



## Palynological signal of the Younger Dryas in the tropical Venezuelan Andes

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### ABSTRACT

The occurrence, or not, of the Younger Dryas cold reversal in the tropical Andes remains a controversial topic. This study reports a clear signal for this event in the Venezuelan Andes, employing high-resolution palynological analysis of a well-dated sediment core from Laguna de Los Anteos, situated around 3900 m elevation, within grass páramo vegetation. The lake is surrounded by some *Polylepis* forests which are close to their upper distribution limit. The section of the core discussed here is 150-cm long and dated between about 14.68 and 9.35 cal kyr BP, using a polynomial age-depth model based on six AMS radiocarbon dates. Between 12.86 and 11.65 cal kyr BP, an abrupt shift occurred in the pollen assemblage, manifested by a decline of *Podocarpus*, *Polylepis* and *Huperzia*, combined with an increase in Poaceae and Asteraceae. The aquatic pteridophyte *Isoetes* also decreased and disappeared, and the algae remains show their minimum values. Pollen assemblages from the Younger Dryas interval show maximum dissimilarity values compared with today's pollen assemblage, and are more similar to modern analogs from superpáramo vegetation, growing at elevations 400–500 m higher. A lowering of vegetation zones of this magnitude corresponds to a temperature decline of between 2.5 and 3.8 °C. During this colder interval lake levels may have been lower, suggesting a decrease in available moisture. The vegetation shift documented in Anteos record between 12.86 and 11.65 cal kyr BP is comparable to the El Abra Stadial in the Colombian Andes but it differs in magnitude. The Anteos shift is better dated and coincides with the Younger Dryas chron as recorded in the Cariaco Basin sea surface temperature reconstructions and records of continental runoff, as well as in the oxygen isotope measurements from the Greenland ice cores. When compared to other proxies of quasi-immediate response to climate, the time lag for the response of vegetation to climate is found to be negligible at a centennial scale. The *Polylepis* pollen curve is especially noteworthy, as it reproduces the overall pollen trends and matches well with paleoclimatic reconstructions based on other proxies. Hence, *Polylepis* might be used as a reliable paleoclimatic indicator in lake sediments close to its uppermost distribution boundary.

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### 1. Introduction

The Younger Dryas (YD) is recognized as an abrupt cold reversal recorded in high latitude Northern Hemisphere paleoclimate records, most recently dated between 12.86 and 11.65 cal kyr BP from Greenland NGRIP ice core (Rasmussen et al., 2006). So far, the main bulk of evidence for the YD has been found in Greenland ice cores and in different paleoclimatic records around the northern Atlantic Ocean (Rodbell, 2000). The absence of YD evidence in other regions, especially at both sides of the southern Pacific Ocean, is against the YD cooling as a global phenomenon (Bennett et al.,

2000; Barrows et al., 2007). Active discussion on the available southern and Pacific evidence is now in progress (Applegate et al., 2008; Barrows et al., 2008). The cause of the YD event is generally considered to be triggered by abrupt changes in Atlantic thermohaline circulation (Alley et al., 2003; Broecker, 2006; Bakke et al., 2009). These changes likely had a profound impact on tropical circulation that would have led to additional feedbacks in the global climate system. The current lack of continuous and well-dated records of Late Glacial atmospheric shifts from mountain regions in the tropics (Rodbell et al., 2009), however, limits the ability to evaluate the role of low latitude circulation in abrupt global environmental changes. Recently, an alternative explanation involving multiple meteorite impacts has been also proposed to explain the YD cooling, but there is still much controversy about the evidence for this hypothesis (Firestone et al., 2007; Van der Hammen and van

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Geel, 2008; Kennett et al., 2009; Surovell et al., 2009; French and Koeberl, 2010).

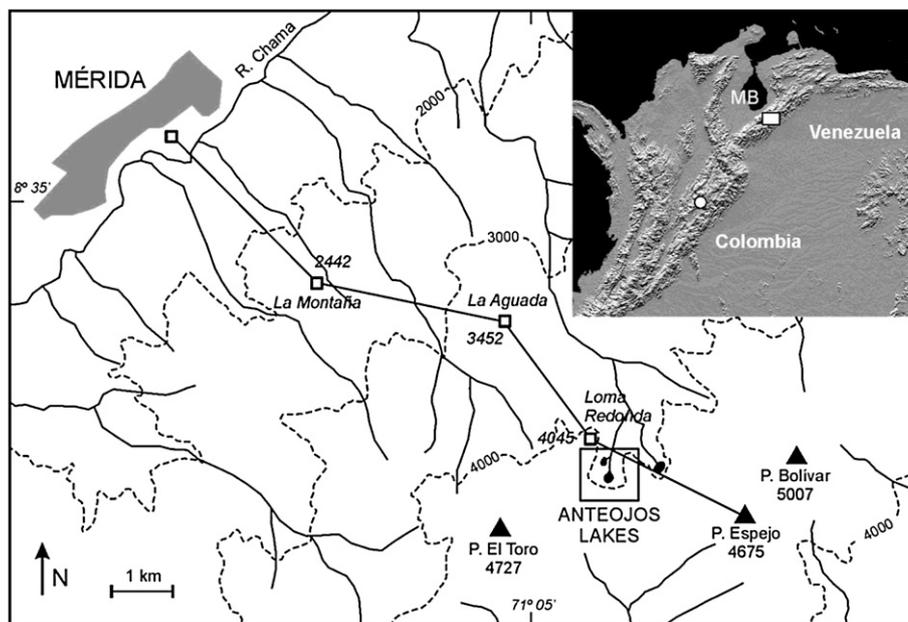
In the northern tropics of South America, the sediments of the Cariaco Basin provide evidence for the YD as a cold and dry event, with increased marine primary productivity caused by the intensification of trade wind driven upwelling (Peterson et al., 2000; Werne et al., 2000; Haug et al., 2001; Lea et al., 2003; Hughen et al., 2004). This has been explained as the result of the combined action of changes in Atlantic circulation and shifts in the position of the Intertropical Convergence Zone (ITCZ). In the tropical Andes, glaciological evidence for the YD event is not conclusive, mainly because of dating uncertainties and the discontinuous nature of most of the terrestrial records (Osborn et al., 1995; Clapperton et al., 1997; Markgraf et al., 2000; Rodbell and Seltzer, 2000). Palynological records from Peruvian and Ecuadorian Andes are similarly unclear (Hansen, 1995). A potential YD equivalent is the El Abra stadial, initially dated between 10.9 and 10.1  $^{14}\text{C}$  kyr BP (12.9–11.7 cal kyr BP), which was recorded by palynological evidence in the Colombian Andes. During this cold and dry event, the temperature decreased by 4–6 °C and the upper forest line was 600–800 m lower than the present (Van der Hammen and Hooghiemstra, 1995). A more recent survey including newly dated sequences concludes that the onset of the El Abra stadial can be placed at 11.2  $^{14}\text{C}$  kyr BP (13.1 cal kyr BP), roughly coinciding with the onset of the YD, but the bracketing (minimum) ages are not conclusive (van't Veer et al., 2000). According to this new interpretation, the El Abra stadial includes both the YD and the earliest Holocene until about 9.0  $^{14}\text{C}$  kyr BP (10.2 cal kyr BP), and the existence of an internal erosional hiatus is suggested. In the Venezuelan Andes, Salgado-Labouriau (1989) reported a cold interval between about 11.7 and 9.4  $^{14}\text{C}$  kyr BP (13.5–10.6 cal kyr BP), termed the Mucubají Cold Humid Phase, in which temperatures were estimated to be 2–3 °C below present averages. It has been suggested that the Mucubají Cold Phase would be a YD equivalent (Rinaldi, 1996), but once more, radiocarbon ages bracketing this event are not precise enough for such an assessment. Other studies show a strong decrease of forest pollen (mainly *Podocarpus*) and the occurrence of characteristic unknown remains

