Biomass-modulated fire dynamics during the last glacial-interglacial transition at the Central Pyrenees (Spain)

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Abstract

Understanding long-term fire ecology is essential for current day interpretation of ecosystem fire responses. However paleoecology of fire is still poorly understood, especially at high-altitude mountain environments, despite the fact that these are fire-sensitive ecosystems and their resilience might be affected by changing fire regimes. We reconstruct wildfire occurrence since the Lateglacial (14.7 cal ka BP) to the Mid-Holocene (6 cal ka BP) and investigate the climate-fuel-fire relationships in a sedimentary sequence located at the treeline in the Central Spanish Pyrenees. Pollen, macro- and micro-charcoal were analysed for the identification of fire events (FE) in order to detect vegetation post-fire response and to define biomass-fire interactions. Mean fire intervals (MFI) reduced since the Lateglacial, peaking at 9-7.7 cal ka BP while from 7.7 to 6 cal ka BP no fire is recorded. We hypothesize that Early Holocene maximum summer insolation, as climate forcing, and mesophyte forest expansion, as a fuel-creating factor, were responsible for accelerating fire occurrence in the Central Pyrenees treeline. We also found that fire had long-lasting negative effects on most of the treeline plant communities and that forest contraction from 7.7 cal ka BP is likely linked to the ecosystem's threshold response to high fire frequencies.

Keywords

Fire history; Quaternary; Lateglacial; palaeoecology; historical biogeography; Iberian Peninsula.

Taxa nomenclature is based on Castroviejo et al. (1986).

1. Introduction

Fire is a well-known transforming agent of the Earth system that, while well studied across different spatial scales, it is best understood at short-term temporal scales. Fire occurrence is determined by a range of factors that interact dynamically, such as climate, fuel availability and flammability, landscape structure, amongst others, defining fire regimes. Sensitive ecosystems to the current global environmental change experience fire regime changes which are often responsible for deep modifications of their biodiversity and resilience patterns (Bond and Keeley, 2005). This could be the case for mountain ranges, which have been spotlighted as one of the most endangered continental ecosystems because of their high levels of plant endemism (Médail and Quézel, 1999) and their particular sensitivity to global change (Engler et al., 2011; Gottfried et al., 2012). Assessing the potential ecosystem transformations caused by future changes in fire regime at mountain ranges requires a comprehensive knowledge of their long-term fire ecology (Gobet et al., 2003; Stähli et al., 2006; Tinner et al., 1999, 2005a). Thus, changes in fire regimes at centennial to millennial time-scales have been thoroughly documented in the Alps (Blarquez and Carcaillet, 2010; Colombaroli et al., 2009, 2010; Stähli et al., 2006; Tinner and Lotter, 2001) and at lower altitudes of the Northern Pyrenees (Rius et al., 2009, 2011a, 2011b). In the Iberian Peninsula, past fire histories and vegetation responses have been explored in the Mediterranean area (Carrión, 2002; Carrión et al., 2004, 2007, 2010a, 2010b; Carrión-Marco, 2005; Franco Múgica et al., 2005; Gil-Romera et al., 2010; Jiménez-Moreno et al., 2013; López-Merino et al., 2009), and in the Eurosiberian region of the Iberian Peninsula (Carrión-Marco et al., 2010; Kaal et al., 2011; López-Merino et al., 2012; Morales-Molino et al., 2013). However, the Iberian investigations are focused on regional fire activity, through examination of micro-charcoal records so they do not tackle locally-occurred fire events due to the absence of contiguous macro-charcoal datasets, thus precluding the estimation of fire frequencies or return intervals (Power et al., 2008; Whitlock et al., 2010a, 2010b). Studies addressing long-term local fire events have been barely carried out in the Iberian Peninsula, and they do not investigate the climate-fire-biomass relationships or the ecosystem response to fire, as the record of Estany de Burg (Fig. 1) (Bal et al., 2011) .

The study presented here is focused on the long-term fire ecology of a fuel-limited alpine site located at the Central Spanish Pyrenees, El Portalet, where a previous palynological analysis described a sequence of environmental changes with high sensitivity to abrupt climate fluctuations since the Lateglacial (González-Sampériz et al., 2006). Our objectives are to 1) analyse the Lateglacial to Mid-Holocene (ca. 14.7-6 cal ka BP) interactions amongst the different agents determining fire occurrence, i.e. climate and fuel availability, in a fuel-limited environment, and 2) determine long-term plant responses and ecosystem resilience to fire disturbance.

2. Material and methods

2.1 Study area

El Portalet site (1802 m asl) is located in the Central-western Pyrenees (Fig. 1), lying on Devonian and Carboniferous shales and limestones. The site is currently a peatland situated within a small glacial cirque. Climate is alpine, with high rainfall (mean annual precipitation ca. 1800 mm) mainly linked to the activity of Atlantic fronts. Annual mean air temperature is 5ºC and daily temperatures are below 0º C for more than 200 days along the year while mean summer temperature is ca. 12º C (AEMET-IM, 2011).

The area is currently devoid of woody vegetation, presenting some bushed spots formed by *Vaccinium myrtillus* and mixed pasture-alpine grasslands (Fig. 2) probably established during the Middle Ages, when intense deforestation was regularly practiced due to pastoral and slash-and-burn activities (Montserrat, 1992). However, the closest west-to-east valleys (Fig. 2) present *Pinus sylvestris* and *P. uncinata* communities reaching the treeline (between 1500 and 1800 m asl), with a mixed scrubland formed by *Juniperus* (*J. communis* ssp. *alpina*, *J. communis* ssp. *hemisphaerica*) and by *Buxus sempervirens* at lower altitudes. *Abies alba* and *Fagus sylvatica* mixed forest appear in shady slopes between 1500 and 1700 m asl. Mixed temperate forests formed by a variety of mesophytes (*Corylus*, *Acer*, *Salix*, *Fraxinus*, etc.) can be found at lower altitudes (1500 to 1600 m asl), often confined to riparian environments. *Betula* communities (*B. pendula* and some remnants of *B. nana*) are present at different altitudes, forming disperse forests, sheltered in areas controlled by moisture availability and reduced sun exposure.

Evergreen and semi-deciduous *Quercus* (*Q. ilex* ssp. *ballota* and *Q. faginea*) become abundant below 1500 m asl, where the latter prefers cooler and wetter locations.

2.2 Chronological framework and sampling resolution

El Portalet age-depth model was constructed from 13 radiocarbon dates obtained from pollen concentrates and a wood fragment, along a 6.08 m long core, recording a time-span between ca. 32 and 5.5 cal ka BP (González-Sampériz et al., 2006). The analyses in this new study have been performed between 14.7 to 12.5 cal ka BP (470-382 cm) and 10 to 6 cal ka BP (364-160 cm), the sections with higher and relatively constant sedimentation rates (Table1) and that provide examples of different climates and biomass availabilities. The criterion to select these intervals is based on sedimentation issues, as the 382-364 cm interval (ca. 12.5 and 10 cal ka BP) corresponds to a period of abrupt changes in the sedimentation rate, with some missing cm of sediments, including some possible hiatuses during the Younger Dryas stadial (Table 1) (González-Sampériz et al., 2006)

Different sampling resolution was applied for the pollen analysis of the two selected sections. The Holocene section (10-6 cal ka BP), with sedimentation rate ca. 15 yr cm^{-1}, (Table 1), enabled a high-resolution approach. Pollen, micro-charcoal (between 10µm and 150µm) and macro-charcoal (particles>150µm) particles were studied from contiguously taken samples (1 cm), permitting time-series analyses and cross-correlation amongst the three proxies. The Lateglacial section (14.7-12.5 cal ka BP), with a sedimentation rate ca. 24 yr cm^{-1}, was contiguously sampled for macro-charcoal analyses (1 cm), and every 2 to 5 cm for pollen and micro-charcoal content (Table 1).

