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Leunda, Maria; González-Sampériz, Penélope; Gil Romera, Graciela; Aranbarri, Josu; Morena, Ana; Oliva-Urcia, Belén ; Sevilla-Callejo, Miguel; Valero-Garcés, B.

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The Late-Glacial and Holocene Marboré Lake sequence (2612 m a.s.l., Central Pyrenees, Spain): Testing high altitude sites sensitivity to millennial scale vegetation and climate variability

Maria Leunda[(a,b)]*, Penélope González-Sampériz[(a)], Graciela Gil-Romera [(a,c)], Josu Aranbarri [(d)], Ana Moreno [(a)], Belén Oliva-Urcia [(e)], Miguel Sevilla-Callejo[(a)] and Valero-Garcés, B. [(a)]

(a) Department of Geoenvironmental Processes and Global Change, Pyrenean Institute of Ecology (IPE-CSIC). Av/ Montañana s/n, 50059 Zaragoza, Spain

(b) Departamento de Ciencias de la Tierra. Universidad de Zaragoza. Pedro Cerbuna, 12. 50009 Zaragoza, Spain

(c) Department of Geography and Earth Sciences, Aberystwyth University, Penglais Campus,SY23, United Kingdom

(d) Departamento de Geografía, Prehistoria y Arqueología, Universidad del Pais Vasco (UPV-EHU). C/ Tomás y Valiente s/n 01006 Vitoria-Gasteiz, Basque Country, Spain

(e) Departamento de Geología y Geoquímica, Universidad Autónoma de Madrid, Francisco Tomás y Valiente 7, 28049 Madrid, Spain

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Abstract

This paper presents the environmental, climate and vegetation changes reconstructed for the last 14.6 kyr cal BP from the Marboré Lake sedimentary sequence, the highest altitude record (2612 m a.s.l.) in the Pyrenees studied up to date. We investigate the sensitivity of this high altitude site to vegetational and climate dynamics and altitudinal shifts during the Holocene by comparing palynological spectra of the fossil sequence and pollen rain content from current moss pollsters. We hypothesize that the input of sediments in lakes at such altitude is strongly controlled by ice phenology (ice-free summer months) and that during cold periods Pollen Accumulation Rate (PAR) and Pollen Concentration (PC) reflect changes in ice-cover and thus is linked to temperature changes. Low sedimentation rates and low PC and PAR occurred during colder periods as the Younger Dryas (GS-1) and the Holocene onset (12.6-10.2 kyr cal BP), suggesting that the lake-surface remained ice-covered for most of the year during these periods. Warmer conditions are not evident until 10.2 kyr cal BP, when an abrupt increase in sedimentation rate, PC and PAR occur, pointing to a delayed onset of the Holocene temperature increase at high altitude. Well-developed pinewoods and deciduous forest dominated the mid montane belt since 9.3 kyr cal BP till Mid-Holocene (5.2 kyr cal BP). A downwards shift in the deciduous forest occurred after 5.2 kyr cal BP, in agreement with the aridity trend observed at a regional and Mediterranean context. The increase of herbaceous taxa during the Late Holocene (3.5 kyr cal BP-present) reflects a general trend to reduced montane forest, as anthropogenic disturbances were not evident until 1.3 kyr cal BP when *Olea* proportions and other anthropogenic indicators clearly expand. Our study demonstrates the need to perform local experimental approaches to check the effect of ice phenology on high altitude lakes sensitivity to vegetation changes to obtain more realistic reconstructions of mountain vegetation belts dynamics.

Key words: Lake ice-cover, moss pollster, vegetation dynamics, Central Pyrenees, Last deglaciation, Holocene

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1. Introduction

Current landscapes have been shaped by long-term climatic, environmental and cultural processes. Particularly, alpine ecosystems are among the most sensitive and fragile to Global Change (Krajick, 2004) and their geological archives offer a great opportunity to understand recent changes in mountain ecosystems in the context of past environmental and climate dynamics. Recent studies have detected a gradual transformation of mid-latitude high mountain plant communities due to the ongoing climate change in several mountain ranges, including the Pyrenees (Gottfried et al., 2012; García et al., 2016). This gradual transformation encompasses both substitutions of cold-adapted plant communities by more thermophilous ones (Gottfried et al., 2012) and treeline altitudinal shifts (Camarero and Gutiérrez, 2004; García-Ruiz et al., 2015; García et al., 2016). Alpine ecosystems show an intense and fast response to recent global warming (Camarero et al., 2015) and land-use changes (Battarbee et al., 2002; Cunill et al., 2012; Geantă et al., 2014; García-Ruiz et al., 2015).

Addressing the response of these ecosystems to changing environmental and climate conditions in the past helps to better constrain the role of different forcings controlling the current climate change processes and impacts. Mountain vegetation has been shown to be particularly sensitive to climate variability (Birks and Ammann, 2000; González-Sampériz et al., 2006; Magny et al., 2013; Pérez-Sanz et al., 2013; Thöle et al., 2016) and particularly at higher altitudes (Birks and Ammann, 2000). In this sense, remote mountain lakes have high potential as past climate and vegetational change archives (Battarbee et al., 2002; Catalan et al., 2002; Ilyashuk et al., 2011). However, interpreting pollen sequences from high altitude sites has some specific challenges, as pollen percentages do not reflect vegetation cover, some taxa are over-represented (pines) and values are highly influenced by sedimentation rates which are likewise influenced by ice-cover season. Alpine lakes can be ice-covered for about 10 months or more, strongly dependent on climate variability (Brown and Duguay, 2010; Sánchez-López, 2016) and since changes in ice-cover timing directly affect sedimentation dynamics, all fluxes associated to environmental proxies are affected too (Catalan et al., 2002; Thompson et al., 2005; Ojala et al., 2008; Tomkins et al., 2009). In order to have a better control on

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pollen representation in fossil sequences we use the absolute amount of pollen deposition per unit area and time (Pollen Accumulation Rate, PAR). This is frequently a more precise index than the more commonly used pollen percentages, particularly when addressing vegetation changes in high altitude lakes to minimize the effect of variable sedimentation rate in a frequent ice-covered lake (van der Knaap et al., 2001; Tinner and Theurillat, 2003; Seppä and Hicks, 2006; Matthias and Giesecke, 2014).

The other limiting factor in high-altitude pollen –based reconstruction is related to the variable intensity and source of the pollen rain. Thus, as pollen produced in lowlands is easily lifted by vertical air-mass movements and deposited at subalpine and alpine zones, it may obscure the local vegetation signal, especially in treeless sites where local pollen production is low, complicating the vegetation history reconstruction (Barthelemy and Jolly, 1989; David, 1993; Birks and Birks, 2000; Tinner and Theurillat, 2003; Ortu et al., 2006; Seppä and Hicks, 2006). To tackle this problem, modern pollen rain is usually characterized along an elevation gradient and it is used as a tool to refine past vertical shifts and changes in vegetation composition (Ortu et al., 2006; Canellas-Bolta et al., 2009; Birks and Bjune, 2010; de Nascimento et al., 2015; Garcés-Pastor et al., 2016, 2017).

Comparisons between fossil and current palynological content, using pollen percentages, PC and PAR values is needed to obtain more accurate interpretations in high altitude settings (Seppä and Hicks, 2006). Finally, factors determining the vegetation response to past environmental change are also obscured at times by the interaction of climate and human activities. While lowlands have often been disturbed by human activities, the high elevation sites have been less affected until recent times (Catalan et al., 2013; Pérez-Sanz et al., 2013; González-Sampériz et al., 2017). Alpine pollen sequences, usually less affected by human activities, represent therefore good archives for the study of past climate changes (Ortu et al., 2006; Pérez-Sanz et al., 2013) with lower human interaction.

Many studies have been carried out in lakes at different mountain ranges in the Iberian Peninsula (e.g. Moreno et al., 2011; Jiménez-Moreno and Anderson, 2012; Morales-Molino et al., 2013; Muñoz Sobrino et al., 2013). Unfortunately, most of the studied Pyrenean sequences cover only part of the

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Holocene (e.g. Pla and Catalan, 2005; Miras et al., 2007; Pèlachs et al., 2011; Pérez-Obiol et al., 2012; Pérez-Sanz et al., 2013; Pérez-Díaz et al., 2015; Garcés-Pastor et al., 2016, 2017) and few of them include the Late Glacial-Holocene transition (LGH) (Montserrat-Martí, 1992; González-Sampériz et al., 2006, 2017; Gil-Romera et al., 2014; Rius et al., 2014) a key interval to provide contrasting boundary conditions for terrestrial ecosystems, particularly at high altitudes (Brisset et al., 2015). After alpine glacier retreat, new environmental conditions developed on freshly ice-free valleys, profoundly modifying mountain landscapes (e.g. Tinner et al., 1996; Heiri et al., 2003; Lotter and Birks, 2003). Defining the timing and dynamics of these changes is crucial for a better understanding of thresholds in the Earth's climatic system (Brisset et al., 2015) particularly in regions (the Pyrenees and the Mediterranean Mountains) were records are relatively scarce.

We present here a reconstruction of the palaeoenvironmental and vegetational dynamics of the last 14.6 cal kyr BP at Marboré Lake (2612 m a.s.l.) located at the Central southern Pyrenees. To ensure a robust interpretation of past vegetation changes at these high altitude environments we use pollen accumulation rates (PAR), pollen concentration (PC), pollen percentages and data from current pollen rain along an altitudinal gradient. We particularly focus on 1) the timing and dynamics of vegetational shifts in the Pyrenees and their relationship with climate variability, 2) the role of ice-cover on PAR and PC changes and how it compares with pollen percentages and sediment deposition rates; 3) testing how well current vegetation is represented in pollen spectra at an altitudinal gradient, and 4) discussing the role of human activities shaping the mountain landscapes.

2. Study area

2.1. Geographical settings

The Pyrenees are an alpine range lying in Northeastern Iberia for about 450 km length from the Cantabrian to the Mediterranean Sea (Fig. 1a). Marboré Lake (42°41'44.27"N, 0° 2'24.07"E) is and alpine glacial lake located at 2612 m a.s.l. (Fig 1b, e) in the central part of the Pyrenees within a glacial cirque limited by the Tucarroya Peak (2818 m a.s.l.) to the north and the Monte Perdido (3355

m a.s.l.) and Cilindro de Marboré (3328 m.a.s.l.) to the south (Fig.1 d). The cirque opens towards the east and ends at the Balcón de Pineta, as a hanged valley to the Pineta glacier Valley (Fig. 1d).

