are higher than in surrounding soils, and periglacial effects are attenuated (Monasterio, 1980a). Accompanying canopy taxa are *Gynoxis* (Asteraceae), *Weinmannia* and *Espeletia*, whereas a relatively high variety of shrubs grow in the understorey.

In the Venezuelan Andes, the history of human disturbance is almost limited to the last centuries, after the European colonization around AD 1500. Former indigenous presence was reduced to small and scattered marginal populations relatively isolated from main cultures from the central Andes, which reached these latitudes only lately, in protohistoric times (Wagner, 1979). Therefore, their influence on regional vegetation and environment at a millennial timescale has been negligible. Concerning introduced plants, the more conspicuous are *Pinus caribbaea* (Pinaceae) and *Rumex acetosella* (Polygonaceae). This last species came after AD 1500 as a weed from Europe with wheat cultivation, which was important during the sixteenth and seventeenth centuries, and ended around AD 1850 (Monasterio, 1980b). At present, *Rumex*



**Figure 1** Graphical display of sampling characteristics. (A) Location map indicating the sampling sites (solid circles). The approximate area below the upper forest line (UFL) is shaded. (B) Sampling gradient sorted by altitude and sample number

develops dense and extensive populations in the numerous, still recognizable, abandoned wheat fields. Pines were planted later for forestry purposes, but they are not under manifest exploitation. According to Salgado-Labouriau (1979), the Venezuelan páramos do not show signs of intensive human disturbance above 3500 m. Below this altitude, the main activities are cattle raising and potato cultivation. The higher part of the altitudinal transect selected for the present study, mainly corresponding to the páramo biome, belongs to a national park, and is therefore under strict protection. However, in the lowermost part, several areas around Santo Domingo village (Figure 1) have been cleared for agriculture and cattle raising.

## Methods

A single altitudinal transect along the Santo Domingo river valley was selected to minimize the variability resulting from the characteristic neotropical heterogeneity in biogeographical and ecological patterns (Bush *et al.*, 2001). The selected transect, called DM, includes the most relevant localities cored so far in the Venezuelan Andes (Rull, 1996, 1999, 2005). Samples were taken in the headwaters of rivers Santo Domingo and Chama, in an altitude gradient ranging from the Santo Domingo village (~2300 m altitude) to the Mucufuque peak (4609 m), one of the highest in the area (Figure 1). Therefore, the DM transect represents the uppermost part of the upper Andean forests, and most of the páramo region. A total of 52 samples were taken, but two were not considered for the

analysis because their pollen/spores content were lower than required for statistical reliability (Rull, 1987). Samples consisted of superficial peat scraps from bogs, swamps and lake shores. In order to minimize sampling errors, most samples (up to 4200 m) were taken by the author during a single field trip, and completed (from 4200 to 4609 m) during a subsequent lake-coring campaign. Laboratory procedures include KOH, HCl and HF treatment, acetolysis and mounting with glycerine jelly (Bennett and Willis, 2001). Pollen counting was conducted until the saturation of diversity using the Shannon-Weaver index (Rull, 1987). Final counts average 559 for pollen and 463 for spores. Pollen and spores identification was based on van der Hammen and González (1960), Murillo and Bless (1974, 1978), Hooghiemstra (1984), Tryon and Lugardon (1991) and Rull (1998). The pollen sum includes all pollen taxa, except those from aquatic and semi-aquatic plants (Cyperaceae, *Oenothera* and *Ranunculus*).

Pollen diagrams were plotted with Psimpoll 4.10 free software written by K.D. Bennett (<http://www.kv.geo.uu.se/psimpoll.html>, last accessed 21 October 2005). Pollen and spore taxa were grouped into trees, shrubs and herbs, following Salgado-Labouriau (1979) and Marchant *et al.* (2002b). Asteraceae were placed within shrubs for plotting simplicity, because it is assumed that, in the páramo samples, most of this pollen is produced by the lignified columnar rosettes of *Espeletia/Espeletiopsis*. However, this is not true for samples below 3000 m, and this fact should be considered in the interpretation. A zonation was attempted only for description purposes, using the optimal splitting by information content (OSIC) method, and the broken stick criterion for the selection