around 12.6 cal kyr BP, but a clear signal of regional vegetation change has not been found (Rull et al., 2005, 2007, 2010). Recently, Mahaney et al. (2008) documented post-glacial sediments and moraines in the Venezuelan Andes containing several peat layers and wood fragments of ages ranging from 18.8 to 12.4 cal kyr BP. Some of them could possibly correspond to the YD, but the lack of bracketing (maximum and minimum) ages limits a definite conclusion. Mahaney et al. (2009) also found a carbon-rich layer (“black mat”) that they believe will support the extraterrestrial impact hypothesis.

A review of palynological evidence from Central and northern South America concludes that only four records from Guatemala, Costa Rica and Colombia indicate a climate reversal occurred at the onset of the YD, but the upper boundary is still insufficiently dated (Leyden, 1995; Islebe and Hooghiemstra, 1997; van't Veer et al., 2000). According to the same authors, most Neotropical pollen records lack sufficient age control between 14.0 and 10.0  $^{14}\text{C}$  kyr BP for detailed correlations with the YD chron. Unfortunately, there are no palynological studies available for comparison in the Cariaco Basin, where the YD has been clearly recorded by other proxies. There are well-dated records from the southern tropical Andes of abrupt Late Glacial climate change (Rodbell and Seltzer, 2000; Rowe et al., 2003; Thompson et al., 2005), but interpretations of the environmental conditions during this interval vary, and the pattern of temperature and aridity changes are not clear. Here, a well-dated continuous pollen sequence from the Venezuelan Andes is reported, showing a distinct vegetation shift that coincides with the YD chron. This event is interpreted in paleoclimatic terms and compared with other studies, in both regional and global context. Potential implications in terms of changes of regional circulation patterns at continental scale are analyzed separately (Stansell et al., 2010).

## 2. Study site

The twin lakes called Lagunas de Los Anteosojos are in the vicinity of the Loma Redonda field station, situated at 4045 m elevation, which belongs to the Mérida aerial cableway (Fig. 1). The watershed



**Fig. 1.** Map of the northern Andes (upper right corner) indicating the position of the region under study (white box) and the approximate location of the El Abra site (white dot) in Colombia (Van der Hammen and Hooghiemstra, 1995; van't Veer et al., 2000). MB = Maracaibo Basin. Below the region under study, showing the itinerary of Mérida-Pico Espejo aerial cableway and its stations. The cirque containing the Anteosojos lakes is highlighted by a white box.

is currently ice free, but was extensively glaciated during the late Pleistocene (Schubert, 1972). The southernmost lake, here Anteojos-S, is the largest and deepest (7.3 m). It is at 3920 m elevation, within a small glacier cirque valley, with the headwall situated around 4400 m elevation. The other lake is called here Anteojos-N, and is smaller and notably shallower.

The Anteojos lakes are on the wettest slope of the Mérida Andes, with a total annual precipitation of about 1550 mm, and a short dry season between January and March (data from Loma Redonda station). The main source of moisture is the tropical Atlantic Ocean and moisture recycling over the Orinoco (Polissar et al., 2006), which provides the necessary water for orographic precipitation via the Chama River valley (Vila, 1960). Total annual precipitation increases with altitude to a maximum of 2280 mm in La Montaña station, which is the maximum recorded for the Mérida Andes (Monasterio and Reyes, 1980), and then decreases until Pico Espejo at an approximate rate of  $-49 \text{ mm}/100 \text{ m}$  (Fig. 2). The annual average temperature at Loma Redonda is around  $3^\circ\text{C}$  with low seasonal variations of  $1\text{--}2^\circ\text{C}$ , but high daily oscillations up to  $30^\circ\text{C}$  (Monasterio and Reyes, 1980). Freezing occurs about 50 days per year. There is also an altitudinal dependence of temperature, which decreases at an average rate of  $-0.6^\circ\text{C}/100 \text{ m}$  elevation (Fig. 2). The Anteojos lakes are within the highest biome of the northern Andes, called páramo (Luteyn, 1999). The páramo is situated between the upper forest line ( $\sim 3000 \text{ m}$  elevation) and the snow line ( $\sim 4700 \text{ m}$ ) (Monasterio, 1980a), and is characterized by open vegetation with three strata. The lower consists of cushion and rosette plants, the intermediate is dominated by graminoid herbs and shrubs, and the upper is characterized by *Espeletia* (Asteraceae) columnar rosettes, which are the most conspicuous element of the landscape (Luteyn, 1999).

Berg and Suchi (2001) studied in detail the arrangement of páramo vegetation along an altitudinal transect including the lakes under study (Fig. 3). On these slopes, cloud forests show their maximum development and reach higher altitudes than in the rest of the Venezuelan Andes because of higher precipitation (Monasterio,

1980a). The upper forest line (UFL) is situated around 3200 m elevation, and the dominant tree is *Podocarpus oleifolius* (Podocarpaceae), accompanied by *Schefflera rufa* (Araliaceae) and *Ocotea* (Lauraceae). The forest–páramo transition, also called subpáramo, is characterized by shrub communities dominated by Ericaceae (*Macleania* and *Befaria*), Asteraceae (*Libanothamus*), Myrtaceae (*Ugni*) and Myrsinaceae (*Cybianthus*). A detailed study of this transition can be found in Yáñez (1998). The páramo proper extends up to 4100 m and is dominated columnar rosettes of *Espeletia schultzii* (Asteraceae), together with *Arcytophyllum* (Rubiaceae), *Calamagrostis*, *Agrostis* and *Aciachne* (Poaceae), *Espeletopsis* (Asteraceae), *Lobelia* (Campanulaceae), *Vaccinium* (Ericaceae), and the fern *Blechnum*. The superpáramo is the uppermost life zone extending up to the snowline, and has been subdivided into two formations: the desert páramo, or lower superpáramo, and the periglacial desert, or upper superpáramo (Monasterio, 1980a). In the study area, the desert páramo is represented by *Coespeletia* and *Pentacalia* (Asteraceae) communities, with *Festuca* (Poaceae), *Niphogeton* (Apiaceae), the fern *Jamesonia*, and the lichen *Thamnolia* (Berg and Suchi, 2001). The periglacial desert is present above 4400 m elevation, in the upper slopes of Bolívar and Espejo peaks, and is characterized by mostly bare soil with disperse herbaceous patches of *Arenaria* (Caryophyllaceae), *Draba* (Brassicaceae), and grasses (*Poa*, *Festuca*), *Espeletia* rosettes are absent. The uppermost limit of plant life is around 4700 m elevation (Fig. 3).