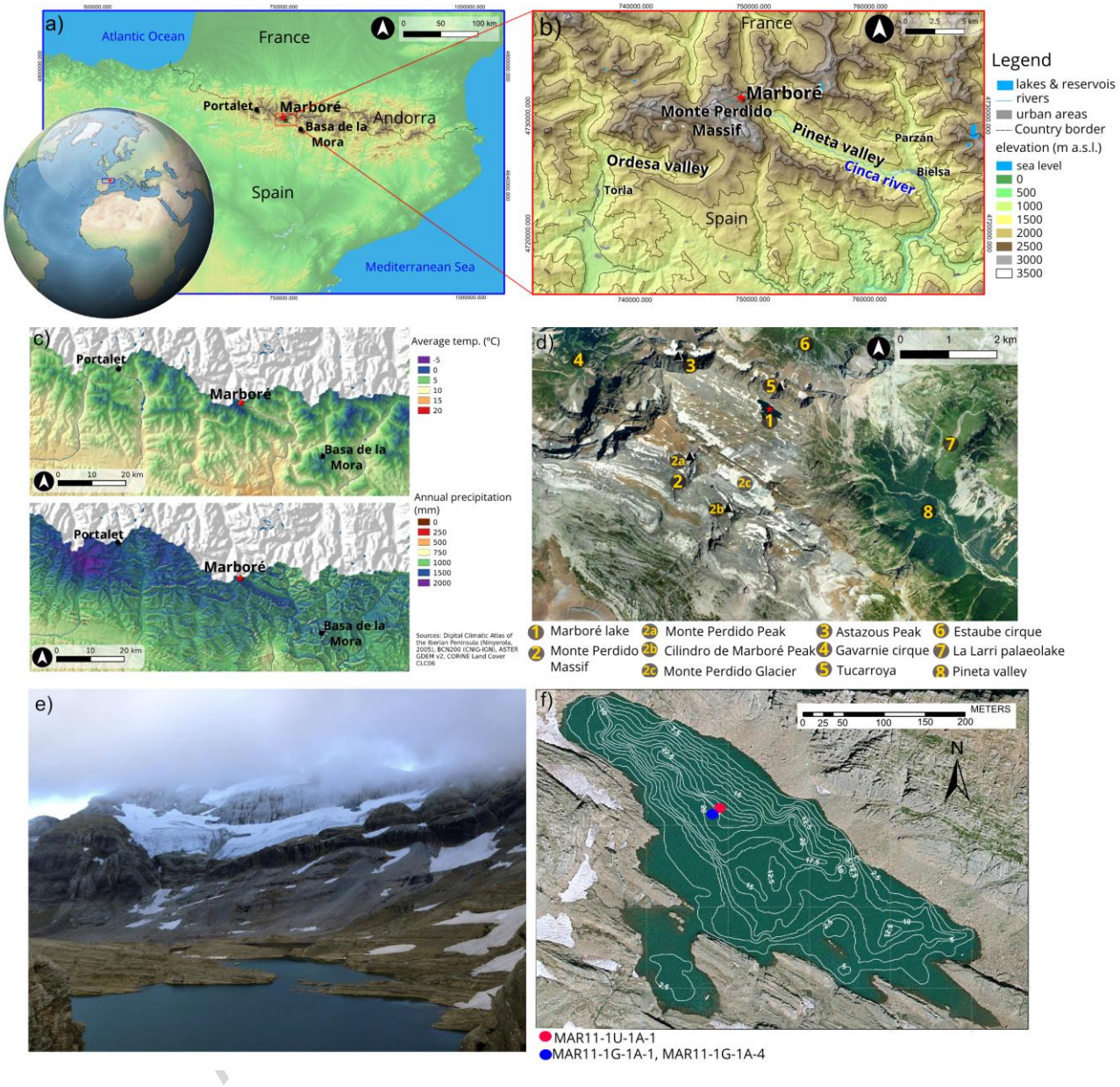

Fig.1. a) Location map of Marboré Lake in the Pyrenees together with nearby Pyrenean records discussed in the study. b) Detailed topographic map of the area where the lake is located. c) Temperature and precipitation maps of the Pyrenees. d) Ortophoto of the Marboré Lake and surrounding area. e) Photography of the Marboé Lake and its nearby area (September 2013). f) Bathymetry of the Marboré Lake with the coring sites for this study.

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Marboré Lake is located in a syncline within the Upper-Cretaceous (Campanian-Maastritchian) Marboré sandstone formation composed of sandy limestones and fine-grain sandstones cemented by a carbonatic matrix (Souquet, 1967). The lake measures ~500 m along the WNW-ESE syncline axis and ~200 m across, with a maximum water depth of 30 m (Fig.1e, f). The outflow of the lake is the headwaters of the Cinca River. The southern limit of the basin includes the remnants of the Monte Perdido and Marboré glaciers, but there are no direct surface connections between the glaciers and the lake basin as they are separated by a topographic high (Fig. 1e) (Garcia-Ruiz et al., 2014).

Most Pyrenean glaciers have been affected by a significant retreat since the Little Ice Age and many of them have even disappeared from 1850 to 2005 (López-Moreno et al., 2016). The Monte Perdido glacier (Fig. 1d) is the third largest glacier still remaining in this mountain range. Recently Garcia-Ruiz et al., 2014 have reconstructed the Late Holocene evolution with a glacier expansion at ca 5.1 kyr BP, probably associated with the Neoglacial period (Davis et al., 2009), followed by a later retreat at 3.4 and 2.5 kyr BP, synchronous with the Bronze/Iron Ages, another glacial advance phase during the Dark Ages (1.4-1.2 kyr BP) and finally, two pulses during the Little Ice Age (LIA), the early 18th century and between 1790-1830 AD. The current shrinkage of the Monte Perdido Glacier began at the end of the LIA and has clearly accelerated after 2000 AD (López-Moreno et al., 2015, 2016).

2.2. Climate and vegetation

The Central Pyrenees encompasses, in a relatively small area, the transition between Mediterranean and Atlantic climate regimes which are mainly different in terms of precipitation amount and seasonality. These mountains are thus affected by both rainfall regimes and they present vegetation communities from both domains. The mean annual temperature during 1982-2011 for Góriz -the nearest meteorological station located at 2220 m a.s.l. - is 4.9 ±0.5ºC. January is the coldest month with mean temperature of -0.7ºC and July is the warmest with 13ºC. Regarding precipitation, the mean annual value for Marboré Lake is ca. 2000 mm (Fig. 1c). Current ice-cover lasts on average 9-10 months, from November-December to mid-July-August.

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Locally, the altitudinal gradient from the valley bottoms to the Monte Perdido massif (3355 m a.s.l.) shows a typical vegetation zonation in alpine mountain environments (Fig. 2), where three main vegetation belts have been described: (1) the montane belt, below 1600 m a.s.l., is characterized by a mixed temperate and pine forest ; (2) the subalpine belt, below 2000 m a.s.l., is dominated by *Pinus uncinata* communities and shrub patches and indeed nowadays the valley treeline is at 2000 m a.s.l. where *P. uncinata* is the main tree species); and (3) the alpine belt, above 2000 m a.s.l, where only some patches of annual and perennial alpine herbs, coping with harsh environmental conditions, are present.

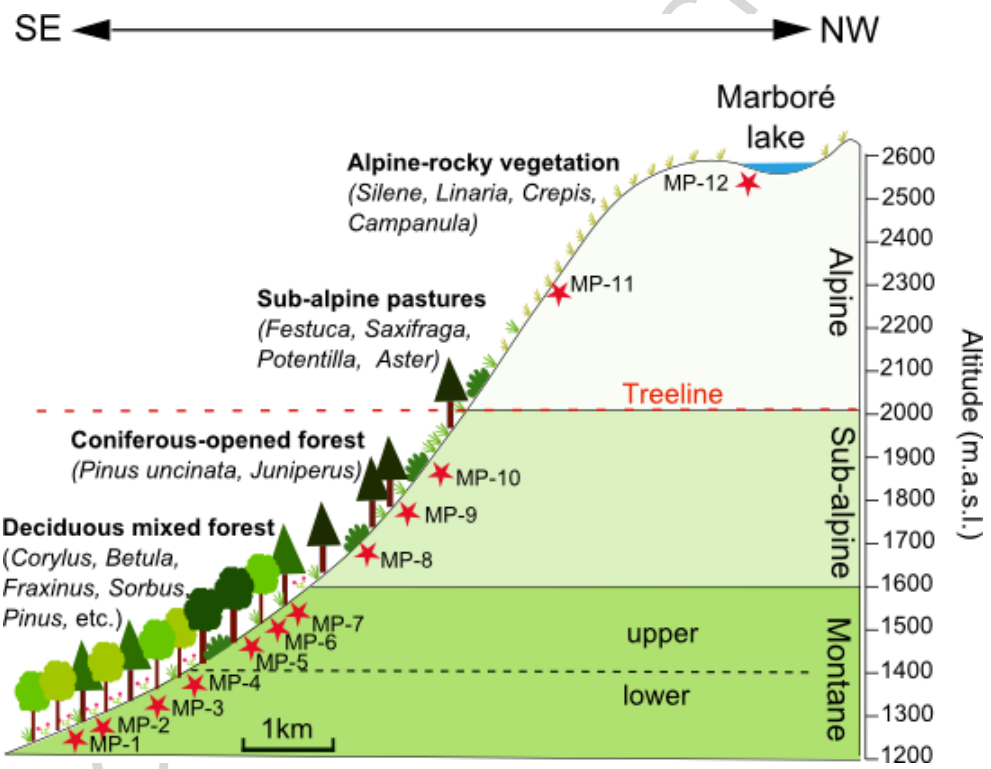

Fig.2. Simplified vegetation transect from the Pineta valley (1200m a.s.l.) to the Marboré Lake (2612m a.s.l.) with main vegetation communities and the vegetation belts defined. Red stars correspond to moss pollster sampling sites.

3. Material and Methods

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In August 2011, 3 piston cores (~7 m long each) and 16 short gravity cores (<1m each) were retrieved using an Uwitec platform and coring equipment of the Pyrenean Institute of Ecology (IPE-CSIC). All the cores were opened, photographed and sampled for biotic and abiotic analyses: radiocarbon dating, X-ray diffraction (XRD), X-ray fluorescence, Total organic (TOC) and inorganic (TIC) carbon analysis, quantitative values of elemental composition (ICP-OES), environmental magnetism measurements (u-channels), pollen and microcharcoal analysis. Sedimentological, geochemical and palaeomagnetism results, as well as details of the chronological model, have already been summarized in (Oliva-Urcia et al., submitted). The composite sequence includes the long core (MAR11-1U-1A-1) and two short cores (MAR11-1G-1A-4 and MAR11-1A-1) correlated by the Pb content measured by ICP-OES at the Ionomic Laboratory of CEBAS-CSIC in Murcia. The short core MAR11-1U-1A-4 was dated by ^{210}Pb ^{137}Cs techniques for the upper 17.5cm (Oliva-Urcia et al., submitted). Due to the absence of large charcoal particles and terrestrial organic matter remains, 16 bulk sediment samples were dated by ^{14}C in the Direct AMS laboratory in Seattle (WA, USA) (Table 1). Radiocarbon ages were calibrated using CALIB Rev 7.0.4 (Stuiver and Reimer, 1993) and the INTCAL13 curve (Reimer et al., 2013). The comparison of the ^{14}C and ^{210}Pb dates allows calculating a reservoir effect of 2230 ^{14}C years which has been considered in the chronological model. Marboré's age-depth model was made with *Clam* 2.2 software (Blaauw, 2010), using ^{14}C AMS dates and 2 tie points inferred from the correlation with Pb peaks (Oliva-Urcia et al., submitted and Fig. 5).

Pollen analysis were carried out in 90 samples from core MAR11-1U-1A prepared using the standard chemical procedure following (Moore et al., 1991) but including Thoulet solution (2.0 g cm^{-3}) for separation and *Lycopodium clavatum* spores to calculate concentration (Stockmarr, 1971). Pollen has been identified under a light microscope, and using the reference collection from the IPE-CSIC, determination keys and photo atlases (Moore et al., 1991; Reille, 1992). The mean of pollen grains counted was 353 per sample (Standard deviation (SD) of 35.2), and 69 different pollen and spore types were identified. Results are expressed in percentages, concentration (pollen grains g^{-1}) and pollen accumulation rates (PAR, considered as number of pollen grains cm^{-2} yr^{-1}), always excluding

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hygrophytes, hydrophytes, *Pteridophyta* spores and non pollen palynomorphs (NPP) from the pollen sum. PAR values were calculated as a product of pollen concentration, sediment density (g cm^{-3}) – measured as mass (g):volume (cm^3) ratio - and sedimentation rate (cm yr^{-1}) in each sample. Pollen diagrams and cluster analyses were used to establish pollen zones and were performed with Psimpoll 4.27 software (Bennett, 2009).