of significant zones (Bennett, 1996, 2002). Numerical analysis includes a set of interdependent standard methods commonly used in pollen calibration studies aimed to: (1) determine the individual response of taxa to altitude by estimating their optimum and tolerance, (2) assess the overall dependence of pollen assemblage on altitude, (3) test the significance of these responses, and (4) obtain pollen–altitude transfer functions (Birks, 1998; Seppä *et al.*, 2004). The overall dependence of pollen data on altitude was tested through correspondence analysis. Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) and detrended canonical correspondence analysis (DCCA) (ter Braak, 1986) were carried out with CANOCO 4.5 (ter Braak and Smilauer, 2002). File conversion for interactive use within different software packages was performed with WinTran 1.4, written by S. Juggins (freely available at <http://www.campus.ncl.ac.uk/staff/Stephen.Juggins/software/wintran.htm>, last accessed 21 October 2005). Percentages were square-root transformed, for variance stabilization (Prentice, 1980), and rare taxa were downweighted. Altitude was used as the only constraining variable in DCCA. The individual relationship of each pollen taxon with respect to altitude was characterized through the optimal altitude and its tolerance, as computed by weighted averaging (WA) (ter Braak and Looman, 1986). The statistical significance of these individual responses was tested using the Huisman–Olf–Fresco (HOF) fitting method, which considers a set of hierarchical models in a generalized linear modelling framework (Huisman *et al.*, 1993; Oksanen and Minchin, 2002). These models are designed as I (flat response, no relationship), II (monotonic), III (plateau), IV (symmetric unimodal) and V (skewed unimodal). The minimum number of occurrences of a taxon to be considered for HOF analysis was 10, and 0.05 was the maximum *p*-value for fitting acceptance (*F* test). HOF 2.3 free software written by J. Oksanen (<http://cc.oulu.fi/~jarioksa/pages/hof2.htm>, last accessed 21 October 2005) was used for this purpose. Pollen–altitude transfer functions were derived from weighted averaging partial least squares (WA-PLS) regression (ter Braak and Juggins, 1993), which has shown better performances than other methods for taxa–environment calibration purposes (Birks, 1998; Seppä *et al.*, 2004). All pollen taxa within the pollen sum were included in the calibration analysis to increase the statistical performance (Birks, 1994). This analysis was carried out using C2 1.4 software (Juggins, 2003). The optimal number of components for the resulting prediction model was determined according to the higher determination coefficient ( $r_{\text{jack}}^2$ ) and the lower root mean square error (RMSEP) between observed and predicted values, using jack-knife resampling or leave-one-out cross validation (ter Braak and Juggins, 1993; Birks, 1995, 1998).

## Results

### Visual analysis

A total of 82 pollen and 26 spore types were identified and counted (Figures 2 and 3). The most abundant taxa are Asteraceae, Poaceae and *Rumex* (*R. acetosella*-type). Three zones were defined using OSIC, with boundaries at 3835 and 2995 m (interpolated altitudes between contiguous samples). The lower limit is very close to the local UFL, while the upper limit is around the lower altitudinal boundary of the superpáramo. In the lowermost zone (~2300 to ~3000 m), trees attain the higher percentage values, the most important being *Alnus*, *Hedyosmum*, *Podocarpus* (which are consistently represented along the whole diagram), *Clusia*-type, *Miconia* and *Poulsenia* (almost restricted to the lower zone). ‘Shrubs’ exhibit intermediate abundances, yet it should be borne in

mind that not all Asteraceae taxa represented necessarily correspond to shrubs (see Methods). Other locally important shrubs are Ericaceae and *Fuchsia*. Herbs show lower values than in other zones; among them, Poaceae are dominant, and Caryophyllaceae (other than *Arenaria*) and Rapateaceae are locally abundant. Cyperaceae vary from almost absent to around 50% of the pollen sum. Among spores, psilate and verrucate monolet forms and *Pityrogramma* show local maxima, alternating with absence or negligible percentages.

The zone between ~3000 and ~3800 m is clearly dominated by herbs (mainly Poaceae and *Rumex*), followed by shrubs (Asteraceae and *Hypericum*-type). The main tree elements show a significant and continuous decrease both individually and as a group, and several of them even disappear. Among shrubs, the increase of *Hypericum*-type, almost absent in the lower zone, is noticeable. A similar pattern but different percentages is shown by the herbs *Rumex* and *Conomorpha*-type. *Arenaria* appears for the first time in altitude and increases, accompanied by other páramo elements such as *Draba*, *Gentiana*, *Geranium* and *Plantago*. In general, subdominant pollen taxa exhibit inverse tendencies compared with in the lower zone. Cyperaceae are abundant only in the lower half of this zone (below 3400 m). Spore taxa, which were abundant in the former zone, are now scarce or absent, while *Isoetes* and *Jamesonia* follow a reverse pattern, at least locally. The uppermost zone (~3800 to ~4600 m) is dominated by Asteraceae shrubs, which show a conspicuous increase in percentage. On the contrary, *Hypericum*-type starts a continuous decrease until its virtual disappearance at the top. Trees (mainly *Alnus*, *Hedyosmum* and *Podocarpus*) show a recovery in some scattered samples. Herbs are consistently lower than in the former zone, where they dominated. Poaceae have notably decreased and *Rumex* has similar percentages than in the intermediate zone. Some páramo herbs are in a similar condition than formerly, but others (*Cerastium*, *Montia*, *Rhizocephalum*, *Valeriana*) appear or increase here. Among aquatic plants, Cyperaceae and *Oenothera* decrease, while *Isoetes* oscillates locally.

It should be stressed that introduced *Pinus* and *Rumex* show very different patterns in modern pollen spectra. The first is almost absent, only two grains could be observed in sample 18 (3880 m altitude), and its frequency is under the representation limit in the diagram. On the contrary, *Rumex* is one of the dominant pollen taxa in the pollen assemblage of the páramo (Figure 2). The pollen morphology of *Rumex* is clearly different from any other pollen taxa found in this analysis and in the páramo plants in general (Luteyn, 1999), and morphologically identical to the European weed *Rumex acetosella* (Reille, 1992). Concerning *Pinus* pollen, although it is morphologically similar to the autochthonous *Podocarpus*, their separation is not problematic due to evident differences in the size of the whole grain and in the sacci/corpus relationship, both conspicuously larger in *Podocarpus* than in *Pinus*.

