Holocene fire and vegetation dynamics in the Central Pyrenees (Spain)

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Abstract

Fire-vegetation relationships are critical to understand transient mountain ecosystems and their long-term landscape dynamics, which is essential for alpine forest conservation. In this paper we aim to (1) reconstruct the Holocene fire history at high altitudes of the southern Central Pyrenees, (2) add evidence to the debate on fire origin, naturally or anthropogenically produced, (3) determine the importance of fire as a disturbance agent for sub-alpine and alpine vegetation, in comparison with the plant community internal dynamics applying conditional inference trees. We present and compare microcharcoal and pollen data series, from two lacustrine sedimentary sequences in the Central Pyrenees: Basa de la Mora (BSM), within the treeline ecotone at the subalpine belt (1914 m a.s.l.) and Marbore Lake, above the treeline at the alpine belt (2612 m a.s.l.). We evidence that, fire activity was not the most important factor in driving vegetation dynamics regionally. Our results suggest that spatially, the fire signal might be site-dependent while over time, climate exerted a strong influence on fire activity during the early-to-mid Holocene, showing more fires during the Holocene Thermal Maximum (HTM) (ca. 7000–6000 cal yr BP) whereas fire activity decreased with the cold Neoglacial period. At ca. 3700 cal yr BP, fire activity increased coinciding with a regional landscape opening, suggesting that human activities may have strengthened the importance of fire. Fire activity remained low over the last two millennia but a remarkable Holocene maximum for the last centuries in both sequences is observed, likely related to increasing human pressure.

Keywords: Microcharcoal; Pollen; Lake sediments; Palaeoclimate; Human impact; Fire-history

1. Introduction

Fire is a relevant disturbance of the Earth system, driving significant changes in ecosystem structure and function, species evolution, biomass dynamics or global carbon cycling (Bond and Midgley, 1995; Bowman et al., 2009; Pausas and Schwilk, 2012; Archibald et al., 2013). Fire regimes are driven by factors such as climate (e.g. Daniau et al., 2012), vegetation through fuel load, connectivity or flammability, soil types, ignition sources-natural or anthropogenic-, and topographical features (Whitlock et al., 2010; Krawchuk and Moritz, 2011). Thus, the sensitivity of any ecosystem to fire depends on its own characteristics.

Sub-alpine and alpine plant communities are formed by alpine pastures and weakly flammable conifer woodlands like *Pinus sylvestris* L*., Pinus uncinata* Ramond ex DC*, Juniperus communis* L. and *Abies alba* Mill*,* which hold no post-fire strategy, especially after crown fires (Keeley et al., 2012). Fire in mountains is associated with the occurrence of woody species (Leys et al., 2014), and is therefore infrequent above the treeline due to the lack of arboreal biomass. Under natural conditions, fire occurrence will generally be controlled by the fuel moisture degree, in turn driven by precipitation and temperature.

The high landscape heterogeneity in mountain areas often implies different fire behaviour (Leys and Carcaillet, 2016; Frejaville et al., 2018) at the sub-regional or local scales. Mountain environments are in addition very sensitive to climate, fire, and land use changes, because of their narrow tolerance capabilities, especially at the boundaries of the treeline (Theurillat and Guisan, 2001; Pauli et al., 2012).

Fire occurrence is generally low in alpine ecosystems under present climatic conditions and land use patterns in the Pyrenees. However, fire activity has changed over time (Jimenez-Ruano et al., 2019) and may have been a more frequent disturbance over the last millennia, with different climatic settings and more intense human activities. In fact, human activities have been modifying natural fire regimes through changing land use (Pausas and Keeley, 2014) since centuries or even millennia (Carracedo et al., 2017; Morales-Molino et al., 2017), using fire as a tool in land management. For instance, during the mid-19th century humans used fire as a common tool to maintain opened mountain landscapes in the Pyrenees (Garcia-Ruiz et al., 2015; Garcia- Ruiz and Lasanta, 2018), modifying the structure of sub-alpine systems. However, due to the abandonment of traditional land uses, the extension of opened areas has been reduced, increasing forest connectivity and the accumulation of standing fuel loads. Consequently, the increase in drought conditions and temperature due to global warming (IPPC, 2014), together with the increase in the amount of standing fuel may enhance the risk of wildfires in southern European mountains (Ryan, 2000; Wastl et al., 2013). This may

reduce forest resilience to wildfires (Stevens-Rumann et al., 2018), while it can also provide an opportunity for ecosystem restoration under particular circumstances (Leverkus et al., 2019).

Understanding to what extent changing fire regimes at longer temporal scales have contributed to the current mountain landscapes is paramount for designing sustainability policies for socio-ecological systems. In this context, long-term ecology research emerges as a critical tool to obtain the needed time series to address environmental changes at centennial to millennial time-scales. Sedimentary microcharcoal analysis improves our understanding on the long-term role of fire as a key ecological factor (Whitlock and Larsen, 2001; Power et al., 2008; Colombaroli et al., 2010; Feurdean et al., 2012), whereas pollen analysis in sediments has been widely used for the study of vegetation changes (Carrion et al., 2010 and references therein; Birks and Bjorn, 2018). Both proxies have facilitated and strengthened our understanding of past disturbances in the landscape.

The comparison of different charcoal records at global scale has revealed significant regional differences in fire activity during the Holocene, probably caused by the complex interplay between climate, vegetation and human impact (Power et al., 2008; Vanniere et al., 2011, 2016; Marlon et al., 2013). Thus, despite climate seems to be the main fire driving force at large spatial scales in fire-prone areas, regional studies evidence that other local factors would be also determining the high temporal variability in biomass burning (e.g. Gavin et al., 2006; Feurdean et al., 2012, 2017; Leys and Carcaillet, 2016). Given this spatial and temporal heterogeneity in variables controlling fire, site-specific histories are needed to show how fire activity has been modulated by microclimate, vegetation, topography and land-use (Gavin et al., 2006; Whitlock et al., 2010; Rius et al., 2011).

Apart from fire, climate and other external disturbances, plant population dynamics are also determined by the ecological memory of a community, defined as the capacity of past states of the system to influence present or future responses (Padisak, 1992; Ogle et al., 2015). In this regard, antecedent taxa dynamics and fire activity may also be relevant explaining the abundance of a taxa at a given time. Therefore, understanding ecological memory may help to assess long-term ecosystem resilience.

Contrary to other European mountain ranges, where long-term fire activity has been widely studied in mountain sites (e.g. Tinner et al., 1998, 2015; Blarquez and Carcaillet, 2010; Colombaroli et al., 2010; Feurdean et al., 2012; Leys et al., 2014; Florescu et al., 2018), we know little about the long-term fire history of the Iberian Peninsula mountain ranges (Perez-Obiol et al., 2012; Carracedo et al., 2017; Morales-Molino et al., 2017) and, in particular, of the Pyrenean mountains. While most studies focus on the eastern part (Ejarque et al., 2010; Bal et al., 2011; Perez-Obiol et al., 2012; Cunill et al., 2013; Garces-

Pastor et al., 2017) presenting the evolution of fire activity during the Lateglacial and Holocene periods very few have been developed at the central part (Gil- Romera et al., 2014), and little is known about the role of fire transforming alpine ecosystems.