In order to study pollen-vegetation relationships along the altitudinal gradient which influences Marboré's palynological content, a total of 12 vegetation surveys (MP-1 to MP-12) were performed, covering different vegetation communities from the Pineta's valley bottom (1282 m a.s.l., montane belt) to the Marboré Lake (2612 m a.s.l., alpine belt) (Fig. 2). Moss samples were used because of their known suitability as pollen traps and their frequent occurrence in the area. Furthermore, their pollen content is an average pollen assemblage of several years, as it occurs in sediments, and provide a good record of local vegetation (Räsänen et al., 2004, 2007; Wilmshurst and McGlone, 2005; Mazier et al., 2006; Lisitsyna and Hicks, 2014). In each site, two moss pollsters were taken and mixed into a single sample. The vegetation surrounding the moss pollsters MP-1 to MP-11 was surveyed at north and south transects in intervals of 1, 2, 3, 4, 6, 8 and 10 m from the moss pollster. For each moss pollster a semi-quantitative vegetation survey was made based on cover estimation within 20m-diameter around each sample. The area surrounding the lake, corresponding to moss pollster MP-12, is mainly bare rock so, transects were not carried out although the few species that were present were described qualitatively. Results have been plotted in a stacked bar chart and classification was conducted with a cluster analysis.

Moss samples were chemically processed including the standard procedure explained above (Moore et al., 1991) but including acetolysis. Pollen identification and results analyses were performed applying the same procedure than for the fossil samples. Pollen accumulation rates have not been calculated for moss pollster pollen samples as it has been demonstrated that these units may not be very reliable when working with moss samples (Lisitsyna and Hicks, 2014). However, pollen

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concentrations for several pollen groups have been used in order to complement pollen percentages and to get more precise information for current pollen samples.

4. Results

4.1. *Current vegetation and moss pollsters*

Current vegetation from Pineta valley (1282 m a.s.l.) up to Marboré Lake (2612 m a.s.l.) presents a strong altitudinal gradient. Fig. 3 shows a comparative stacked bar chart between the vegetation cover of a 20 m diameter around the moss pollster (Fig. 3a) and the pollen signal recorded in each of them (Fig. 3b). Plant cover for taxa such as *Pinus* (the most abundant arboreal taxon), *Corylus* (the principal taxon within the deciduous forest group) and Poaceae (an important component within the herbaceous group) has been compared with its representation in pollen percentages for each moss pollster (Fig. 4). The plant cover distribution around each sample site shows a high agreement with the pollen abundances found on it (Fig. 3a, b). Both, pollen data and plant cover define a three-zone classification corresponding to:

a) Montane belt (Zone I, up to 1600 m a.s.l.). This zone is a well-developed deciduous forest (~28%) (Fig. 3a) (sometimes mixed with conifers) with species like *Corylus avellana, Fraxinus excelsior, Acer campestre, Betula pendula, Sorbus aria, Fagus sylvatica and Pinus sylvestris* with sparse shrubs as *Buxus sempervirens, Juniperus communis, Crataegus monogyna*, *Taxus baccata, Ilex aquifolium, or Rhamnus sp.,*. Montane pastures appear within forest clearings (~50%) with, among others, *Plantago sp., Fragaria vesca, Trifolium sp*., *Aconitum napellus, Viola sp., Ranunculus sp., Vicia sp., or Knautia* and several Poaceae species. The lower part of the montane belt (Zone I-A, below 1400 m a.s.l) shows a better developed and denser deciduous forest (~30%), while in the upper part (Zone I-B, 1400-1600 m a.s.l.) this proportion is lower (<10%), and montane pastures acquire more relevance. *Pinus* is the most frequent pollen type for the montane belt sites (Fig. 3b, Zone I), (~50-60%) and it is clearly over-represented since no pines are found around the sample sites (Fig. 3a, Fig. 4). On the contrary, deciduous forest pollen (~20%) dominated by *Corylus*, *Fraxinus* and *Betula,* among others

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shows a good correlation with plant cover (Figure 4). *Olea* is also an over-represented taxon since it does not grow in this belt and always appears on the samples. Herbs are under-represented in pollen content (~15%) as it can be seen for example with Poaceae (Fig. 4).

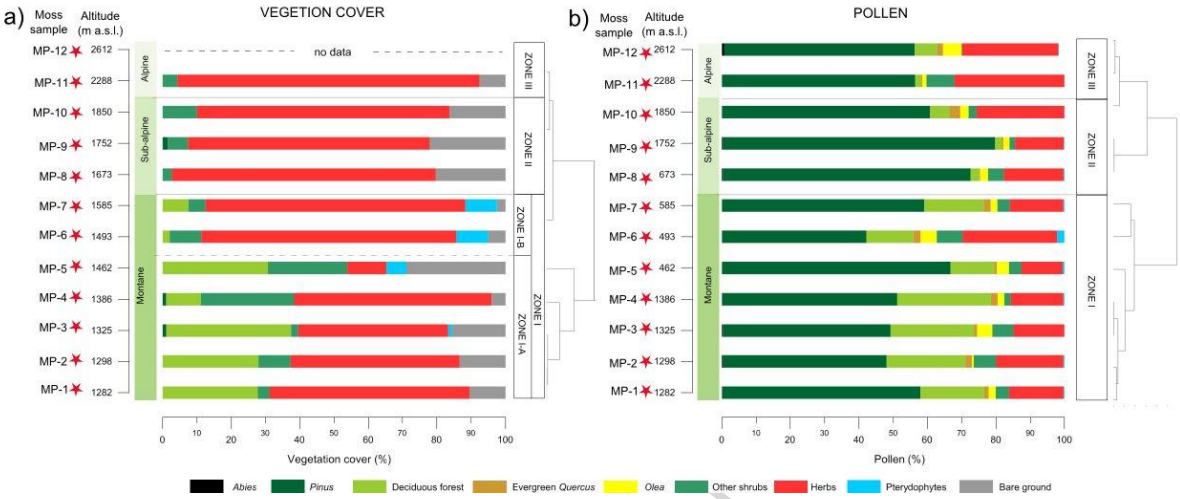

Fig.3. Bar-chart comparison between a) vegetation cover (%) existing around moss pollsters and b) pollen rain captured (%) in each moss pollster.

b) Sub-alpine domain (Zone II, 1600-2000 m a.s.l.). Arboreal communities are scarcer in this belt (Fig. 3a), and *Pinus uncinata* is the principal species up to the treeline (2000 m a.s.l.). Shrubs such as *Juniperus communis, Rhamnus alpina* and *Amelanchier ovalis* appear sparsely. Herbs dominate the land cover (~80%) within this belt with species such as *Potentilla alchemiloides, Galium sp., Campanula sp.,* and several Poaceae, forming extended sub-alpine pastures. However, herbaceous pollen group reach only around 25%. Pollen from deciduous taxa, *Olea* and other shrubs occur in lower percentages (~5%). Pollen from moss pollsters (Fig. 3b, Zone II) also show *Pinus* as the main taxon (~70%), clearly over-represented (Fig. 4). It is worth noticing that *Pinus* pollen could be produced by both *Pinus sylvestris,* occurring in the montane belt and *P. uncinata,* appearing in the subalpine belt and featuring the timberline and treeline.

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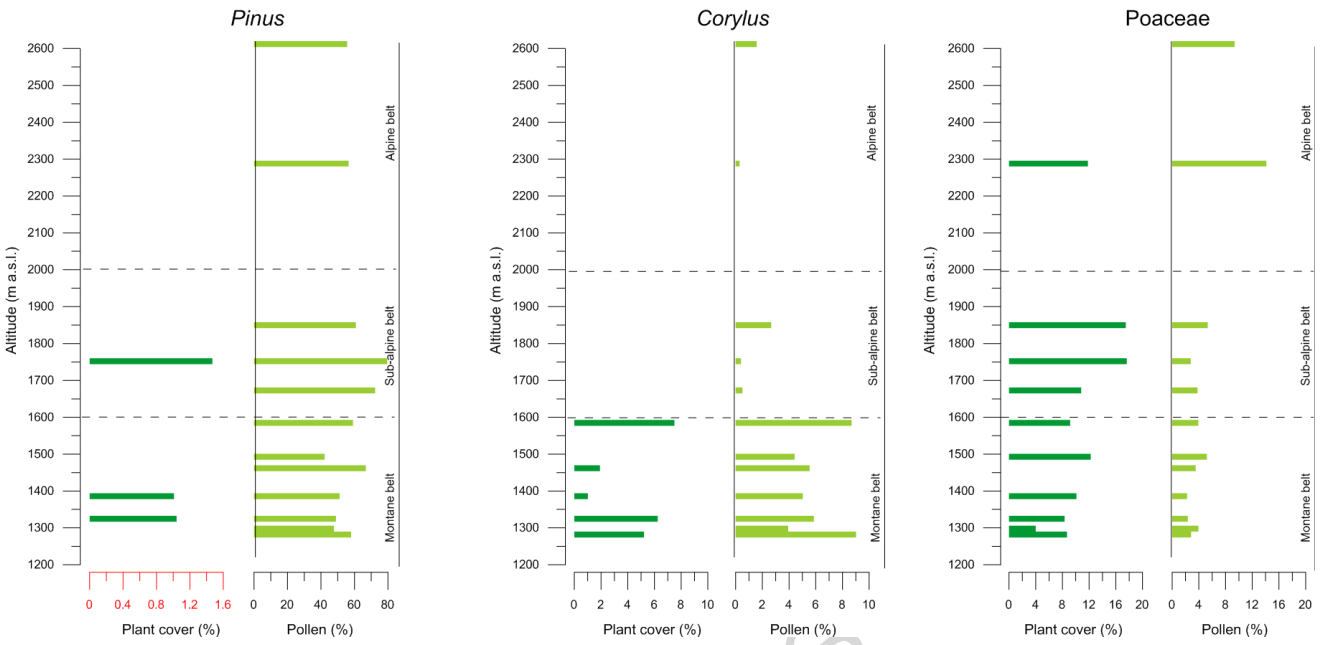

Fig.4. Comparison between plant cover (%) of selected taxa (*Pinus*, *Corylus* and Poaceae) and its representation in pollen (%) for each moss pollster. Note the different x-axis scales, in the case of *Pinus* marked with red.

c) Alpine belt (Zone III, 2000-2600 m a.s.l.). The vegetation at 2288 m a.s.l. (Fig 3a) represents the transition between the sub-alpine and the alpine belts but it already shows alpine characteristics as it is dominated by taxa from alpine meadows and rocky-environments as *Saxifraga aizoides, Leontopodium alpinum, Globularia sp., Horminum pyrenaicum, Paronychia capella* and Poaceae. The upper most sample, at 2612 m a.s.l., is located in bare ground but species as *Galium pyrenaicum, Leucantemopsis alpina, Linaria alpina, Potentilla nivalis, Doronicum grandiflorum,* amongst others were sparsely frequent. Pollen preserved in alpine moss pollsters (Fig. 3b, Zone III) shows the highest herbaceous elements percentages (~30 %) with a good representation of Poaceae (Fig. 4). *Pinus* pollen is still the principal taxon (~55%) despite does not grow at this altitude. Deciduous forest components are also present, but in low proportions.