Other communities, called azonal by Berg and Suchi (2001), are present only around favorable microhabitats, as is the case of dwarf forests and aquatic vegetation. They initially grow as isolated patches on rock debris, and are small and relatively open forests dominated low trees of *Polylepis sericea* (Rosaceae) and *Gynoxys* (Asteraceae), with *Valeriana* (Valerianaceae) and *Ribes* (Grossulariaceae) in the shrubby stratum. The aquatic vegetation is poorly represented in the transect studied, and is restricted to flooded sites and lake shores. Typical genera are *Rhizocephalum* (Campanulaceae), *Lachemilla* (Rosaceae), *Orithrophium* (Asteraceae) and *Carex* (Cyperaceae). The aquatic pteridophyte *Isoetes* is frequent in lake shores, where it lives submerged until about the depth of light penetration. A number of sites around the cableway stations have been disturbed by human activities, and some plantations of exotic trees such as *Pinus*, *Cupressus* and *Eucalyptus* can be seen in the lowermost páramo levels.

The lakes Los Anteojos are in the upper part of the páramo proper, close to the lower superpáramo boundary (Fig. 3). According to the classification of Berg and Suchi (2001), two main páramo communities grow around the lakes. One is the *Espeletia schultzii*–*Aciachne acicularis* community (9), which develops a typical páramo landscape with a lower grass layer spiked by columnar rosettes up to 1 m high. At present, this community is subjected to extensive grazing. The other is the *Arcytophyllum nitidum*–*Lobelia tenera* community (10), which can be a shrubland or a mixture of shrubs and columnar rosettes of *E. schultzii*, with an herbaceous stratum of grasses and other herbs such as *Baccharis tricuneata* (Asteraceae) and *Draba pulvinata* (Lamiaceae). Among the superpáramo communities surrounding the lakes, the more significant are those dominated by tall rosettes (up to 1.5 m) of *Coespeletia moritziana*, belonging to two associations: one with *Pentacalia* cf. *sclerosa* and *Jamesonia canescens* (11), and the other with *Festuca toluensis* (13), as differential species. In addition, a few small patches of *Polylepis* forests (16) and cushion pastures of *Aciachne acicularis* (17) can be identified around lake Anteojos-S (Fig. 4).

### 3. Materials and methods

The sediment section studied is part of a 425 cm continuous percussion piston core (A3/3 B07) collected in the deepest part of

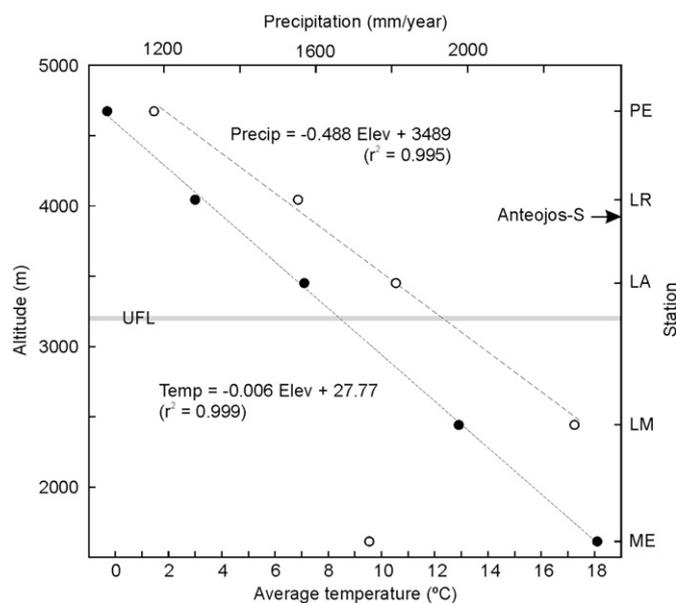
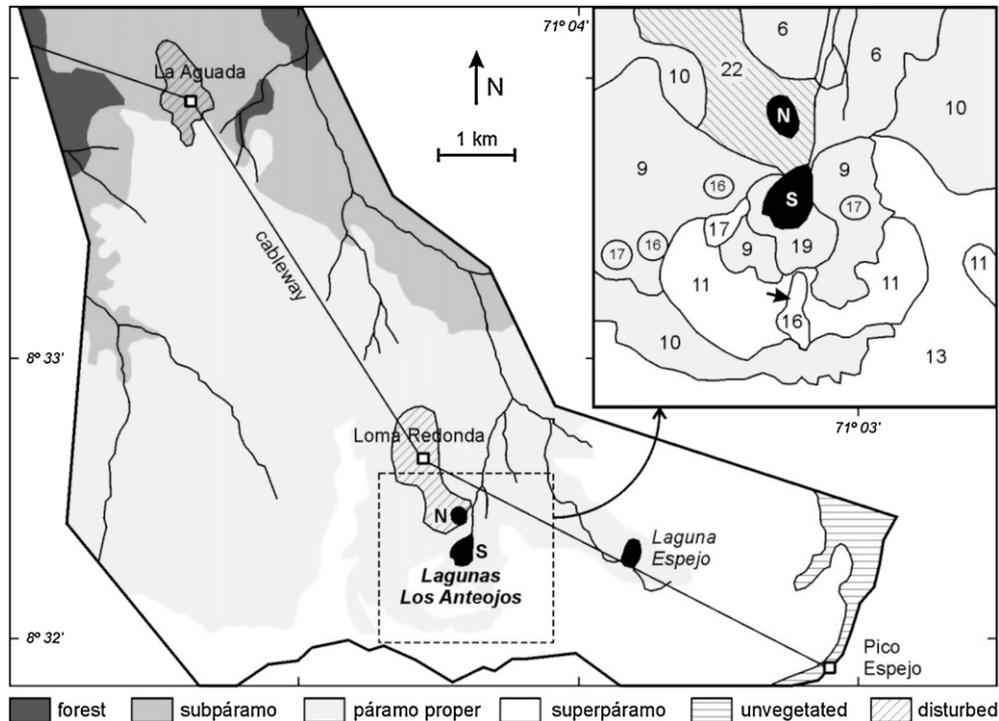


Fig. 2. Altitudinal relationships for temperature (black dots) and precipitation (open dots) in the Mérida-Pico Espejo transect, based on data from Monasterio and Reyes (1980) and Veillon (1989). The lapse rate for each parameter (expressed as the rate of change per 100 m elevation) is 100 times the slope that is:  $-0.6^\circ\text{C}/100 \text{ m}$  for average temperature, and  $-48.8 \text{ mm}/100 \text{ m}$  for precipitation. ME = Mérida, LM = La Montaña, LA = La Aguada, LR = Loma Redonda, PE = Pico Espejo.