In the current research we aim to (1) reconstruct the long-term fire history in the southern Central Pyrenees, (2) add evidence to the debate on fire origin, naturally or anthropogenically driven, comparing our Holocene fire series with other local and regional evidence, and (3) compare the relative influence of antecedent values of pollen abundance and fire activity versus concurrent fire activity on the dynamics of several taxa. We present an encompassing comparison of well-dated Holocene sedimentary charcoal records and their fossil pollen assemblages from the sub-alpine, Basa de la Mora Lake (BSM) (at the treeline) and alpine Marbore Lake (MAR) (above the treeline).
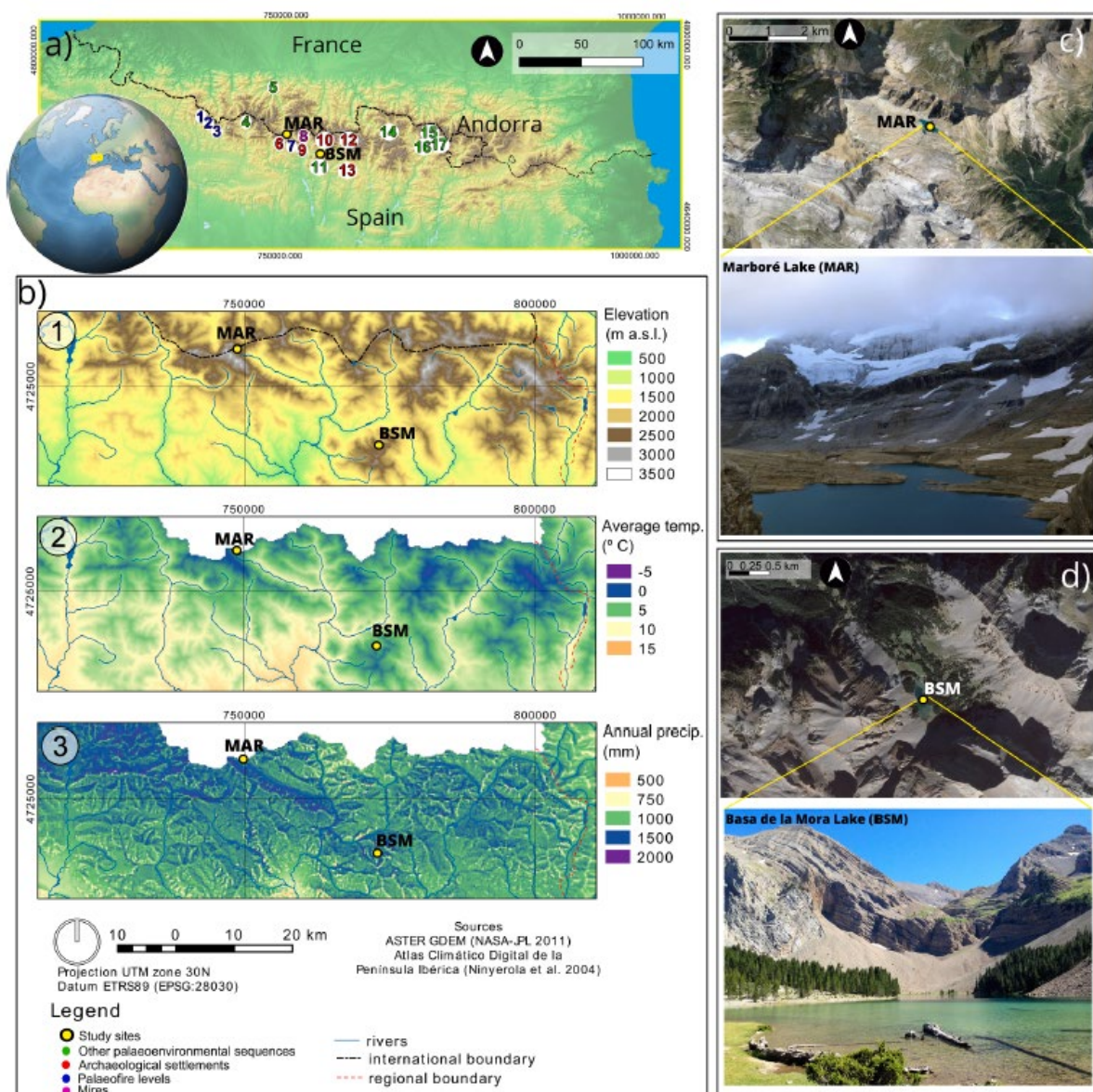

Fig. 1. (a) Location map of the study lakes Marbore (MAR) and Basa da la Mora (BSM) in the Pyrenees together with other existing records; in blue: dated palaeofire levels; in red: archaeological settlements; in green: other existing fire and pollen records; in pink: mires. 1: Plandaniz (Gonzalez-Samperiz et al., 2019); 2:

Aragues (Gonzalez-Samperiz et al., 2019); 3: Las Blancas (Gonzalez-Samperiz et al., 2019), 4: Portalet peatbog (Gonzalez-Samperiz et al., 2006; Gil-Romera et al., 2014); 5: Lourdes Lake (Rius et al., 2011); 6: Barranco Pardina (Laborda et al., 2017); 7: Valle Pardina (Gonzalez-Samperiz et al., 2019); 8: Parzan mires; 9: Corotrasito (Clemente et al., 2016); 10: Puyascada (Baldellou, 1987); 11: Armena-A294 Ice Cave (Leunda et al., 2019); 12: Hospital de Benasque (Ona and Calastrenc, 2009); 13: Els Trocs (Rojo et al., 2013); 14: Bassa Nera (Garces-Pastor et al., 2017); 15: Estanilles peatbog (Perez-Obiol et al., 2012); 16: Plaus de Bodis-Montarenyo (Cunill et al., 2013); 17: Burg (Pelachs et al., 2011). (b) Topographic (1), Temperature (2) and Precipitation (3) maps of the study areas. c) Ortophoto and photography of the MAR Lake and surrounding area. d) Ortophoto and photography of BSM and surrounding area (Google, Imagery 2019. CNES. Institut Cartografic de Catalunya, Landsat. Copernicus, Maxar Technologies, Map data 2019).

2. Regional setting

The Pyrenees are a mountain range located in north eastern Iberian Peninsula (Fig. 1a), between the Atlantic Ocean and the Mediterranean Sea. Water availability in the Pyrenees is controlled by an important west-east rainfall gradient (2000 to 1000 mm) driven by the North Atlantic Oscillations (Araguas-Araguas and Diaz Teijeiro, 2005). The western Pyrenees have a direct Atlantic influence with a humid climate, while the eastern Pyrenees have a stronger Mediterranean influence, with a drier and warmer season. Beyond these general features, there is also a high-climatic variability controlled by topography and elevation, with highest mean annual precipitation (MAP) values occurring at the highest elevations (2000–2500 mm), and a temperature lapse rate of ca. −0.6°/100 m (Garcia-Ruiz et al., 2015) with a mean annual temperature gradient that goes from 5 to 10 °C in the valleys, to below 0 °C in the high massifs (Ninyerola et al., 2005; Fig. 1b).

The altitudinal gradient defines the main vegetation belts in the Pyrenees (Fig. 2). The low montane community (ca. 1200–1400 m a.s.l.) is characterized by mosaics of croplands and open mixed areas of *Quercus ilex* L., *Quercus faginea* Lam. /*cerrioides* Willk. & Costa, and *P. sylvestris* with a dense shrub land of different juniper species, *Buxus sempervirens* L. and *Genista scorpius* (L.) DC. among others. The upper montane community (ca. 1400–1600 m a.s.l.) features well-developed broadleaf forests mainly composed of *Corylus avellana* L.*, Betula pendula* Roth*, Fraxinus excelsior* L.*, Acer campestre* L.*, Sorbus aria* (L.) Crantz*, Sorbus aucuparia* L. mixed with *P. sylvestris, P. uncinata or A. alba*. The sub-alpine belt (ca. 1600–2000 m a.s.l.) is dominated by coniferous forests of *P. uncinata* with sparse shrubs like *J. communis* or *Rhododendron ferrugineum* L. Although slope orientation, soil formation, microclimate and past human activities interact to determine the upper limit of the closed forest, the timberline is located at ca. 1700–1900 m a.s.l. Both timberline and treeline (up to ca. 2000–2200 m a.s.l.) are communities where the dominant tree is *P. uncinata* (Fig. 2). Alpine and sub-nival communities (higher than ca. 2000 m a.s.l.) are formed by alpine herbs and dwarf shrubs.

Fires in the Pyrenees occur mostly in forested areas (Cubo et al., 2012; Vazquez de la Cueva, 2016) and they are mostly naturally produced, triggered by lightning as the main ignition source in high altitude locations (Amatulli et al., 2007; Cubo et al., 2012; Vazquez de la Cueva, 2016), during summer storms (Font, 1983; Vazquez de la Cueva, 2016). Despite human-caused fires do happen as well, these take place in the more fragmented areas in the montane zone (Amatulli et al., 2007).