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4.2 Sedimentary sequence

4.2.1. Sedimentology and Chronological model

The Marboré Lake sedimentary sequence comprises laminated fine silts and silty clays with very low organic matter content (TOC values < 1%). The sequence has been divided into 4 main units: Unit 4 (721-582 cm depth) is characterized by the lowest TOC values of the whole sequence and the presence of several TIC and Ca peaks. Relatively higher TOC, less defined lamination and the occurrence of associated Ca-Mn peaks defines Unit 3 (582-270 cm depth). Unit 2 (270-220 cm depth) is characterized by a decrease in TOC values and the increase in the magnetic properties of the sediments. Well defined laminations, relatively higher TOC and the occurrence of two Pb peaks characterized Unit 1 (220-0 cm depth) (Oliva-Urcia et al., submitted).

The comparison between ^{210}Pb and ^{14}C chronologies for the upper part of the sedimentary sequence suggests an important ^{14}C reservoir effect. In order to estimate it, two cores were correlated using Pb (XRF counts) peaks and the ^{210}Pb age markers from the MAR11-1G-1A core were transferred to the long core MAR11-1U-1A. The average sedimentation rate according to ^{210}Pb chronology is 0.095 cm yr^{-1}, providing an age of 340 cal yr BP for the base of the short core (32.5 cm depth). A ^{14}C sample at that depth gave an age of 2570 cal yr BP, much older that the age provided by the ^{210}Pb model. The ^{14}C reservoir effect was then calculated as 2230 years by subtracting both ages. Since we could not calculate reservoir effect for other periods, we had to assume a constant reservoir effect during the Holocene, and applied to all ^{14}C dates (Table 1). Three radiocarbon dates have been excluded from the final depth age model as presented reversal ages (Table 1, Figure 5). According to this age model, the sequence covers the last 14.6 kyr cal BP.

Although the assumption of a constant reservoir effect for the whole sequence is not supported by other absolute dating methods, several lines of evidence give credibility to this age model. The occurrence of Pb peaks is in agreement with regional mining and metallurgic activities in Roman, Medieval and contemporaneous times. The age of the spread of *Abies* (5.8 cal yr BP) and *Tilia* (8 ky

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cal BP) in the Marboré sequence are consistent with their timing for expansions in other Pyrenean records (González-Sampériz et al., 2006; Miras et al., 2007; Pérez-Sanz et al., 2013). According to this model, the mean sedimentation rate is 0.049 cm yr^{-1}, with a sharp change at 10.2 kyr cal BP from 0.0216 cm yr^{-1} to 0.061 cm yr^{-1} (Fig. 5).

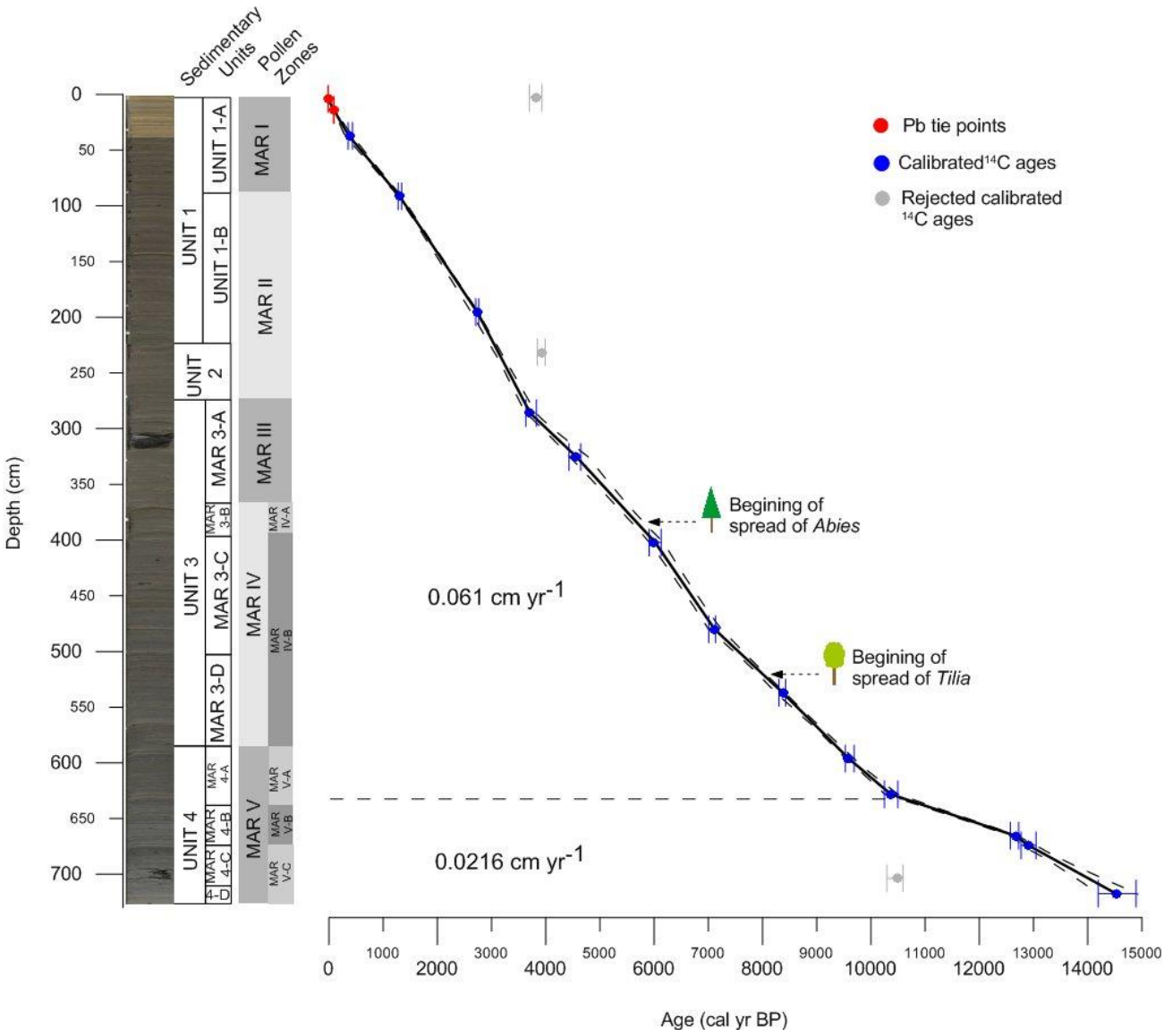

Fig.5. Depth-age model for the Marboré Lake sequence based on 13 AMS ^{14}C dates and two Pb tie points (Oliva-Urcia et al., submitted). The spread of *Abies* and *Tilia* reinforces the model.

4.2.2. Palynological sequence

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According to the cluster analysis, 5 main vegetation zones (MAR-I to MAR-V) have been defined (Fig. 6).

MAR V, Sedimentary Unit 4 (721-582 cm depth; 14.6-9.3 kyr cal BP)

Based on the fluctuations of *Pinus* and the deciduous forest pollen-group, 3 subzones have been defined:

-MAR V-C, Sedimentary Units 4d, c (721-667 cm depth; 14.6-12.6 kyr cal BP)

The beginning of this sub-zone (Fig. 6) is characterized by the highest proportions of NAP, mainly dominated by *Artemisia*, Poaceae, Chenopodiaceae and Lamiaceae; after 710 cm depth NAP sharply decreases and AP expands (~80%) through the rest of the sub-zone. *Pinus* is the principal taxon, although the deciduous forest is also well represented (20-30%), mainly by *Corylus* and in lower proportions by *Betula, Ulmus, Alnus* and *Quercus*. *Juniperus* is also present with percentages around 5%. These percentages might suggest a forested landscape, but if we consider PC and PAR for all taxa (Figs. 7 and 8) the values are quite low with just small peaks at 678 and 667 cm depth (13.1 and 12.6 kyr cal BP respectively).

-MAR V-B, Sedimentary Unit 4b (667-622 cm depth; 12.6-10.2 kyr cal BP)

Pinus and *Corylus* percentages sharply fluctuate while other taxa like *Juniperus* and NAP show lower values (Fig. 6). The PC and PAR values are the lowest of the whole sequence (Figs. 7 and 8) regardless of taxa. Some AP components such as *Carpinus* and *Juglans* are present, although anecdotally.

-MAR V-A, Sedimentary Unit 4a (622-582 cm depth; 10.2-9.3 kyr cal BP)

A slight decline in pine and a coeval increase in *Corylus* abundances occur while *Artemisia*, Chenopodiaceae and Lamiaceae decrease. Peaks with the highest PC and PAR values of the whole record occur at the top of the subzone (up to 116 10^3 grains cm^{-2} yr^{-1}), generally in AP and NAP, and specifically in pines and *Corylus* (Figs.7 and 8).

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MAR IV, Sedimentary Unit 3d, c, b (582-360 cm depth; 9.3-5.2 kyr cal BP)

Similarly to previous unit, the fluctuations of *Pinus* and deciduous taxa group define 2 subzones:

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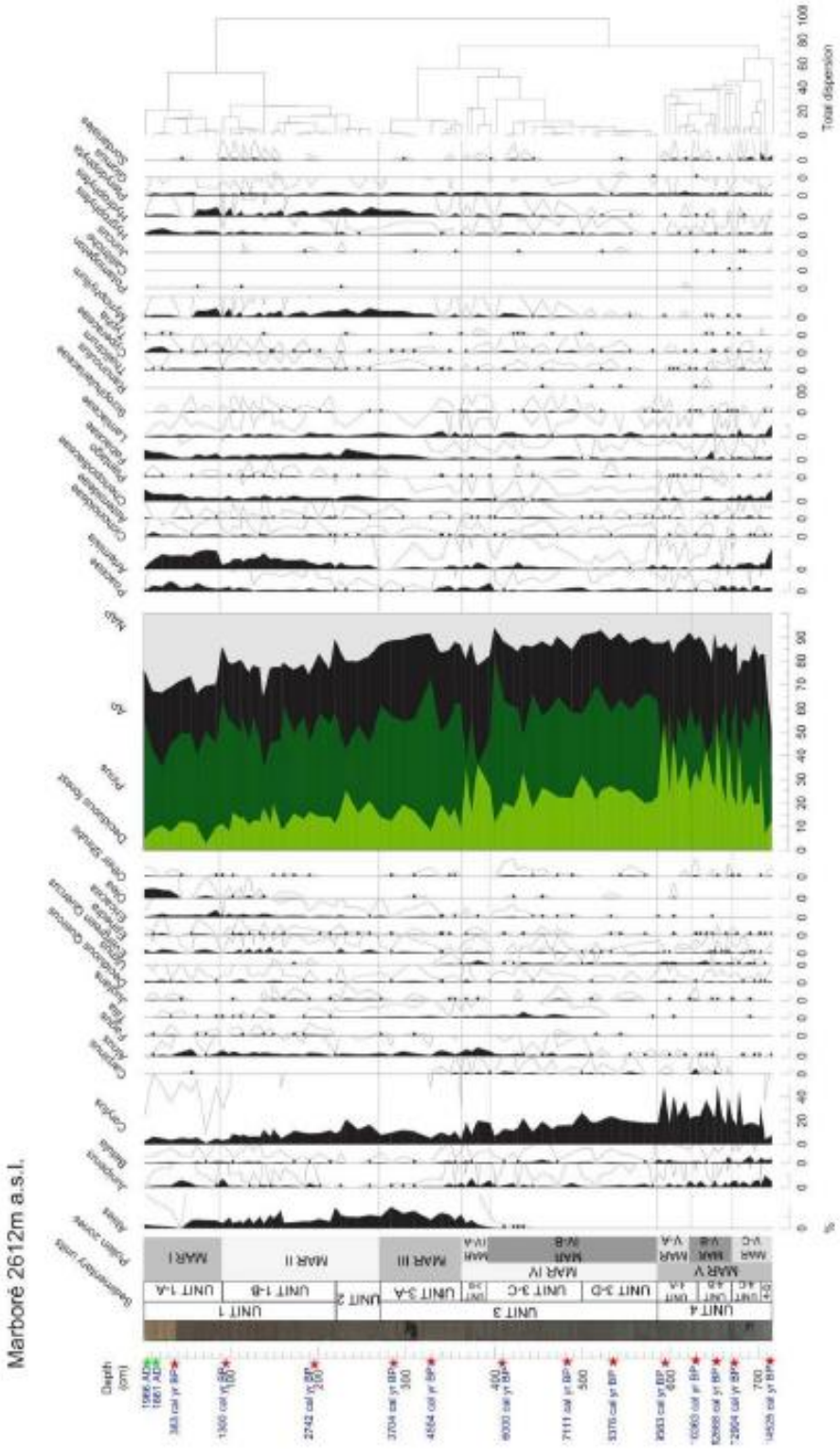