### Numerical analysis and calibration

WA optimum and tolerance values for pollen taxa included in the analysis are depicted in Figure 4. About two-thirds of the taxa found (65%) have their optimum within the intermediate páramo zone, while 24% are in the forest zone and around 11% in the uppermost superpáramo zone. In general, pollen taxa tend to be arranged according to the preferred altitudinal range of their parent taxa, except for three forest trees: *Hedyosmum*, *Podocarpus* and *Alnus*, whose optimum in the modern pollen rain lies around 500 m above the UFL, and close to the optima of dominant pollen taxa such as Poaceae and Asteraceae. HOF fitting shows that 28 pollen taxa (35%)



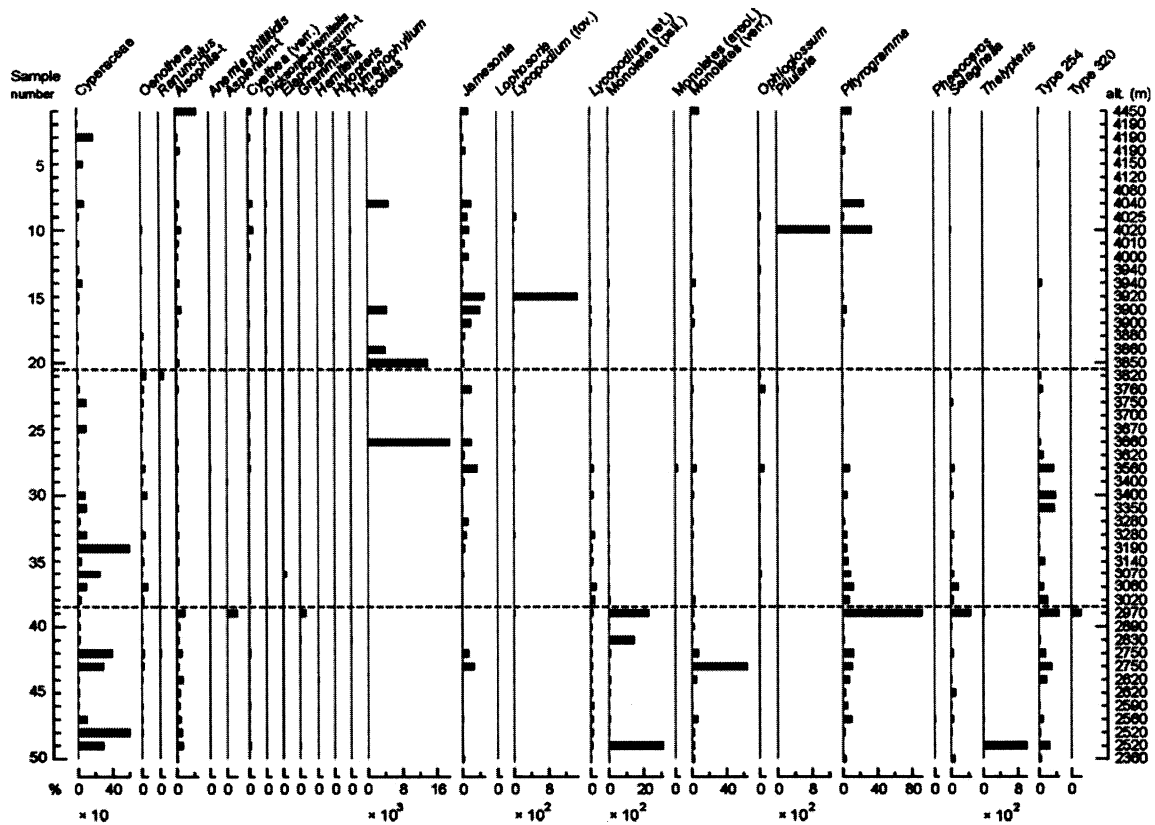


Figure 3 Percentage diagram of the elements outside the pollen sum, which include pollen from aquatic and semi-aquatic plants and fern spores. Types 254 and 320 refer to the nomenclature of Hooghiemstra (1984)

noteworthy that pollen from *Hedyosmum*, *Podocarpus* and *Alnus*, which showed anomalous altitude optima with respect to the habitat of their parent trees, have no significant responses to altitude.

A significant negative correlation between the first DCA axis (which accounts for 16.7% of the total variance) and altitude

exists for the whole data set. Axes 2 and 3 account for low percentages of the total variance and are not correlated to altitude (Table 2). Similarly, DCCA shows that the first axis is highly correlated with altitude when used as the only constraining variable. Therefore, the altitude gradient explains the major trends in variation of the whole DM pollen data set.