MAR is an alpine glacial lake located at 2612 m a.s.l. at the base of the Monte Perdido Glacier (Fig. 1c). BSM (1914 m a.s.l.) is a shallow glacial lake located on the north-facing slope of the Cotiella Peak (Fig. 1d). Although both lakes in this study lay at the Central Pyrenees and are ca. 30 km from each other, each lake presents quite different geographical and ecological characteristics summarized in Table 1. MAR does not present woody vegetation around the lake, as it is placed in the alpine belt. The treeline is located 600 m below, thus, fires are less likely locally. However, BSM is currently located in the sub-alpine belt, and thus, within the treeline ecotone dominated by *P. uncinata* communities. Fires can potentially occur in the vicinity of the lake, although fire activity is nowadays low in this place. Furthermore, the modern fire activity at a regional scale in both areas is weak, with ca. 1 to 2 fire events occurring every 30 years, invariably set by natural causes (mostly summer storms) that, however, often create mid-to-large fires with a burnt area between 10 and 100 Ha (Vazquez de la Cueva, 2016).
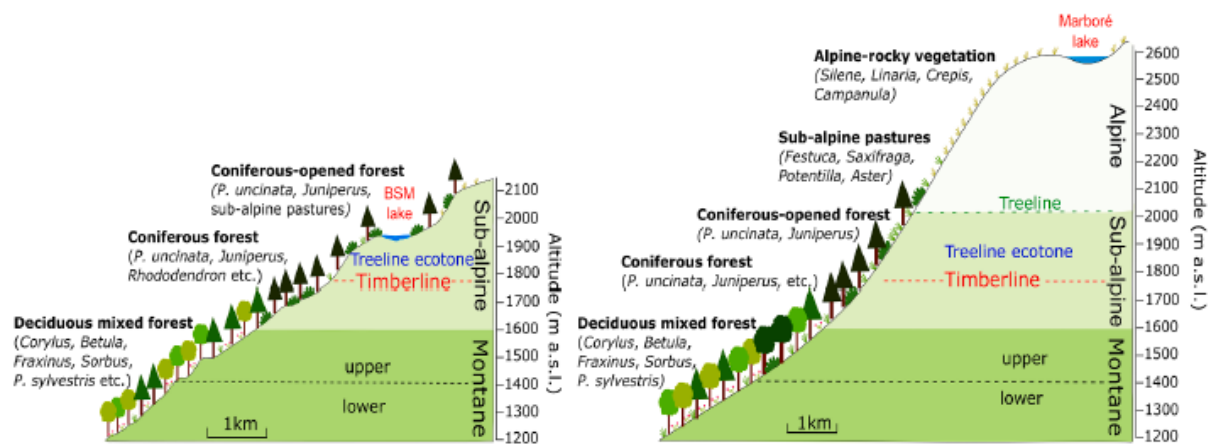

Fig. 2. Simplified vegetation transects for Basa de la Mora (left) and Marbore (right) sites.

3. Materials and methods

3.1. Lake-coring, chronology and pollen analysis

Previous multiproxy analyses of both sedimentary records have already been published, Perez-Sanz et al. (2013) for BSM Lake and Leunda et al. (2017) and Oliva-Urcia et al. (2018) for MAR Lake. In the present study we focus on the Holocene section of both sequences. BSM depth-age model is based on 13 14C terrestrial plant macrofossil dates along 11 m depth (mean sedimentation rate: 0,149 cm/yr), and MAR depth-age model is based on 9 14C bulk sediment dates along 6 m depth (mean sedimentation rate:

0,061 cm/yr). In both cases, the most recent part has been dated with 210Pb/137Cs. Depth-age models were carried out with Clam 2.2 software (Blaauw, 2010) using linear interpolation between dated levels (Fig. 3). Pollen analysis for both sequences was conducted in Perez-Sanz et al. (2013) and Leunda et al. (2017) following the standard chemical procedure (Moore et al., 1991) but including Thoulet solution (2.0 g/cm3) 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 Pyrenean Institute of Ecology (IPE-CSIC), determination keys and photo atlases (Moore et al., 1991; Reille, 1992). Results have been calculated both in percentages and pollen accumulation rates (PAR #/cm2yr). More details about the chronological framework and pollen analysis are provided in Perez-Sanz et al. (2013) and Leunda et al. (2017).

3.2. Microcharcoal analysis

We present here microcharcoal series for BSM and MAR as fire proxy, aiming to achieve our first objective, i.e. to reconstruct the long-term regional fire activity. The term microcharcoal refers to small carbonized particles (Fig. S1) produced during vegetation fires (Jones et al., 1997) and transported by aeolian and fluvial agents from the combustion site to the sedimentation basin. In lakes charcoal preserves well due to its relatively high resistance to chemical and microbial decomposition (Habib et al., 1994; Hart et al., 1994; Verardo, 1997; Hockaday et al., 2006; Quenea et al., 2006).

Microcharcoal analyses were carried out in a total of 108 samples for MAR and 130 samples for BSM. We sampled microcharcoal at the same depths of the pollen samples previously analysed. In BSM sample resolution was every 5 cm with a mean temporal resolution between samples of ca. 70 years, while MAR sampling was performed every 5– 10 cm with a mean temporal resolution between samples of ca. 109 years, except for the upper part, where sampling was every 2 cm. Sediment samples were processed using the chemical procedure following Daniau et al. (2009, 2013) at the UMR-EPOC laboratory (CNRSUniversite de Bordeaux). The microcharcoal extraction technique consisted of a chemical treatment of 37% HCl, 68% HNO3 and 33% H2O2 performed over 24 h on 0,3 g of dried sediment, followed by a dilution of 0,1 applied to the residue. The suspension was then filtered onto a cellulose acetate membrane containing nitrocellulose of 0,45 μ m porosity and 47 mm in diameter. A portion of this membrane was mounted onto a slide.

The identification and quantification of microcharcoal was performed using automated image analysis with an automated Leica DM6000M microscope at x500 magnification in transmitted light and following the criteria proposed by Boulter (1994), identifying charcoal as being black, opaque and angular with sharp edges. This technique allows identifying microcharcoal particles automatically, once colour and lightning settings are established for identifying them, reducing considerably the counting task. Identification

of unburned particles, characterized by the absence of plant structures and distinct level of reflectance, was used to set the best-fit threshold level to secure identification of microcharcoal by image analysis. Critical particles were distinguished from dark minerals by reflected light (Clark, 1984) and in order to have a good statistical representation of each sample, 200 view fields (200 images) of 0,0614 mm2 were taken in colour with a 1044 × 772 pixels digitizing camera (1 pixel = 0,276 μm). The surface scanned by the microscope represented a surface area of 12,279 mm2. Although this technique has primarily been applied in marine sediments (Daniau et al., 2009, 2013) it has also been successfully used for lake sediments (e.g. Tinner et al., 1999; Leys et al., 2014; Remy et al., 2018). Microcharcoal particles below 10 μm have not been considered, as theoretical considerations showed that particles smaller than 5–10 μm in diameter are difficult to identify (Clark, 1988).

From the microcharcoal measurements, three parameters were calculated for each sample: (i) the concentration of microcharcoal (CCnb: #/g); (ii) the concentration of microcharcoal surface (CCs), which is the sum of all surfaces of microcharcoal in one sample per gram (μm2/g) and (iii) microcharcoal accumulation rate or influx (CHAR: #/cm2yr), in order to have a time-fitted value of charcoal. 1 cm3 of sediment was sampled with a syringe and weighted (g) in order to calculate sediment density (g/cm3) and multiply it with charcoal concentration (#/g) and sedimentation rate (cm/yr) to obtain microcharcoal accumulation rate (#/cm2yr).

Several replicate analyses were done (7 for MAR and 10 for BSM) randomly analysing 10 times each. For this replicate samples, the mean value and standard deviation was calculated. For the comparison of both sequences, microcharcoal influx data was normalized with Zscores (Glantz et al., 2016).

3.3. Numerical analyses: Conditional inference trees

Accomplishing the third objective of our research implied estimating to what extent long-term fire dynamics is a relevant variable shaping the sub-alpine and alpine Pyrenees landscape. We thus calculated the effect that antecedent and concurrent fires (CHAR) have on the abundance of certain taxa (PAR). On the other hand, we intend to quantify to what extent PAR itself is determined by its own antecedent values. In doing so, we incorporate a quantitative approach to the ecological memory concept (Ogle et al., 2015). In order to analyse the effect of past and concurrent CHAR and past PAR on each PAR value, we aligned the samples of each site with their antecedent ones, generating a data structure with a lag of order 1, following the model expressed in Eq. (1):

PAR~CHAR + CHAR. antecedent + PAR.antecedent   (1)

PAR is the response, with the same age and depth as CHAR, which represents concurrent fire, while CHAR.antecedent and PAR.antecedent have the age and depth of

the previous sample, and represent the effect of past states on the dynamics of the system.