Fig.6. Pollen diagram of selected taxa from Marboré sequence, plotted in depth. Deciduous forest group is composed of: *Betula*, *Corylus*, *Carpinus*, *Castanea*, *Acer*, *Salix*, *Alnus*, *Fraxinus*, *Fagus*, *Tilia*, *Populus*, *Juglans*, deciduous *Quercus*, *Ulmus* and *Sorbus*. Other shrubs are: *Rhamnus*, *Buxus*, *Tamarix*, *Phyllirea*, *Myrtus*, *Pistacea*, *Prunus* and *Genista*. Hygrophytes curve content: *Ranunculus*, Cyperaceae, *Thalictrum and Typha*. Hydrophytes group is formed by: *Myriophyllum* and *Potamogeton*. As usually AP includes all the arboreal taxa (trees and shrubs) and NAP the herbaceous component (all taxa plotted in the diagram and also Caryophyllaceae, Brassicaceae, *Gentiana*, Cistaceae, Saxifragaceae, Ranunculaceae, Poligonaceae, Apiaceae, Boraginaceae, *Sedum*, *Urtica*, *Campanula*, *Asphodelus*) excluding aquatics and ferns. Sedimentary units and pollen zones, as well as both radiocarbon dates (red stars) and ^{210}Pb dates (blue stars), are also indicated in the figure.

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MAR IV-B, Sedimentary Unit 3d, c (582-400 cm depth; 9.3-6 kyr cal BP)

Pinus reaches its maximum abundance (up to 80%) but no major changes occurred in the NAP abundance (Fig. 6). *Tilia* appears continuously at 521 cm depth, 8kyr cal BP (Figs. 5 and 6) consistent with the other records in the Central Pyrenees (Montserrat-Martí, 1992; González-Sampériz et al., 2006; Miras et al., 2007; Pèlachs et al., 2007; Pérez-Sanz et al., 2013). After 9.3 kyr cal BP (Figs. 7 and 8) a correlation among PC, PAR and percentage trends is more consistent till the top of the sequence (Fig.7). *Abies* initially appearance occurs at 432 cm depth (6.4 kyr cal BP).

MAR IV-A, Sedimentary Unit 3b (400-360 cm depth; 6-5.2 kyr cal BP)

Arboreal pollen slightly declines in this unit (Fig. 6), due mainly to *Pinus* reduction (~ 45%), as deciduous forest pollen percentages and PAR values increase mostly due to *Corylus* and *Alnus* (Fig. 7). *Abies* continues expanding from the base of this zone (400 cm depth, 6 kyr cal BP; Figs. 5 and 6) also coherent with its expansion inferred from other records from the region (Montserrat-Martí, 1992; González-Sampériz et al., 2006; Miras et al., 2007; Pèlachs et al., 2007; Pérez-Sanz et al., 2013).

MAR III, Sedimentary Unit 3a (360-270 cm depth; 5.2-3.5 kyr cal BP)

This vegetation zone is characterized by a *Pinus* recovery (~60%), and a deciduous forest group decrease both in abundances and PAR (Figs. 6 and 7). *Abies* continues expanding reaching its maximum abundance (18%) at the top of this zone. A rise in hygrophytes is mostly due to the increase of *Myriophyllum*.

MAR II, Sedimentary Units 2, 1b (270-90 cm depth; 3.5-1.3 kyr cal BP)

During this zone, the herbaceous taxa abundance expands progressively, dominated by *Artemisia*, Chenopodiaceae and Fabaceae, whereas AP experiments a continuous decrease due to the decline in *Abies*, *Corylus, Tilia* and *Alnus*. Among the shrubs, Ericaceae abundance increases towards the top of the sequence but the values never exceed 4% (Fig. 6). *Fagus* consistently appears in this zone, instead of causally as in previous sections (543 cm depth, 8.5 kyr cal BP). Both hygro-hydrophytes

groups also appear continuously with minor fluctuations and PAR values increase and reach their maximum for the sequence (except for unit MAR V-A) and coupled to percentage fluctuations (Fig. 7).

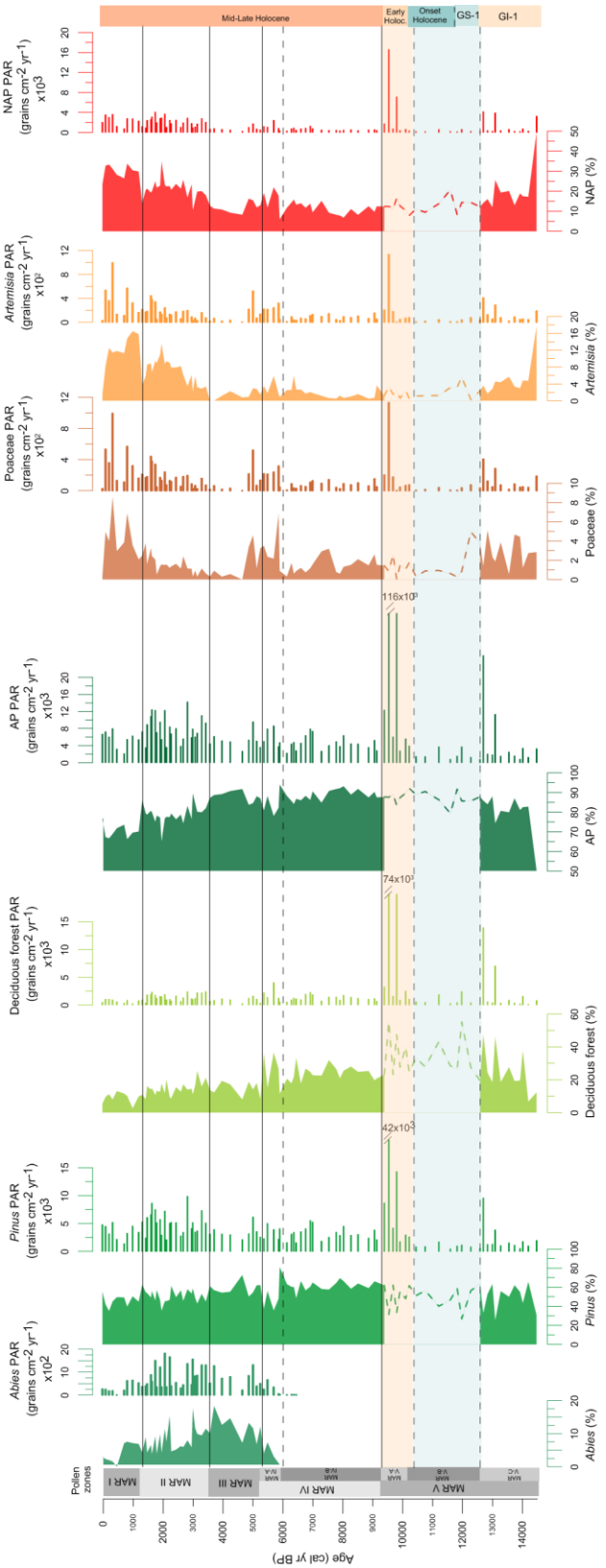

Fig.7. Comparisons of usual percentages and PAR values form selected pollen taxa and AP-NAP pollen groups. Note the different x-axis scales.

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MAR I, Sedimentary Unit 1a (90-0 cm depth; 1.3-0 kyr cal BP)

This zone is characterized by increasing *Olea* abundances and the significant and sharp decrease of *Abies* towards the top while *Pinus* declines, with some fluctuations. NAP abundance rises steeply (up to 30-35%) led by *Artemisia*, Poaceae, Chenopodiaceae and Fabaceae (Fig. 6). PAR for all these taxa present similar trends (Fig. 7).

5. Discussion

5.1 Keys to interpret the pollen sequence of Marboré Lake

Two issues must be considered when interpreting a pollen sequence from a high altitude lake. First, the record might be more influenced by regional vegetation rather than local one, which is usually very scarce. Second, long periods of ice-cover in the lake may produce different responses of the sedimentation dynamics (eg. distinct sedimentation rate). Marboré record shows a complex pattern of pollen assemblage changes during the Late Glacial and Holocene (Figs. 6 and 7). The reconstruction of vegetation dynamics from pollen data obtained in high altitude sites needs to understand the source, transport and deposition of pollen grains in such settings. As during present times, it seems clear that the source area of arboreal pollen in Marboré Lake has always been regional and that the treeline did not reached the Marboré cirque during the last 14.6 kyr. The watershed has an abrupt orography, no well-developed soils and it is mainly dominated by bare rocks (Fig. 1). The lack of woody plant macrofossils representing local forest vegetation along the sedimentary sequence also favors this interpretation. Arboreal pollen in Marboré is a regional signal and interpreting the regional pollen signal implies understanding pollen-vegetation altitudinal correlations (Fig. 3) as well as depositional processes in the lake (sedimentation rates) and limnological features (ice-cover) that could influence pollen fluxes.

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Our pollster transect shows an, unsurprisingly, relevant *Pinus* over-representation (Figs. 3 and 4). *Pinus* pollen in high-altitude environments has been shown to have a large source area (Sugita et al., 1999; Tonkov et al., 2001; van der Knaap et al., 2001; Jensen et al., 2007; Canellas-Bolta et al., 2009; Birks and Bjune, 2010). On the other hand, we found a high correlation between the deciduous forest pollen group and its actual presence at the montane belt, where deciduous communities are abundant (Fig. 3). Deciduous pollen types are also frequent, but to a lesser extent, in moss pollsters at high altitude sites (~5%), where this vegetation is no longer present, proving some wind pollen drift uphill transport. As expected for anemophilous (wind pollinated) taxa as e.g. *Corylus, Betula, Tilia* pollen is long transported upwards in mountain regions (Canellas-Bolta et al., 2009).On the other hand, herb pollen types are under-represented (Fig. 3), as it has been documented in several studies and in agreement with data recorded in a similar moss pollster transects in the Pyrenees (Canellas-Bolta et al., 2009; Rieradevall et al., in press).

