



Environmental history and vegetation dynamics in response to climate variations and human pressure during the Holocene in Bassa Nera, Central Pyrenees



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ABSTRACT

With the aims of investigating the causes of environmental changes in high mountain ecosystems during the Holocene in relation to climate forcings and identifying thresholds for vegetation community shifts, we performed a multi-proxy palaeoecological reconstruction based on two sediment cores from Bassa Nera, a lentic system located close to the montane–subalpine ecotone in the Central Pyrenees. Using pollen, plant macroremains, charcoal, chemical elements and loss-on-ignition at centennial to decadal resolution, we reconstructed the vegetation and lacustrine dynamics during the last 10,000 years. A montane pollen ratio was used as a palaeoecological indicator to track altitudinal shifts in high mountain vegetation, which was compared to the ice-rafted debris index (IRD) as a proxy for summarizing the climatic influence of the North Atlantic Circulation. Our results show upward shifts of deciduous forest and its presence in Bassa Nera from the onset of the Holocene until 4200 cal yr BP, when it was replaced by coniferous taxa. The montane ratio showed a link between vegetation and North Atlantic influence, while changes in *Sphagnum* macroremains and aquatic taxa allowed description of local ontogenic changes from the initial pond to the present peatland. The loss-on-ignition record showed some flood events at Bassa Nera between 4500 and 3900 cal yr BP. The studied proxies allowed inferences concerning anthropic pressure in the catchment through grazing activities by 7300 cal yr BP and the appearance of cereal agriculture around 5190 cal yr BP. The highest human pressure occurred in the late Bronze Age, Roman Period and Middle Ages.

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1. Introduction

The development of environmental assessment tools to predict how current climate change will affect natural ecosystems is essential to apply proper management measures. Palaeoenvironmental reconstructions are crucial to understand ecosystem sensitivity and past environmental shifts, as they help to distinguish between the effects of climatic and anthropogenic forcings (Last and Smol, 2001; Willis and Birks, 2006; Catalan et al., 2013). Mountain ecosystems

are well-suited to study such changes, since their hard environmental conditions make them less prone to intensive human influence.

The onset of the Holocene, characterised by relatively warmer temperatures and an increase in humidity in Europe (Walker, 1995), prompted a rapid expansion of deciduous forests in southwest European mountains (Jalut et al., 2009; Pérez-Obiol et al., 2011), including the Pyrenees (Benito et al., 2008; Montserrat-Martí, 1992). By the Middle-Holocene, a southward shift of the North Atlantic westerly jet (Bond et al., 2001) led to a change in precipitation seasonality (Pla and Catalan, 2005), a drastic decline in deciduous taxa and a progressive consolidation of conifers in the Pyrenees (González-Sampérez et al., 2006; Pèlachs et al., 2011). Such changes in plant community composition suggest that the North Atlantic climatic variability had sufficient magnitude and duration to affect the Pyrenean ecosystems and force them to cross a threshold into a different state. However, the precise

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features in the response of deciduous and conifer species to climatic shift are not yet fully understood, and their study becomes even more complicated when anthropogenic influence is taken into account.

With the aim of investigating how the high mountain ecosystems of the Central Pyrenees responded to the Holocene climate and anthropogenic forcings, we performed a multi-proxy palaeoecological reconstruction of Bassa Nera (BSN), a pond with a ring of *Sphagnum* moss close to the montane-subalpine boundary of the Aiguamòg valley (Aran valley). There are several palaeoecological studies in the Central Pyrenees covering the Holocene that record a marked climate variability with well-defined arid and cold events (Pla and Catalan, 2005; González-Sampériz et al., 2006; Pérez-Sanz et al., 2013), vegetation responses through treeline shifts and biomass-fire interactions (Cunill et al., 2013; Gil-Romera et al., 2014).

Regarding human influence, the Central Pyrenees have been occupied and exploited by prehistoric societies since at least the Neolithic (Ejarque et al., 2010; Gassiot et al., 2014) through fire and complex land use management (Bal et al., 2010; Pérez-Obiol et al., 2012). Phases of higher anthropogenic pressure in high mountain areas are known since the Early and Middle Neolithic, with an important threshold in the Early Bronze Age (Gassiot and Jiménez, 2006; Miras et al., 2007). Since then, it has been widely assumed that the configuration of high mountain landscapes has been influenced by humans (Ejarque et al., 2010; Bal et al., 2011; Cunill et al., 2013), or at least that humans have accentuated the effects of climatic constraints on vegetation during the late Holocene (Jalut et al., 2009) through mining activities, farming or cattle raising (Pèlachs et al., 2009a; Cunill et al., 2013; Garcés-Pastor et al., 2016). In this study, we perform a high-resolution reconstruction of vegetation in order to detect the onset of the anthropic pressure in Bassa Nera caused by grazing and agriculture farming.

Pèlachs et al. (2011) found a close coupling between regional climatic patterns using the ice-rafted debris index (IRD; Bond et al., 2001) from the North Atlantic and the accumulation of organic matter in a mountain wetland system in the Central Pyrenees (Pèlachs et al., 2011). However, it is advisable to check whether this coupling between climatic influence and organic matter deposition may be generalized to other lentic systems in order to test the applicability of the IRD to palaeoecological reconstructions. Hence, this paper studies the response of organic matter accumulation in Bassa Nera to North Atlantic regional climatic patterns and compares it with similar regional essays. In a previous study, Garcés-Pastor et al. (2016) introduced a montane pollen ratio that was useful for monitoring local upward migrations of the montane-subalpine boundary. The present work uses this montane ratio to track the response of high mountain vegetation to the Holocene climate variability and North Atlantic influence (IRD) and, if possible, to identify possible thresholds in vegetation communities. In this paper, we combine diverse proxies (pollen, charcoal, macroremains, organic matter, chemical elements and sedimentology) from two independent records of Bassa Nera spanning the Holocene with the following objectives: (1) To reconstruct the local vegetation dynamics of BSN; (2) to evaluate the ecosystem response of the area to climate forcings and North Atlantic influence, describing the main arboreal dynamics at the local level as well as identifying thresholds in vegetation communities and their possible causes; (3) to test the response of organic matter indicators such as LOI in front of North-Atlantic regional climatic patterns (IRD), comparing the results from BSN to those obtained from other Pyrenean systems; and (4) to assess the human influence on the BSN region, determining the point at which this influence became strong enough to be detectable and how it was affected by the climatic patterns.

2. Study area

2.1. Environmental and geographical settings

The Bassa Nera (42° 38' 18.5" N, 0° 55' 27.6" E, 1891 m a.s.l.) is a small lentic system from glacial origin located in the peripheral zone

of "Aigüestortes i Estany de Sant Maurici" National Park (PNAESM) (Fig. 1). Its surface area is 2.01 ha, with a maximum depth of 5 m, and it drains by a small outlet into the Aiguamòg River. This pond is surrounded by mixed peat bogs and it is currently in the final stages of infilling (Pérez-Haase and Ninot Sugrañes, 2006, 2017). The climate is subalpine with Atlantic influence and precipitation is well distributed along the seasons (annual average = 1152 mm) (Ninyerola et al., 2003). Mean annual temperature is 4.25 °C, being January the coldest month (−3 °C in average) and July the warmest (14 °C in average). The BSN basin lies on a granodiorite bedrock from the Maladeta batholith, which dates from the Carboniferous-Permian age (Roca i Adrover et al., 2010). The main peat communities are geogenous fens (*Scheuchzeria-Caricetea fuscae*) and ombrogenous bogs (*Oxycocco-Sphagneteta*) (Pérez-Haase et al., 2012). The BSN is surrounded by a mixed conifer forest of *Pinus mugo* subsp. *uncinata* (Ramond) Domin. and *Abies alba* Mill., with *Rhododendron ferrugineum* L. in the understory and Poaceae meadows. Cañellas-Boltà et al. (2009) described the montane and sub-alpine vegetation altitudinal belts where the catchment area lies. The montane belt (<1600 m) is composed by deciduous oak forests of *Quercus petraea* (Mattuschka) Liebl. with *Betula pendula* Roth.; riverine forests (dominated by *Alnus glutinosa* L., *Fraxinus excelsior* L., and *Salix* spp.); forests with *Tilia platyphyllos* Scop., *Prunus avium* L., and *Corylus avellana* L.; and mixed forests of *Betula pendula* Roth. and *Pinus sylvestris* L. The subalpine belt (1600–2250 m) is dominated by coniferous forests of *Abies alba* and *Rhododendron ferrugineum* at the lowest parts and *Pinus mugo* subsp. *uncinata* with *R. ferrugineum* at the upper stages. Wetlands are mainly occupied by *Trichophorum cespitosum* subsp. *cespitosum* (L.) Hartm. communities, assemblages of *Juncus balticus* Willd. subsp. *pyrenaicus*, *Carex rostrata* Stokes beds., *Caltha palustris* L. flushes and *Sphagnum* peat bogs (carpets and hummocks) (Pérez-Haase and Ninot Sugrañes, 2006). This part of the valley has experienced low human pressure through pasturing and farming during the last millennium (Garcés-Pastor et al., 2016). Since the rural exodus of mid-20th century to the creation of the PNAESM in 1955, grazing, forest exploitation and hydroelectric electricity generation were the only activities. Afterwards, tourism has become an important activity in the national park.