**Fig. 3.** Vegetation map of the region under study, redrawn from Berg and Suchi (2001). The general picture includes only the main vegetation types, while the enlarged box at the upper right corner displays the communities defined by Berg and Suchi (2001). The original numerical identification of these authors has been maintained for consistency. The arrow indicates the *Polylepis* forest patch seen in Fig. 4.

the lake Anteosjos-S, in January 2007 (Stansell et al., 2010) (Fig. 4). For the present study, we used the 307–455 cm interval. Thirty-three volumetric samples ( $2\text{ cm}^3$ ) were taken at 2–5 cm intervals for pollen analyses. A modern (sediment surface) sample was taken in the same place with a small percussion corer. An additional modern sample from Laguna Negra (Mucubají) obtained previously with a Glew core collected during a field season in 2002, was also analyzed for comparison. These samples were processed using standard palynological techniques (Bennett and Willis, 2001), with some modifications, which have shown to be especially efficient for Andean lake samples (see Supplementary Material). Slides were mounted in silicone oil without sealing. Pollen and spore



**Fig. 4.** General view of the Anteosjos lakes facing South. The approximate coring site in Anteosjos-S is marked with an asterisk. The arrow indicates the largest patch of *Polylepis* forest around the lakes (see Fig. 3) (Photo M. Bezada).

identification was made according to Van der Hammen and González (1960), Murillo and Bless (1974, 1978), Hooghiemstra (1984), Salgado-Labouriau (1984), and Tryon and Lugardon (1991). In reference to identification, it is important to note that the *Acaena*–*Polylepis* pollen type is attributed to *Polylepis* because, in the study area, *Acaena* is only present in Community 8 of Berg and Suchi (2001), which occurs at lower altitudes and is not present neither around the lake nor in its basin (Fig. 3). On the contrary, *Polylepis* gallery forests are conspicuous along the creeks that feed the lake (Figs. 3 and 4). In the Venezuelan Andes, this pollen type has a little dispersion power and is mostly local or downwater transported. Indeed, modern pollen sedimentation studies have shown that the presence of *Acaena*–*Polylepis* pollen type is associated to the presence of *Polylepis* forests close to the sampling site or upstream (Rull, 2006). Counts were conducted until a minimum of 300 pollen and spores were tabulated (excluding the superabundant *Isoëtes*), but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts range between 319 and 495, with an average of 346. Pollen sum values, including all pollen types, range from 253 to 406 (average 299). Pollen taxa are grouped in the diagrams according to the vegetation composition (Salgado-Labouriau, 1979; Monasterio, 1980a; Berg and Suchi, 2001). Pollen diagrams were plotted with PSIMPOLL 4.26, using a time scale derived from an age-depth model based on six AMS radiocarbon dates (Table 1). The zonation method was the Optimal Splitting by Information Content (OSIC), and the number of significant zones was determined by the broken-stick model test (Bennett, 1996). Pollen types with over 5% were used for zonation, and their percentages were square-root transformed. Interpretation is based on comparison with the surface samples previously mentioned. The differences between modern and Late Glacial samples were measured using the Squared Euclidean Distance (SEUCLID), using only taxa included in the pollen sum. Previous modern analog studies along altitudinal transect from the

**Table 1**

AMS radiocarbon dates for the core studied, based on aquatic macrofossils (Stansell et al., 2010).

Lab number	Depth (cm)	<sup>14</sup> C yr BP	Cal yr BP (median, 95% conf. int.)
UCI-37511	326	8850 ± 20	10,012 (9780–10,153)
UCI-37538	372	10,180 ± 25	11,889 (11,760–12,025)
UCI-37539	406	11,060 ± 30	12,975 (12,905–13,068)
UCI-37540	425	11,880 ± 35	13,749 (13,656–13,833)
UCI-37623	446	12,430 ± 80	14,480 (14,136–14,905)

montane forest to the superpáramo (Salgado-Labouriau, 1979; Rull, 2006) were used for interpretation. Numerical reconstructions using the available transfer functions (Rull, 2006) have not been attempted because modern samples on which they are based were taken in soils, peat bogs, mosses and lakes, and taphonomic differences may introduce errors. Furthermore, these transfer functions were developed in an altitudinal transect from the dry páramo slopes, where climatic gradients are different (Monasterio and Reyes, 1980). The known autoecology of taxa identified (Marchant et al., 2002) was also considered.

## 4. Results

### 4.1. Modern sample

The modern sample differs from the Late Glacial sequence by the presence of three exotic pollen types that are absent below: *Rumex*, *Plantago* and *Pinus*. The *Rumex* pollen found is of the type *R. acetosella*, and represents 4.72% of the pollen sum, while *Plantago* (of the *P. lanceolata* type) is 6.87%, and *Pinus* is represented by one single grain. In order to make the percentages of modern sample comparable to that of the diagram below, a new pollen sum was calculated excluding these three exotic types. The new percentages are displayed at the top of the diagrams (Figs. 5 and 6). The percentage of pollen from Andean forest trees is slightly above 30%, with *Podocarpus* reaching >10%. Among páramo elements, herbs dominate (~40%) while Asteraceae are notably lower (~10%). Spores are largely dominated by *Huperzia*-type (~25%). Concerning aquatic remains, the more abundant is *Botryococcus* (>300% of the pollen sum). *Zygnema* and an unknown remain similar to type 317 of van Geel et al. (1980/1981) are also worth mentioning (3–5%), while *Isoëtes*, *Mougeotia* and *Spirogyra* are scarce (<1%).

### 4.2. Late Glacial sequence

Overall, the pollen diagram is dominated by páramo herbs and shrubs, mainly Poaceae and Asteraceae, followed by trees from the Andean forest (*Podocarpus*, *Alnus* and *Hedyosmum*) and from the high altitude *Polylepis* forests (Fig. 5). Among spores, the more abundant is the *Huperzia*-type. The total pollen and spore concentration is oscillating, with two major peaks, slightly above the center and at the top of the diagram, respectively. The stratigraphic variations of the pollen and spore assemblages allowed subdivision into the following zones.

#### 4.2.1. Zone A3-1 (145–97 cm; 14.68–12.86 cal kyr BP; 12 samples)

This zone is dominated by Poaceae (40–50%), followed by *Podocarpus* (up to 25%). Less abundant (up to 10%) are *Alnus*, *Hedyosmum*, *Polylepis*, Asteraceae and Cyperaceae. *Huperzia*-type and the psilate *Cyathea* spores are also around 10%. The lowermost part of this zone is slightly different, because of the low percentages of *Podocarpus* and *Huperzia*-type (<5%), and the comparatively higher abundance of *Alnus* and *Hedyosmum* (~10%). *Podocarpus* is constantly increasing throughout the zone, peaking near the top. Dissimilarity values with the modern sample assemblage are

intermediate. The aquatic elements show their maxima in the lower half of this zone, especially *Isoëtes*, *Pediastrum*, *Botryococcus* and cf. type 317 (Fig. 6). In the upper half, only *Isoëtes* spores are abundant. *Pediastrum* and *Botryococcus* drastically decline and cf. type 317 disappears.

#### 4.2.2. Zone A3-2 (97–58 cm; 12.86–11.65 cal kyr BP; 8 samples)

A sudden decline of *Podocarpus* and *Polylepis*, together with an increase of Poaceae, marks the beginning of this zone. *Huperzia*-type also decreases. *Polylepis* disappears around the middle of the zone, while Poaceae are around 70% of the pollen sum. Above this point (77 cm; 12.28 cal yr BP), *Polylepis* occur again, but with lower numbers (<5%), and Asteraceae show a local maximum (20%). This is the zone of maximum dissimilarity with the modern assemblage, especially in its lower half. *Isoëtes* spores experience a sudden decrease at the beginning and are almost absent in this zone, showing a recovery at the end. The algae remain in their lower values.