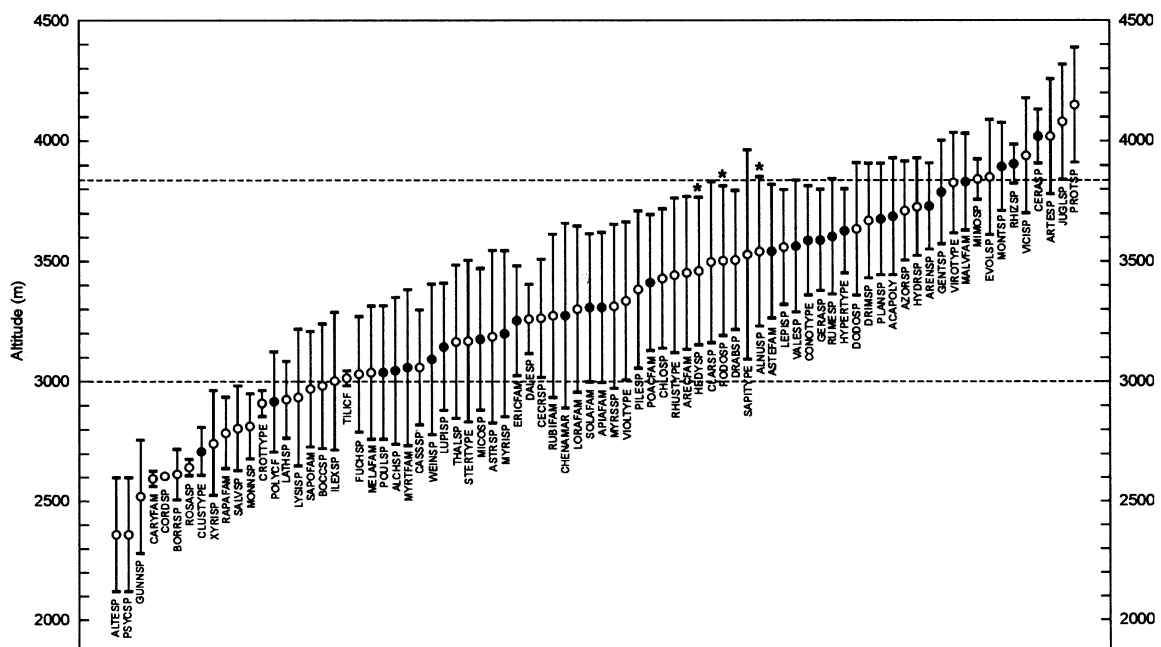


Figure 4 Altitudinal arrangement of weighted averaging (WA) optima (circles) and tolerances (error bars) for the taxa considered in the analysis. Solid circles indicate the taxa with significant fitting after HOF correlation analysis. Forest trees with anomalous optima with respect to their altitudinal habitat (*Hedyosmum*, *Podocarpus* and *Alnus*) are indicated with an asterisk. See Appendix for taxa codes

**Table 1** Individual response models for pollen taxa with significant HOF fitting

Taxon	Model	N	Optimum	Tolerance
<i>Cerastium</i>	V	15	4020	223
<i>Rhizocephalum</i>	IV	16	3906	163
<i>Montia</i>	V	20	3894	365
Malvaceae	V	10	3831	402
<i>Gentiana</i>	II	29	3788	429
<i>Arenaria</i>	IV	35	3730	359
Acaena/Polylepis	II	22	3687	485
<i>Plantago</i>	II	25	3676	464
<i>Hypericum</i> -type	IV	36	3627	350
<i>Rumex</i>	IV	45	3604	480
<i>Geranium</i>	IV	25	3589	420
<i>Conomorpha</i> -type	IV	33	3588	454
<i>Valeriana</i>	V	21	3564	547
Asteraceae	II	50	3543	556
Poaceae	IV	50	3412	565
Apiaceae	II	33	3308	625
Solanaceae	II	36	3308	617
Chenopodiaceae/Amaranthaceae	II	12	3275	769
Ericaceae	IV	24	3254	457
<i>Myrica</i>	II	12	3200	691
<i>Miconia</i>	II	29	3177	589
Lupinus	II	21	3145	530
<i>Weinmannia</i>	II	24	3094	625
Myrtaceae	II	11	3059	647
<i>Alchornea</i>	II	20	3047	610
<i>Poulsenia</i>	V	24	3039	554
cf. Polygonaceae	IV	12	2917	416
<i>Clusia</i> -type	IV	10	2710	201

N, number of occurrences. Optima and tolerance (in metres altitude) were obtained by WA analysis, and rounded to whole numbers. Taxa are sorted by altitude, according to their estimated optima.

Samples are well separated in the space of the first two axes (Figure 6). Sites below the UFL are clearly segregated from the rest by axis 1, while páramo samples are differentiated by axis 2. The altitude dependence of axis 1 is also evident in Figure 5, with the exception of the highest (1, 4450 m) and the lowest (50, 2330 m) samples, which deviate from the main body of samples as outliers. If these samples are deleted from the analysis, the goodness of fit between the first axis and altitude increases in both DCA ( $r = -0.884$ , 17.5% of variance) and DCCA ( $r = -0.926$ , 14.2% of variance).

In principle, all the taxa included in the pollen sum are considered for calibration purposes, but some observations are pertinent. As stated before, *Rumex acetosella* has been introduced recently in historical times (after AD 1500); hence it should be considered only for transfer functions aiming to reconstruct the palaeoenvironments of the last four to five centuries. On the other hand, it would be interesting to test if a

reduced calibration set including only those taxa with significant HOF fitting with altitude, produce better transfer functions than the whole set. In this way, four different calibration sets were analysed: DM, including all pollen taxa within the pollen sum; DM-R, in which *Rumex* has been removed; DMs, including only the 28 taxa with significant relationship with altitude; and DMs-R, which is DMs without *Rumex*. The performance of the different transfer functions obtained using the four calibration sets considered is shown in Table 3. In general, the response is better when the whole data set is used ( $r_{\text{jack}}^2 = 0.774$  and RMSEP = 319 for DM-R), and the performance significantly drops when only pollen taxa with significant fitting with altitude are considered ( $r_{\text{jack}}^2 = 0.581$  and RMSEP = 386 for DMs-R). Therefore, sets DM and DM-R are preferred for calibration of modern (last centuries) and past (back to about AD 1500) palaeoaltitude estimation, respectively. When the two outlier samples detected by DCA (Figure 6) are deleted (sets DM\* and DM-R\*), the performance increases (Table 3, Figure 7). In this way, for a given fossil pollen assemblage, it is possible to estimate the apparent palaeoaltitude (and hence, the past vertical distance to the UFL or the snowline) with an error of  $\pm 256$  m, which corresponds to the 12% of the total altitude gradient length for the present calibration set. Similarly, using the present-day lapse rate of  $-0.6^\circ\text{C}/100$  m altitude (Salgado-Labouriau, 1979), the temperature anomaly, ie, the deviation from the present annual average temperature of a given coring site, can be estimated with  $\sim 1.5^\circ\text{C}$  accuracy.