3. Material and methods

3.1. Coring, sampling, dating and sedimentology

Two cores (PATAM-12 and BSN-6), separated by 47 m, were retrieved from the *Sphagnum* mire surrounding Bassa Nera (Fig. 1). Core PATAM-12 provides a detailed record of the last seven millennia, but lacks the beginning of the Holocene. For this reason, we also studied core BSN-6, which covers the last ten thousand years and provides a wider environmental framework. The core BSN-6 (core A, 270 cm long) was collected in 2011 through the percussion and recover in one step of a 3 m PVC tube on a hummock composed by *Sphagnum magellanicum* and *S. capillifolium* (Fig. 1). The core PATAM-12 (core B, 706 cm long) was obtained in 2007 with a "Russian" corer (Jowsey, 1966) on the *Sphagnum* quaking carpets (*Caricion lasiocarpae*) that surround the pond. Core A was sliced every 1 cm and core B every 3 to 5 cm. The chronological framework was based on AMS radiocarbon dates from peat and macroremains obtained at Beta Analytic Radiocarbon Dating laboratory (Miami, USA) and Keck Carbon Cycle (Irvine, USA), published in Pèlachs et al. (2016) and Garcés-Pastor et al. (2016). The radionuclide analysis (^{210}Pb) for dating purposes of the uppermost 40 cm of core A was carried out at the Laboratory of Environmental Radioactivity of the Universitat Autònoma de Barcelona (UAB, Spain). The supported ^{210}Pb was found at 30 cm depth and ^{210}Pb activities were determined by α -spectrometry through ^{210}Po in equilibrium (Sanchez-Cabeza et al., 1998). Ages were calibrated with IntCal13.14C curve (Reimer et al., 2013) and the age–depth models (Fig. 2) were performed with Clam 2.2. software using *Smooth*

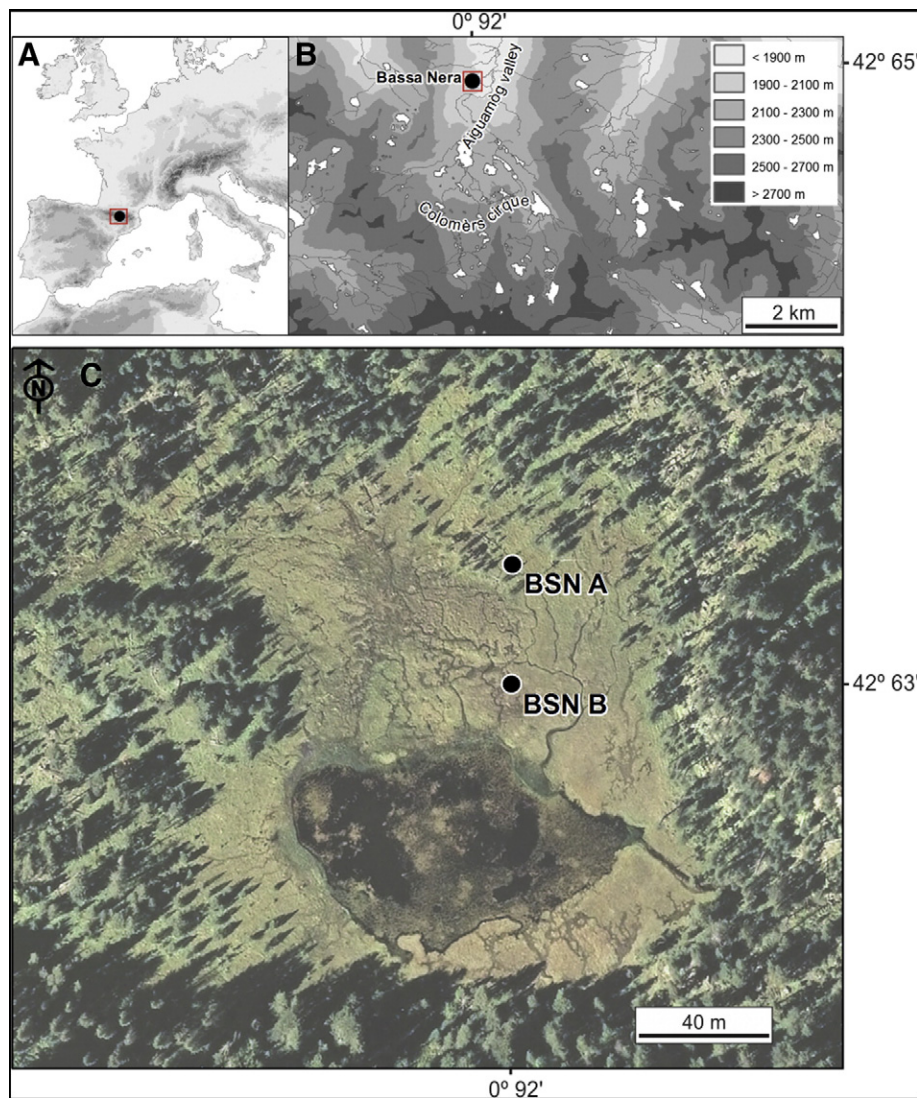


Fig. 1. Location of the study area (A) Map indicating the relative location of Bassa Nera Pond in the Iberian Peninsula. (B) Topographic map of the terrain surrounding Bassa Nera. (C) Coring sites where the cores A and B were retrieved.

Spline function (Blaauw, 2010). The sedimentary facies of the cores were described following Schnurrenberger et al. (2003) (Fig. 2).

3.2. Pollen, charcoal and macroremains

Pollen analyses were carried out in two different laboratories. A total of 62 samples along 270 cm (core A) and 114 samples in 706 cm (core B) were processed according to standard chemical methods (Moore et al., 1991) with KOH, HCl, HF digestions and mineral separation in heavy liquid (Thoulet solution; density 2.0 g/cm³) at the Universitat Autònoma de Barcelona and the Catalan Institute of Human Paleocology and Social Evolution. The pollen record from the first 330 cm from core B (51 samples) has been already studied in Garcés-Pastor et al. (2016). Pollen grains were identified according to Faegri and Iversen (1989) and Reille (1992), and counted until diversity saturation (Rull, 1987). Because most slides had *Pinus* superabundance that could hide vegetation dynamics, counts were increased in order to get a representative sample (minimum 200 pollen grains without *Pinus*). Stomata, non-pollen palynomorphs and algal remains were also counted. The palynological results are presented as percentage of the pollen sum excluding *Pinus*, spores and wetland plant pollen. Diagrams were plotted using *Psimpoll* 4.27 software (Bennett, 2002) and statistical significant pollen zones were calculated

using the method of *Optimal Splitting by Information Content* (Bennet, 1996) on taxa showing abundances >1% (Figs. 3 and 4). Some pollen taxa which appear in Fig. 4 have been excluded from Fig. 3 since they were less represented due to localisms. The montane pollen ratio used by Garcés-Pastor et al. (2016), based upon the modern pollen indicators of montane and subalpine/alpine stages identified by Cañellas-Boltà et al. (2009), was calculated to estimate altitudinal variations of the montane belt. This ratio was calculated using taxa that have a significant correlation between the abundance of pollen and local occurrence of parent taxa in montane and subalpine-alpine belts in this valley. Montane pollen types included *Alnus*, *Betula*, *Buxus*, *Corylus*, *Fraxinus*, deciduous *Quercus*, *Tilia* and *Salix*, while subalpine-alpine indicators included Asteraceae, *Calluna*, *Campanula*, Ericaceae, *Plantago* and Poaceae. The percentages of the montane pollen were summed and divided by the sum of the percentages of subalpine-alpine pollen (see more information in Garcés-Pastor et al., 2016). Values of 2.5 indicate the close presence of montane belt, while higher values imply the upward montane migration of the latter within Bassa Nera basin. It is important to highlight that this ratio has been inferred from only one altitudinal transect and has been useful for the palaeoenvironmental interpretation of BSN catchment (Garcés-Pastor et al., 2016), but it should be interpreted with caution if used in other areas or landscape mosaics.

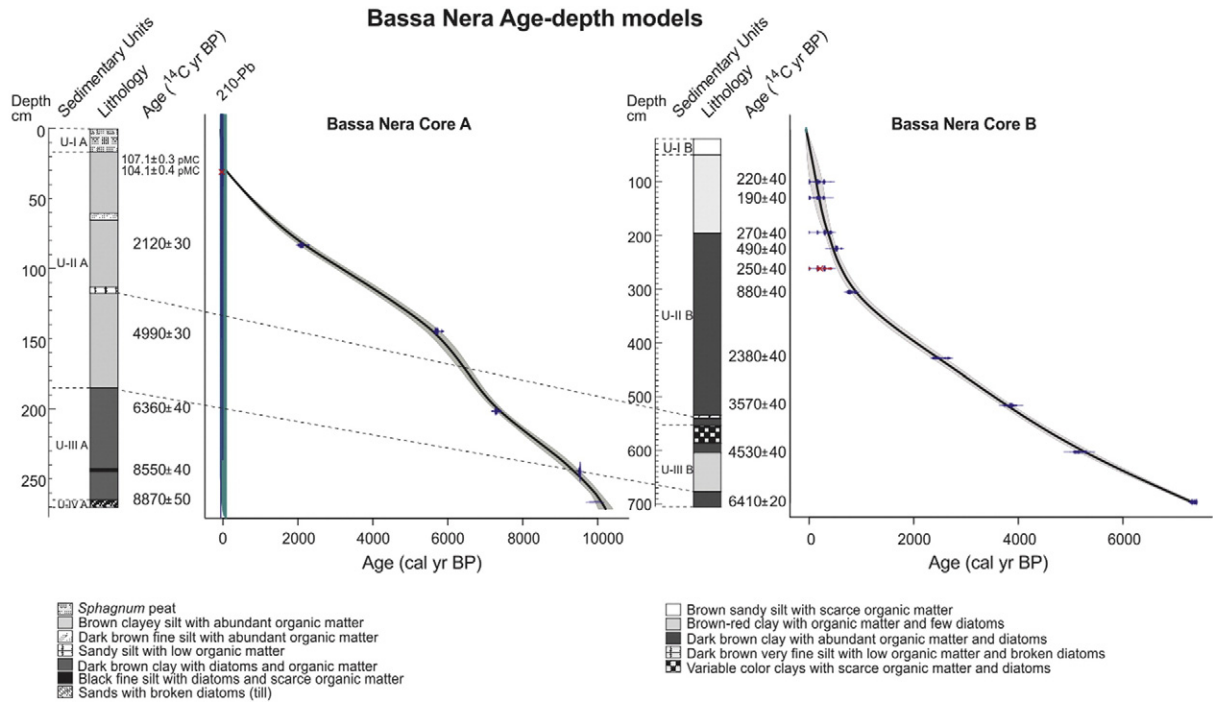


Fig. 2. Age-depth models of Bassa Nera cores based on radiocarbon dating, performed with Clam 2.2 software using Smooth Spline function (Blaauw, 2010) and correlation between their sedimentary facies. Core A presents the ^{210}Pb dates (marked in blue). In cores A and B, one radiocarbon date was rejected as stratigraphically incongruent, likely because roots might have dragged down the wood macroremain.