#### 4.2.3. Zone A3-3 (58–1 cm; 11.65–9.35 cal kyr BP; 13 samples)

The main features of this zone are the manifest increase of *Polylepis* (up to 25% at the end of the zone), Asteraceae (up to 30%), and *Huperzia*-type (10–15%), coinciding with the gradual and consistent decrease of Poaceae (from around 50% to 20%). This is the zone of maximum similarity (minimum Euclidean distance) with modern assemblages. *Isoëtes* spores and *Botryococcus* are abundant again, but not as high as in A3-1. *Pediastrum* slightly increases at the end, and *Debarya* shows a continuous increase throughout the zone.

## 5. Interpretation

### 5.1. Present pollen–vegetation relationships

Pollen from typical páramo herbs and shrubs are dominant, with an important contribution from introduced plants, indicative of human disturbance from cattle and agriculture. *Rumex acetosella* (Polygonaceae) was introduced by Europeans in the 16th century as a weed associated with wheat cultivation, which ended around 1850 AD (Monasterio, 1980b). At present, *Rumex* develops extensive populations in the abandoned wheat fields, and its pollen is present and abundant (up to 40%) in all surface samples from around 3000 to 4500 m elevation (Rull, 2006). *Plantago lanceolata* (Plantaginaceae) is also a herbaceous weed introduced from Europe. Other species of *Rumex* and *Plantago* occur in the páramos (Vareschi, 1970; Rahn, 1974; Hooghiemstra, 1983; Luteyn, 1999), but the morphological similarity of the pollen types found with well-known human-introduced species, together with their strong increase in the modern sample are remarkable. *Pinus* is of even more recent introduction, as the plantations of *P. caribbaea* date from the past century. The pollen from Andean forest trees (notably *Podocarpus*) is far more abundant than in other locations situated at the same altitude, and similar to the values recorded at the forest–páramo transition zone or subpáramo (Salgado-Labouriau, 1979; Rull, 2006). This would be caused, in part, by the maximum elevation reached by the UFL, owing to the wetter climate of these slopes (see above). However, taphonomic differences between peat and lake sediments should also be considered. The relatively high ratio of herbaceous to Asteraceae pollen, representing mainly the *Espeletia* rosettes, is consistent with the more herbaceous character of these páramos, as compared with those from other (drier) Andean valleys (Monasterio, 1980a; Berg and Suchi, 2001). Despite the small area occupied by *Polylepis* forests (Fig. 3), the pollen of these trees is relatively well represented (>5%) in the modern pollen assemblage. This might be due to the fact that the larger



## Laguna Anteoijos-S (core A3/3 B-07)

Analysts: V. Rull, E. Montoya

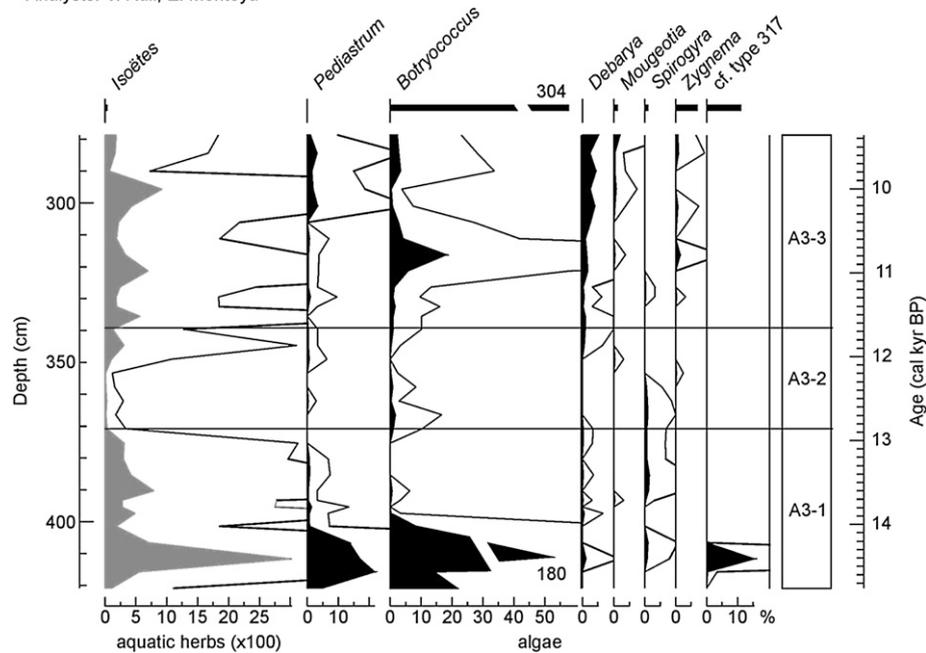


Fig. 6. Percentage diagram of aquatic remains. Solid lines represent  $\times 10$  exaggeration. Values for the modern sample are represented by bars at the top of the diagram.

*Polylepis* patch around the cored lake lies in its headwall, on a slope draining straight into the lake (Fig. 4), thus facilitating water transport. Previous studies showed that *Polylepis* pollen has low dispersion power and is commonly absent or rare, unless the sampled sediments are very close or inside the forests (Rull, 2006). However, the pollen of these trees can dominate the assemblage in lakes entirely surrounded by *Polylepis* forests (Table 2). Among spores, the high percentages of *Huperzia*-t support previous observations of Hansen et al. (2003), by which these spores were characteristic of high, cold and wet páramos. In summary, the modern sample reflects the present vegetation around the Anteoijos lakes, in agreement with páramo samples taken at similar altitudes in previous modern analog studies on the Venezuelan Andes (Salgado-Labouriau, 1979; Rull, 2006).

### 5.2. Late Glacial trends

The regional vegetation corresponding to zone A3-1 (14.68–12.86 cal kyr BP) was not substantially different from today, but the density of Asteraceae tall rosettes was lower, in relation to grasses. Most modern elements were already present, including *Polylepis*, and its abundance suggests a patchy pattern similar to today. The increase of *Podocarpus* at the end of the zone culminated around 13.26 cal kyr BP, and may be indicative of a slightly higher UFL. However, the other trees do not show the same trends. A similar situation in a coeval pollen zone from another Andean lake of the same region was interpreted in terms of intensified orographic winds, resulting in more efficient upward transport of the highly anemophilous *Podocarpus* pollen (Rull et al., 2005). The similar abundances of some pelagic elements (*Botryococcus* and cf. type 317) suggest the presence of lake levels similar to today between about 14.68 and 14.01 cal kyr BP. However, the contrasting percentages of *Isoetes* and *Pediastrum* suggest differences from present-day limnological conditions. It is possible that the lake level was slightly lower than today (note the lower *Botryococcus* percentage) and littoral, shallow-water environments were more

extensive, favoring the development of *Isoetes* communities. Between about 14.01 and 12.86 cal kyr BP, the synchronous decrease of the dominant algae and the intermediate values of *Isoetes* likely indicate the existence of shallower waters.