## Discussion and conclusions

Numerical analysis of the Santo Domingo-Mucuñuque modern data set (DM) shows that altitude is the main parameter controlling the composition of pollen assemblages. This allows obtaining transfer functions to estimate altitude from pollen abundances with a known statistical reliability. These functions can be applied to past pollen records for quantitative reconstructions of vertical displacements in the UFL/snowline and, indirectly, palaeotemperature change. The best performance is obtained using WA-PLS regression on the whole data set, after elimination of two outlier samples. The use of two DM calibration sets is recommended: DM\* (all pollen taxa within the pollen sum) for records after AD 1500, and DM-R\* (excluding *Rumex*) for older surveys.

The performances of the recommended transfer functions obtained in the present work:  $r_{\text{jack}}^2 = 0.77-0.78$  and RMSEP = 256–257 m ( $\sim 1.5^\circ\text{C}$  and  $\sim 12\%$  of the gradient length) are similar to other studies of the same nature based on pollen and other biological proxies. A representative literature review of papers using the same methods on pollen data shows that correlations ( $r_{\text{jack}}^2$ ) range from 0.33 to 0.889, whereas root mean square errors of prediction (RMSEP) are between  $0.89^\circ\text{C}$  and  $2.57^\circ\text{C}$ , which represents 8.8–22.2% of the total temperature

**Table 2** Results, of DCA and DCCA on the whole calibration data set (DM)

	DCA			DCCA		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalue	0.223	0.089	0.061	0.165	0.075	0.065
Gradient length/SD	1.578	1.518	1.177	1.502	1.499	1.763
Cumulative variance (%)	16.7	23.4	28.0	12.4	18.1	22.9
Correlation with altitude	-0.822*	-0.192	-0.255	-0.888*	–	–

Correlation values significant at  $p < 0.001$  are indicated with an asterisk. SD = standard deviation.

gradients (Lotter *et al.*, 2000; Seppä and Birks, 2001; Rosén *et al.*, 2001; Bigler *et al.*, 2002; Seppä *et al.*, 2004). Other works using different proxies (chironomids, cladocera, diatoms, chrysophycean cysts) and the same numerical procedures, give values of 0.46–0.89 for  $r_{\text{jack}}^2$ , and 0.7°C to 2.23°C for RMSEP (9–15.8% of the total gradient length) (Lotter *et al.*, 1997, 1999; Walker *et al.*, 1997; Rosén *et al.*, 2000; Larocque *et al.*, 2001; Bigler and Hall, 2002; Bloom *et al.*, 2003; Heiri *et al.*, 2003; Pla and Catalan, 2005). Therefore, DM\* and DM-R\* are comparatively reliable calibration data sets for palaeoaltitude and palaeotemperature estimation. The WA-PLS method has not been used so far in tropical areas, and it is thus not possible to compare the results of the present study with others from regions of similar latitude. The most used calibration methods in low-latitude regions (mainly from Africa and South America) have been the biome approach (Marchant *et al.*, 2001a,b, 2002a, 2004), and the modern analogue technique (MAT) based on response surfaces (Bush, 2000; Gajewski *et al.*, 2002; Markgraf *et al.*, 2002). The first is semi-quantitative and deals mainly with pollen–vegetation relationships, while the second, although quantitative, does not provide reliability and prediction parameters able to be compared with those of WA-PLS regression analysis.

The prediction accuracy of DM\* and DM-R\* data sets, namely  $\pm 256$  m altitude and  $\pm 1.5^\circ\text{C}$  temperature, imposes some limitations. According to palaeoecological studies based

on fossil pollen developed so far in the Venezuelan Andes, the range of variation for temperature has been of the order of 4–7°C for the late Pleistocene, and 1–2°C for the Holocene (Salgado-Labouriau, 1989; Rull, 1998, 2005; Rull *et al.*, 1999). Therefore, DM transfer functions are useful to record Pleistocene and major Holocene variations. The most outstanding Holocene shift recorded so far in the region is the Piedras Blancas cold phase, correlated to the ‘Little Ice Age’, which extended between the fourteenth and seventeenth centuries (Rull *et al.*, 1987). The estimated temperature lowering was of about 2°C compared with the present (Rull and Schubert, 1989), which is within the DM detection limit. Other Holocene temperature shifts, however, have been of the order of 1°C or less, and will be undetectable with enough statistical accuracy by the DM calibration data set, although the main trends would be recorded. It should be also taken into account that the lapse rate temperature is dependent on the moisture content of the atmosphere (McGregor and Nieuwolt, 1998) and can change under some circumstances. For example, Wille *et al.* (2001) estimated that during the last glacial maximum, the temperature decrease with altitude in a Colombian Andes slope was of  $-0.76^\circ\text{C}/100$  m, instead of the present-day  $0.6$ – $0.65^\circ\text{C}/100$  m. This would introduce an additional factor error in any transfer function using altitude as an indirect measure of temperature, which could be avoided by using a direct pollen–temperature calibration tool. Such procedure, however, is only