PAR values of *Pinus*, *Abies*, *Betula*, *Corylus*, and Herbs were used as response variable for both sites. Deciduous *Quercus* was only modelled in BSM because MAR records very low and sparse *Quercus* PAR values. The models were fitted with conditional inference trees (Hothorn et al., 2006) through the ctree function of the R package partykit (Hothron and Zeileis, 2015). Conditional inference trees are recursive partition models that use a permutation test to find on each iteration the threshold of any predictive variable that better splits the data into two homogeneous partitions. The process is repeated on each data partition until further data splitting is not possible, or the terminal nodes of the recursive partition tree reach a minimum sample size.

The resulting model is a regression tree, in which variables located higher up in the tree hierarchy are more important to explain patterns in the data than variables located in lower nodes. Regression trees are easy to interpret, represent partial interactions among predictive variables, and do not rely on assumptions about the properties of the data in the way linear models do. Despite the fact that they are generally underused in ecology, conditional inference trees have proved to be extremely useful in conservation biology (Johnstone et al., 2014).
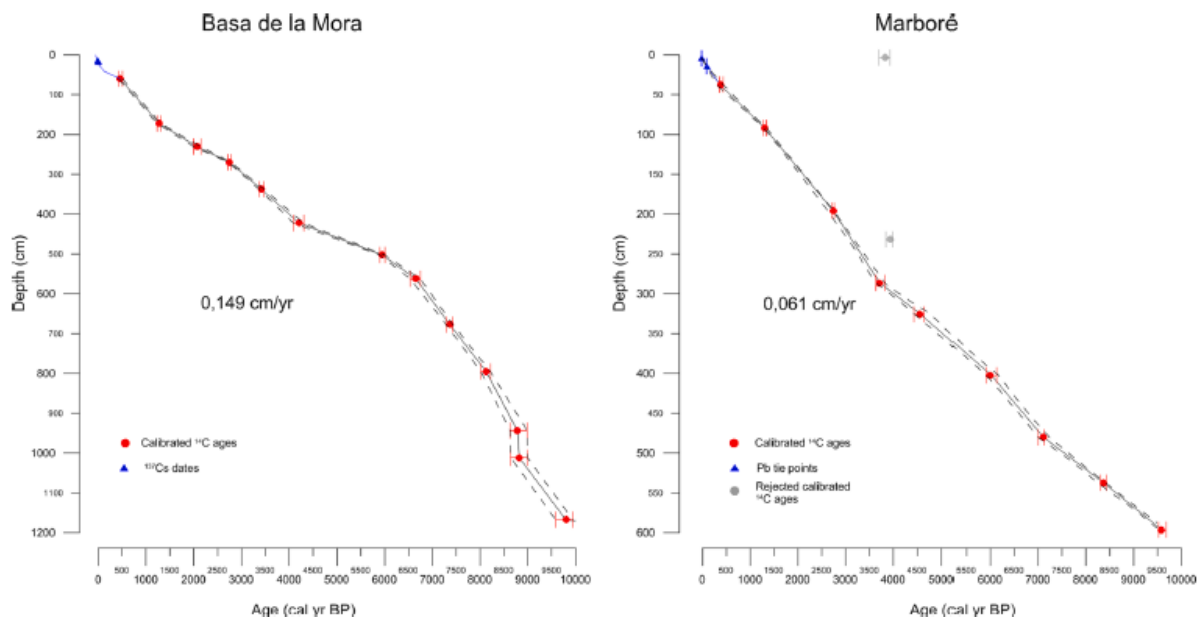

Fig. 3. Holocene depth-age models for both sequences based on Perez-Sanz et al. (2013) and Leunda et al. (2017).