In this new study, a total of 292 samples were analysed for macro-charcoal, from which 235 were used for micro-charcoal and pollen analyses. The 2006 study was limited to 100 pollen samples for this period, and both micro- and macro-charcoal were not count (14.7-12.5 and 10-6 cal ka BP).

2.3 Laboratory methods

2.3.1 Charcoal analyses

Sedimentary macro-charcoal particles (>150 µm) have been proved to be a good indicator of past local fire events (FE) at different time scales (Clark and Royall, 1996; Clark et al., 1996; Higuera et al., 2010; Whitlock and Larsen, 2002). Estimating mean fire intervals (MFI) implies detecting local FE from macro-charcoal particles (>150µm) (see discussion in Whitlock and Larsen, 2002). Thus, macro-charcoal particles were chemically processed and sieved at 150 µm mesh and retrieved particles were counted on a binocular microscope (x40). Charcoal identification was accomplished according to existing literature, counting opaque, angular particles (Clark et al., 1996; Finsinger and Tinner, 2005; Tinner and Hu, 2003; Turner et al., 2004). Micro-charcoal particles (>10 µm) were counted on pollen slides under an optical microscope (x250) being a proxy for regional fire activity. More details on laboratory methods can be followed in Supplementary data.

Micro- and macro-charcoal concentrations (charcoal particles cm^{-3}) were transformed into accumulation rates (particles cm^{-3} yr^{-1}). The macro-charcoal accumulation rate is referred as CHAR hereafter.

2.3.2 Pollen analysis

Palynological samples were chemically treated and a minimum of 300 terrestrial pollen grains were counted, despite some of the samples displayed low counts (minimum=215, maximum=560, mean=402.84, STD=106.7), excluding from the pollen sum spores, hydro- and hygrophyte pollen types, and expressed in abundance (%). Mesophytes, other trees, shrubs and herbs pollen types were grouped for representation and data analyses purposes. See Supplementary data for more details.

No plant macro-remains have been found in El Portalet sequence, and therefore fossil pollen is our only proxy for vegetation change.

2.4 Data analyses

2.4.1 Fire events (FE) and Mean Fire Intervals (MFI)

Identifying FE – one or several fires occurring within the time resolution of a sample in a core (Higuera et al., 2010; Whitlock and Larsen, 2002)– implies isolating charcoal peaks equivalent to the signal related to local fire occurrence (Carcaillet et al., 2001; Gavin et al., 2006; Lynch et al., 2002). Peak identification was performed using CharAnalysis (Higuera et al., 2009). MFI for particular periods are calculated as the age between the first and the last fire event divided by the number of fire intervals in that period. Fire frequencies (FF, number of fires/time unit) have been estimated every 500 years. See more details on methods in Supplementary data.

2.4.2 Vegetation dynamics: numerical approach

Pollen assemblage zones and diagram plotting were performed with software Psimpoll 4.27(Bennett, 2009). Palynological richness was estimated by rarefaction analysis, implemented in the open software Analytic Rarefaction 2.0, and a Spearman's R correlation with different taxa and group of taxa was performed to check whether richness is led by any of them. These were done in R v. 2.0.5 (R Core Team, 2012).

Cross-correlation analyses between CHAR and those pollen taxa with expected fire interactions following the ecological literature (Paula et al., 2009) were performed to explore the effect of biomass accumulation on fire occurrence and the potential feedbacks between local wildfire and vegetation response. Thus, 235 samples (corresponding to the 10-6 cal ka BP section) analysed at the same time resolution for pollen and macro-charcoal were used after potential trends were removed by linearly detrending both data series (Blarquez and Carcaillet, 2010; Colombaroli et al., 2007, 2008). CHAR was cross-correlated to pollen percentages as a way to control potential common trends in sedimentation rates, avoiding potential spurious correlations (Tinner et al., 1999). Cross-correlation coefficients were calculated at ±10 lags corresponding to ±150 years (each lag corresponds to the mean time difference between two adjacent samples, i.e. 15 years for the Holocene section of the record). Negative lags represent the effect of the second variable (taxa abundance) over the first (CHAR) while positive lags are a measure of the influence of the first variable (CHAR) over the second (taxa abundance). Cross-correlation analyses were completed with the package TSA of R v. 2.0.5 (R Core Team, 2012). There is more related information in Supplementary data.

3. Results and discussion

We interpret the Lateglacial and Holocene fire dynamics in El Portalet (Fig 3) as naturally produced, with lightning as the main ignition source as it happens currently in high altitude areas of the Pyrenees (Amatulli et al., 2007). Neither evidence of human indicators appeared in the pollen assemblages at the studied period, nor archaeological sites are present in the area. Magdalenian, Azilian or Mesolithic settlements at the subalpine belt have not been found. Some trans-Pyrenean migratory routes existed in the area, but they were located in lowland natural passes (Utrilla and Rodanés, 1997; Utrilla and Montes, 2007).

3.1 Climate-biomass-fire interactions at the Central Pyrenees: wetter is better

Macro-charcoal analyses resulted in the identification of eighteen FE, most of them (seventeen) occurred between 13.7-12.5 and 9.8-7.7 cal ka BP (Fig. 3B), whereas a single FE appears at ca. 14.6 cal ka BP. Between 7.7 and 6 cal ka BP there was very low to nil macro-charcoal counts and no fire episodes were detected (Fig. 3A). MFI decreased from ca. 314 years during the Lateglacial (14.7-12.5 cal ka BP) to 190 years during the Early-Mid Holocene (9.8-7.7 cal ka BP; (Fig. 3A).

Unlike the Mediterranean ecosystems, where fire regimes have played an important role shaping the plant landscape before and after human presence (Keeley et al., 2012 and quotes herein), the high altitude plant communities of the Pyrenees are not usually exposed to high wildfire frequencies (Amatulli et al., 2007). Hence, the MFIs found at El Portalet (between ca. 190 to 314 years) (Figs. 3 and 4) points to the low frequency of natural wildfire occurrence, which agrees with present-day fire frequency in the high altitude areas of the Pyrenees, where virtually no natural fire has been recorded from 1974 and 2000

(Vázquez de la Cueva et al., 2006). Despite general low frequencies for the period analysed, a clear pattern on wildfire behaviour in El Portalet is detected as MFIs reduced since the Lateglacial to the Early-Mid Holocene. Similarly, lower fire activities during the Lateglacial than during the Early Holocene have been reported in several Northern Hemisphere sites (Carcaillet et al., 2012; Higuera et al., 2011, 2009; Power et al., 2008) and particularly in high-altitude European mountain sites (Feurdean et al., 2012; Tinner and Lotter, 2001; Tinner et al., 2005; Vescovi et al., 2007), where climate was colder and drier during this time compared to the Holocene. Changes in temperature during the Lateglacial did not play a significant role in MFIs variability. The nearest chironomid-derived palaeotemperature curve in the Col d'Ech Northern Pyrenees site (700 m asl, Fig. 1, Lourdes Basin, France) (Millet et al., 2012), shows an important increase in temperature of ca. 2ºC at ca. 14.7 cal ka BP, coeval with the Bølling onset. Likewise, the also chironomid-inferred paleotemperature from Laguna de la Roya (NW Spain) (Muñoz Sobrino et al., 2013) indicates an increase of 2.5ºC during the Bølling. This thermic rise did not apparently promote large wildfire ignition in El Portalet, with a single FE recorded (Fig. 4). On the one hand, it is possible that the temperature rise during this period would have been gradual rather than abrupt as it has been found for the Mediterranean Sea (Cacho et al., 2001) and continental Iberia (Moreno et al., 2012), where maximum temperature values were identified during the Allerød (Fig. 4). Considering the complex Lateglacial Interstadial palaeoclimate scenario and El Portalet's altitude (1800 m asl), we argue that the gradual increase in temperature during the Bølling, with both cool summers – with still reduced summer solar insolation (Fig. 4) – and extreme winter temperatures, could explain the low fire frequency between 14.6 and 13.9 cal ka BP. Afterwards, during the warmer intervals GI-1c (13.9-13.3 cal ka BP) and GI-1a (13.1-12.9 cal ka BP) (Lowe et al., 2008), and as summer temperature progressively increased during the Allerød, fire frequency increased (Fig. 4), supporting the climatically driven character of these fires. Similarly, and somehow coeval with the more frequent warm episodes within the Allerød (Fig. 4), FE in El Portalet area modestly increased ca. 13.5 cal ka BP from 2 to 3 fires per 500 years, and similarly regional fire activity moderately enhanced as indicated by micro-charcoal influx (Fig. 5).