A major change in pollen spectra occurred after 12.86 cal kyr BP, as manifested in the dominant elements and the dissimilarity

Table 2

Results of the pollen analysis of a surface sample taken in the deepest part of Laguna Negra de Mucubají (~3500 m altitude), which is encircled by a dense and extensive *Polylepis* forest.

Pollen taxa	Vegetation type	% of $\Sigma$ P
<i>Podocarpus</i>	Andean forest	4.71
<i>Hedyosmum</i>	Andean forest	6.52
<i>Alnus</i>	Andean forest	2.90
<i>Dodonaea</i>	Andean forest	1.45
<i>Miconia</i>	Andean forest	1.45
<i>Alchornea</i> -t	Andean forest	1.45
<i>Weinmannia</i>	Andean forest	0.72
URTICALES	Andean forest	0.72
Other trees	Andean forest	0.36
<i>Polylepis</i>	<i>Polylepis</i> forest	35.14
ASTERACEAE	Páramo shrubs	14.49
POACEAE	Páramo herbs	15.22
<i>Rumex</i>	Páramo herbs	1.81
CYPERACEAE	Páramo herbs	1.45
<i>Plantago</i>	Páramo herbs	0.72
APIACEAE	Páramo herbs	0.72
<i>Arenaria</i>	Páramo herbs	0.72
<i>Valeriana</i>	Páramo herbs	0.36
<i>Draba</i>	Páramo herbs	0.36
<i>Gentiana</i>	Páramo herbs	0.36
Other herbs	Páramo herbs	2.54
Undiff. dicots	Páramo herbs	5.80
Monoletes (psilate)	Ferns and lycopods	5.43
<i>Jamesonia</i>	Ferns and lycopods	3.26
<i>Polypodium</i> (verrucate)	Ferns and lycopods	2.17
<i>Huperzia</i> -t	Ferns and lycopods	1.81
<i>Cyathea</i> (psilate)	Ferns and lycopods	1.81
<i>Cyathea</i> (verrucate)	Ferns and lycopods	0.36

curve, which indicate vegetation patterns different from today. Pollen assemblages of this zone are similar to those found in the uppermost modern samples analyzed so far in the region, which correspond to the lower part of the periglacial desert, around 4400–4500 m (Rull, 2006). This suggests a lowering of bioclimatic zones and is consistent with the decline in Andean forest trees, which is indicative of a lowering of the UFL. The lack of *Polylepis* pollen, indicates the disappearance of such forests from around the lakes. These peculiar, almost monospecific, communities occur as isolated forest patches within the páramo landscape. They grow in a wide range of precipitation regimes, from the driest (700 mm) to the wettest (>1500 mm) sectors of the Mérida Andes (Monasterio, 1980a), hence, their disappearance is unlikely caused by moisture changes. More significant is the fact that *Polylepis* forests attain their maximum altitude (4300 m) in the study area (Monasterio, 1980a) and their disappearance is consistent with a lowering in this climatic boundary. Indeed, the pollen of *Polylepis* has a low dispersion power and is regularly found only downstream, below its uppermost distribution boundary (Rull, 2006). The whole picture suggests the existence of high superpáramo environments around the Anteojos lakes, which were probably near the limit between the desert páramo and the periglacial desert (lower and upper superpáramo, respectively). Today, this boundary is around 4400 m elevation (ca 500 m above the lake). On the other hand, a lowering of at least 400 m is needed to push the *Polylepis* forests below the Anteojos lakes. Therefore, the expected vegetation depression can be estimated as 400–500 m altitude. Using the present-day lapse rate of  $-0.6\text{ }^{\circ}\text{C}/100\text{ m}$ , the estimated decrease in annual average temperatures is of  $2.5\text{--}3.0\text{ }^{\circ}\text{C}$ . Using a lapse rate of  $-0.76\text{ }^{\circ}\text{C}/100\text{ m}$ , calculated by Wille et al. (2001) for the Colombian Andes during the LGM, the estimated temperature decline would be of  $3.0\text{--}3.8\text{ }^{\circ}\text{C}$ . These might be considered minimum and maximum estimates, respectively. Cooling lasted until around 12.65 cal kyr BP, when it began to revert until the end of the zone at 11.65 cal kyr BP.

During this cold episode, the climate was likely drier as deduced from almost all moisture indicators. Among the sporomorphs, the main proxy for moisture is *Huperzia*, which has been considered indicator of cold and wet páramos (Hansen et al., 2003; Rull et al., 2005). In this interval, *Huperzia* shows a clear decline with respect to the other pollen zones and the modern sample, suggesting a lowering in the available moisture (i.e. precipitation/evaporation ratio). On the other hand, the synchronous shift in aquatic indicators occurred around 14.01 cal kyr BP still persisted suggesting the maintenance of lower water levels, but the sharp decline of *Isoetes* suggests that water level was even lower, though the lake was not completely dry. The decline of sedges (Cyperaceae), a well-known indicator of local flooding (Marchant et al., 2002), supports this interpretation. In summary, though internal ecological reorganizations cannot be dismissed, the whole picture strongly suggests a decrease in available moisture during this period. In present-day conditions, a downward shift of 400–500 m in altitude indicates a precipitation decrease of around 200–250 mm per year (at a rate of  $-49/100\text{ m}$ , see above). However, this could be not considered an accurate estimate for the time interval under study, as it only considers the influence of orography, and does not take into account potential changes in local and regional precipitation patterns due to circulation re-arrangements. In addition, it is expected that evaporation was slightly reduced due to the lower temperatures.