Fig. 4. Comparison of different indicators from both MAR and BSM lake sequences: (a) and (g) Microcharcoal z-scores from MAR and BSM sequences (the red shade indicate values above 0 in the z-scores standardized values), selected pollen taxa from MAR: (b) *Pinus*, (c) *Abies*, (d) *Betula*, (e) *Corylus*, and (f) Herbs (Leunda et al., 2017), selected pollen taxa from BSM: (h) *Pinus*, (i) *Abies*, (j) *Betula*, (k) *Corylus*, (l) Deciduous *Quercus* and (m) Herbs (Perez-Sanz et al., 2013), (n) Chironomid-based Holocene summer temperature reconstruction from BSM (Tarrats et al., 2018) and (o) distribution and probability sum of calibrated radiocarbon dates of archaeological settlements (in red) and palaeofire layers, referring to layers in a soil, paleosoil, stratified scree or ravine which contain abundant charcoal particles of past fires (in blue) in the Central Pyrenees. Palaeofires: Las Blancas, Abrigo Valle Pardina; Plandaniz, Aragues (Gonzalez-Samperiz et al., 2019). Archaeological settlements: Hospital de Benasque (Ona and Calastrenc, 2009), Barranco Pardina (Laborda et al., 2017), Coro Trasito (Clemente et al., 2016), Puyascada (Baldellou, 1987) Els Trocs (Rojo et al., 2013). HTM: Holocene Thermal Maximum. LIA: Little Ice Age.
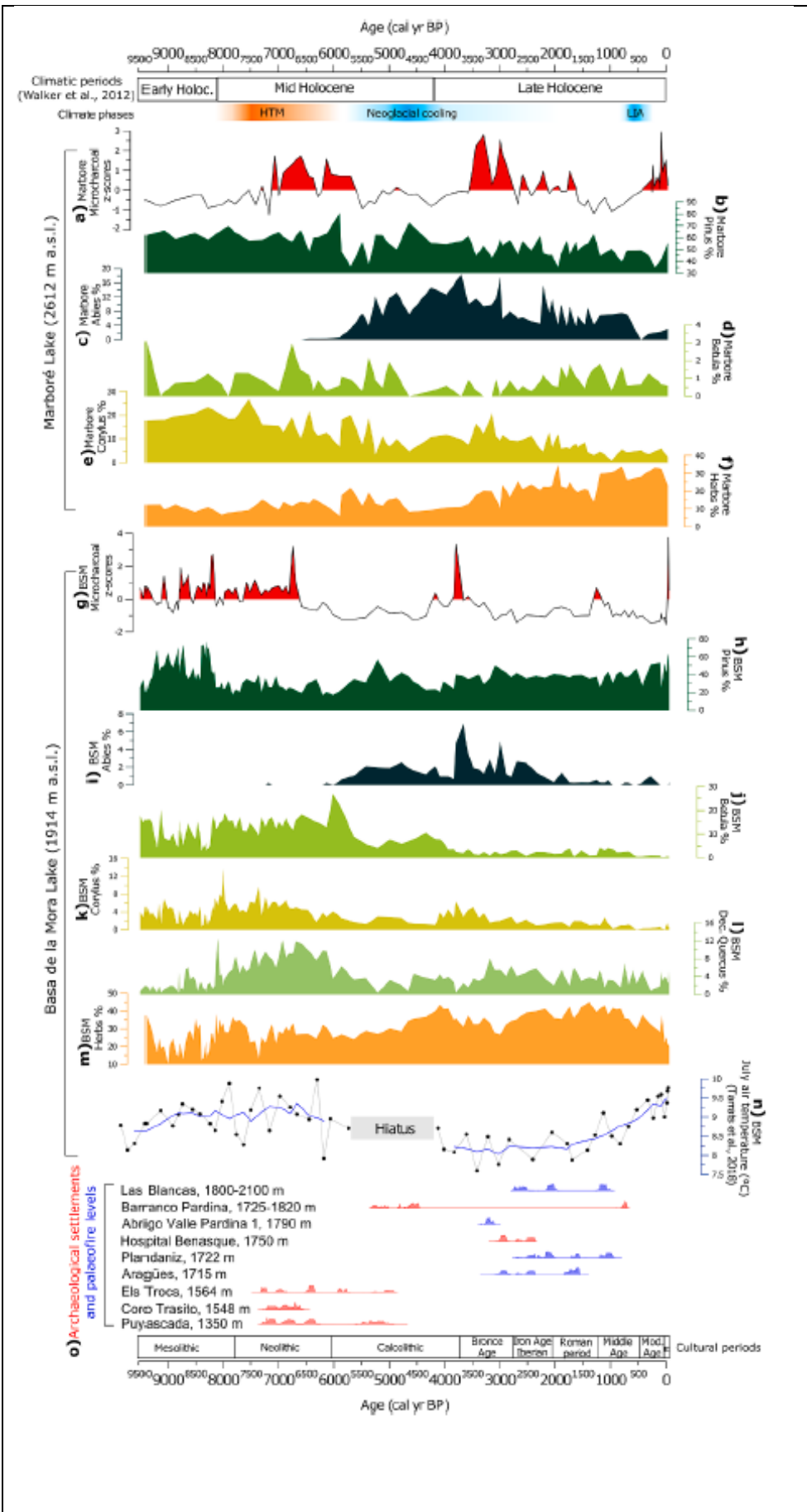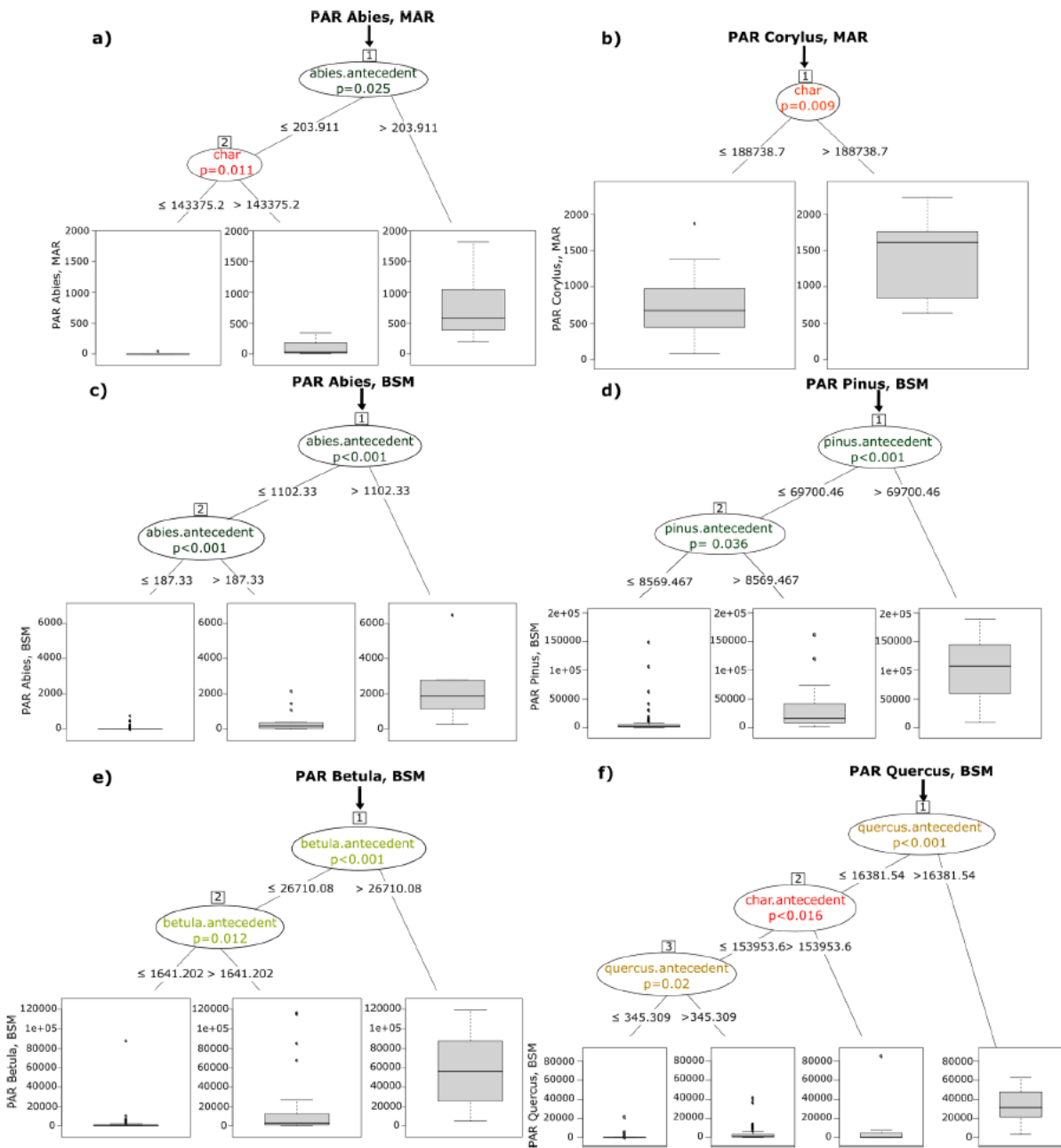
Fig. 5. Conditional inference trees for selected taxa in both MAR and BSM sequences: (a) PAR *Abies* in MAR, (b) PAR *Corylus* in MAR, (c) PAR *Abies* in BSM, (d) PAR *Pinus* in BSM, (e) PAR *Betula* in BSM and (f) PAR *Quercus* in BSM. At the top of each regression tree, the initial PAR values for each taxa are indicated. Each of the circles (with a number e.g. 1,2,3) show the best explanatory variable (with the corresponding p value) from all the considered variables (CHAR, CHAR.antecedent or PAR.antecedent) for the initial PAR values for each taxa. The boxplots, represent mean values of each PAR series classified according to the explanatory variables.

Table 1

Summary of main features of Marboré and Basa de la Mora Lakes. MAP: mean annual precipitation; SP: summer precipitation; WP: winter precipitation; MAT: mean annual temperature; SMMT: summer mean maximum temperature. Climatic data have been extracted from Ninyerola et al. (2005) and Batalla et al. (2018).

	Basa de la Mora (BSM)	Marboré (MAR)
Coordinates	42°32′N, 0°19′E	42°41′N, 0°2′E
Altitude (m a. s. l.)	1914	2612
Lake type and dimensions	· Holomictic lake · ~300 m length · ~100 m across · Maximum water depth of 4.5 m	· Cold Dimictic lake · ~500 m length · ~200 m across · Maximum water depth of 30 m
Lake basin characteristics	· Shallow glacial lake ·Glacial over-deepened basin enclosed by a frontal moraine, surrounded by steep limestone walls ·Catchment consists of Mesozoic limestones and sandy limestones	· Alpine glacial lake ·Glacial over-deepened basin within a glacial cirque at the border between the northern and the southern slopes of the Pyrenees ·Sandy limestones and fine-grain sandstones cemented by a carbonatic matrix
MAP	1500 mm	2000 mm
SP	ca. 180 mm	ca. 230 mm
WP	ca. 150 mm	ca. 200 mm
MAT	5 °C	0 °C
SMMT	15 °C	10 °C
Vegetation belt	Sub-alpine	Alpine
Treeline altitude in the valley (m a.s.l.)	2000–2200	2000–2100
Timberline altitude in the valley (m a.s.l.)	1700–1900	1700–1900
Local vegetation	Treeline ecotone: *P. uncinata* together with *J. communis*, *R. ferrugineum* and sub-alpine pastures	Patches of annual and perennial herbs such as *Silene acaulis*, *Linaria alpina* and *Crepis pygmaea*

4. Results

4.1. Temporal trends in microcharcoal records

Variations in microcharcoal concentrations (CCnb and CCs) in each lake show very similar fluctuations (Fig. S2). This confirms that both CCnb and CCs record the same pattern of microcharcoal concentration variability, suggesting that there is no microcharcoal overrepresentation as the result of potential fragmentation during particle production or transport and thus, both units could be used to interpret the fire record (Daniau et al., 2012). CHAR values also follow similar concentration variability in both sequences (Fig. S2).