Regardless of the climate setting during this period, vegetation in El Portalet between the Bølling (GI-1e) and part of the GI-1c events (ca. 14.6-13-6 cal kyr BP) (Fig 4) was regionally dominated by pines, most likely Scots and mountain pines (*Pinus sylvestris* and *P. uncinata* respectively), while local vegetation was probably composed of less pollen productive types as junipers, most likely *J. communis* ssp. *alpina* and *J. communis* ssp. *hemisphaerica*, and patchy grasslands of Poaceae, *Artemisia* and Chenopodiaceae (Fig. 5), pine forests would have probably provided enough fuel for regional fires to happen while the local sparse vegetation would have not represented an important and well-connected biomass to feed local fires, despite relatively warmer conditions.

The mesophyte forest developed to unprecedented extensions from 13.5 cal ka BP, during the latest Allerød warm phase (González-Sampériz et al., 2006) (Fig. 5). The rising temperatures and still likely high amounts of winter precipitation at a regional scale (Genty et al., 2006; Morellón et al., 2009; Moreno et al., 2010) probably favoured temperate, drought-intolerant communities during this time in El Portalet and this is a well-documented pattern across European sites and in some other Iberian records (Carrión et al., 2004; Fletcher et al., 2010; López-Merino et al., 2012). The location of our site in a south-facing, less steep slopes of the Central Spanish Pyrenees, would have promoted the faster upwards migration of birch forests from its lowland locations when conditions improved. We suggest that since ca. 13.5 cal ka BP, El Portalet held locally dense mesophyte communities formed by dwarf birches (*Betula alba* ssp. *nana*) similar to those currently present in the nearby valleys at the same altitude (Fig. 2). Birch at El Portalet Lateglacial landscapes would have played a pioneer role as it is a well-dispersing tree in poor, oligotrophic soils and its heliophytic character favours its development at early successional stages. Interestingly, intensified fire frequencies from 13.5 cal ka BP concurs with expanding moisture-demanding communities, which may seem a counterintuitive idea as wetter environments would prevent large wildfires. However, these conditions induce a major biomass production (Clark et al., 1989; Daniau et al., 2007; Power et al., 2012) facilitating the expansion of mesophytic communities that grow faster than conifers (Blarquez and Carcaillet, 2010), and creating a remarkable cover of flammable fuel necessary for intense wildfires

(Krawchuk and Moritz, 2010). This controlling role of a particular forest composition on local fire could be even more patent during the Early Holocene in El Portalet.

Fire frequencies varied from 1 fire per 500 years at 9.8-9 cal ka BP, to 3 fires per 500 years at 9-7.7 cal ka BP (Figs. 3C and 4) and the *Pinus* : mesophytes ratio varying drastically (Fig. 4). Climatically, the Early Holocene in the Mediterranean region was marked by wetter and warmer conditions than in Lateglacial times (Cacho et al., 2002; Roberts et al., 2004), which in El Portalet stimulated the continuous development of mesic forests (González-Sampériz et al., 2006) (Fig. 5). Accordingly, vegetation landscapes in El Portalet became then even more biomass-rich than during the Allerød period, as a denser *Corylus*-dominated shrubland spread synchronous with the rise in temperature, followed by a new expansion of *Betula* ca. 9.3 cal ka BP. Thus, increasing fire frequencies between 9-7.7 cal ka BP would have most likely been driven by the mesophytes expansion (Figs. 4 and 5).

Mesophytic biomass control of fire frequency during the Holocene is supported by cross-correlation results (Fig. 6), where birch and other mesophytes, as well as total tree percentages, have a positive effect on local wildfire at different lags since 150 years before fire occurrence. Bushes and herbs are, unsurprisingly, negatively affecting fire occurrence as they prevent large wildfires in a less connected landscape. Regarding trees, the major effect of mesic communities on local fire responds to the biomass accumulated from 120 to 30 years prior to a fire event (mesophyte cross-correlation, Fig. 6). Our results are coherent with a recent study by Pausas and Paula (2012) on the present role of plant productivity, community structure and climate-fire relationships on fire dynamics in the Iberian Peninsula. These authors showed that differences in fire activity across an aridity gradient are not linked to the frequency of fire-prone climate conditions but by the vegetation sensitivity to fire under those conditions, which resulted higher in wetter and more productive regions. Conversely, herbs and shrubs are negatively affecting fire ignition in El Portalet (Fig. 6), reinforcing the hypothesis of more likely wildfire incidence at dense, encroached temperate forests. Indeed, pine presence does not seem to positively influence fire occurrence, reflecting either the less flammable character of *Pinus uncinata/P. sylvestris* stands than *Betula* (Fernandes et al., 2008; Tapias et al., 2004), or a forest structure with relatively thin pine woodlands and young stands with no significant ageing processes, both preventing large, more frequent fires.

The Early to Mid-Holocene transition reflects a sharp decline in local fire activity and after 7.7 cal ka BP no fire is recorded. We postulate that relatively humid conditions could have partially prevented fire occurrence, while the gradual contraction of tree cover probably yielded less effective fuel to be burnt precluding large local wildfires. Summer insolation decreased during the Early to Mid-Holocene transition, favouring relatively cooler summers and milder winters (Webb III et al., 1993). Regional indicators of moisture availability are less clear, and while some Northern Mediterranean and Northern European records showed drier conditions (Magny et al., 2003; Roberts et al., 2004), nearer sequences indicate a regional increase in water availability (Morellón et al., 2008; Pérez-Sanz et al., 2013; Aranbarri et al., 2014).

The Holocene decrease of local FE does not find a counterpart in El Portalet regional fire activity, as micro-charcoal is still recorded along the sequence (Fig. 5), proving that charcoal sources might not be associated. The vegetation-regional fire relationships should be cautiously taken though, as pollen and micro-charcoal may have different source areas difficult to identify. Some experiments trying to overcome this issue proved that charcoal particles <50 µm are likely deposited from 10 to 15 km away from a 200 m diameter lake (Duffin et al., 2008). The original surface area of El Portalet lake is unknown but the current peatland diameter is over 200 m, and the whole basin is not much larger (15 ha), and micro-charcoal source area most likely exceeds 10 km, implying fire happening in the lowlands, where active burning might still have occurred. Relevant source area for pollen, as well as its productivity, are unidentified; however, the immediate response of some taxa (*Pinus*, *Juniperus*, and *Betula*) to local fire occurrence indicates a local to sub-regional pollen input (<10 km) with some regional contribution, particularly from those highly productive and well-dispersed taxa as *Pinus*.

Considering that *Betula* and *Corylus* pollen proportions decreased to less than 15% after 7.7 cal ka BP, we suggest that both taxa locally disappeared and only remained in patched formations at closer valleys and at lower elevations, as they occur nowadays (Fig. 2). These small patches would be located farther away than the 10 km charcoal source area limit and, consequently, they would not contribute to the macro-charcoal input to El Portalet site. Most importantly, this proves that the local sensitivity to fire-climate relationship is mostly mediated by flammable biomass and not only by climate (Pausas and Paula, 2012), as this site would have received a relatively high rainfall amount during the Holocene.