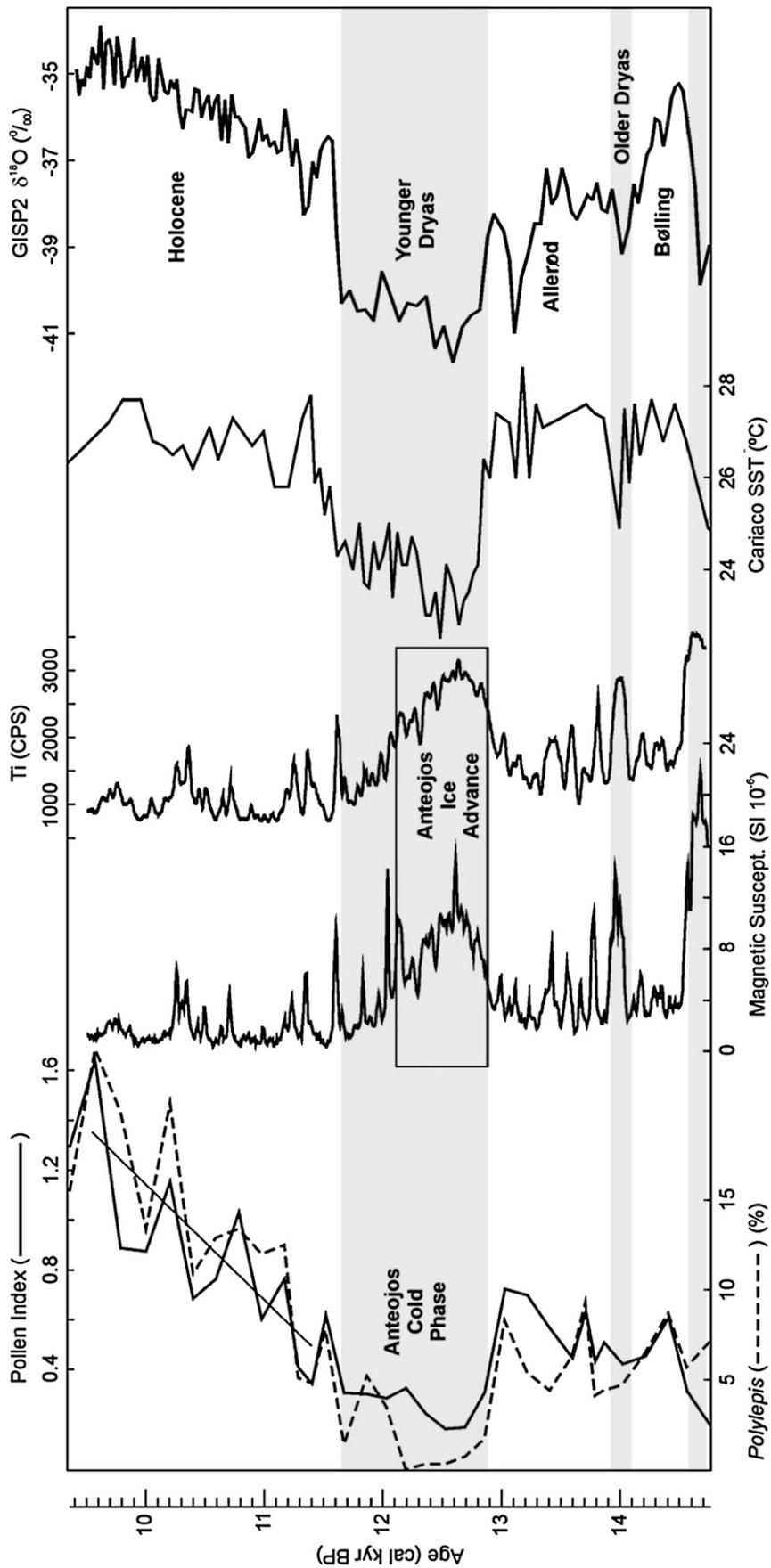
From 11.65 to 9.35 cal kyr BP, the vegetation was more similar to today than in the rest of the sequence (see dissimilarity values), but some minor differences remain. For example, the regional vegetation seems to have been less herbaceous and have more dense communities of Asteraceae (including the *Espeletia* rosettes). In

addition, the recovery of *Polylepis* forests around the lake was striking, with maximal values at the top (around 9.55 cal kyr BP), which are close to values recorded in sediments from lakes completely encircled by these forests (Table 2). In summary, the vegetation was slightly more closed than today and certainly much more than in zone A3-2. This suggests the return to warmer conditions, not very different from today, but perhaps warmer around 9.96 cal kyr BP. Lake levels appear to be higher, but did not attain the present magnitude, not even that of zone A3-1 between 14.68 and 14.01 cal kyr BP.

## 6. Discussion

The Laguna de Los Anteojos record provides strong evidence from the Venezuelan continent of a rapid climate reversal during the YD. The glacial flour record shows a rapid increase in clastic sediment flux starting after 12.86 kyr BP (Stansell et al., 2010). The strength of the record, however, comes from the multi-proxy approach that identifies clear vegetation changes during periods of ice margin fluctuations that are inferred from the clastics record. Clastic sediments can be interpreted in a number of ways that are not necessarily controlled by climatic influences, but combined with palynology and biogenic silica data, they both provide strong supporting evidence of temperature and humidity changes during the Late Glacial. Here we discuss the Lake Anteojos record in the context of other paleoclimate records from the tropics and high latitudes.

The vegetation shift documented in the Anteojos lake sediment record during the 12.86–11.65 cal kyr BP cold reversal is comparable to the record of the El Abra Stadial in the Colombian Andes. Changes in pollen diagrams may vary in magnitude, depending on the elevation of the study site, but there is a decline of Andean/subandean forest elements, accompanied by an increase of páramo elements, mainly Poaceae and Asteraceae (Van der Hammen and Hooghiemstra, 1995). In Colombia, the signal is more pronounced and involves forest trees, such as *Alnus* and *Quercus*, while in the Venezuelan Andes the indicator trees are *Podocarpus* and *Polylepis*. These differences are likely caused by the altitude of the sampling sites and their corresponding regional vegetation, which in Colombia is around the forest–páramo transition, and in Venezuela lies around the páramo–superpáramo boundary. The *Podocarpus* decrease was also recorded in another superpáramo locality of the Mérida Andes, at 12.6 cal kyr BP (Rull et al., 2005). Furthermore, there is a biogeographic component, as *Quercus* is absent in Venezuela, during both the modern and last glacial cycle (Hooghiemstra, 2006; Kappelle, 2006). According to Van der Hammen and Hooghiemstra (1995), the UFL was 600–800 m lower than today and average temperatures were  $4\text{--}6\text{ }^{\circ}\text{C}$  below present values. van't Veer et al. (2000) reconsidered the palynological evidence for El Abra stadial in the original Colombian sections (El Abra and Fúquene), and obtained a more conservative temperature estimate of  $1\text{--}3\text{ }^{\circ}\text{C}$  lower than today. Our estimates for Anteojos ( $2.5\text{--}3.8\text{ }^{\circ}\text{C}$ , average  $3.1\text{ }^{\circ}\text{C}$ ) fall within this range, in agreement with previous estimates of Salgado-Labouriau (1989) for the Mucubají cold phase ( $2\text{--}3\text{ }^{\circ}\text{C}$ ), characterized by similar pollen changes. Concerning moisture availability, the Anteojos sequence favors the existence of dry climates during the cold reversal, coinciding with van't Veer et al. (2000), who propose the occurrence of a prolonged drought during the El Abra biozone. These authors suggest the existence of an intra-El Abra hiatus, as the cause for dating uncertainties that prevent direct comparison of the El Abra stadial with the YD. However, no evidence of a similar hiatus has been found in the Anteojos section analyzed here. The dryness in El Abra is supported by the increase of drought indicators like Cactaceae and *Sapium* (van't Veer et al., 2000). No similar evidence has



**Fig. 7.** Correlations of the Pollen Index (PI) and the *Polylepis* curves with selected physico-chemical paleoclimatic proxies measured in the same core (Stansell et al., 2010) and referential paleoclimatic reconstructions containing the YD event (Cariaco and GISP). Gray bands represent the stadials based on the GISP isotopic curve. The glacier advance defined by Stansell et al. (2010) in the Anteojos core is indicated by a box around MS and Ti curves. Raw data have been downloaded from the IGBP PAGES/World Data Center A for Paleoclimatology - NOAA/NGDC Paleoclimatology Program at [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov). (Lea et al., 2003, Cariaco Basin Foraminiferal Mg/Ca and SST Reconstruction, Data Contribution Series #2003-067; Alley, 2004; GISP2 Ice Core Temperature and Accumulation Data, Data Contribution Series #2004-013).

been found in Anteojos, and our interpretation relies on the likely occurrence of lower water levels, reflected in the dramatic decline of aquatic elements, and the possible decrease in orographic precipitation caused by the altitudinal shift. Future research will contribute to clarify this point.