To study the sedimentary charcoal, the Carcaillet protocol for lacustrine sediments was adjusted to peat bog (Carcaillet et al., 2001). Consequently, wet weight was used instead of volume in order to minimize the differences of density inside the peat bog. A total of 295 samples from core A were digested according to Carcaillet et al. (2001) and counted with a stereomicroscope at $40\times$ magnification. Charcoal counts were combined and divided by sample weight to calculate charcoal concentration (mm^2/g) and divided by sedimentation rate to calculate the charcoal accumulation rate (CHAR, $\text{mm}^2/\text{g}/\text{yr}$). (Fig. 3).

Plant macroremains at 64 depths from core A were analysed. Samples were processed according to Mauquoy et al. (2010) with KOH and sieved with a mesh of $150\ \mu\text{m}$ (Birks and Birks, 1980). Taxonomic identification was done according to Brugués et al. (2007), Smith and Smith (2004) and Daniels et al. (1990) using a stereomicroscope and an episcopic microscope. Some *Sphagnum* macroremains were identified at species level while others could only be identified to their taxonomic section. In those cases, we could refine the identification within each section to a couple of taxa (*S. papillosum* or *palustre* and *S. denticulatum* or *subsecundum*). Results are expressed as presence/absence and *Sphagnum* percentage in Fig. 3.

3.3. Loss-on-ignition and chemical elements

To estimate the organic matter content, 295 samples of core A were dried at $60\ ^\circ\text{C}$ to determine the weight loss and burned at $550\ ^\circ\text{C}$ for 4 h to oxidize organic matter, after absence of carbonates had been verified (Heiri et al., 2001; Luque, 2003). The loss-on-ignition results (LOI) are expressed as percentage of dry weight (Fig. 3). In this work only Titanium (Ti) and Manganese (Mn) were considered as proxies of soil erosion and water oxygenation (Davies et al., 2015). For this purpose, 98 samples from core A were moulded and digested in a microwave oven (CEM, Mars model) using a solution of HNO_3 , HCl and HF with a parallel blank digestion. The extracted solutions were analysed with an inductively coupled plasma mass spectrometer (ICP-MS, Argilent model 7500 ce) at the Chemical Analytic Service of the UAB.

4. Results

4.1. Chronology and sedimentology

Fig. 2 shows the age-depth models, the lithology and the correlation of the two cores. Seven radiocarbon dates and 31 ^{210}Pb dates were used to construct the core A age-depth model. It covers the last 10,211 cal yr BP in 270 cm with an average confidence interval error of ca. 220 yr and a sedimentation rate of $0.07 \pm 0.21\ \text{cm}\ \text{yr}^{-1}$, ranging from 0.016 to $0.86\ \text{cm}\ \text{yr}^{-1}$. Date $104.1 \pm 0.4\ \text{pMC}$ was rejected because lack of consistency with the ^{210}Pb dating at the same depth (30.2 cm). Core A shows four sedimentary units: Unit I-A (0–17 cm) is composed of living *Sphagnum* peat with abundant roots. Unit II-A (17–185 cm) is the largest of the record and is composed of a peat bog texture with light to dark-brown clayey silt and abundant organic matter. Two intercalated layers can be distinguished: one characterised by dark-brown fine silt with abundant organic matter (60–64 cm) and another with low organic sandy silt (115–117 cm). Unit III-A (185–263 cm) is composed of brown-black clay with imbedded pennate diatoms and organic matter and shows an intercalated layer of black fine silt with coarse-quartz sands and pennate diatoms (243–244 cm). Unit IV-A (264–270 cm) presents a transition from quartz pebble to coarse sands (till) and broken diatoms.

The age-depth model of core B was built with ten radiocarbon dates. One date ($250 \pm 40\ \text{AMS}\ ^{14}\text{C}\ \text{yr}\ \text{BP}$), obtained from a woody macroremain, was rejected as stratigraphically incongruent (see detailed information in Garcés-Pastor et al., 2016). The model spans ca. 7490 cal yr BP to the present, with an average confidence interval error of ca. 150 yr and an average sedimentation rate of $0.2 \pm 0.18\ \text{cm}\ \cdot\ \text{yr}^{-1}$, ranging from 0.04 to $0.78\ \text{cm}\ \cdot\ \text{yr}^{-1}$. It presents 3 sedimentary units: Unit I-B (0–50 cm) consists of massive brown sandy silt with scarce vegetal matter. Unit II-B (50–553 cm) is formed by brown-red clay with abundant vegetal matter and few pennate diatoms (50–195 cm), and dark brown massive clays with abundant organic matter (195–553 cm) with an intercalated layer of very fine silt

Bassa Nera: core A

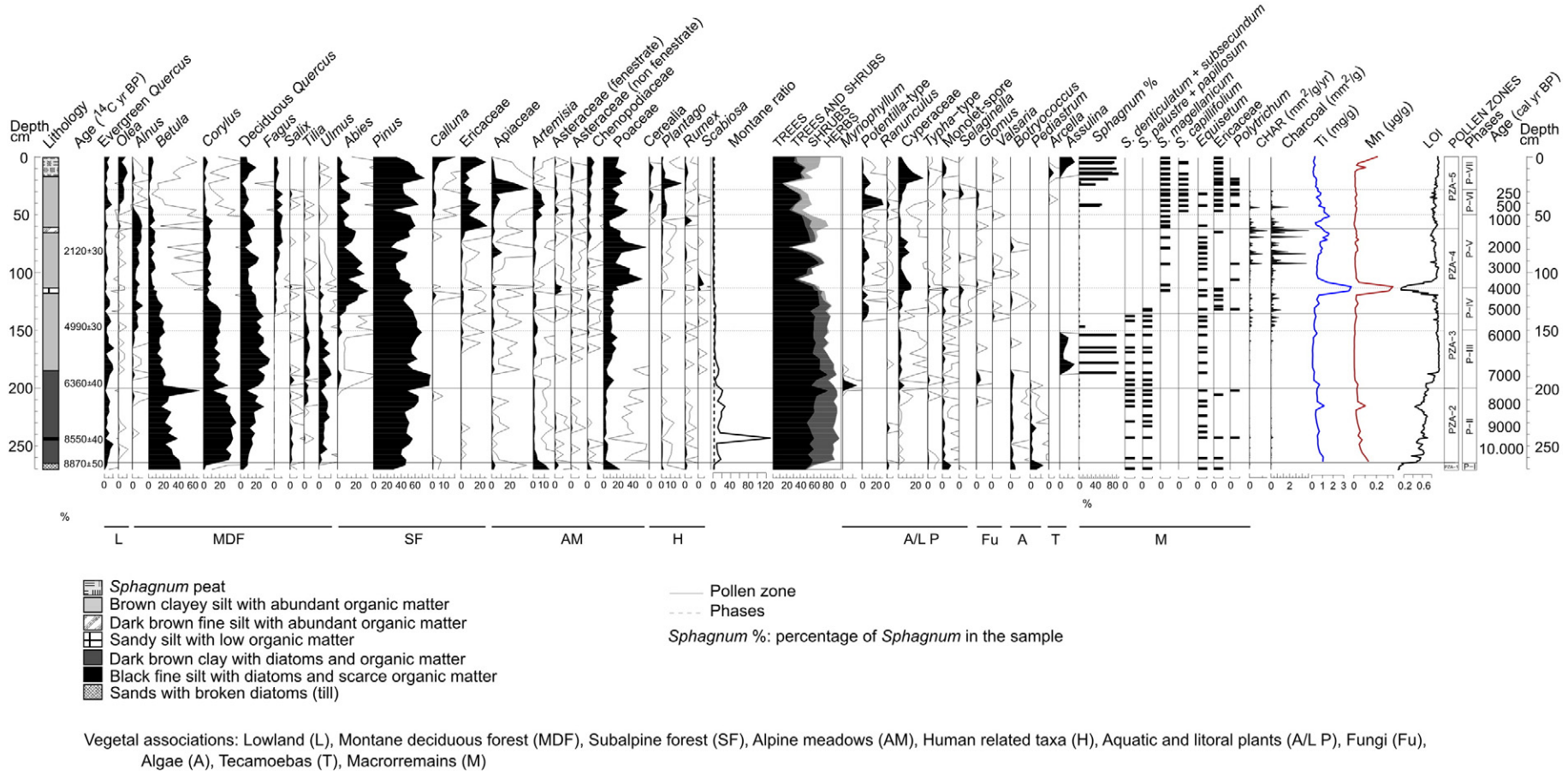


Fig. 3. Percentage diagram of sporomorphs of core A including: the total pollen (relative abundance $\geq 1\%$), montane ratio, aquatic elements and plant macroremains, charcoal concentration (mm^2/g) and charcoal accumulation rate (CHAR, $\text{mm}^2/\text{g}/\text{yr}$), chemical elements and Loss on Ignition. *Pinus* pollen, wetland plants and fern spores were excluded from the pollen sum (ΣP). *Pinus* percentage was calculated with the pollen sum plus *Pinus* pollen. *Sphagnum palustre* or *papillosum* and *Sphagnum denticulatum* or *subsecundum* means that the two species could not be distinguished. The dotted line in montane ratio corresponds to the threshold value of 2.5, which indicates the close presence of montane-subalpine ecotone. Higher values imply the occurrence of upward montane vegetation in Bassa Nera. Vegetal associations: Lowland (L), Montane deciduous forest (MDF), Subalpine deciduous forest (SDF), Alpine meadows (AM), Human related taxa (H). The continuous horizontal lines correspond to statistically significant zones (Bennett, 1996).

with some broken diatoms and low organic matter (536–539 cm). Unit III-B (553–706 cm) is composed of clays with colours varying from grey to brown. This unit has little organic matter and scarce diatoms (553–586 cm) and brown-black clay with pennate diatoms and organic matter (586–706 cm), with an intercalated section of brown-red clay with abundant vegetal matter and few diatoms (603–677 cm).