In addition to pollen productivity, sources and transport processes, some physical features of water bodies located at high altitudes make the pollen-vegetation comparison even more challenging. Excepting subglacial lakes, lacustrine sedimentation requires ice-free conditions at least during some part of the year (Heiri et al., 2014). The catchment area of the lake needs to be also ice-free, as without water availability, there is no sediment input into the lake (including pollen transported within sediments). Lake-ice is sensitive to climate variability (Brown and Duguay, 2010; Sánchez-López, 2016), as ice phenology has typically been associated with variation in air temperatures while ice thickness tends to be more associated to changes in snow cover (Brown and Duguay, 2010). The ice-covered period has important implications in biological processes (e.g., diatom productivity) and also in sedimentation rate and all geochemical fluxes (Catalan et al., 2002). Diatom records and sediment pellets that have been used as indicators of changes in ice cover duration (Lotter and Bigler, 2000; Smol et al., 2005; Ojala et al., 2008; Tomkins et al., 2009).

The lower part of the Marboré palynological record shows abrupt changes in PC and PAR values that unlikely reflect rapid changes in regional pollen rain. We proposed during colder periods with a frozen

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catchment area and no thawing of the lake ice-cover during several consecutive summers, pollen grains would have remained trapped on the lake ice cover and catchment area. Pollen deposition would have not occurred until complete thawing occurred, causing a higher pollen deposition in the lake and abrupt changes of PC and PAR. Abundances are affected by changes in differential pollen deposition and sedimentation rates that cannot be clearly traced with percentages as there is no absolute value of pollen production. PC and PAR are standardized measures by volume of sample and unit of time and thus sedimentation rate variations caused by ice-cover fluctuations during glacial or stadial periods can be identified. Therefore, we propose the existence of long-lasting ice-covered periods when low PC and PAR values occurred while high PC and PAR would indicate abrupt thawing and a subsequent sudden deposition of pollen accumulated during the ice-cover period.

5.2 The deglaciation and the beginning of the Holocene (14.6-9.3 kyr cal BP)?

Several studies (e.g. Sancho et al., 2003; Lewis et al., 2009; García-Ruiz et al., 2013) proved the maximum extent of glaciers in the Pyrenees to have occurred during the Late Pleistocene, at about 64 ± 11 kyr BP, not concurring with the timing for the global Last Glacial Maximum (LGM), 23-19 kyr cal BP (e.g. Mix et al., 2001; Clark et al., 2009). Sedimentation in the Marboré Lake started at least 14.6 kyr ago, indicating that the Marboré cirque was at least partially deglaciated by that time (Oliva-Urcia et al., submitted; Salazar-Rincón et al., 2013). Some studies carried on in the Mediterranean Alps, also attest that glacial cirques above 2000 m a.s.l. were deglaciated since the Bølling/Allerød (Brisset et al., 2015).

Thus, during Greenland Interstadial (GI-1) (14.6-12.9 kyr cal BP) (Rasmussen et al., 2014), proglacial sedimentation characterized Marboré Lake deposition. Sedimentation rate is generally low during GI1, Greenland Stadial 1 (GS-1 or Younger Dryas) (12.9-11.7 kyr cal BP (Rasmussen et al., 2014) and the Holocene onset (HO). Both PC and PAR values also remain low during GI1 and even lower in the subsequent GS-1 and HO (Figs. 7 and 8). The Thompson et al., (2005) ice-cover model indicates that

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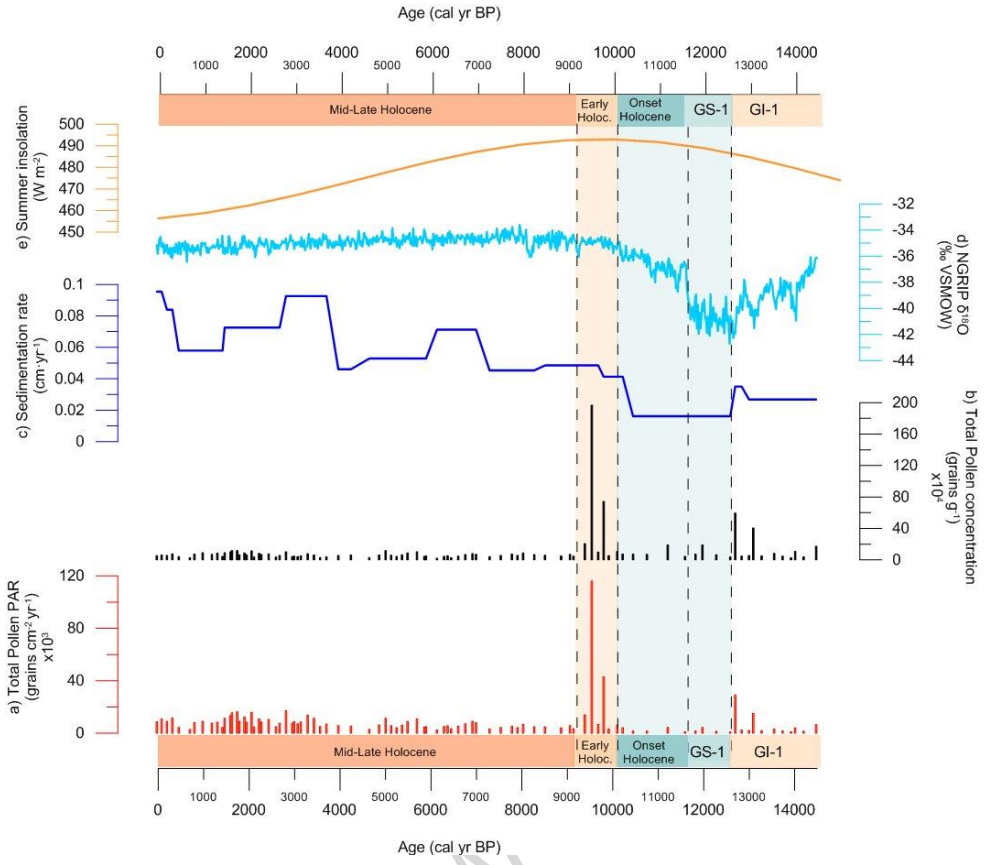

Fig.8. Inferences of the Marboré Lake ice-cover duration. a) Total pollen PAR values. b) Total pollen concentration (PC). c) Sedimentation rate. d) Temperature changes reconstructed from $\delta^{18}O$ content in Greenland NGRIP core (Rasmussen et al., 2014). e) Summer insolation 42ºN curve calculated by means of PAST software (Hammer et al., 2001).

under current temperatures the ice-cover duration for a lake located at 2600 m a.s.l. would be ~225 days. Current observations carried out in the Marboré Lake confirm this figure and suggest that some years ice-cover can last even for ~245 days. According to this calibration model, an estimated Tª decrease of ~ 2ºC at ~2600 m a.s.l. during the GS-1 (Millet et al., 2012; Muñoz Sobrino et al., 2013; Bartolomé et al., 2015) would increase the ice cover duration of the lake in ~30 more days compared to current times. Thus during the GS-1 and HO complete ice-cover length could easily correspond to 10-11 months, or even the whole year during some particularly cold years as well as a frozen catchment area. Sedimentological data from this time interval show the absence of the brown laminae

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which has been linked to the summer season, suggesting that the lake would have been frozen most of the year and deposition dominated by fine clastic sedimentation (Oliva-Urcia et al., submitted).

A sharp increase of sedimentation rate occurs from 10.2 cal Kyr BP onwards parallel to an increase in organic productivity in the lake and a change in lamination features (Oliva-Urcia et al., submitted). These limnological changes are concurrent with several abrupt PC and PAR peaks (Figs. 7 and 8) ca. 9.8 and 9.5 kys cal BP, possibly linked to increasing productivity values as temperature rises. A chironomid-based July air-temperature reconstruction from a mountain lake in the Alps (2796m a.s.l.) reveals the highest temperatures for the Early Holocene during this time-interval (10-8.6 kyr cal BP) (Ilyashuk et al., 2011). The increase in sedimentation rate, PC and PAR values could be coupled to longer ice-free seasons with higher glacier meltwater, sediment availability and strengthen runoff processes. In agreement with these new data from Marboré record, a similar delayed response of Pyrenean and Mediterranean communities to the Early Holocene warmer and moister conditions has previously identified in several regional sequences (Morellón et al., 2009; Pérez-Sanz et al., 2013; Aranbarri et al., 2014; González-Sampériz et al., 2017).

Maximum summer insolation during this period (Fig. 8) would have increased the number of years with a complete melt of the catchment area and the lake ice-cover during summer months, causing a sudden bottom lake deposition of the accumulated pollen on the lake surface during the previous years with limited ice cover thaw.

This complex pollen deposition pattern during the proglacial phase of the lake adds potential artifacts to the interpretations of vegetation dynamics, especially if we only consider percentages from pollen content, which do not reflect reliable vegetation cover at a local or regional scale. To tackle this problem, common in high altitude records, we propose to use PAR and PC for periods with potential longer ice-cover seasons, which indicate a widely open landscape at high altitudes. Similar artifacts may have occurred in Marboré afterwards at centennial or decadal scales during Holocene cold periods (e.g., during the Neoglacial or the Little Ice Age-LIA) but our time resolution does not allow detect them.

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5.3. An overview of Holocene vegetation dynamics in the Central Pyrenees

From 9.3 kyr cal BP onwards sedimentation rate, PC and PAR experienced fluctuations but no abrupt shifts have been detected, suggesting that there were multi-annual periods with no ice-free summers. Most likely during the Holocene, the lake was free of ice lake for several months per year (probably 3-4 months, similar to nowadays). Thus, during this period pollen percentages as well as PC and PAR can be used to interpret regional and local Holocene vegetation patterns (Fig. 7).

5.3.1. Vegetation responses during the Early-Mid Holocene (9.3-5.2 kyr cal BP)

Marboré Lake is strategically located in the Central Pyrenees to investigate changes in the extent of Atlantic versus Mediterranean influences during the Holocene along a West – East gradient. Many studies have demonstrated that vegetation responded differently during the beginning of the Holocene through the Iberian Peninsula, depending on their location relative to the Atlantic – Mediterranean gradient. More temperate and moister conditions were inferred from the Atlantic-influenced pollen sites (Muñoz Sobrino et al., 2005, 2007; Moreno et al., 2011; Iriarte-Chiapusso et al., 2016) where a rapid spread of deciduous forest occurred, while continental and Mediterranean sequences show high proportions of pines and/or junipers (Carrión et al., 2010; Rubiales et al., 2010; Morales-Molino et al., 2013; Aranbarri et al., 2014, 2015), indicating still intense hydrological stress due to maximum seasonality during the Early Holocene.

Pyrenean records show examples of both hydrological situations. In the easternmost sites (e.g., Miras et al., 2007; Pérez-Obiol et al., 2012) marked Mediterranean, more continental conditions with dominant coniferous communities prevailed, while westwards locations with a more Atlantic climate regime such as El Portalet (González-Sampériz et al., 2006; Gil-Romera et al., 2014) show a great and rapid expansion of mesophytes since the Bolling-Allerod transition and throughout the Holocene (Fig. 9f). The Central Pyrenees contains the boundary between both climate regimes and so, pollen sites could help to identify the history of the shifting boundary during the Holocene (Fig. 1). In La Basa de la Mora sequence (Pérez-Sanz et al., 2013), in a southeastern location of the Central Pyrenees

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area and a relatively lower elevation (1914 m a.s.l), the high abundance of pines and junipers reflects a more Mediterranean-influence during the Early Holocene, and progressive changes into a more deciduous dominated landscape during the Early-Mid Holocene transition, suggesting more humid conditions (Fig. 9e). Interestingly, the Marboré sequence, located between El Portalet and Basa de la Mora and a higher altitude (Fig. 1), also presents a pine-dominated community, with *P. uncinata* (at treeline), and *P. sylvestris* (at the timberline), but the importance of the deciduous taxa (Fig. 9b) suggests humid conditions, similar to Atlantic-influenced sites like El Portalet (Fig. 9f) during the Early Holocene. Atlantic influence would have been stronger in higher and northern areas in the Central Pyrenees during the Early Holocene, while lower elevations and more southern areas would already have been more affected by Mediterranean dynamics since the Early Holocene.