In order to compare our interpretation with other regional and global reconstructions, a correlation tool was built using the more sensitive taxa, *i.e.* those experiencing conspicuous shifts during the YD. This pollen index (PI) was defined as the ratio between the decreasing (*Podocarpus*, *Polylepis*, *Huperzia*-t) and the increasing (Poaceae, Asteraceae) elements, in the 12.86–11.65 cal kyr BP interval. In the present state of knowledge, this is an arbitrary and uncalibrated pollen index, but some inferences are possible on the basis of the known climatic and ecological requirements of the involved taxa. The decreasing components are elements from the upper layer of the montane forest (*Podocarpus*), which abundance is directly related to the altitude of the UFL (Salgado-Labouriau, 1979) that is mainly controlled by annual average temperature, and elements from humid páramo environments (*Polylepis*, *Huperzia*) (Marchant et al., 2002; Rull et al., 2005). The decreasing elements are dominant in open páramo environments and, given their high taxonomic level (family), it is not possible to be more precise concerning their ecological requirements. Therefore, the PI index should *a priori* increase with warmer and wetter climates and decrease with colder and dryer ones. Concerning representativity, PI summarizes the 82% of the total information contained in the pollen diagram. The good match between PI and the *Polylepis* curve ( $r^2 = 0.814$ ) suggests that *Polylepis* may be also used as a correlaton tool by itself (Fig. 7). The chronological coincidence of pollen zone A3-2, in which the Anteojos cold phase has been defined, with the YD chron and the matching of pollen reversal with regional and quasi-global paleoclimatic reconstructions are striking. The chronology is constrained by a highly reliable age–depth model based on five AMS radiocarbon dates on macrofossils in a 147 cm interval (1 date each 30 cm, in average) (Stansell et al., 2010). Furthermore, two of these dates (12,975 and 11,889 cal yr BP) closely bracket the YD boundaries (Table 1), which provides additional confidence. Possible equivalents for Older Dryas stadial, and Bølling and Allerød interstadials are also present in the pollen curves, but the resolution should be improved to test these hypotheses. The global warming trend that occurred at the beginning of the Holocene, known as Early Holocene Warming (EHW) (Kaufman et al., 2004; Kaplan and Wolfe, 2006), is also suggested by the PI and *Polylepis* curves. In the Cariaco Basin, the Titanium content of marine sediments, a proxy for continental moisture, indicates drier climates during the YD chron (Haug et al., 2001), coinciding with the palynological interpretation in Anteojos, and also in the Colombian Andes. According to van't Veer et al. (2000) and Lea et al. (2003), dry climates dominated over northern South America during the YD.

The chronological coincidence of palynological curves combined with independent paleoclimatic reconstructions implies a rapid response of sensitive taxa to climatic change during the YD. To properly test this assumption, avoiding circular reasoning, direct comparison of pollen curves with independent proxies of known rapid response to climatic shifts, measured in the same core, is needed. Fig. 7 shows that changes in geochemical proxies representing changes in clastic flux and glacial ice cover, and pollen curves are synchronous. Indeed, the vegetation change proceeded parallel, with no evident delay, to the Anteojos glacier advance initiated at 12.86 cal kyr BP and culminating at 12.65 cal kyr BP (Stansell et al., 2010), which perfectly matches with pollen evidence. Therefore, the time lag in the response of sensitive taxa is lower than sampling resolution, which is of  $\sim 170$  years per sample (centennial), higher than the usual for the Venezuelan Andes,

where multi-centennial to millennial records are the norm (Rull et al., 2010). Even so, higher resolution sampling is needed for a more precise estimation of this parameter. The most sensitive taxa are *Podocarpus* and *Polylepis*, which reacted rapidly at the onset of the YD (Fig. 5). The case of *Polylepis* is worth noting, because it is characteristic of the majority of the pollen trends in the PI, and matches well with other paleoclimatic reconstructions (Fig. 7). As a consequence, *Polylepis* pollen would be tentatively-considered a good paleoclimatic indicator in lake sediments close to their upper distribution boundary, in locations similar to the studied lake. So far, this could be considered a working hypothesis emerged from this study, to be confirmed or not with further research. No other estimations of time lags in the response of neotropical vegetation are available for comparison. Studies developed in mountain lakes from northern Europe estimate short time lags of less than a decade between isotopic records and vegetation responses, during the YD (Ammann et al., 2000; Seppä and Bennett, 2003; Birks and Birks, 2008). Recent studies on living montane communities have shown a synchronous and surprisingly high migration speed ( $\sim 2$  m altitude per year in average) of dominant taxa as a consequence of recent climate change, with imperceptible response lags (Kelly and Goulden, 2008).

The palynological evidence from the Venezuelan Andes supports the glacial-geologic data of an abrupt Late Glacial cooling event in the northern tropics that began at  $\sim 12.86$  ka BP (Stansell et al., 2010). In general, ice margins in the southern tropical Andes advanced just prior to, or at the start of the YD, but mountain glaciers retreated during most of the interval (Rodbell et al., 2009). This is somewhat contradictory because the ice core records from tropical glaciers suggest that conditions were colder and wetter during the YD (Thompson et al., 2005). Based on the available evidence, Rodbell and Seltzer (2000) concluded that the YD was a period of increased aridity in the tropical Andes, but the record of temperature changes is not clear because continuous records of mountain glaciations and environmental shifts have previously not been available. Glaciers in the Venezuelan Andes are mostly temperature sensitive (Stansell et al., 2005; Polissar et al., 2006), and ice margins were able to advance in the northern tropics during the YD even though conditions were more arid. Our evidence of advancing glaciers (Stansell et al., 2010) and lower lake levels (this paper) in the Venezuelan Andes supports the conclusions of Rodbell and Seltzer (2000) that conditions in the tropical mountains were colder and more arid during the YD.

## 7. Conclusions

A cold and likely dry phase, called the Anteojos cold phase (ACP), has been recorded after pollen analysis of a sediment core from Lake Anteojos, in the tropical Venezuelan Andes. This event occurred between 12.86 and 11.65 cal kyr BP, coinciding with the YD cold reversal in the northern hemisphere. The ACP was marked by a sudden decline in *Podocarpus* and *Polylepis* pollen, and an increase in Poaceae and Asteraceae. A general vegetation displacement downward of 400–500 m has been estimated during the maximum of this event, occurred around 12.65 cal kyr BP, which corresponds to an average temperature decrease of 2.5–3.8 °C (average 3.1 °C). The ACP is also correlated both chronologically and paleoecologically with the El Abra stadial from the neighbor Colombian Andes, which has been considered an equivalent of the YD, at least in part. Both are characterized by similar biotic altitudinal displacement and analogous estimated temperature drops, as well as indications of drier climates. The Anteojos pollen shifts are notably synchronous, considering the resolution sampling, with paleoclimatic reconstructions based on physical

proxies and stable isotopes, showing the suitability of pollen to record rapid climatic changes in the tropical Mérida Andes. *Poly-lepis* pollen seems especially well suited for such task, near its upper distribution limit.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quascirev.2010.07.012.

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