The two cores were correlated according to their sedimentological features (Fig. 2). One stratigraphic correlation was carried out between the sandy silt layer of Unit II-A and the very fine silt layer of Unit II-B. The second correlation was made between the base of Unit II-A and the brown-red clay and dark-brown clay layers located at 677 cm in Unit III-B. The lithological differences between the studied cores are likely due to the concave shape of the basin and the relative position of the sampling points. In summary, core A contains 10,211 years in 270 cm and core B 7490 years in 706 cm. Given the different temporal resolutions between the two records, core A will show the main palaeoenvironmental features of the Holocene, and core B the last 7000 years at a higher resolution.

4.2. Loss-on-ignition and metals

The LOI values come from three different sedimentary environments (Fig. 3): (I) peat bog (0–184 cm), with >70% of organic material, showing an abrupt drop to 14% at 105–120 cm; (II) clays (185–263 cm), with an organic content between 30 and 94% and a sharp decrease below 194 cm; and (III) sands with <19% organic matter content (264–270 cm). Ti shows an increasing trend with an important drop at 60–64 cm (Fig. 3). Since then, it displays relatively stable values except for a prominent peak at 112–116 cm and a smaller peak at 215 cm. On the other side, Mn shows low variability (3–46 µg/g), with two small peaks at 10 cm and 215 cm and one large peak at 112–116 cm (311–346 µg/g).

4.3. Palynological interpretation

The diverse sedimentation rates of the cores and their different locations within the lake basin make them suitable to reconstruct the palaeoenvironmental conditions in different ways. The information provided by the pollen, charcoal and macroremains of core A is used to show the main palaeoenvironmental events and vegetal dynamics that occurred in the BSN catchment during the Holocene, while the pollen from core B details the most relevant landscape dynamics (Figs. 3 and 4). The entire record is mainly dominated by arboreal pollen, where the deciduous species that abound at the base are replaced by coniferous taxa at around 4000 cal yr BP. Shrubs and herbs increase along the record. Mediterranean taxa are present during the entire sequence, while anthropogenic indicators and charcoal rise by the middle of the sequence. Seven phases are described and summarized according to statistically significant pollen zones.

4.3.1. Phase I

This phase is dominated by herbs, mainly Poaceae and *Artemisia*, suggesting that the pond was surrounded by steppe-like grasslands (10211–10,070 cal yr BP, core A: 270–264 cm, 2 samples). The lowest montane ratio values and high proportions of *Betula* point to a nearby birch forest. This agrees with studies that indicate an early phase of birch colonization in the Pyrenees during the Late Glacial-Holocene transitional period (Reille and Lowe, 1993; Cunill et al., 2013; Gil-Romera et al., 2014). Therefore, this phase could be a transition from the steppe taxa that abounded during the colder and more-arid Younger Dryas to a deciduous forest, characteristic of the start of the Holocene (González-Sampérez et al., 2006; Reille and Lowe, 1993; Jalut et al., 1992).

The maximum values of planktonic algae (*Pediastrum*, *Botryococcus*) might indicate an increase of primary production (Jankovská and

Komárek, 2000) as a result of the relative increase of temperatures in a cold freshwater environment. The presence of *Sphagnum denticulatum* or *Sphagnum subsecundum* macroremains is characteristic of semi-submerged or flooded areas. The occurrence of *S. palustre* or *S. papillosum* also points to the early presence of *Sphagnum* lawns or low hummocks. The sediment granulometry and the lowest LOI values also suggest an open water phase with scarce vegetation. The presence of *Ranunculus* and ferns implies high moisture and an increase in the lake primary production, while the sands with broken pennate diatoms (sedimentary unit IV-A) suggest intense hydrodynamic material input events.

4.3.2. Phase II

A drop in herbaceous taxa together with the highest frequencies of deciduous taxa characterise this phase (10070–7343 cal yr BP, core A: 264–199 cm, 14 samples). Even though that there is no noticeable increase of montane taxa, the decrease in subalpine-alpine taxa prompted by a drop in Poaceae and Asteraceae led to an increase in the resulting montane ratio. According to modern analogues, the high montane ratio values correspond to the presence of the lower montane altitudinal belt (Garcés-Pastor et al., 2016). In this period, the forest shifted from a *Betula* woodland to a mixed *Corylus* and *Betula* forest with deciduous *Quercus*, *Ulmus* and some *Pinus* (Fig. 3). Meadows became scarce. The replacement of the sun-tolerant *Betula* by *Corylus* matches the natural succession of secondary species. The higher frequencies of *Corylus* compared to deciduous *Quercus* during the entire phase emphasize the colonizing capacity of the former and suggest stronger oceanic influence (González-Sampérez et al., 2006; Montserrat-Martí, 1992). This coincides with studies that reported the warmest summer temperatures during the early Holocene in the Northern Hemisphere due to maximum summer radiation and minimum winter radiation (Heiri et al., 2003; Anderson et al., 1988; Cacho et al., 2010).

In the aquatic system, the decrease in freshwater algae (*Botryococcus*, *Pediastrum*) could indicate shallower or more-turbid waters (Jankovská and Komárek, 2000), which is consistent with the presence of pennate diatoms in sedimentary unit III-A. On the other hand, the co-occurrence of species with affinity for moist (*Sphagnum denticulatum* or *subsecundum*) and dry conditions (*Sphagnum palustre* or *papillosum*, *Polytrichum*, Ericaceae) evidences a complex *Sphagnum* landscape. The decrease in Ti and Mn, with a change from sands to clays, suggests decreased sedimentary input (Nesje and Dahl, 2001). This coincides with the establishment of forests surrounding BSN, which would have promoted the rise of LOI, stabilized the soils and limited the erosion input into the lake (Fig. 3). The intercalated layer of fine silt between 9397 and 9358 cal yr BP coincides with an important montane ratio peak (243 cm), suggesting a punctual event of higher moisture that might have favoured the growth of deciduous forest. This could be related to the meltwater events of 9300 cal yr BP described in the Pyrenees and Mediterranean regions, when increased snow accumulation in winter and large snowpack melt during warmer summers led to higher run-off (Pérez-Sanz et al., 2013). Shortly later, between 9195 and 8789 cal yr BP, the drastic decrease in montane values with the rise of meadows (Apiaceae, *Artemisia* and Asteraceae) would point to colder and drier conditions. This period coincides with an episode of forest decline at around 9200 cal yr BP in the western Mediterranean (Fletcher et al., 2013) and a cold and arid event registered at 8800 cal yr BP in Bassa de la Mora Lake and the rest of the Iberian Peninsula (Pérez-Sanz et al., 2013).

By 8164 cal yr BP, the occurrence of Ti and Mn peak and a drop in LOI shortly followed by the presence of chlamydozooids of the mycorrhizic fungus *Glomus* suggest punctual runoff events (López-Vila et al., 2014). The posterior decline of the montane ratio reflects a downward shift of montane forest led by a *Betula* decrease which can be also found in Bassa de la Mora lake and the Portalet peat bog, which could point to drier summer conditions (Pérez-Sanz et al., 2013; González-Sampérez et al., 2006). The shallower waters, inferred by decrease of algae and rise of Cyperaceae and *Typha*-t pollen, could have prompted the

increase of emerged littoral areas. The drier conditions, the peaks of Ti and Mn and the drop in LOI could be related to the 8200 cal yr BP cold event that brought generally cold and dry conditions to the Northern Hemisphere (Alley and Ágústssdóttir, 2005; Rohling and Pälike, 2005) and the Central Pyrenees (González-Sampérez et al., 2006).

4.3.3. Phase III

This phase is characterised by a sharp decrease in *Corylus* and *Betula*, as the forest succession evolves (7343–5832 cal yr BP, 11 samples core A: 199–150 cm; 13 samples core B: 706–632 cm). The montane ratio decreases and fluctuates around a value of 20, which suggests punctual episodes of montane forest downward migration. Even so, the lower montane belt was still present at the site, composed of a mixed *Corylus* and deciduous *Quercus* woodland with some *Betula*, *Tilia* and *Ulmus*. Meadows increase, indicated by the rise of Poaceae and *Artemisia*. *Salix* slightly drops and *Ulmus* shows a decreasing trend, while *Alnus* rises around the end of the phase. *Abies* appears in the beginning of this phase and rises by 6356 cal yr BP. This is in line with the east-to-west colonization of the Central Pyrenees by firs (Pèlachs et al., 2009b; Matías et al., 2016). The marked reduction in *Pinus* around 7000 cal yr BP observed in core B could point to an increase in temperature and precipitation, as reported across the Iberian Peninsula (Pérez-Díaz et al., 2016) (Fig. 4). On the other hand, a higher fire frequency is inferred from the noteworthy increment of charcoal by 6200 cal yr BP (150 cm). The rise of Cyperaceae points to shallower waters and higher extent of littoral areas and, which is corroborated by the differences between both records due to small-scale spatial variability.