Reconstructing both treeline and timberline shifts is hindered by the absence of macrofossils originating from trees and shrubs representing forest vegetation in the records (e.g. Tinner and Theurillat, 2003; Birks and Bjune, 2010). In the Pyrenees, a montane ratio based on pollen-vegetation relationships has recently been applied by Garcés-Pastor et al.,(2016, 2017) to detect vegetation altitudinal shifts during the Holocene. In Marboré, we establish a consistent pollen-vegetation relationship finding that changes in the deciduous montane belt position may be easier to infer as there is a good correspondence between deciduous taxa in current vegetation and pollen rain from moss pollsters (Figs. 3 and 4). Treeline is mainly influenced by summer temperatures (Körner, 2012) but, studies on the timberline and treeline response to climate and human impact in the Alps suggest a stronger sensitivity of the timberline than the treeline (Tinner, 2013), therefore supporting the relevance of high altitude sites as better sensors of montane than alpine communities, that are generally less productive in terms of both biomass and pollen.

Pollen assemblages from 9.3-5.2 kyr cal BP period show an average of 23.55% (6.95 SD) of deciduous forest pollen group (SI, Table 1). This pollen values would correspond to the modern montane belt at 1300 m a.s.l. where a 22% (3.05 SD) of deciduous forest pollen is represented in pollster sites (Figs. 3a and 3b). Nowadays the deciduous forest upper limit is ca. 1500 m a.s.l. thus,

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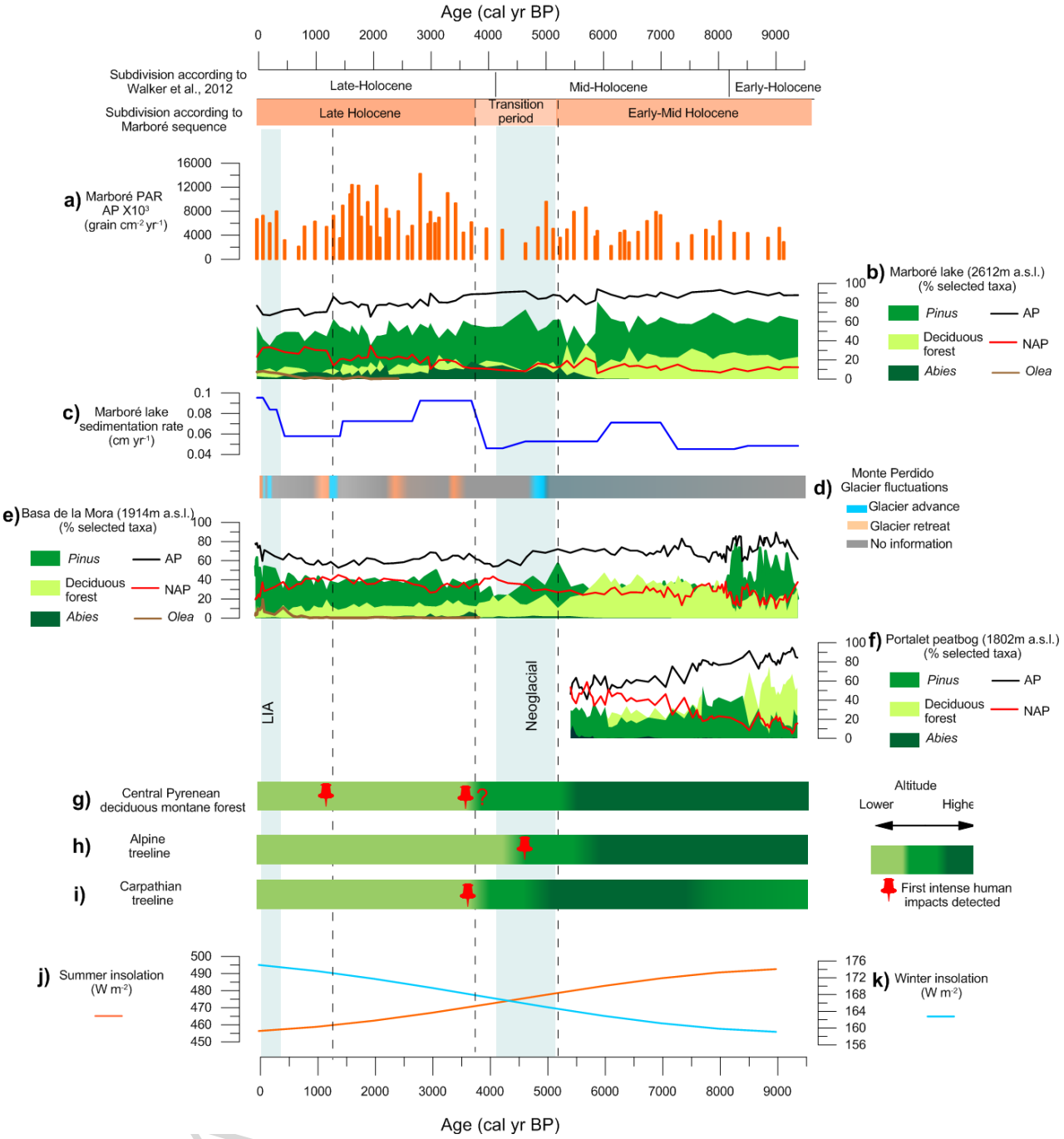

Fig.9. Comparison of the Marboré Lake sequence (pollen-based ecological groups, PAR values and sedimentation rate) with selected records from the Pyrenees for the Holocene. a) AP PAR values for Marboré. b) Selected taxa for Marboré Lake (Deciduous forest pollen group includes: *Betula, Corylus, Carpinus, Castanea, Acer, Salix, Alnus, Fraxinus, Fagus, Tilia, Populus, Juglans*, deciduous *Quercus, Ulmus* and *Sorbus).* c) Marboré Lake sedimentation rate evolution. d) Monte Perdido Glacier

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fluctuations (Garcia-Ruiz et al., 2014). e) Selected pollen taxa for Basa de la Mora (Deciduous forest pollen group includes: *Betula, Corylus, Fagus, Tilia*, deciduous *Quercus, Alnus*, *Salix, Ulmus, Populus* and *Juglans* (Pérez-Sanz et al., 2013). f) Selected pollen taxa for Portalet peatbog (Deciduous forest pollen group includes: *Betula, Corylus*, deciduous *Quercus, Alnus, Ulmus, Acer, Salix, Tilia, Fraxinus, Populus, Fagus, Juglans* and *Castanea*) (González-Sampériz et al., 2006; Gil-Romera et al., 2014). g) Simplified reconstruction of the variations in the Central Pyrenean deciduous montane forest altitudinal shifts. h) Simplified reconstruction of Alpine treeline variations in altitude (Tinner and Theurillat, 2003; Heiri et al., 2014). i) Simplified reconstruction of the altitudinal variations in the Carpathian treeline (Magyari et al., 2012; Geantă et al., 2014; Feurdean et al., 2016). j ,k) Summer and winter insolation 42ºN curve calculates by means of PAST software (Hammer et al., 2001).

considering both current and fossil data, we suggest that between 9.3-5.2 kyr cal BP the deciduous forest shifted to higher altitudes, even reaching the subalpine belt. Basa de la Mora (Pérez-Sanz et al., 2013) also reveals the highest abundance of deciduous forest between 8.1-5.7 kyr cal BP (Fig. 9e). In the Alps, in a lake situated at a similar altitude (Sshwarzsee ob Sölden Lake, 2796m a.s.l., Austrian Alps) show similar deciduous forest dynamics (Ilyashuk et al., 2011).

Although no tree macrofossils were preserved both pine communities at the timberline (*Pinus sylvestris)* and treeline (*Pinus uncinata*) could have shifted a bit higher than nowadays In any case, the Central Pyrenean treeline would have always been below 2600 m a.s.l.

Macrofossil-based estimation of treeline changes in the Swiss Alps show the highest treeline position during ~10-5 kyr cal BP, rising over 2100 m a.s.l. (Heiri et al., 2014) and reaching up to ~2500 m a.s.l. (Tinner and Theurillat, 2003) (Fig. 9h). Studies carried out in the Carpathian Mountains also show that both timberline and treeline were higher during warm early and mid-Holocene, being higher than today after 8.5 kyr cal BP (1900 m a.s.l.) (Magyari et al., 2012; Geantă et al., 2014; Feurdean et al., 2016) (Fig.9 i).

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These data from Iberian, central and southern European mountain sites reflecting montane belt evolution suggest that the Early-Holocene increasing summer temperature would have favored fast-growing, pioneering, thermophilous deciduous forest (Lotter et al., 2006; Wehrli et al., 2007) and both treeline and timberline expansion.

5.3.2. Changing environments after 5.2 kyr cal BP

Large landscape changes have been reported since ~ 6-5 kyr cal BP onwards in European mountains both related to climate and human action (Ilyashuk et al., 2011; Pérez-Obiol et al., 2012; Pérez-Sanz et al., 2013; Heiri et al., 2014; Feurdean et al., 2016; Thöle et al., 2016; González-Sampériz et al., 2017; Oliva-Urcia et al., submitted). However, discerning climatic and human impact in these sites has always been a matter of discussion (Carrión et al., 2010; González-Sampériz et al., 2017). In the Alps, after 6 kyr cal BP treeline and timberline shifted downhill, particularly after 4.5 kyr cal BP (down to ~2000 m a.s.l.), and it has been primarily attributed to anthropogenic impact, with cooler climates playing a subordinate role (Tinner and Theurillat, 2003; Tinner, 2013; Heiri et al., 2014) (Fig. 9h). In the Carpathians, a thinning of the timberline found from ~4.9 kyr cal BP (Fig. 9j) has been interpreted as responding to cooler summers in the Northern Hemisphere (Berger and Loutre, 1991; Feurdean et al., 2016). In this area, clear evidences for the contribution of human activities to the decline of the treeline and timberline are not found until 3.5 kyr cal BP (Feurdean et al., 2016).

Our study documents a large qualitative vegetation change from 5.2-3.5 kyr cal BP, marked by an important decrease of deciduous forest (Fig. 9b), reaching modern analogues values in the montane and sub-alpine transition belts (SI, Table1). During this period, deciduous forest belt shifted progressively to lower altitudes, although it would still be located at higher altitudes than nowadays. La Basa de la Mora (Fig. 9e) also presents this pattern. This change characterizes the Mid-Holocene in Mediterranean regions (e.g. Jalut et al., 2010; Roberts et al., 2011) and it has been interpreted as colder and/or drier conditions, although most authors do not discard a regional human impact intensification as indicated by the increasing openness of forest environments and the increase of pasturelands (Galop and Catto, 2014; González-Sampériz et al., 2017).