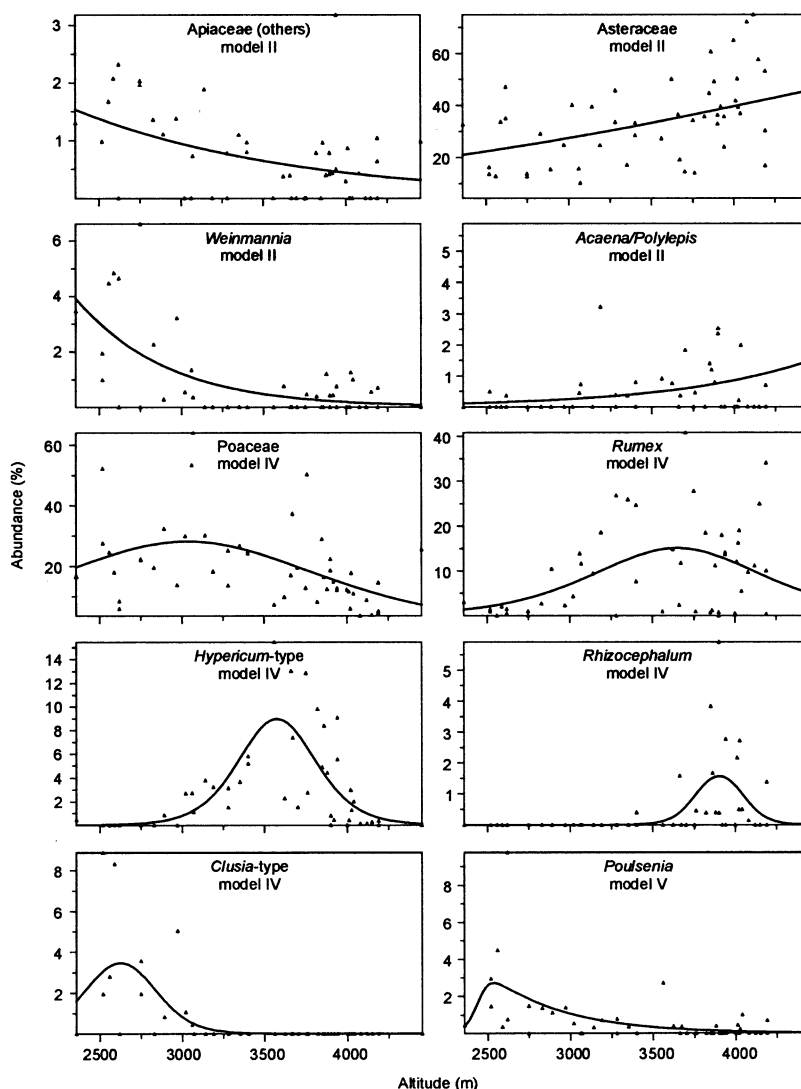
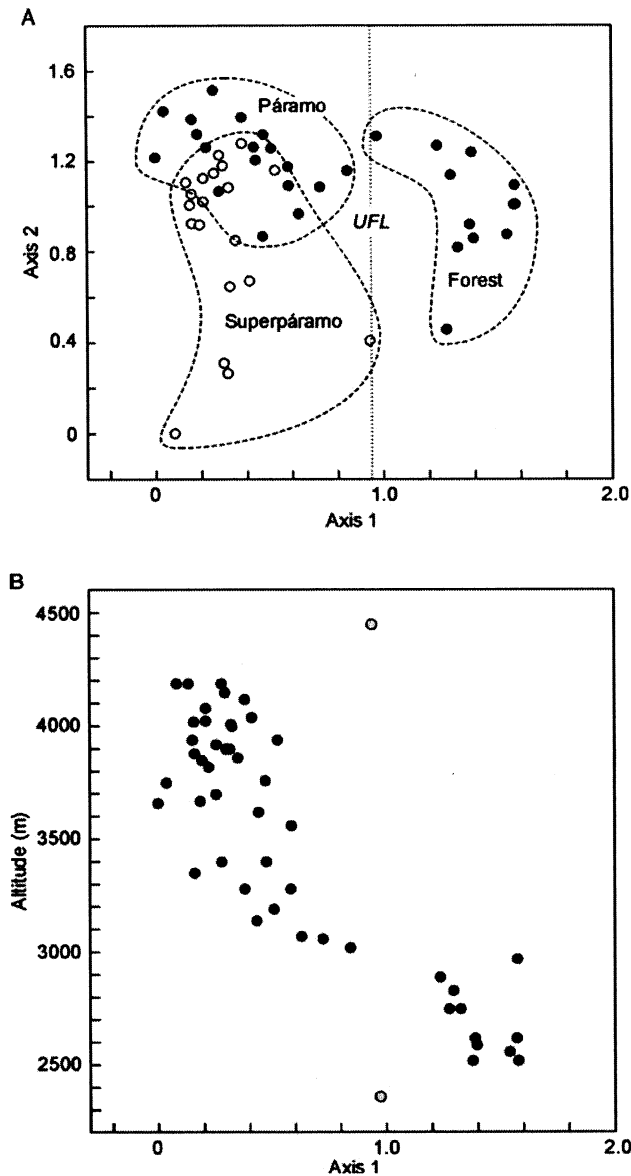


Figure 5 Selected plots of HOF response analysis showing examples of the significant models found. See Table 2 for more information



**Figure 6** Results of detrended correspondence analysis on set DM. (A) Sample arrangement according to the first two axes, accounting for the 23.4% of total variance. (B) Scatter plot showing the inverse significant relationship between axis 1 and altitude. The two outlier samples (1 and 50) are depicted as grey circles

possible in regions with a suitable net of climatic data, which is not the case for the tropical Andes.