These findings confirm the trends found in other Holocene European records, where fire intensity and frequency are strengthened since the beginning of the Holocene until the Early-Mid Holocene transition (Colombaroli et al., 2007; Feurdean et al., 2012; Feurdean et al., 2013; Tinner et al., 1999; Vescovi et al., 2007). However, in the closest Holocene Col d'Ech fire record (Lourdes basin, France, ca. 700 m asl; Rius et al., 2011a, 2011b), a different fire regime pattern is found (Fig 3F). Despite little temporal overlap with El Portalet, fire activity intensification in the Lourdes basin from 7.8 to 4 cal ka BP is discussed by the authors considering three features: a change in the sedimentation rate (from silt to peat ca. 8.2 cal ka BP); an increasing effect of human activity; and progressively warmer summers and flammable-prone conditions due to a lagged effect on temperature of Laurentidae ice sheet deglaciation (Renssen et al., 2009). El Portalet presents a change in sedimentation rate much later than Col d'Ech (ca. 6.5 cal ka BP), thus, in our study the lack of fire activity from 7.7 cal ka BP would not be associated with depositional factors. As discussed before, anthropogenically-induced environmental changes are less likely at higher altitudes and, unlike at the Col d'Ech, no evidence of human activity has been documented in the area during the Early Holocene. Mid-Holocene warmer summers (Holocene Thermal Maximum) have been modelled at the Northern hemisphere spatial scale, suggesting that cooler summers than expected due to summer insolation before 7 cal ka BP arose from a combination of the inhibition of Labrador Sea deep convection by the flux of melt water from the ice sheet, which weakened northward heat transport by the ocean, and the high surface albedo of the ice sheet (Renssen et al., 2009). However, our findings in El Portalet may not fit in this model as the occurrence of a high local fire activity from 9 to 7 cal ka BP in a relatively fuel-limited environment as the Central Spanish Pyrenees treeline, supports the importance of orbital forcing on the mesophyte development (Fig. 5) and the role of the latter in modulating fire activity (Daniau et al., 2007; Pausas and Paula, 2012; Power et al., 2011).

3.2 *Vegetation–fire interactions, plant responses to disturbance and ecosystem resilience*

The current plant communities at the mid to high altitudes of the Pyrenees do not show any fire trait implying a clear adaptation to fire (Fulé et al., 2008; Montané et al., 2009; Paula et al., 2009). Modern fire frequencies are relatively higher in the Central Pyrenees compared to the MFI found in El Portalet (1 to 5 FE, both wildfire and attempted arsons, for the last 10 years, Spanish Forestry Database (MAGRAMA, 2012)). Hence, it should be considered that FE identified in El Portalet sequence responds to large wildfires, probably implying both crown and surface fires, while current statistics do not distinguish these criteria (size or fire type). It is not surprising then that local wildfires have a long-term negative effect at different time-lags on most studied tree taxa in El Portalet and that taxa favoured by fire are those forming open-landscape communities, as herbs and shrubs, which are also those preventing fire occurrence (Fig. 6). An exception to this pattern is *Pinus*, most likely represented by *Pinus sylvestris* / *P. uncinata* in El Portalet, which are not fire-adapted pines, unlike the Mediterranean pines (*Pinus pinaster*, *P. pinea*, *P. nigra* and *P. halepensis*) that are showing serotiny, bark thickness and bud resistance to fire (Fernandes et al., 2008; Paula et al., 2009). Despite some previous studies in the Alps having proved a positive relationship between fire and *Pinus sylvestris* (Stähli et al., 2006), we suggest that in El Portalet the Pinus-fire correlation might be associated with temporal exclusion of *Pinus* competitors, rather than to a direct positive effect of fire over pine occurrence, enabling pine recolonization from the edge of burnt areas or from sheltered refugia in rocky outcrops (Keeley et al., 2012).

The long-term role of birch in the sub-alpine/alpine belt of the Central Spanish Pyrenees is partially in agreement with its documented early-successional character after disturbances, as revealed by other Holocene sequences (Feurdean and Astalos, 2005; Morales-Molino et al., 2011; Pérez-Sanz et al., 2013) and modern ecology studies on their resprouting ability (Reyes and Casal, 1998). Interestingly, *Betula* in El Portalet is a main factor building-up fuel but its development is negatively affected by fire in the first 150 years after the fire event. This is common with most of the mountain trees, supporting the idea of the alpine ecosystem as a long-term fire-sensitive environment. Indeed it is worth considering that more recurrent fires during the Early-Mid Holocene transition would have had a long-term impact on the birch development as it is the only mesophyte that clearly decreases from 7.5 cal kyr BP. However, this does not necessarily preclude birch communities pioneering the treeline recuperation as one amongst the first forestalls types able to spread after fires, especially considering that most trees respond negatively to fire (Fig. 6).

Palynological richness (rarefaction index) gradually increased as large wildfires reduced from 7.7 cal ka BP (Fig. 5), and despite its long-term variation, richness does not show any clear pattern linked to local fire occurrence (Fig. 6). A long-term positive fire effect on plant richness has often been argued, especially in those ecosystems where plants present fire-resistant seedbanks (Beckage and Stout, 2000; Johst and Huth, 2005; Montané et al., 2009). However, we argue that El Portalet increasing palynological richness during the Holocene is not led by fire disturbance, but it seems to be a consequence of the tree cover decline and the spread of non-arboreal communities, as semi-open landscapes represent a main driver of palynological richness and show larger diversity than closed forests (Colombaroli and Tinner, 2013; Feurdean and Astalos, 2005). We actually found that the non-arboreal pollen abundance presents a Spearman's R= 0.75 ($p<0.05$) (Table 2) with the rarefaction values for the 10-6 cal ka BP period (Fig. 5), supporting the idea of richer ecosystem in more open landscapes but not necessarily linked to fire disturbance.

4. Conclusions

The high resolution pollen and charcoal records at El Portalet enabled long-term analyses on fire regime, biomass-mediated fire occurrence and vegetation response to disturbance at the Central Spanish Pyrenees treeline. The main findings of our study are:

1) Local wildfire frequency varied since the Lateglacial (14.7 cal ka BP) to the Mid-Holocene (6 cal ka BP) at El Portalet, where the mean fire intervals progressively decreased during the fire-active periods, between 13.6-12.5 and 9.8-7.7 cal ka BP.

2) Variation in fire activity was not linked to human presence in El Portalet but to climate and biomass fluctuations. Mesophyte forest expansion (led by *Betula* and *Corylus* communities), as a fuel-creating factor, triggered increasing fire frequencies in the Central Spanish Pyrenees treeline. Hence, fire regimes in this region proved to be long-term sensitive to insolation changes and biomass abundance.

3) Fire has long-lasting negative effects on most of the treeline plant communities. These are not currently fire-prone forests, exhibiting no clear fire-trait, and El Portalet sequence shows that this is a long-term ecological feature of the subalpine/alpine Pyrenees communities.

4) Forest contraction from 7.7 cal ka BP could be linked to a threshold response of the system to recurrent fire frequencies as climate was not unfavourable for forest development. Palynological richness increased from that time coeval with the openness of the landscape.

Long-term fire ecology is proved to be a useful tool to explore Quaternary fire regime changes, especially in those fire-sensitive ecosystems where changing fire regimes may determine vegetation composition and resilience.

Besides, our findings are relevant under the current and predicted scenarios of global change, as warming would stimulate more frequent fire events in biomass-rich environments and therefore influencing environmental resilience vulnerability levels. Interestingly, these results from Quaternary scenarios concur with the local knowledge on current forest management, as both would stress the importance of keeping low levels of woody encroachment and promoting traditional forest use in order to prevent fuel accumulation and avoid virulent fires, with catastrophic effects both in this fire-sensitive ecosystem and in the local communities.