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Geomorphological and climatic aspects could help to identify the human or climate origin of mid to late Holocene deciduous forest shifting in the Central Pyrenees (Fig. 9g). A glacial expansion occurred during the Neoglacial (5.1 kyr ± 0.1 kyr) as a large push moraine has been identified and dated at the Monte Perdido (Fig. 1; Fig. 9d) (Garcia-Ruiz et al., 2014). Radiocarbon ages from the Troumouse Cirque, located 9 km to the north on the French side of the Pyrenees, also revealed an intensification of glacial activity between 5190 ± 90 and 4654 ±60 yr BP (Gellatly et al., 1992), with glaciers larger than those developed during the Litlle Ice Age-LIA (1300-1850 AD). During this Mid-Holocene glacial reactivation worldwide new glaciers formed and/or advanced (Davis et al., 2009). In general terms, this cold period in the mountains coincided with an arid phase in the Western Mediterranean (Jalut et al., 2000, 2009). Changes in the magnetic properties of the sediments, the lamination patterns and a decrease in sedimentation rate in Marboré Lake (Oliva et al., submitted) occurred during this period (Fig. 9c). PAR (Fig. 9a), decreased to the lowest Holocene values. A coeval decrease, although shorter in time, is noticed in both PAR and sedimentation rate at around ca. 1.2-1.5 kyr cal BP during the Early Medieval times when, another stage of glacier expansion occurred in Marboré cirque (Garcia-Ruiz et al., 2014) (Fig. 9d) in response to relatively colder and more humid conditions of the Dark Ages (Moreno et al., 2012; Morellón et al., 2011, 2012). No similar changes have been detected during the LIA. No clear evidences of increasing duration of the lake ice-cover have been detected for these cold pulses in comparison to the YD and HO, possibly because the shorter duration of these events and the resolution of our proxies.

A clear human imprint is not recorded in the Marboré sequence between 5.2-3.5 kyr cal BP, although evidences of cultural landscape transformations have been detected in the lowlands since 4 kyr cal BP (i.e., Galop and Jalut, 1994; Bal et al., 2010, 2011; Rius et al., 2012). The first human-induced deforestations were detected at around 4 kyr cal BP in the Tramacastilla sequence (1380m a.s.l.) by Montserrat-Martí (1992), although the forest recovered afterwards. The decreasing trend observed in the PAR values of Marboré during ~5-4 kyr cal BP (Fig. 9a) could however be responding to first regional deforestations, similar to those recorded by Montserrat-Martí (1992). In agreement with

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Montserrat's hypothesis, Marboré forest recovered in following centuries, as shown by the maximum values reached by PAR at around 2.5-2 kyr cal BP (Fig. 9a). However no other anthropogenic indicators are found during this period so, as previously mentioned, this decrease could also be associated with colder climatic conditions.

Over the last 3.5 kyrs, herbs (mainly *Artemisia*, Chenopodiaceae, Fabaceae and Poaceae) progressively expanded indicating a more consistently open, landscape. In the literature, herbaceous pollen percentages greater than 30% have been interpreted as a treeless alpine environment (Tinner and Theurillat, 2003; Berthel et al., 2012; Geantă et al., 2014). AP tends to descend progressively (Fig. 9b) primarily because of the decline in the deciduous forest which is also visible in the PAR values (Fig. 9a), interpreted as a deciduous-montane belt shift downwards, or a greater reduction of this community in general terms (Fig 9g). A similar trend has also been identified in many other Pyrenean sequences located at both high (e.g. Tramacastilla, Montserrat-Martí, 1992; Redón, Pla and Catalan, 2005; Burg, Pèlachs et al., 2011; Estanilles, Pérez-Obiol et al., 2012; Basa de la Mora, Pérez-Sanz et al., 2013), and low altitudes (González-Sampériz et al., 2017) and linked to the continuous spread of human impact. However, increasing heliophytes may point to climatic drivers leading the landscape change (Pérez-Sanz et al., 2013).

For instance, the rise of *Artemisia* in Basa de La Mora after 3000 cal BP (Pérez-Sanz et al., 2013) fits well with the results obtained in Marboré sequence, without any clear evidences of human perturbations in the nearby forests. The coeval decrease in humid-demanding taxa like *Corylus* and *Abies*, coupled with the rise in evergreen *Quercus*, indicate a drier climate background. Coherently, the geochemical data from Marboré sequence (Oliva-Urcia et al., submitted) show another major change characterized by an increase in most magnetic parameters and in Mn oxides which also indicates a generally drier period with a lower lake level.

It is not until the last 1.3 kyrs, when Marboré records the spread of human activities at a regional-scale with, the noticeable rise of the NAP component in percentages and PAR (Fig. 9b). *Artemisia* continues as the main herb taxa, but followed by Cichorioideae, Chenopodiaceae, Ericaceae and Fabaceae

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which suggest an intensification of landscape management. The rise in Poaceae points to the expansion of alpine meadows at high-altitudes as also shown in Basa de la Mora (Pérez-Sanz et al., 2013) (Fig. 9e). As a consequence AP from both Marboré (Fig. 9c) and Basa de la Mora (Fig. 9e) experienced an important reduction, more intense in the deciduous forest. As shown in SI, Table 1, deciduous pollen percentages reached the lowest values during this period, suggesting that the deciduous forest boundary would have stabilized at an altitude similar to the current one (~1500 m). The vegetation replacement during the last millennium seems linked to anthropogenic activities rather than climate drivers since the expansion of *Olea* cannot be explained exclusively by natural causes. In fact, the spread of olive cultivars in the lowlands has been widely documented in many pollen sequences (Morellón et al., 2011; Rull et al., 2011; Pérez-Obiol et al., 2012; Pérez-Sanz et al., 2013; González-Sampériz et al., 2017) and archaeobotanical studies at regional-scale (Alonso et al., 2014).

In sum, high altitude pollen sequences in the Central Pyrenees are good archives for understanding the regional vegetation variability and the montane vegetation altitudinal shifts without any significant human imprint, at least until the last millennium. Due to the high sensitivity of these high altitude lakes to environmental change, and how strongly they affect sedimentological and biological processes and pollen transport and deposition in the lake, caution should be taken when interpreting pollen percentages where ice-cover may preclude pollen deposition over long periods of time during colder periods.

6. Conclusions

1. The Marboré sequence offers the opportunity to investigate the sensitivity of high altitude systems as archives of climate and environmental changes during the Late-Glacial and Holocene in Southern European mountains (last 14.6 kyr cal BP).
2. The unique setting (high altitude, prolonged snow and ice – covered periods, varied pollen sources) possess some challenges to reconstruct past vegetation dynamics based on pollen records. A modern altitudinal transect of pollster pollen rain sites and the use of PC and PAR

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instead of pollen percentages has helped to better constrain the vegetational history of the Central Pyrenees and the altitudinal shifts of the montane forest during the Holocene.

3. Lower sedimentation rate, PC and PAR occurred in Marboré during colder periods of GS-1 and HO (~12.6-10.2 kyr cal BP) indicating longer ice-cover periods. Increasing sedimentation rate and the occurrence of several abrupt PAR peaks during Early Holocene (10.2-9.3 kyr cal BP) were caused by longer ice-free seasons due to higher temperatures.

4. Pollen percentages for cold periods as ~12.6-9.3 kyr cal BP are not reliable as indicators of vegetation composition because of differential pollen deposition depending on the ice-cover duration.

5. The comparison between current vegetation cover and modern pollen spectra shows a good correlation between deciduous pollen assemblage and actual plant cover. This fact enables us to infer altitudinal shifts of the deciduous forest timberline. *Pinus* pollen type is always the dominant taxa in moss pollster and it is always over represented in all samples. On the contrary, herbaceous taxa are generally under-represented.

6. The lack of arboreal plant macrofossils along the whole sequence, suggest that the treeline never reached Marboré site (2600 m a.s.l.) for the last 14.6 kyr cal BP. However, the comparisons carried out with fossil pollen abundances and modern spectra from moss pollsters, suggest that the maximum altitude reached by deciduous-montane forest was quite higher (1600-1900 m a.s.l.) than nowadays (1500 m a.s.l.), reaching the subalpine belt between 9.3-5.2 kyr cal BP time period.

7. A progressive decrease in deciduous forest, sedimentation rate and PAR values occurred around 5.2 kyr cal BP, primarily attributed to the colder climatic conditions of the Neoglacial. Similarly, both sedimentation rate and PAR slightly decrease during the colder Dark Ages. No evidences of longer ice-cover duration changes have been identified for either period, probably as a consequence of their short duration and the low resolution sampling.

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8. The expansion of herbs started around 3.5 kyr cal BP and intensified after 1.3 kyr cal BP. Coevally, an important reduction of AP occurred (especially in deciduous forest), which could be related to the intensification of human activities at lower altitudes as it has been documented regionally. A clear anthropogenic signal is not found until recent times ~700 kyr cal BP, with the expansion of *Olea* pollen content, suggesting the regional intensification of Olive groves in the lowlands.

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Table 1. AMS radiocarbon dates from core MAR11-1U-1A and two tie points corresponding to the two Pb peaks. Note that rejected dates are indicated in italics.

Direct AMS code	Name	Composite Depth (cm)	Radiocarbon date (^{14}C AMS yr)	Age error (yr BP)	Reservoir effect (substracted before cal)	Calibrated age (2σ) (cal yr BP)	Mean calibrated age (cal yr BP)
-	MAR11-1G-1A-4 cm 6-FirstPbpeak	4	-16	2.76	0	-	-16
-	MAR11-1G-1A-4 cm 14 SecondPbpeak	14	89	7.62	0	-	89
D-AMS 1217-203	*MAR11-1A-1U-1 cm 8-10*	-	*5771*	*46*	*2230*	-	-
D-AMS 001189	MAR11-1A-1U-1 cm 39-41	37.2	2514	25	2230	353-435	383
D-AMS 1217-204	MAR11-1A-1U-2 cm 53-56	91.4	3611	28	2230	1275-1340	1300
D-AMS 001190	MAR11-1A-1U-2 cm 142-144	195.4	4820	28	2230	2707-2765	2742
D-AMS 1217-205	*MAR11-1A-1U-3 cm 27-30*	-	*5853*	*30*	*2230*	-	-
D-AMS 1217-206	MAR11-1A-1U-3 cm 71-74	286.1	5675	31	2230	3632-3828	3704
D-AMS 001191	MAR11-1A-1U-3 cm 102-104	325.5	6294	39	2230	4429-4646	4554
D-AMS 1217-	MAR11-1A-1U-4 cm 17-21	402.2	7464	55	2230	5909-6129	6000

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D-AMS 001192	MAR11-1A-1U-4 cm 88-90	480.1	8447	39	2230	7006-7133	7111
D-AMS 1217-208	MAR11-1A-1U-4 cm 139-141	537	9787	43	2230	8305-8427	8376
D-AMS 001193	MAR11-1A-1U-5 cm 27-29	596.1	10852	47	2230	9525-9689	9583
D-AMS 001194	MAR11-1A-1U-5 cm 53-55	628.2	11434	47	2230	10248-10496	10363
D-AMS 010873	MAR11-1A-1U-5 cm 82-86	665.3	12945	56	2230	12573-12727	12668
D-AMS 010100	MAR11-1A-1U-5 89-93 cm	674	13269	46	2230	12769-13045	12904
D-AMS 1217-209	*MAR11-1A-1U-5 cm 113-116*	*703.6*	*11521*	*47*	*2230*	-	-
D-AMS 010101	MAR11-1A-1U-5 cm 124-128	717.3	14656	50	2230	14192-14893	14528

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Highlights

- Variations of a Pyrenees lake ice-cover duration have been inferred for the GS-1 and Holocene onset, based on sedimentation rate and Pollen Accumulation Rate (PAR) values.
- The deciduous-montane forest is the community best reflected when comparing current vegetation and pollen from modern surface samples.
- The deciduous forest reached the maximum altitude between 9.3-5.2 kyr cal BP likely spreading to the sub-alpine belt.
- Human impact is not clearly identified at high altitudes until very recent times.

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