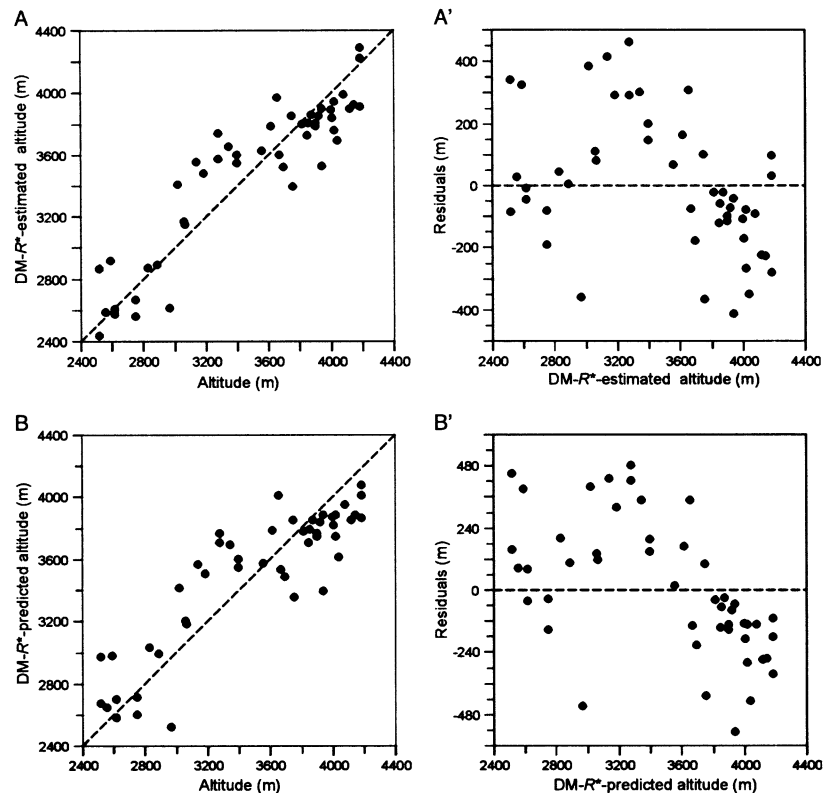
Another important matter to be considered is the geographical validity of the obtained transfer functions, that is, the potential of the DM training set for palaeoenvironmental

reconstructions outside the Santo Domingo-Chama headwaters. So far, any answer to this question is speculative. As stated above, the studied area was selected because it holds the most important coring sites of the Venezuelan Andes, as well as many other potentially interesting localities. Also, a single-valley transect was considered to improve calibration accuracy, which could be compromised by the high physiographical and biogeographical heterogeneity of the neotropics (Bush *et al.*, 2001; Weng *et al.*, 2004). New studies are needed for a definite assessment. Two complementary strategies are either to perform studies such as the present one on other single-altitudinal transects and compare them, or to develop extensive sampling programmes in order to find potential training sets of regional validity. In this sense, an important conclusion of the present work is that such studies are worthwhile, since altitude (and hence temperature) is the main parameter explaining variations in modern pollen assemblages, and WA-PLS regression is a reliable method of finding quantitative inference models. Finally, it should be stressed that the DM training set has been developed for palaeoecological studies based on cores from peat bogs, swamps and glacio-fluvial deposits, from which superficial samples have been taken. The use of this calibration set for lake sediments is *a priori* not recommended, but future studies are required to clarify this issue. In such case, a regional approach is mandatory, because no single altitudinal transect contains enough lakes for a reliable statistical study.

The 'anomalous' behaviour, ie, the lack of relationship of important upper montane forest trees such as *Hedyosmum*, *Podocarpus* and *Alnus* with respect to altitude, deserves a comment. Previous studies carried out on the same region suggested that the pollen of *Alnus* is more or less evenly represented at any altitude in the páramos because of its high dispersion power. Contrarily, the moderate dispersion power of *Podocarpus* and *Hedyosmum* makes their quantity diminish with altitude in a way that can be used to roughly estimate the vertical distance of a given deposition site with respect to the upper forest line (Salgado-Labouriau, 1979). In the present study, however, no significant pollen–altitude response is found for any of these tree pollen types, probably because of their comparatively high values in several uppermost samples (Figure 2). This could be the cause for the upward WA optimum displacement (Figure 4) and the fitting with the non-significant model I in the HOF regression. It has been reported, and the present study adds new evidence in this sense, that pollen percentages from mountain forest trees can be over-represented in samples from the high Andean environments, because of the scarcity of pollen from local plants (eg, Hansen and Rodbell, 1995; Hansen *et al.*, 2003). This fact was also recognized by Salgado-Labouriau (1979), who recommended caution in the interpretation of pollen percentages of these pollen taxa in samples with low total pollen content (<16 grains/mg). The disagreement between this paper and