Among the aquatic and littoral elements, the spatial differences illustrate two scenarios. Core A shows the peatland development at the shore of the lacustrine system by 6866 cal yr BP, likely forming lawns. This is inferred from the increase in *Sphagnum* percentages dominated by *S. palustre* or *S. papillosum* with the occurrence of the cercozoan *Assulina* (185–150 cm), characteristic of non-water-saturated topsoils (Charman et al., 2000). The rise in LOI and Cyperaceae together with a decrease in planktonic algae and the change from clay with abundant diatoms to peat also supports this interpretation. In core B, the dominance of *Botryococcus*, fewer sedimentary diatoms (unit III-B) around 6822 cal yr BP and low Cyperaceae frequencies points to some water level. The change from brown-dark to brown-red clay with organic matter suggests periods of subaerial exposure or hydric fluctuations (Fig. 2). These changes in lake level might have increased water turbidity in shore environments, perhaps affecting algae development and favouring the disappearance of *Pediastrum* in core A (Jankovská and Komárek, 2000), while *Botryococcus* and *Mougeotia* rise in the shallow waters of core B. Nearby localities such as Portalet and Estanilles peat bogs and Burg Lake also recorded a transition from a lake to a peat system at similar times (González-Sampérez et al., 2006; Pérez-Obiol et al., 2012; Pèlachs et al., 2011).

4.3.4. Phase IV

A transition from deciduous to coniferous taxa marks this phase. The decrease in deciduous *Quercus* and the drop in *Betula* and *Corylus* indicate a downward shift of deciduous forest (5832–3912 cal yr BP, 10 samples core A: 150–112 cm; 19 samples core B: 632–525 cm). However, montane ratio values around 5 indicate the occurrence of upper montane forest on the site. On the other hand, *Abies* expanded and *Fagus* appeared by 4492 cal yr BP. This vegetation shift could point to rainy and warm summers, where *Abies* rose in altitude to avoid the warming, and a change to greater precipitation might have promoted a downward displacement of optimal deciduous habitats (Alba-Sánchez et al., 2010; Pèlachs et al., 2011). The replacement of *Ulmus* by *Alnus* in 5286–4054 cal yr BP is coherent with the decline of elm in the rest of the Pyrenees (Montserrat-Martí, 1992; Reille and Lowe, 1993). The establishment of emerged lands and lakeshore environments might have favoured colonization by *Alnus*

(Pérez-Obiol et al., 2016; Revelles et al., 2015). The alpine meadows continued their rising trend, dominated by Poaceae, *Artemisia* and some Apiaceae. This coincides with an intensification of anthropic pressure, as inferred by the increase in fires and agropastoral pollen indicators (*Centaurea*, *Cerealia-t*, *Potentilla*).

In the wetland plant communities, littoral site A has a peaty marsh environment, as inferred by the occurrence of aquatic plants (*Ranunculus-t* and *Typha-t*) and *Selaginella-t* since 5526 cal yr BP and a drastic decrease in *Sphagnum* percentages. Around 5043 cal yr BP, both *S. palustre* or *papillosum* and *S. denticulatum* or *subsecundum* disappeared in conjunction with a rise in Ericaceae and some *S. magellanicum*. The ombrotrophic affinity of these taxa points to drier peaty habitats. On the other hand, the water level increased at site B, as indicated by the occurrence of *Myriophyllum* and planktonic algae (*Botryococcus* and *Mougeotia*) (Grosjean et al., 2001; Van Geel, 2001). Subsequently (590 cm), the watershed shrank, giving rise to marshy conditions with the increase of *Potamogeton* and Cyperaceae and the reduction of diatoms in clay sediments, leading to peat formation by 4359 cal yr BP with a change to dark-brown clay.

A remarkable increase in erosion, likely due to a rise in the recurrence of flood events, occurred around 4049 cal yr BP, as evidenced by a sharp decrease in LOI, peaks in Ti and Mn and the presence of an inorganic silt layer in both cores. This event might have damaged the forest that surrounded the pond, with a decrease in deciduous *Quercus*, *Abies* and *Pinus* and may have prompted the rise of the montane ratio, possibly explained by the colonization of the degraded terrain by *Betula*. The presence of *Equisetum* and the absence of Ericaceae at site A, characteristic of pond margins, also suggest an increase in moisture around 3992 cal yr BP (Pérez-Haase and Ninot Sugañes, 2006). These flood events that appear locally exaggerated in BSN are in accordance with a period of wetter conditions registered between 4500 and 3900 cal yr BP at nearby study sites such as Basa de la Mora Lake and the rest of the Iberian Peninsula, such as Sanabria and Enol Lakes (Pérez-Sanz et al., 2013; Jambrina-Enríquez et al., 2014; Moreno et al., 2011). Indeed, lakes from France and Italy have also registered phases with increasing humidity in this period (Magny et al., 2013; Simonneau et al., 2013), a dynamics attributed to positive synergies between cold climatic oscillations and human-induced soil destabilization and erosion.

4.3.5. Phase V

The highest abundances of coniferous taxa suggest that the vegetation surrounding the pond was dominated by *Abies* and *Pinus* with some mixed montane forest (deciduous *Quercus*, *Betula* and *Fagus*) (3912–792 cal yr BP, 14 samples core A: 112–50 cm; 45 samples core B: 525–290 cm). Although the montane ratio continued to decline, the values around 2.75 indicate the proximity of the montane upper limit to BSN; *Alnus* still dominated the riverine forest. On the other hand, a higher anthropic pressure (3000 cal yr BP) through forest clearance is evidenced by the intensification of fires, the noteworthy rise of shrubs (Ericaceae) and the increase of agropastoral indicators (*Cerealia-t*, *Potentilla*).

Regarding the aquatic system, site A continues showing a pond margin scenario at 4049–1455 cal yr BP with the continuity of *Equisetum* and the absence of Ericaceae, while site B still has some water level, as inferred by the rise of *Myriophyllum* and the presence of diatoms in the sediment (Grosjean et al., 2001). However, their decrease at 3169–2303 cal yr BP points to shallower waters and matches a period of intensified aridity in the Pyrenees and across the Mediterranean (Pérez-Sanz et al., 2013; Jalut et al., 2000). The chemical elements remain stable along the phase until 1369–1231 cal yr BP, when an important drop in Ti coincides with an intercalated layer of fine silt (unit II-A) and Ericaceae macroremains at site A, pointing to a period of dried substrate and lower sedimentary input.

4.3.6. Phase VI

This phase is marked by the highest values of *Prunus-t* and a notable rise in herbs (Poaceae, *Artemisia*, Chenopodiaceae/Amaranthaceae) (792–386 cal yr BP, 3 samples core A: 50–38 cm; 21 samples core B: 290–200 cm). *Abies* and *Pinus* forest remained in detriment of deciduous vegetation (deciduous *Quercus*, *Fagus* and *Betula*), which experienced a downward shift, supported by montane values below 2.75. The increase of meadows and the co-occurrence of charcoal and anthropogenic pollen indicators (*Secale cereale*, Cerealia-t) indicate the continuity of forest clearances for agropastoral purposes.

In the wetland community, *Sphagnum* values >40% in site A show the development of drier *S. magellanicum* and *S. capillifolium* hummocks, with Ericaceae and *Polytrichum* (Pérez-Haase and Ninot Sugrañes, 2006) between 499 and 465 cal yr BP. At site B, the transition from *Myriophyllum* to *Potamogeton* by 544 cal yr BP points to a lower lake level. Moreover, a paleoecological study of the last 1000 years in BSN (Garcés-Pastor et al., 2016) reported extreme fluctuations of diatom concentrations and a decrease of planktonic frequencies, which were interpreted as responses to periods of strong seasonality and hydric fluctuations (Fig. 4).

4.3.7. Phase VII

The highest values of Poaceae and lowland pollen (evergreen *Quercus*, *Olea*) characterise this phase (386 cal yr BP–present, 8 samples core A: 38–0 cm; 16 samples core B: 200–0 cm). A conifer forest (*Abies*, *Pinus*) surrounded BSN, while the low montane ratio values show the continuity of the montane boundary at lower altitudes. The understorey (Ericaceae) and alpine meadows grew. The decrease in fires and agropastoral indicators (*Prunus-t*, Cerealia-t), with the highest values of *Potentilla* between 160 and 110 cm, suggest a complex agroforestral system with a dominance of pastoral activities (Garcés-Pastor et al., 2016).

On the aquatic system, the dominance of Cyperaceae points to the continuity of a thin water layer. The establishment of the peat bog at site B at around 370 cal yr BP was marked by a change from dark-brown to red-brownish fibrous peat moss. At the littoral site A, the disappearance of *Equisetum* by 171 cal yr BP suggests less moisture. Finally, the higher percentages of *Sphagnum* (*S. capillifolium* and *S. magellanicum*) and Ericaceae point to the establishment of an ombrotrophic hummock in recent times.