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Tables

Table 1: Criteria used for the selection of different core sections and analyses carried out in each of them.

Table 2: Spearman's R of some taxa and group of taxa and palynological richness. Asterisks are significant values at p< 0.05.

Figures

Figure 1: Digital elevation model of the Western-central Southern Pyrenees. Sites mentioned in the text: 1) El Portalet, 2) Estany de Burg, 3) Col d'Ech.

Figure 2: Vegetation map of the principal plant communities of the Western-central Spanish Pyrenees The upper panel displays in red the mesophyte forest, including *Betula* and *Corylus* distributions in the area. See Supplementary data in Supporting Information for taxa included in the different groups. Colour figure available online.

Figure 3: A) Raw charcoal accumulation rate values (CHAR) (grey bars); transformed Log C interpolated (variance stabilisation is achieved by log-transforming C interpolated series into Log C interpolated) (solid black line); Log C background (Detrending Log C interpolated resulted in background charcoal (Log C background) (red line). B) Fire events (FE) (red crosses) and detected fire peaks that did not pass the threshold for FE (red dots). C) Fire return intervals (FRI) for the two studied periods, expressed as years between fire events. D) Fire frequency (FF) every 500 years. E) Microcharcoal- accumulation rate. No samples were analysed between 364 and 382 cm - more details are given in the text –. Colour figure available online. F) Fire frequency (FF) every 500 years and fire events (FE) (black crosses) at Col d'Ech (site 3 in Fig 1) during the Holocene period concurrent with our site. See more details on the methods in the Supporting Information.

Figure 4: *Pinus:*mesophyte ratio plotted against local fire occurrence (fire frequency and peak magnitude) and July summer insolation (42ºN) (Laskar, 2004) in an age scale. Chronology from Lateglacial climate events are defined after Lowe et al. (2008) except for the Allerød warm event as El Portalet pollen and

sedimentary signals found in González-Sampériz et al. (2006), marked as *Allerød/GI-1a** with a dotted-line box in this figure, do not chronologically agree with the recent chronology presented in Lowe et al. (2008). Colour figure available online.

Figure 5: Synthetic pollen diagram with relevant selected taxa. Pollen values are abundances (%) represented as filled black areas. Fire activity is characterized by micro-charcoal area concentration, and local fire events are represented by red crosses. Palynological richness is represented with confidence intervals and measured in number of taxa. See Supplementary data for taxa included in the different groups. Colour figure available online.

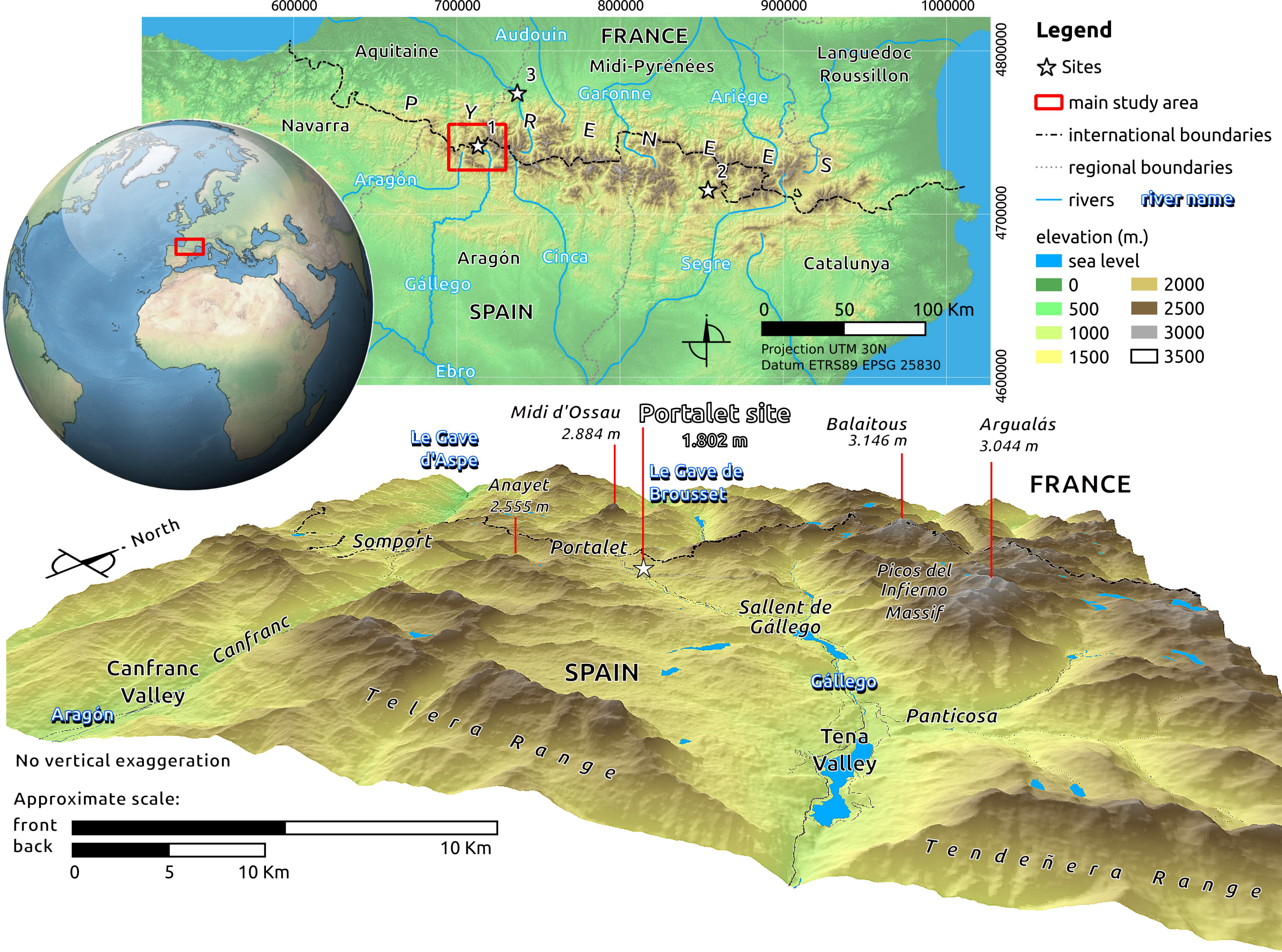
Figure 6: Cross-correlograms of detrended macro-charcoal influx versus detrended pollen percentages for the 6-10 cal kyr BP period. Every lag corresponds to the average time difference between two adjacent samples, both containing pollen and charcoal (15 yr cm^{-1}). Lag 0 is the ordinary linear correlation coefficient between two variables at a particular time. Positive lags measure the influence of the first variable on the second, ie., how charcoal affects pollen, after a particular time lag; negative lags measure the influence of the second variable (pollen) on the first (charcoal) with reference to the lag. Dotted lines correspond to the significance level $p<0.05$.