**Table 3** Performance parameters for the WA-PLS transfer functions obtained for the four calibration sets, using jack-knife leave-one-out cross-validation. Sets in which outlier samples have been deleted are indicated with an asterisk

	DM	DM*	DM-R	DM-R*	DMs	DMs-R
Component	3	2	3	1	4	4
$r^2$	0.932	0.898	0.937	0.838	0.852	0.839
RMSE	148.46	172.30	142.47	216.49	218.23	228.01
Average bias	0.00	0.68	2.70	0.30	-1.21	4.00
Maximum bias	166.34	229.79	129.99	335.26	279.30	232.72
$r_{\text{jack}}^2$	0.713	0.774	0.702	0.776	0.566	0.581
RMSEP	309.72	256.66	319.36	256.17	394.58	386.01
Average bias (pred.)	3.86	3.00	9.85	2.10	2.59	7.14
Maximum bias (pred.)	863.72	381.61	753.77	391.12	1511.26	1299.64



**Figure 7** Performance of WA-PLS transfer function obtained for set DM-R\* (see also Table 3). (A-A') Scatterplot and residuals of observed and estimated altitudes. (B-B') Scatterplot and residuals of observed and predicted altitudes using jack-knife leave-one-out cross-validation

previous assumptions regarding *Podocarpus* and *Hedyosmum* pollen in the same area could be a result of differences in both the length of altitude gradient considered (previous transect: 1240 m, this work: 2090 m), the number of samples considered (previous transect: 18 samples, this work: 50 samples), and the fact that Salgado-Labouriau's (1979) assessments are not based on statistical treatment of data but on visual interpretation. However, no generalization can be made so far about the palaeoclimatological usefulness of *Podocarpus* and *Hedyosmum* pollen, which is one of the important issues to be addressed in future surveys.

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## Appendix 1

Codes of the taxa used for numerical analysis

ACAPOLY	<i>Acaena-Polylepis</i>
ALCHSP	<i>Alchornea</i>
ALNUSP	<i>Alnus</i>
ALTESP	<i>Alternanthera</i>
APIAFAM	Apiaceae (others)

ARECFAM	Arecaceae
ARENSP	<i>Arenaria</i>
ARTESP	<i>Artemisia</i>
ASTEFAM	Asteraceae
ASTRSP	<i>Astronium</i>
AZORSP	<i>Azorella</i>
BOCCSP	<i>Bocconia</i>
BORRSP	<i>Borreria</i>
CARYFAM	Caryophyllaceae (others)
CASSSP	<i>Cassia</i>
CECRSP	<i>Cecropia</i>
CERASP	<i>Cerastium</i>
CHENFAM	Chenopodiaceae-Amaranthaceae
CHLOSP	<i>Chlorophora</i>
CLARSP	<i>Clarisia</i>
CLUSSP	<i>Clusia</i> -type
CONOTYPE	<i>Conomorpha</i> -type
CORDSP	<i>Cordia</i>
CROTTYPE	<i>Croton</i>
DALESP	<i>Dalea</i>
DODOSP	<i>Dodonaea</i>
DRABSP	<i>Draba</i>
DRIMSP	<i>Drimys</i>
ERICFAM	Ericaceae
EVOLSP	<i>Evolvulus</i>
FUCHSP	<i>Fuchsia</i>
GENTSP	<i>Gentiana</i>
GERASP	<i>Geranium</i>
GUNNSP	<i>Gunnera</i>
HEDYSP	<i>Hedyosmum</i>
HYDRSP	Hydrocotyle
HYPERTYPE	<i>Hypericum</i>
LATHSP	<i>Lathyrus</i>
ILEXSP	<i>Ilex</i>
JUGLSP	<i>Juglans</i>
LEPISP	<i>Lepidium</i>
LORAFAM	Loranthaceae
LUPISP	<i>Lupinus</i>
LYSISP	<i>Lysipomia</i>

MALVFAM	Malvaceae
MELAFAM	Melastomataceae (others)
MICOSP	<i>Miconia</i>
MIMOSP	<i>Mimosa</i>
MONNSP	<i>Monnina</i>
MONTSP	<i>Montia</i>
MYRISP	<i>Myrica</i>
MYRSSP	<i>Myrsine</i>
MYRTFAM	Myrtaceae
PILESP	<i>Pilea</i>
PLANSP	<i>Plantago</i>
POACFAM	Poaceae
PODOSP	<i>Podocarpus</i>
POLYCF	cf. Polygonaceae
POULSP	<i>Poulsenia</i>
PROTSP	Proteaceae
PSYCSP	<i>Psychotria</i>
RHIZSP	<i>Rhizocephalum</i>
RHUSSP	<i>Rhus</i> -type
ROSASP	Rosaceae (others)
RUBIFAM	Rubiaceae (others)
RUMESP	<i>Rumex</i>
SALVSP	<i>Salvia</i> -type
SAPISP	<i>Sapium</i> -type
SAPOFAM	Sapotaceae
SOLAFAM	Solanaceae
RAPAFAM	Rapateaceae
STERTYPE	Sterculiaceae
THALSP	<i>Thalictrum</i>
TILICF	cf. Tiliaceae
VALESP	<i>Valeriana</i>
VICISP	<i>Vicia</i>
VIOLTYPE	<i>Viola</i> -type
VIROTYPE	<i>Virola</i> -type
WEINSP	<i>Weinmannia</i>
XYRISP	<i>Xyris</i>

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