5. Discussion

5.1. Vegetation response to the North Atlantic influence: montane ratio and IRD

The ice rafted debris (IRD) index from the North Atlantic (Bond et al., 2001) has been used as an indicator of general climatic patterns during the Holocene in regions influenced by North Atlantic Ocean circulation (Battarbee et al., 2004). High IRD values have been correlated with southward displacements of the Atlantic westerly jet, prompting increased precipitation and higher water levels in mid-European lakes (Magny et al., 2001; Magny, 2004). Likewise, in the Pyrenees, González-Sampériz et al. (2006) reported a translation of climate variability from the North Atlantic to the mid-latitudes, and Pélachs et al. (2011) found a correlation between IRD and deciduous tree pollen percentages in Burg Lake, where high IRD corresponded to wetter and occasionally colder conditions.

With the aim of evaluating the North Atlantic influence in BSN vegetation shifts, we compared the montane ratio with the IRD index (Fig. 5). Cores A and B present different behaviour because of their varying sedimentation rates. Core A shows a smoothed curve along the record since it has a lower sedimentation rate. On the other hand, core B offers a greater detail of the altitudinal shifts due to its higher sedimentation rate and resolution. Similar montane ratio and IRD trends are apparent during the first half of our records

(between 10,200 and 5300 cal yr BP), when high IRD values (the main Bond events 6, 5 and 4 and other secondary peaks) coincide with increases in the montane ratio (10,000; 9400; 8100; 7300; 6800; 5750; 5500; 5300 cal yr BP). The remarkable montane peak at around 9400 cal yr BP (core A), which could be related to a punctual high moisture event, has also been registered in Burg and Redon Lakes as a phase of low LOI and colder winter/spring temperatures (Pla and Catalan, 2005; Pélachs et al., 2011). However, by the end of Bond event 4, the montane ratio starts to decouple from IRD, and fully decoupled trends can be seen henceforth during the most recent half of our records, when the montane ratio maintains stably low values, despite the occurrence of several Bond events with high IRD values (Fig. 5). Therefore, montane ratio peaks during the first half (10200–5300 cal yr BP) may be related to the growth of deciduous taxa in response to a regional rise of moisture in the Northern Hemisphere, in agreement with Pélachs et al. (2011). However, the increasing mismatch between both trends suggests that other pressures besides the North Atlantic climate (probably at a more local level) have ultimately influenced BSN vegetation. Regarding those pressures, charcoal notably increased around 6700 cal yr BP, indicating that fires in the area might have affected the montane forest and prompted the early decrease of the montane ratio by 6650 cal yr BP. Shortly later, in 6400–6100 cal yr BP, charcoal becomes recurrently abundant, coinciding with a notable decrease of *Betula* and the montane ratio. Indeed, *Betula* and the montane ratio fall to even lower values around 6140 cal yr BP, when a notable charcoal peak occurs (Fig. 5). During that period, frequent fires might have interfered with the response of montane vegetation to the regional moisture increase inferred from higher IRD. By 5700 cal yr BP, charcoal notably increased, suggesting higher fire frequency. This coincides with a drop of *Corylus*, suggesting that fires may have burnt the montane forest and favoured resprouting species such as Ericaceae. Even though the fire frequency was reduced around 5400 cal yr BP, the montane ratio did not respond to the rise of IRD by 5250 cal yr BP. However, a period with less fires could have prompted the recovery of the montane ratio by 5100 cal yr BP, which responded to IRD with a slight delay until 4750 cal yr BP.

Thus, the montane vegetation responded to climatic forcing from 10,200 to 6700 cal yr BP, followed by a transition period (5700–5250 cal yr BP) when fires could have affected the resilience of deciduous vegetation, hampering its response to climate. These results agree with those found in the nearby Basa de la Mora Lake, which also presented a retreat in deciduous taxa from 5700 cal yr BP, when frequent fires and climatic forcings overcame the regeneration capacity of the vegetation (Lasheras-Álvarez et al., 2013). Although Portalet peat bog shows a hiatus by this transition period, it also recorded a contraction of deciduous forest from 7700 cal yr BP, attributed to a threshold response of the ecosystem to high fire frequencies (Gil-Romera et al., 2014). Burjachs and Expósito (2015) also noted that vegetation in the Mediterranean area of the Iberian Peninsula was more resilient during the first half of the Holocene than in the recent Holocene. By 5250 cal yr BP, climate and fires could have weakened the resilience of deciduous vegetation beyond a threshold that prompted the progressive downward shift of montane vegetation between 5300 and 4200 cal yr BP in BSN. Indeed, Pla and Catalan (2005) showed that the climate was more continental before 4000 cal yr BP, whereas Jalut et al. (2000) and Pérez-Sanz et al. (2013) reported a change in precipitation seasonality towards more frequent summer droughts, namely, a transition from a significant Atlantic influence to a typical Mediterranean climate that affected the deciduous forest composition and resilience while promoting fires.

5.2. Local differences in the response of organic matter accumulation to the North Atlantic influence: LOI and IRD

The close correlation found between Bond IRD oscillations and the accumulation of organic matter reported in Burg Lake (1821 m a.s.l.)

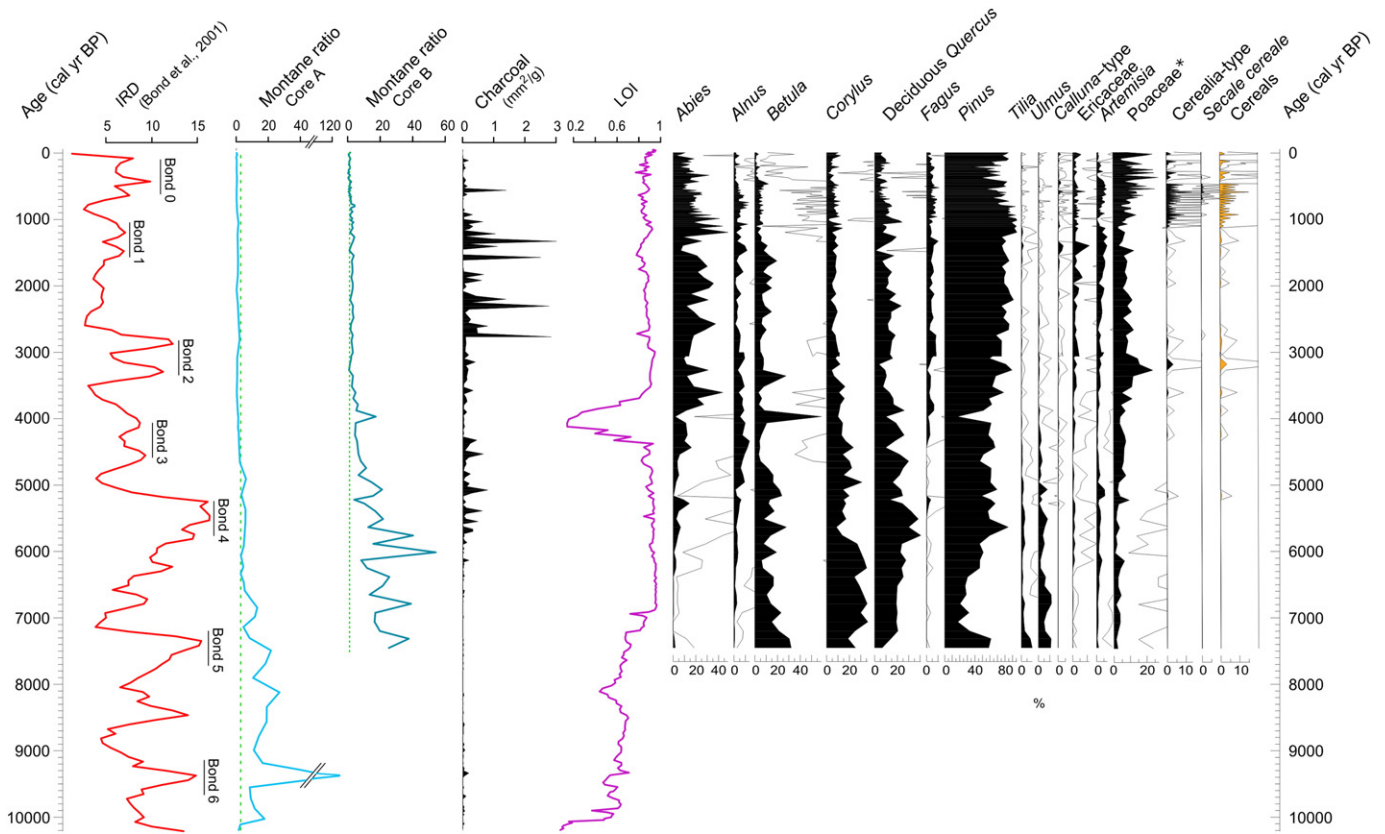


Fig. 5. Summary diagram grouping IRD (Bond et al., 2001), Bond events, montane ratio of cores A and B, Charcoal concentration (mm²/g), LOI and relevant selected pollen taxa of core B.