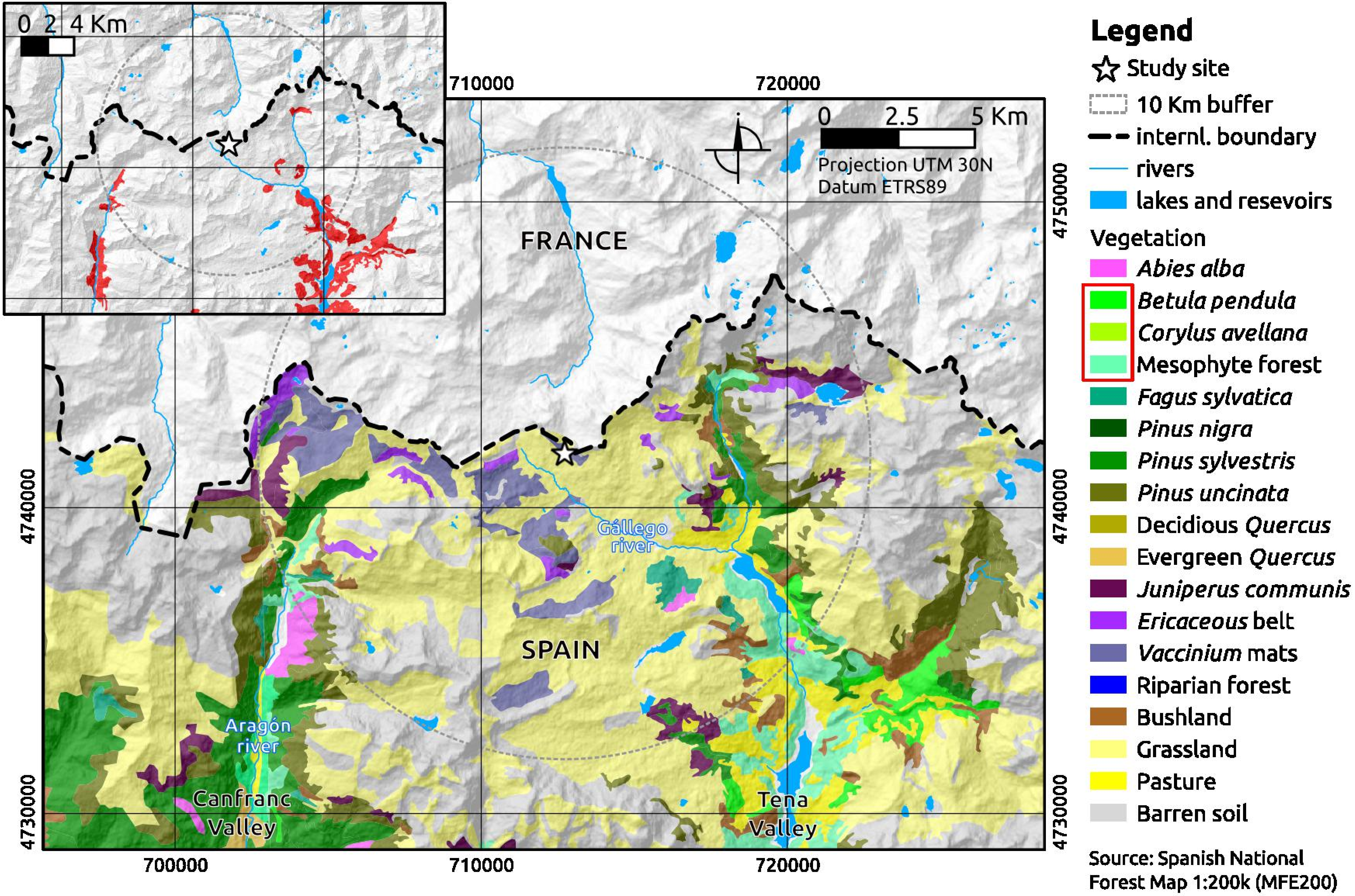
Table 1

Depth (cm)	Age (cal kyr BP)	Analysis	Criteria
60-160	5 to 6	No analyses	Peatland to lake transition; different environmental settings for charcoal deposition
160-364	6 to 10	High resolution pollen, micro- and macro-charcoal (1 cm^3, every 1 cm)	Sedimentation rate meets the demands for decomposition of time series and peak-fire detection (15 yr/cm)
364-381	10 to 11.5	No analyses	Sedimentation rate too low in the very few available samples
381-382	11.5 to 12.5	No analyses	Possible hiatus corresponding to the Younger Dryas
382-471	12.5-14.7	Pollen and micro-charcoal every 2-5 cm, macro-charcoal every 1 cm	Sedimentation rate is high enough (24 yr/cm) fitting the required for peak-fire detection while pollen analysis was performed in the available samples from the original core
471-608	14.7-32	No analyses	Glacial influence and low presence of potentially local taxa were not suitable for the proposed objectives.