4.1.1. MAR lake microcharcoal sequence

The beginning of the sequence shows a low microcharcoal influx between ca. 9500–7000 cal yr BP (mean influx of 9×10^4 #/cm2yr; SD $2,3 \times 10^4$ #/cm2yr). Microcharcoal increases from 7000 to 6500 and 6200–5700 cal yr BP (mean influx of $1,7 \times 10^5$ #/cm2yr; SD $3,9 \times 10^4$ #/cm2yr). A significant decrease is appreciated from 5700 to 3600 cal yr BP (mean influx of 1×10^5 #/cm2yr; SD $2,8 \times 10^4$ #/cm2yr). Fluctuating CHAR values are found between 3600 and 1600 with several local maxima (up to an influx value of $2,6 \times 10^5$ #/cm2yr). The signal becomes weak between 1600 and 1000 cal yr BP but an abrupt and consistent charcoal increase is observed afterwards until present day, reaching maximum values (maximum influx value $3,1 \times 10^5$ #/cm2yr) (Fig. S2 and Fig. 4a).

4.1.2. BSM lake microcharcoal sequence

At BSM, low but fluctuating values are present during 9500–6600 cal yr BP (mean influx $1,6 \times 10^5$ #/cm2yr; SD 2×10^5 #/cm2yr) with a significant microcharcoal peak at ca. 6700 cal yr BP (microcharcoal influx of $2,2 \times 10^5$ #/cm2yr). Subsequently, the signal is weakened with sustained low microcharcoal values until ca. 3700 cal yr BP (mean influx $5,4 \times 10^4$ #/cm2yr; SD $2,4 \times 10^4$ #/cm2yr), where it increases showing a marked isolated

maximum (microcharcoal influx of $2,2 \times 10^5$ #/cm2yr). Microcharcoal signal maintains low afterwards, until almost recent times (mean influx $4,4 \times 10^4$ #/cm2yr; SD $2,3 \times 10^4$ #/cm2yr) with the exception of a minor fire peak at ca. 1200 cal yr BP. The maximum microcharcoal signal is found for the last decades (up to an influx value of $2,4 \times 10^5$ #/cm2yr) (Fig. S2 and Fig. 4g).
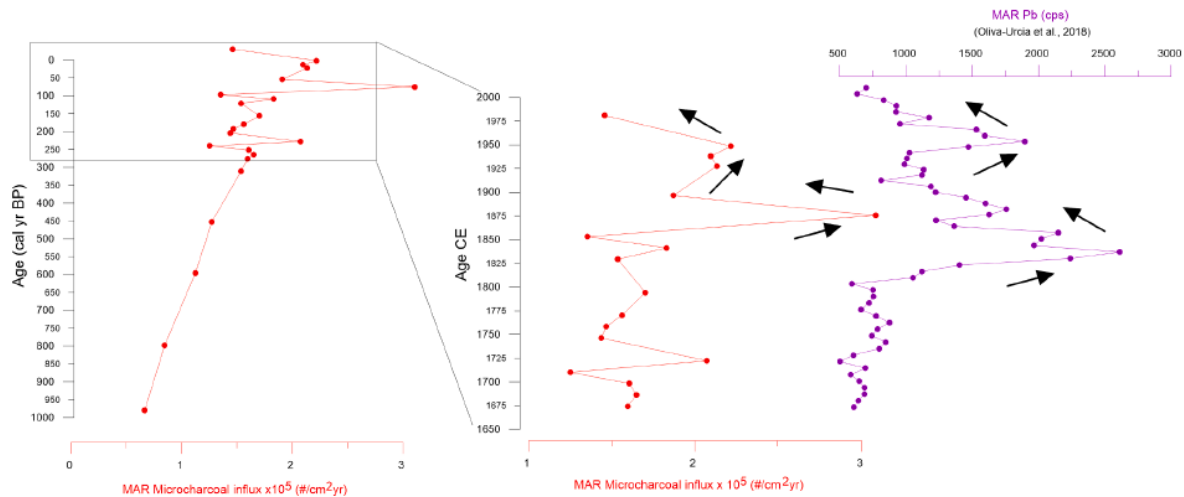

Fig. 6. Microcharcoal influx in MAR for the last 1000 years (left side) with a zoom over the last 300 years and compared it with Pb element profile (Oliva-Urcia et al., 2018) in MAR (right side).

4.2. Conditional inference trees

Conditional inference trees (Fig. 5 and Fig. S3 for all taxa and sites) found significant patterns of influence of the explanatory variables we have used (antecedent PAR, antecedent CHAR and CHAR) on PAR, except in the case of *Pinus* and *Betula* in MAR (Fig. S3a,b). For most taxa, PAR.antecedent, which represents the endogenous dynamics of the taxa, is the best explanatory variable (Fig. 5a,c,d,e,f and Fig. S3c,d,e). Hence, larger values of antecedent PAR seem to have a positive effect on the taxa's abundance, at any given time, especially in BSM. Antecedent CHAR had a significant and positive effect on *Quercus* PAR in BSM (Fig. 5f), while concurrent CHAR influenced positively the pollen abundance of *Abies* and *Corylus* in MAR (Fig. 5a,b). The boxplots represent mean values of each PAR series classified according to the explanatory variables. For instance, looking at *Abies* MAR (Fig. 5a), abies.antecedent is the best explanatory variable determining large *Abies* values (right boxplot), only when abies.antecedent is low, concurrent CHAR succeeds predicting *Abies* PAR to a certain threshold, producing the next classified group (central boxplot).

5. Discussion

5.1. Pollen and microcharcoal source: Considerations for the studied sequences

Comparing these two sequences brings forward the need to look at site-specific settings, as these might be determining different fire behaviour and, what it is most important, source area for biological proxies and transport pathways (Corella et al., 2018). The study sites are defined by both catchment dimensions and altitude, thus, several studies have evidenced that higher elevations may record best regional rather than local environmental variations (Escudero et al., 2016; Corella et al., 2018).

MAR (2612 m a.s.l.) is placed ca. 600 m higher than the current treeline (Figs. 1c and 2), and we infer that due to the absence of tree macrofossils along the sedimentary sequence (Leunda et al., 2017), the treeline would have not reached the Marbore cirque during the Holocene. Moreover, MAR lies in an open cirque wind-exposed supporting that the source area of both arboreal pollen and microcharcoal particles would come from large areas both from northern and southern slopes of the Pyrenees, having a wide catchment area and thus registering fires and vegetation dynamics from far. Indeed, regional tropospheric circulation becomes a more important factor in particle transport and deposition above ca. 2100 m a.s.l., whereas below this altitude horizontal regional transport is less patent (Escudero et al., 2016).

On the other hand, BSM is currently located in the sub-alpine belt (1914 m a.s.l.) at the treeline ecotone (Figs. 1d and 2). During the Holocene the lake would have been likely colonized by different forest communities (Perez-Sanz et al., 2013), enabling fires to also occur locally. Thus, the source area of both tree pollen and microcharcoal could be partially a background signal but still more local than in MAR, with an important input from nearby forest communities.

5.2. Fire history through the Holocene in the Central Pyrenees

5.2.1. Low fire activity during the early Holocene (ca. 9500–7000 cal yr BP)

Fire activity was relatively low during the early Holocene, as inferred from both BSM and MAR sequences, although they show differing patterns; MAR holds a lower variability compared to BSM which evidences a fluctuating fire activity (Fig. 4a,g). A rather low fire activity is also detected in other Pyrenean sequences (Cunill et al., 2013; Gil- Romera et al., 2014; Garces-Pastor et al., 2017). Pine communities dominated both lakes at a regional scale (ca. 70% of pine pollen; Fig. 4b,h), and despite the lack of treeline reconstructions for the early Holocene in the Pyrenees, Cunill et al. (2013) demonstrated the existence of pine biomass at 2200 m a.s.l. in the eastern Pyrenees, indicating that BSM could already be surrounded by pines. On the other hand, the importance of mesophytes (mainly *Corylus* and *Betula*) is clear in the MAR sequence, similar to more Atlantic sites like El Portalet (Gonzalez-Samperiz et al., 2006; Gil-Romera

et al., 2014). In this regard, significant differences in vegetation composition have been recorded along the Pyrenees during the early Holocene related to the more Atlantic (Gonzalez-Samperiz et al., 2006; Gil-Romera et al., 2014; Leunda et al., 2017) vs. more Mediterranean influence (e.g. Miras et al., 2007; Perez-Obiol et al., 2012; Perez-Sanz et al., 2013; Connor et al., 2019).