by Pèlach et al. (2011) suggests a direct North Atlantic influence on climate fluctuations in the Central Pyrenees. Of the Pyrenean studies that have used loss on ignition as an organic matter indicator (Pla and Catalan, 2005; González-Sampérez et al., 2006; Pèlach et al., 2011), Burg is the only lentic system with a continuous record that can be compared to our results. The proximity between BSN and Burg (34.5 km) makes them suitable places to study the response of subalpine ecosystems at the regional level. However, the LOI trend at BSN differs from the oscillating record at Burg. In BSN, the LOI values approach 90% by 6900 cal yr BP (Figs. 3 and 5) and stay rather constant except for a remarkable decrease around 4049 cal yr BP. Conversely, Burg has stronger LOI oscillations, reaching 90% values by 5100 cal yr BP and fluctuating thereafter following the IRD trend (Pèlach et al., 2011). Although both records have a different response amplitude, they present some similarities in 5500–3800 cal yr BP, and we hypothesise that this corresponds to a wetland phase, according to a sediment change from organic silt to peat and higher LOI values at both sites. In this general trend, several aridity phases have been identified at different moments on the Iberian Peninsula during the Middle Holocene, for example, between 6200 and 5600 and 4600–4300 cal yr BP (Pérez-Sanz et al., 2013; Pèlach et al., 2007; Azuara et al., 2015). The LOI at BSN is less sensitive to global climate changes than at Burg and thus shows a high influence of local factors, which might have hidden any direct relationship between IRD oscillations and BSN peat bog development (Mäukilä, 1997). The accumulation of organic matter in a wetland is promoted by temperature and/or water inundation (Crawford et al., 2003), the latter being mainly controlled by precipitation (Charman et al., 2009). Therefore, we can attribute differences in the LOI trends between both sites to contrasting water inundation patterns. The higher and more constant values of LOI in BSN suggest less water table variations than Burg. These differences could have been influenced by the orographic conditions of both sites, which would have determined the precipitation regime. Although significant environmental changes

occurred in BSN during the entire record, these shifts do not seem to have influenced the LOI values, highlighting that the local influence is too important to allow climatic inferences from this variable. On the other side, Burg could have been more dependent on precipitation that would have prompted an increase of paludification and LOI fluctuations. On the other hand, the Portalet peat bog (1802 m a.s.l.) was established after 6400 cal yr BP, reached LOI values around 40% and fluctuated thereafter due to alternate periods of peat and shallow clastic lake deposition, until a hiatus in 5300 cal yr BP (González-Sampérez et al., 2006). Finally, the Molina peat bog, located in north-west Spain (Cantabrian region) was established around 6000 cal yr BP and reached LOI values close to 90% and then remained stable until the last millennium (Pérez-Obiol et al., 2016). These different scenarios show how local influence could limit the suitability of LOI as a paleoclimate indicator in the case of peat bog systems. However, it may be more useful in environments with higher Mediterranean influence where climatic oscillations are more pronounced (Azuara et al., 2015).

5.3. Anthropogenic influence: fire and crops

The low fire frequency and the absence of anthropic indicators between 9968 and 8548 cal yr BP in Bassa Nera could be attributed to natural fires prompted by the large amounts of deciduous biomass, as occurred in the nearby Portalet peat bog and Basa de la Mora Lake in the same period (Gil-Romera et al., 2014; Lasheras-Álvarez et al., 2013).

The BSN catchment is surrounded by many archaeological sites that evidence human occupation and exploitation of the high mountains of the Pyrenees since the Neolithic (from 9000 to 8571 cal BP) (Gassiot et al., 2014). The first anthropic evidence in the PNAESM area is some hunting artefacts from 7650 to 7325 cal yr BP found in Sardo cave, located 9 km from BSN (Gassiot et al., 2012). Shortly after, the rise in agropastoral indicators in BSN (*Artemisia*, *Asteraceae*, *Potentilla*, *Galium*, *Centaurea*, *Rumex*) and charcoal particles indicate grazing activities

between 7343 and 5832 cal yr BP. This is coherent with agropastoral activities recorded in the nearby records of Sardo cave (Gassiot et al., 2012), Bosc dels Estanyons (Miras et al., 2007) and the Estanilles peat bogs (Cunill et al., 2013). The intermittent presence of Cerealia-t pollen in our records between 5190 cal yr BP and 2000 cal yr BP, together with agropastoral indicators and charcoal, might be evidence of some cereal-based agriculture near BSN. Although the first record is a punctual event (5190 cal yr BP), it fits with the development of cereal-based subsistence in the area, coinciding with cereal seeds found in Sardo cave and Cerealia-t pollen recorded in the Burg lake and Madriu valley records (Pèlachs et al., 2007; Miras et al., 2007; Gassiot et al., 2014). A higher fire frequency in 5190–4300 cal yr BP and the rise in pastoral indicators (*Potentilla*, *Rumex*) suggest an increase in grazing activities in BSN, coinciding with an intensification of archaeological settlements found in PNAESM (Sardo cave, Estany de la Coveta I, Obagues de Ratera and Saboredo). These lines of evidence of high mountain exploitation in the Central Pyrenees (Gassiot et al., 2014; Pèlachs et al., 2007; Jalut et al., 2000) were probably prompted by the increased frequency of dry summers around 4600–4300 cal yr BP in the Mediterranean area (Jalut et al., 2000; Azuara et al., 2015). The rise of fires during the Bronze Age and the scattered presence of Cerealia-t (4230–3500 cal yr BP) point to forest clearance and occasional crops. The spread of *Fagus*, which occurred in the same period (Fig. 4), could have been favoured by the resulting open spaces from anthropogenic disturbance followed by a change to higher precipitation (Miras et al., 2007; Pèlachs et al., 2009b). The rise of *Fagus* in BSN fits with its expansion in the Pyrenees and Cantabrian mountains (Pérez-Sanz et al., 2013; Montserrat-Martí, 1992; Magri, 2008). During the Late Bronze Age (3150–2650 cal yr BP), agricultural landscapes were established in BSN with the rise of Cerealia-t and agropastoral indicators (*Centaurea*, *Potentilla*, *Artemisia*, *Asphodelus*). This agrees with the record of higher anthropic pressure through farming and pasturing activities found in the nearby Burg, Estanilles and Bosc dels Estanyons peat bogs (Bal et al., 2011; Pérez-Obiol et al., 2012; Miras et al., 2007). Fires increased by 2800 cal yr BP, and Cerealia-t reappeared with the Roman Period (2000 cal yr BP). By the Middle Ages (1100 cal yr BP), an intensification of agriculture and livestock is indicated by the rise of Cerealia-t, grazing indicators (*Galium*, *Potentilla*) and fires, coinciding with an increase of human settlements in PNAESM and the Central Pyrenees (Catalan et al., 2013). At 800 cal yr BP, the appearance of *Secale cereale* together with the rise of Poaceae, agropastoral and arboriculture indicators (*Rumex*, *Artemisia*, *Castanea*, *Juglans*) point to crop diversification and an increase of pastures (Garcés-Pastor et al., 2016). The rise of *Prunus*-t in this period could be related to cultivated species such as *P. domestica* or *P. avium*. From 450 cal yr BP, the scattered cereal presence and the higher amounts of Poaceae and pastoral pollen (*Potentilla*, *Urtica*) suggest the abandonment of farming, the spread of meadows and the highest grazing exploitation period of the sequence. The resulting opening of the landscape would have led to the higher upward flow of *Olea* and evergreen *Quercus* from an increase of agricultural practices in the lowlands (Cañellas-Boltà et al., 2009). Since 120 cal yr BP, the forest clearance and a peak in Poaceae might be the result of an increased need for supplies and raw materials during the Industrial Revolution (Garcés-Pastor et al., 2016). Later, the disappearance of cereals and the reduction of agropastoral pollen indicate crop abandonment. However, the presence of *Potentilla* suggests some grazing activity until the establishment of the PNAESM in 1955 cal AD and the protection of its surroundings in 1990 cal AD.

Agriculture in BSN has passed through short exploitation phases interspersed with periods of land abandonment and grazing. Some authors suggest that these human occupation phases could be a result of the synergic effects between climate changes and human activity (Gassiot et al., 2012; Jalut et al., 2009). To check whether the occupation phases in BSN could have been prompted by climate, we compared IRD with the Cerealia-t pollen frequencies (Fig. 5). Our results suggest that cereals rise when IRD presents low values (c. 5200, 4250, 3600, 3180,

1950, 1300 cal yr BP), in agreement with Pèlachs et al. (2011) in Burg lake. The only occurrence of cereals with high IRD values occurs with *Secale cereale* in 750–500 cal yr BP, known for its resistance to cold environments and which is also cultivated in the Estanilles peat bog (Cunill et al., 2013; Pérez-Obiol et al., 2012). In agreement with the appearance of cereals in other studies of the Central Pyrenees and coinciding with Magny (2004) the development of cereal-based subsistence in BSN could have been prompted by the rise of the regional population and by dry conditions. The farming activities in BSN and their influence in the environment became evident during the Bronze Age and intensified in the Roman period and Middle Ages.

6. Conclusions

In this multi-proxy study we reconstructed the palaeoecological and ontogenic events recorded in Bassa Nera during the last 10,200 cal yr BP. Changes in aquatic taxa, macroremains and sedimentary units show a non-linear development of the peat bog over the larger previous lake. The study of two separated cores allowed us to compare some remarkable spatial differences that took place within the same catchment. The pollen and the montane ratio were useful to infer structural and altitudinal changes in montane forest through the last 10,200 cal yr BP. Vegetation strongly responded to climate during the first half of the Holocene (10200–6700 cal yr BP) with punctual episodes of downward shift in the montane forest. *Abies* appeared by 6356 cal yr BP and expanded. Then, a transition period took place (5700–5250 cal yr BP) when climate and fires prompted a progressive downward shift of montane vegetation and its replacement by coniferous taxa, which has dominated the catchment with some mixed montane forest since 3912 cal yr BP. The montane ratio was a useful tool for summarizing palaeopalynological data, enabling the assessment of the potential correlations between changes in vegetal communities and the climatic forcing indicated by the IRD, and highlighting the different responses of the vegetation to the North Atlantic influence in Bassa Nera during the Holocene. The study of LOI and sedimentary units allowed us to infer important flood events between 4500 and 3900 cal yr BP. From 7300 cal yr BP onwards, charcoal and pollen indicators evidence human disturbance through grazing, pointing to the use of fire as a tool for forest clearance or maintaining open spaces. The first cereal crops in Bassa Nera occurred around 5190 cal yr BP and coincided with dry climate conditions until the cultivation of cold resistant species like *Secale cereale*. The second half of the Holocene features phases with increased occurrence of agricultural practices alternating with land abandonment and grazing. Notable periods of anthropic pressure include the Late Bronze Age, with the establishment of agricultural landscapes, followed by the Roman Period and Middle Ages. The results from this study highlight the sensitivity of the high-mountain vegetation of the Central Pyrenees to climate changes and anthropic pressures.