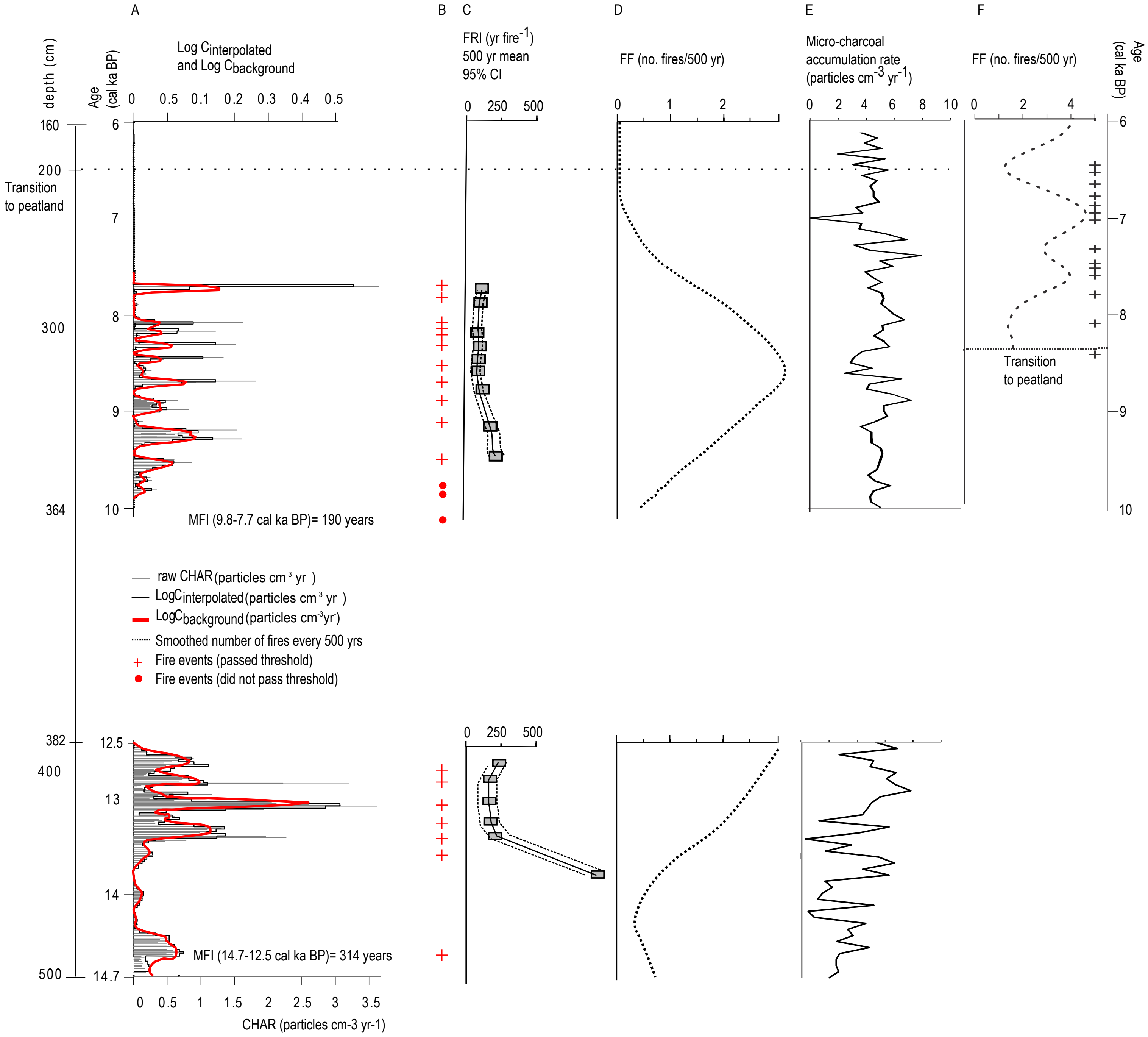
Table 2

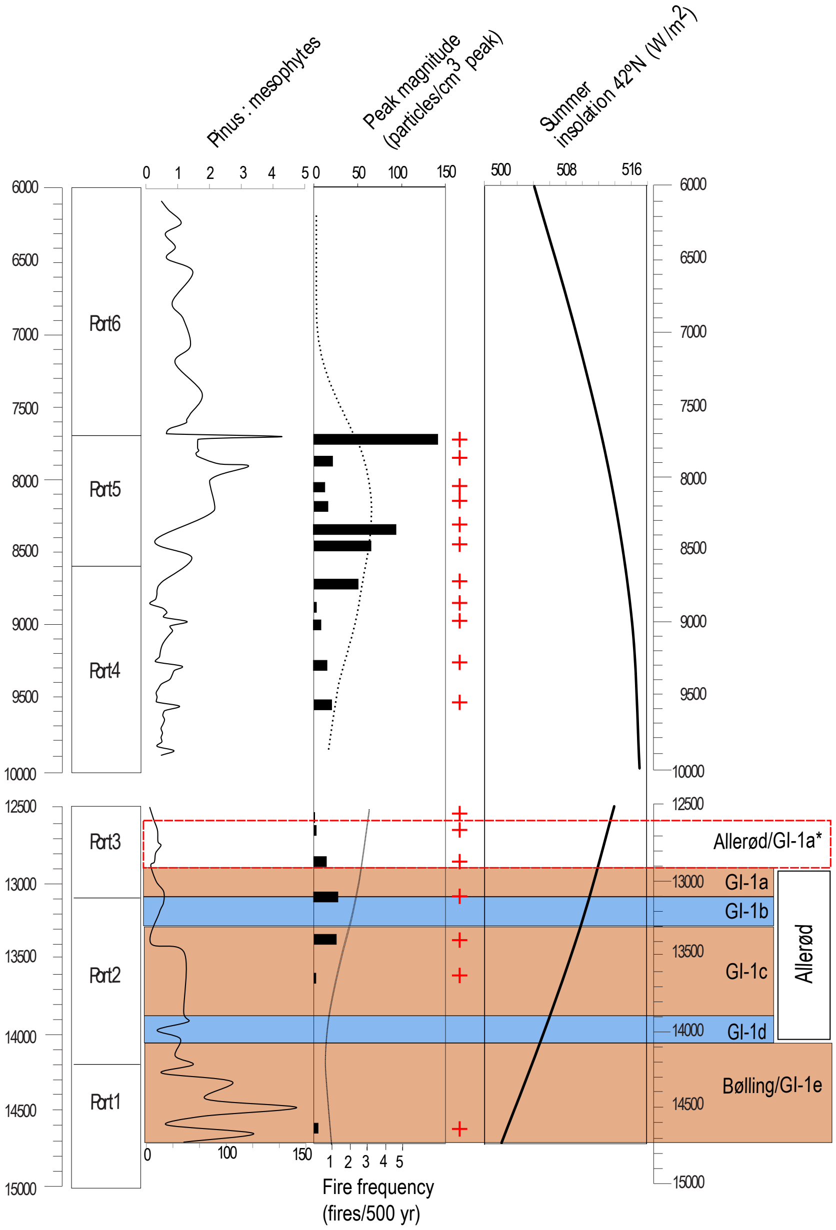
Taxa or group of taxa	**Spearman's R**
Trees	-0.42 *
Mesophytes	0.27
Shrubs	0.65 *
Poaceae	0.34
Herbs	0.83 *
Non arboreal (shrub and all herbs)	0.75 *
Pinus	-0.20
Betula	-0.32
Corylus	-0.29

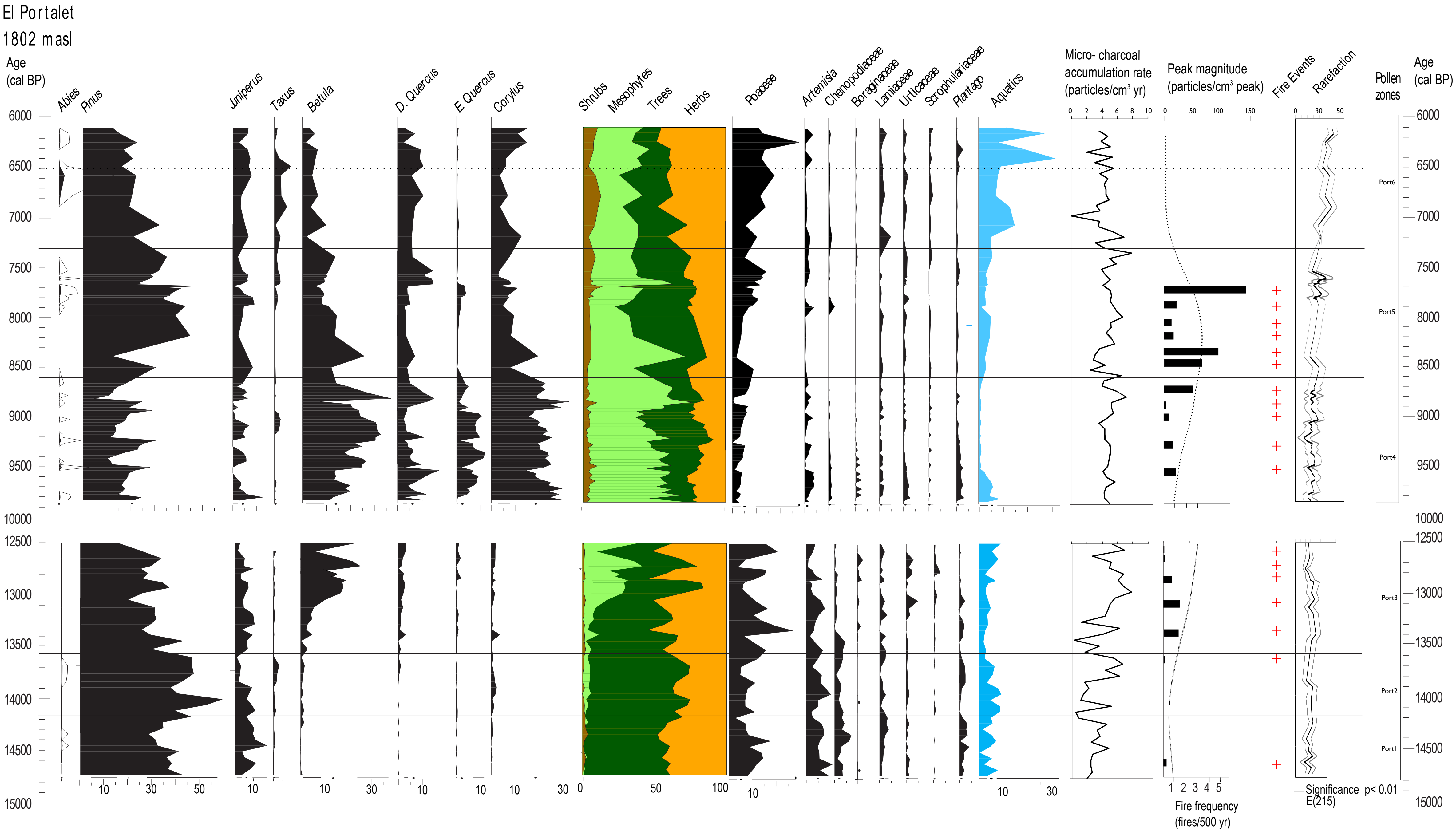

600000
700000
800000
900000
1000000
4800000
4700000
4600000
Legend
☆ Sites
main study area
international boundaries
regional boundaries
rivers
river name
elevation (m.)
sea level
0
500
1000
1500
2000
2500
3000
3500
FRANCE
Aquitaine
Audouin
Midi-Pyrénées
Garonne
Ariège
Languedoc Roussillon
Navarra
P Y R E N E E S
1
2
3
Aragón
Aragón
Cinca
Segre
Catalunya
Gállego
SPAIN
Ebro
0
50
100 Km
Projection UTM 30N
Datum ETRS89 EPSG 25830
Midi d'Ossau
2.884 m
Portalet site
1.802 m
Balaitous
3.146 m
Argualás
3.044 m
Le Gave d'Aspe
Le Gave de Brousset
Anayet
2.555 m
FRANCE
North
Somport
Portalet
Picos del Infierno Massif
Sallent de Gállego
Canfranc
Canfranc Valley
Aragón
SPAIN
Telera Range
Gállego
Panticosa
Tena Valley
Tendeñera Range
No vertical exaggeration
Approximate scale:
front
back
10 Km
0
5
10 Km