Thus, the different patterns between BSM and MAR in terms of fire activity could be related to the differences in biomass type and availability and to the lakes geographical settings, which today is characterized by different amounts of rainfall (Fig. 1b). Especially, the rainfall gradient has a critical effect on the landscape flammability as, if biomass is available, dry settings will more easily become flammable. This would have been the case in BSM, located at a denser vegetated, drier and more continental lower altitude (Perez-Sanz et al., 2013) compared to the alpine, locally wetter MAR site.

Even if fire severity and extent is difficult to infer from microscopic charcoal data alone, pollen assemblages variation (e.g. an increase in herbaceous pollen taxa) can be used as indirect evidence for high severity fires (Minckley and Shriver, 2011). As there are no evidences of landscape opening in terms of herb expansion, it is likely that these fires did not play a significant role in vegetation dynamics. In addition to this, no human occupation signs have been detected for the Central Pyrenees at this period. The livelihood of Mesolithic (11700–7800 cal yr BP) people was hunting-gathering in small nomadic groups (Valdeyron et al., 2008; Ejarque et al., 2010), which implies weak environmental imprints (Montes et al., 2016; Rojo-Guerra et al., 2018).

5.2.2. Increasing fire activity at HTM (ca. 7000–5500 cal yr BP)

Fire activity increased over the mid-Holocene in both sequences. MAR records an earlier increase starting at ca. 7000 cal yr BP and, although fluctuating, lasting until ca. 5500 cal yr BP (Fig. 4a), whereas the increase in fire activity in BSM occurs at ca. 6700 cal yr BP (Fig. 4g). Other eastern Pyrenean sequences such as in Estanilles peatbog also show a fire increase (Perez-Obiol et al., 2012).

The expansion of mesophytes (especially *Betula*, deciduous *Quercus* and *Corylus*) in BSM occurred during the mid-Holocene (8200–5500 cal yr BP; Fig. 4 j,k), when *Betula* could have reached the sub-alpine belt (Perez-Sanz et al., 2013; Leunda et al., 2019). The treeline, mainly composed of *Pinus*, would have reached the highest levels during this period (Cunill et al., 2013; Leunda et al., 2019). This biomass expansion has been closely related to a summer temperature increase. In fact, the chironomid based July temperature reconstruction for the Holocene in BSM, shows that the maximum summer temperatures occurred between 8000 and 6500 cal yr BP (Fig. 4n) which is in agreement with other European summer temperature reconstructions defining the HTM (Renssen et al., 2009; Samartin et al., 2017). Thereby, favourable climate conditions for burning

established supported by the constant and increasing biomass availability. Nevertheless, fires were probably neither intense nor virulent, since vegetation does not show important changes.

In addition to this, scatter Neolithic archaeological sites have been found at lower elevations in the Central Pyrenees where sparse *fumier* levels (succession of animal manure, soil and plant remains, which besides being naturally fermented, were sometimes burned to sanitize the enclosure; Alday et al., 2012; Montes and Alday, 2012) were identified (Fig. 1a and Fig. 4o). However, no pollen evidence for agropastoral activities are detected in MAR and BSM nor in the nearby palaeoenvironmental sequences at this time (Gonzalez-Samperiz et al., 2017). Nevertheless, a rather early human impact with punctual presence of cereal pollen grains since the Neolithic onset (ca. 7000 cal yr BP) or even earlier (Ejarque et al., 2010; Perez-Obiol et al., 2012) has been detected in the eastern Pyrenean palaeoenvironmental sequences, where sparse sub-alpine Neolithic settlements were found (Gassiot Ballbe et al., 2014; Gassiot Ballbe, 2016).

Thus, even if it is not possible to discard punctual anthropogenic burning practices during the Neolithic period, it is not likely that they would leave a large imprint at high altitude sites as evidences for human presence occur locally at lower altitudes (Gonzalez-Samperiz et al., 2019). Thus, the driving mechanism for the increase in fire activity at both sites at ca. 7000 cal yr BP might be related to both biomass availability and increasing summer temperatures.

5.2.3. Fire activity decline during the Neoglacial period (ca. 5500–3700 cal yr BP)

Both in BSM and MAR there's a general fire activity decline concurrent at regional (Rius et al., 2011; Garces-Pastor et al., 2017) and subcontinental scales (Vanniere et al., 2011) at ca. 5700 cal yr BP (Fig. 4a,g). Wildfire weakening coincides with the beginning of the Neoglacial period (Davis et al., 2009; Kumar, 2011) where a glacier expansion occurred at ca. 5100 cal yr BP, in both southern (Garcia-Ruiz et al., 2014) and the northern (Gellatly et al., 1992) slopes of the Central Pyrenees. We lack an independent temperature reconstruction for 6000–4200 cal yr BP period due to low chironomid contents in BSM. However, during the late-Holocene (4200–2000 cal yr BP) inferred temperatures were the lowest through the Holocene (Fig. 4n; Tarrats et al., 2018).

A lower proportion of archaeological settlements were present in the Central Pyrenees at this time (Fig. 4o), as societies may have also been affected by the wetter/cooler oscillations of the Neoglacial period. Rius et al. (2011) also indicated fewer signs of human activities at the northern slope of the Pyrenees. This scenario suggests that climatic control is still dominant in promoting fire occurrence during the mid-tolate-Holocene transition.

Simultaneously, *Abies* spread from ca. 6000 cal yr BP in both BSM and MAR (Fig. 4c,i) and in other Pyrenean records (Miras et al., 2007; Perez-Sanz et al., 2013; Garces-Pastor et al., 2017). *Abies* is a mesophilous, late-successional tree species very shade tolerant and considered to prefer cool and moist sites (Villar et al., 1997). Different studies have also demonstrated that *Abies* is a fire sensitive taxon, being negatively affected by fire activity (Tinner et al., 1999; Schworer et al., 2015). So, we argue that the fir spread could be favoured by both the temperature descent and a weaker fire activity until ca. 3500 cal yr BP (Fig. 4a,g).

Deciduous trees progressively declined during this period in our study sites following the same pattern as other Pyrenean sequences (Gonzalez-Samperiz et al., 2006; Miras et al., 2007; Pelachs et al., 2007; Perez-Sanz et al., 2013; Garces-Pastor et al., 2017; Leunda et al., 2017), very likely related to these changing climatic conditions.

5.2.4. High variability of fire activity over the last 3700 years

A great increase in fire activity is appreciated in both sequences; at ca. 3700 cal yr BP in BSM, followed by the rise in MAR between 3500 and 3000 cal yr BP. In regard to the eastern Pyrenean palaeoenvironmental sequences, a general intensification of fire occurrence is observed for the last ca. 4000 years, with an alternation of higher and lower periods, denoting spatial and temporal disparities in fire activity (Bal et al., 2011; Rius et al., 2011; Garces-Pastor et al., 2017). Dated palaeofire layers also appear more frequently from ca. 3000 cal yr BP onwards, indicating the occurrence of fires.

Herbs increase significantly both in MAR and BSM (reaching values > 30%) (Fig. 4f,m), indicating a regional opening of the landscape where fire may have played an important role. Previous fires were probably not as severe as those occurred over the last four millennia. Hence, fire did not provoke important biomass losses, contrarily to what may have occurred over the last ca. 3700 years. *Abies* decreased (Fig. 4c,i), suggesting again that fir's populations may have been negatively affected by fires.

Regarding climatic factors, reconstructed summer temperatures in the area are the lowest for the whole Holocene (Fig. 4n; Tarrats et al., 2018), which apparently may have not favoured fire occurrence. A decoupling of fire and climatic control has been attributed to human impact, overriding the effect of natural ignition in alpine ecosystems (Colombaroli et al., 2010). However, there is a significant gap of archaeological settlements during the Bronze-Iron Age, from 4000 cal yr BP onwards, both in the Central (Fig. 4o; Gonzalez-Samperiz et al., 2019) and in the eastern Pyrenees (Gassiot Ballbe et al., 2014), despite an intensification of agricultural and grazing indicators has been detected in the eastern Pyrenean sequences (Miras et al., 2007; Pelachs et al., 2007; Bal et al., 2011; Perez-Obiol et al., 2012; Garces-Pastor et al., 2017).