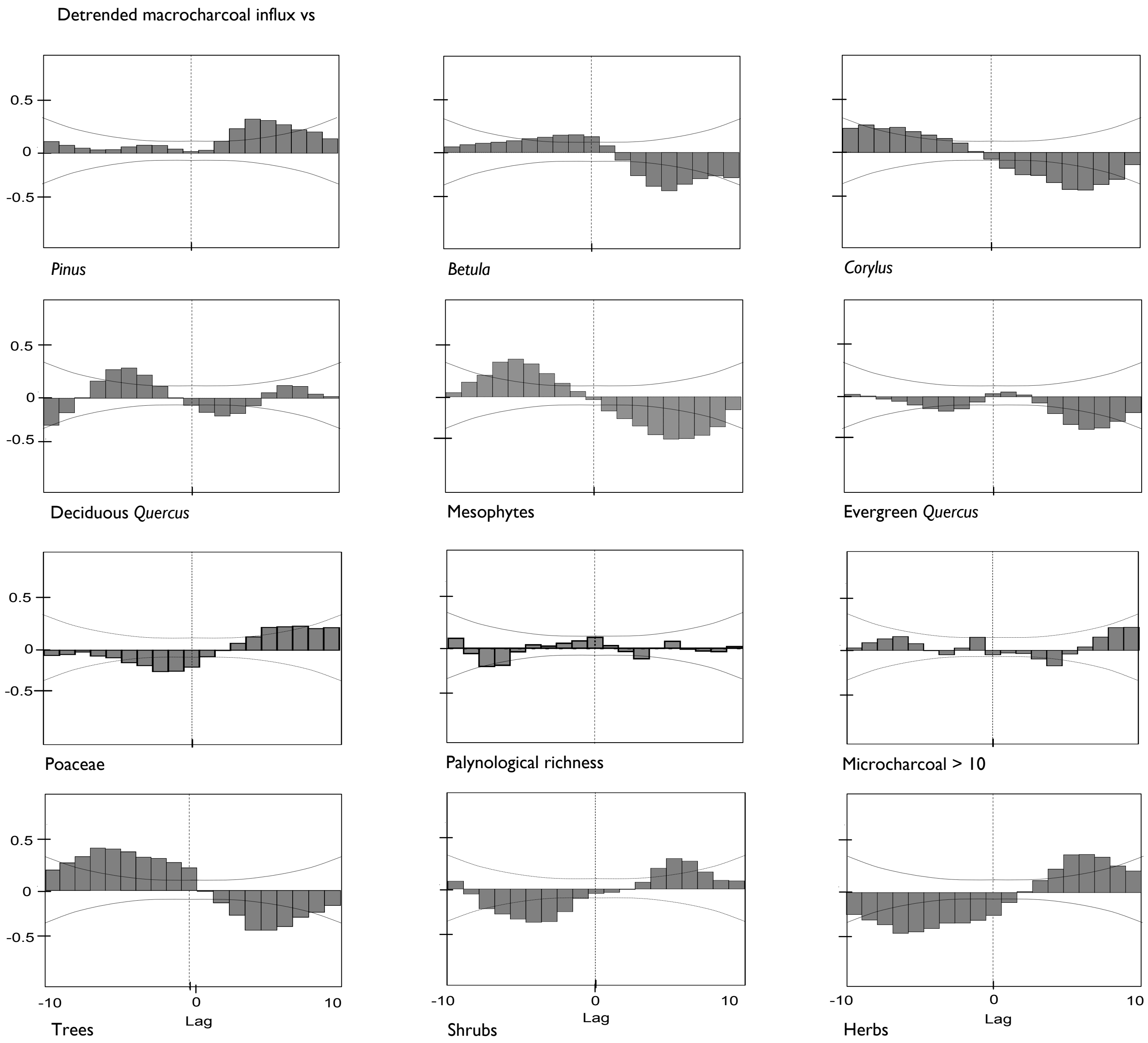


Source: Spanish National Forest Map 1:200k (MFE200)


A
B
C
D
E
F
depth (cm)
Age (cal ka BP)
Log Cinterpolated and Log Cbackground
0 0.5 0.1 0.2 0.3 0.4 0.5
FRI (yr fire-1) 500 yr mean 95% CI
0 250 500
FF (no. fires/500 yr)
0 1 2
Micro-charcoal accumulation rate (particles cm-3 yr-1)
0 2 4 6 8 10
FF (no. fires/500 yr)
0 2 4
Age (cal ka BP)
160
200
Transition to peatland
300
364
382
400
500
6
7
8
9
10
12.5
13
14
14.7
MFI (9.8-7.7 cal ka BP)= 190 years
raw CHAR (particles cm-3 yr-)
LogCinterpolated (particles cm-3 yr-)
LogCbackground (particles cm-3yr-)
Smoothed number of fires every 500 yrs
+ Fire events (passed threshold)
● Fire events (did not pass threshold)
Transition to peatland
0 250 500
MFI (14.7-12.5 cal ka BP)= 314 years
0 0.5 1 1.5 2 2.5 3 3.5
CHAR (particles cm-3 yr-1)


Pinus : mesophytes
Peak magnitude (particles/cm^3 peak)
Summer insolation 42ºN (W/m^2)
0 1 2 3 4 5
0 50 100 150
500 508 516
6000
6500
7000
7500
8000
8500
9000
9500
10000
12500
13000
13500
14000
14500
15000
Port6
Port5
Port4
Port3
Port2
Port1
0 100 150
1 2 3 4 5
Fire frequency (fires/500 yr)
Allerød/GI-1a*
GI-1a
GI-1b
GI-1c
GI-1d
Bølling/GI-1e
Allerød


El Portalet
1802 masl
Age (cal BP)
Abies
Pinus
Juniperus
Taxus
Betula
D. Quercus
E. Quercus
Corylus
Shrubs
Mesophytes
Trees
Herbs
Poaceae
Artemisia
Chenopodiaceae
Boraginaceae
Lamiaceae
Urticaceae
Scrophulariaceae
Plantago
Aquatics
Micro- charcoal accumulation rate (particles/cm³ yr)
0 2 4 6 8 10
Peak magnitude (particles/cm³ peak)
0 50 100 150
Fire Events
Rarefaction
0 30 50
Pollen zones
Port6
Port5
Port4
Port3
Port2
Port1
Age (cal BP)
6000
6500
7000
7500
8000
8500
9000
9500
10000
12500
13000
13500
14000
14500
15000
10 30 50
10
10 30
10
10
10 30
0 50 100
10
10 30
1 2 3 4 5
Fire frequency (fires/500 yr)
Significance p< 0.01
E(215)


Detrended macrocharcoal influx vs
0.5
0
-0.5
Pinus
Betula
Corylus
Deciduous *Quercus*
Mesophytes
Evergreen *Quercus*
Poaceae
Palynological richness
Microcharcoal > 10
Trees
Shrubs
Herbs
-10
0
10
Lag