This heterogeneous pattern in fire activity, during an arguable period of anthropogenic fire dynamics, could be associated with a steady but non-permanent human impact in

mountain areas during the Bronze Age and onwards in a complex landscape scenario. Human-induced fires, would have locally maintained more open landscapes in specific areas (Gonzalez-Samperiz et al., 2019).

A great spatial variability in terms of fire activity has also been observed in other European mountain ranges such as the Alps (Colombaroli et al., 2010; Leys et al., 2014) and in the Carpathians (Feurdean et al., 2012; Florescu et al., 2018) but generally indicating increasing human related landscape transformations during the last 4000 years.

The slight increase of fire activity in BSM during the Medieval Period (Fig. 4g) could be related to the intensification of the landscape opening over the last 1000 years, (increase in *Artemisia,* Poaceae, Cichorioideae, Chenopodiaceae) (Fig. 4f,m) and with the high presence of human settlements in the eastern Pyrenees (Gassiot Ballbe, 2016). Simultaneously, and perhaps with a synergistic effect to human activity, drier conditions during the Medieval Climate Anomaly (MCA), a period of aridity recognized in most of south-western Europe (Seager et al., 2007; Moreno et al., 2012), could have also favoured fire occurrence.

In addition to this, historical documents record mining activities to exploit iron, silver and lead at least since Medieval times (Bielza de Ory et al., 1986) in the Bielsa-Parzan area (Fig. 1a) as well as in other Pyrenean areas (Pelachs et al., 2009). The increase in herbs at this time, could be very likely related to the land-use intensification that occurred, as miners were given lands in order to ensure their permanence in the valley (Bielza de Ory et al., 1986). Both mining and smelting activities very likely affected forests through deforestation and burning due to increasing energy demand (Bielza de Ory et al., 1986; Jouffroy et al., 2005; Pelachs et al., 2009). However, no signs of contamination in terms of trace metal deposition increase is detected in MAR and BSM lakes at this time (Corella et al., 2018; Oliva-Urcia et al., 2018), probably related to the low intensity of the mining activities to cause a regional imprint.

MAR shows a prominent charcoal peak at the end of the 19th century, which stays relatively high until ca. 1930 CE (Fig. 6). This tendency concurs with the Pb enrichment in MAR Lake sediments (Fig. 6; Corella et al., 2018; Oliva-Urcia et al., 2018) likely related to the onset of large-scale Pb production in the Parzan area which started by the end of the 19th century lasting until 1930 CE, when the closure of the mines occurred due to the decrease in Pb prices (Nieto-Callen, 1996; Fanlo et al., 1998). The historical metal mining in this area ended at this time. This Pb enrichment is not detected in BSM, probably related to the lake characteristics and its lower altitude, that greatly reduce the lake sensitiveness to record historical pollution of trace metals as suggested by Corella et al. (2018).

For more recent times, the significant increase in fire activity registered in BSM at 1980 CE (being the maximum microcharcoal peak; Fig. 4g) could be related to the large fires that occurred in summers of 1980 CE, 1981 CE, 1986 CE and 1991 CE in the Central Pyrenees where 2200 to 6500 Ha of woodlands were burnt in each fire (El Pais, 1980; Vazquez de la Cueva, 2016).

5.3. How determinant was fire modifying alpine landscapes in the Pyrenees during the Holocene?

Regardless the site-to-site variations that seem to determine fire activity most, an interesting finding is that fire at these altitudes has not generally played a critical role in vegetation dynamics. This finding suggests that, as occurs in the present, past alpine and sub-alpine vegetation communities were not, broadly speaking, fire-prone neither fire-driven ecosystems (Leys et al., 2014). Thus, fire regimes may have not been the most relevant factor on forest dynamics, unlike Mediterranean ecosystems, which are composed of highly flammable sclerophilous vegetation (Keeley et al., 2012). This situation has also been observed in other studies in mountain areas e.g. in the Dolomites (Leys et al., 2014).

According to our data, the selected forest taxa in BSM and MAR are best characterised by their own endogenous effect, i.e., a higher antecedent presence of a particular taxa has a positive effect on its abundance (Fig. 5a,c,d,e,f). In other words, a larger population will cope better with environmental change and disturbances, and remain large until a certain threshold in a specific forcing is reached. While in MAR fire may have played a more important role for *Corylus* and *Abies* (Fig. 5a,b), we interpret inter-site differences as a consequence of the proxy potential source area, as several studies have evidenced that higher elevations may record best regional rather than local environmental variation (Escudero et al., 2016; Corella et al., 2018).

Fire at BSM might be indeed reflecting local but scattered events that, according to our data, do not imply any response for most taxa, except for deciduous *Quercus* (Fig. 5f) (likely *Quercus pubescens* or *Q. humilis*). This taxon, unlike all the others, may have not been locally present nearby the lake (Perez-Sanz et al., 2013). However, it successfully sprouts after fire generally out-competing non-serotinous pines like the ones present in the sub-alpine belt (Sanchez-Pinillos et al., 2018) as the ones present in BSM. MAR, more exposed to tropospheric circulation due to its higher altitude, is possibly reflecting an even more regional picture of both vegetation and fire variability. This fact implies, on the one hand, that proxies might be recorded with larger lags than expected. On the other hand, it indicates that environmental variability from different locations might be harmonized by sedimentary processes at these altitudes that prevents evidencing spatial cooccurrent effects of disturbance on vegetation response. Such might be the case of the positive effect that CHAR has on *Abies* if antecedent PAR values are under the threshold

(Fig. 5a). This would be one example of a, probable, lack of spatial simultaneity on fire occurrence and vegetation response where charcoal and pollen might be arriving from different areas. While this might be the case for all other taxa in MAR too, concurrent CHAR is the only variable with a positive influence on *Corylus* PAR in this site (Fig. 5b). In this particular case, hazel is indeed a clear case of a temperate tree where both neo- and palaeoecology studies (Tinner et al., 1999; Finsinger et al., 2006) have evidenced a fast and positive fire response given its resprouting ability after burning (Delarze et al., 1992). Besides the post-fire strategy, hazel pollen production is enhanced when vegetation is opened by disturbance (Aaby, 1986; Begeot, 1998). This fact is likely explaining why the concurrent rather than the antecedent fire is more critical in affecting *Corylus* presence, as resprouting and pollination would happen very soon after fire.

Finding that fire might not be the most critical factor shaping the long-term dynamics of the analysed tree taxa has important consequences for conservation practices, as fire occurrence has been predominantly low in these sub-alpine areas. Thus, future scenarios with more active fires might threaten the treeline ecosystems. In fact, the abandonment of agro-pastoral activities in mountain areas during the past decades in the Pyrenees has provoked bush encroachment, which concurring with the rise in average temperatures, may increase fire risk during the next decades forced by the synergistic effect of both climate conditions and human impact.

6. Conclusion

Here we present the comparison of two long-term fire activity records from different altitudes in the Central Pyrenees providing a better understanding of the Holocene fire-vegetation dynamics in this mountain range. Our results highlight that caution should be taken when comparing the results of different lacustrine sequences, even if they are in the same mountain range, and just few km away, as site-specific settings may determine different fire behaviour and source areas. We argue that fire activity during the early-to-mid-Holocene was relatively low and mostly controlled by climate. High summer temperatures together with high biomass accumulation led to a prolonged period of high fire activity during ca. 7000–6000 cal yr BP as recorded in MAR with a coeval increase in fire activity, but shorter in duration, in BSM at ca. 6700 cal yr BP. Burning decreased, concurring with the Neoglacial period, which suggests that climatic control was still dominant in promoting fire occurrence until 3700 cal yr BP, when fire activity increased coevally to the opening of the landscape and decoupled from climate as the only fire driver. Although from ca. 3000 cal yr BP onwards fire activity decreased, the increasing human pressure over the last centuries lead to a remarkable rise in fire activity. Our results highlight that, overall fire activity does not seem to be a critical factor shaping alpine ecosystem through the Holocene. However, the increase in arboreal biomass due

to abandonment of traditional land uses in mountain areas together with the rise in average temperatures during the last decades, may increase fire risk in the nearby future, as occurred in the HTM.

Data and code availability

The code and data are available in this GitHub link: https://github.com/BlasBenito/PyreFire, and are deposited in Zenodo under the DOI https://doi.org/10.5281/zenodo.3266002.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2019.104411.

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