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References

- Alba-Sánchez, F., López-Sáez, B., Pando Linares, B., Nieto-Lugilde, D., López-Merino, L., 2010. Past and present potential distribution of the Iberian *Abies* species: a phytogeographic approach using fossil pollen data and species distribution models. *Divers. Distrib.* 16, 214–228.
- Alley, R.B., Ágústssdóttir, A.M., 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. *Quat. Sci. Rev.* 24, 1123–1149.
- Anderson, P.M., Barnosky, C.W., Bartlein, P.J., Behling, P.J., Brubaker, L., Cushing, E.J., Dodson, J., Dworetzky, B., Guetter, P.J., Harrison, S.P., Huntley, B., Kutzbach, J.E., Markgraf, V., Marvel, R., McGlone, M.S., Mix, A., Moar, N.T., Morley, J., Perrott, R.A., Peterson, G.M., Prell, W.L., Prentice, I.C., Ritchie, J.C., Roberts, N., Ruddiman, W.F., Salinger, M.J., Spaulding, W.G., Street-Perrott, F.A., Thompson, R.S., Wang, P.K., Webb, T.L., Winkler, M.G., Wright, H.E.J., 1988. Climatic changes of the last 18,000 years: observations and model simulations. *Science* 241 (4869) (p. 1043–1052 241, 1043–1052).
- Azuara, J., Combourieu-Nebout, N., Lebreton, V., Mazier, F., Müller, S.D., Dezileau, L., 2015. Late Holocene vegetation changes in relation with climate fluctuations and human activities in Languedoc (Southern France). *Clim. Past Discuss.* 11:4123–4157. <http://dx.doi.org/10.5194/cpd-11-4123-2015>.
- Bal, M.C., Rendu, C., Ruas, M.P., Campmajo, P., 2010. Paleosol charcoal: reconstructing vegetation history in relation to agro-pastoral activities since the Neolithic. A case study in the Eastern French Pyrenees. *J. Archaeol. Sci.* 37, 1785–1797.
- Bal, M.-C., Pelachs, A., Perez-Obiol, R., Julia, R., Cunill, R., 2011. Fire history and human activities during the last 3300 cal yr BP in Spain's central Pyrenees: the case of the Estany de Burg. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 300, 179–190.
- Battarbee, R.W., Gasse, F., Stickley, C.E., 2004. Past climate variability through Europe and Africa. *Developments in Palaeoenvironmental Research*. <http://dx.doi.org/10.1007/978-1-4020-2121-3>.
- Benito, M., Sánchez de Dios, R., Sainz, H., 2008. The evolution of the *Pinus sylvestris* L. area in the Iberian peninsula from the last glacial maximum to 2100 under climate change. *The Holocene* 18, 705–714.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol.* 132 (1), 155–170.
- Bennett, K.D., 2002. Documentation for PSIMPOLL 4.10 and PSCOMB 1.03. C Programs for Plotting Pollen Diagrams and Analysing Pollen Data. Cambridge.
- Birks, H.J.B., Birks, H.H., 1980. *Quaternary Palaeoecology*. London.
- Blaauw, M., 2010. Methods and code for “classical” age-modelling of radiocarbon sequences. *Quat. Geochronol.* 5, 512–518.
- Bond, G., Kromer, B., Beer, J., Muscheler, R., Evans, M.N., Showers, W., Hoffmann, S., Lottibond, R., Hajdas, I., Bonani, G., 2001. Persistent solar influence on North Atlantic climate during the Holocene. *Science* 294, 2130–2136.
- Brugués, M., Cros, R.M., Guerra, J., 2007. Flora Briofítica Ibérica. Sphagnales, Andreales, Polytrichales, Tetraphidales, Buxbaumbiales, Diphyssiales.
- Burjachs, F., Expósito, I., 2015. Charcoal and pollen analysis: examples of Holocene fire dynamics in Mediterranean Iberian peninsula. *Catena* 135:340–349. <http://dx.doi.org/10.1016/j.catena.2014.10.006>.
- Cacho, I., Valero-Garcés, B.L., González-Sampérez, P., 2010. Revisión de las reconstrucciones paleoclimáticas en la Península Ibérica desde el último periodo glacial.
- Cañellas-Boltà, N., Rull, V., Vigo, J., Mercadé, A., 2009. Modern pollen-vegetation relationships along an altitudinal transect in the central Pyrenees (southwestern Europe). *The Holocene* 19 (8), 1185–1200.
- Carcaillet, C., Bouvier, M., Fréchette, B., Larouche, A.C., Richard, P.J.H., 2001. Comparison of pollen-slide and sieving methods in lacustrine charcoal analyses for local and regional fire history. *The Holocene* 11, 467–476.
- Catalan, J., Pla-Rabés, S., Wolfe, A.P., Smol, J.P., Rühland, K.M., Anderson, N.J., Kopáček, J., Stuchlík, E., Schmidt, R., Koinig, K.A., Camarero, L., Flower, R.J., Heiri, O., Kamenik, C., Korhola, A., Leavitt, P.R., Pensner, R., Renberg, I., 2013. Global change revealed by palaeolimnological records from remote lakes: a review. *J. Paleolimnol.* 49, 513–535.
- Charman, D.J., Hendon, D., Woodland, W.A., 2000. The Identification of Testate Amoebae (Protozoa: Rhizopoda) in Peats. Technical Guide, London.
- Charman, D.J., Barber, K.E., Blaauw, M., Langdon, P.G., Mauquoy, D., Daley, T.J., Hughes, P.D.M., Karofeld, E., 2009. Climate drivers for peatland palaeoclimate records. *Quat. Sci. Rev.* 28:1811–1819. <http://dx.doi.org/10.1016/j.quascirev.2009.05.013>.
- Crawford, R.M.M., Jeffree, C.E., Rees, W.G., 2003. Paludification and forest retreat in northern oceanic environments. *Ann. Bot.* 91:213–226. <http://dx.doi.org/10.1093/AOB/MCF185> (Spec No).
- Cunill, R., Soriano, J.M., Bal, M.C., Pélachs, A., Rodríguez, J.M., Pérez-Obiol, R., 2013. Holocene high-altitude vegetation dynamics in the Pyrenees: a pedoanthracology contribution to an interdisciplinary approach. *Quat. Int.* 3 (289), 60–70.
- Daniels, R.E., Eddy, A., Institute of Terrestrial Ecology, A. (Alan), 1990. *Handbook of European Sphagna*. Natural Environment Research Council, Institute of Terrestrial Ecology.
- Davies, S.J., Lamb, H.F., Roberts, S.J., 2015. Micro-XRF Core Scanning in Palaeolimnology: Recent Developments. Springer, Netherlands:pp. 189–226. http://dx.doi.org/10.1007/978-94-017-9849-5_7.
- Ejarque, A., Miras, Y., Riera, S., Palet, J.M., Orengo, H.A., 2010. Testing micro-regional variability in the Holocene shaping of high mountain cultural landscapes: a palaeoenvironmental case-study in the eastern Pyrenees. *J. Archaeol. Sci.* 37, 1458–1479.
- Faegri, K., Iversen, J., 1989. *Paysages du Néolithique à nos jours dans les Pyrénées de l'Est d'après l'écologie historique et l'archéologie pastorale*. Textbook of Pollen Analysis. fourth ed. The Blackburn Press, New Jersey.
- Fletcher, W.J., Debret, M., Goni, M.F.S., 2013. Mid-Holocene emergence of a low-frequency millennial oscillation in western Mediterranean climate: implications for past dynamics of the North Atlantic atmospheric westerlies. *The Holocene* 23:153–166. <http://dx.doi.org/10.1177/0959683612460783>.
- Garcés-Pastor, S., Cañellas-Boltà, N., Clavaguera, A., Calero, M.A., Vegas-Vilarrubia, T., 2016. Vegetation shifts, human impact and peat bog development in Bassa Nera pond (Central Pyrenees) during the past millennium. *The Holocene*. <http://dx.doi.org/10.1177/0959683616670221>.
- Gassiot, E., Jiménez, J.P.A., 2006. Nuevas Aportaciones al Estudio de la Prehistoria y la Protohistoria en las Zonas Altas del Pallars Sobirà: Planteamientos, Resultados y Potencialidad. *Simbolismo, Arte E Espacios Sagrados Na Pré-História Da Península Ibérica*. Actas Do IV Congreso de Arqueología Peninsular. Promotoria Monográfica 05. p. Faro. Universidade do Algarbe, pp. 169–179.
- Gassiot, E., Mazzucco, N., Clemente, I., Antón, D.R., Ortega, D., 2012. Circulación e intercambio en el poblamiento y la explotación de la alta montaña del Pirineo en los milenios V-IV a.n.e. *Rubricatum Rev. del Mus. Gavà* 0, 61–68.
- Gassiot, E., Rodríguez Antón, D., Pélachs, A., Pérez Obiol, R., Julià, R., Bal, M.C., Mazzucco, N., 2014. La alta montaña durante la Prehistoria: 10 años de investigación en el Pirineo catalán occidental. *Trab. Prehist.* 2, 261–281.
- Gil-Romera, G., González-Sampérez, P., Lasheras-Álvarez, L., Sevilla-Callejo, M., Moreno, A., Valero-Garcés, B., López-Merino, L., Carrión, J.S., Pérez Sanz, A., Aranbarri, J., García-Prieto Fronce, E., 2014. Biomass-modulated fire dynamics during the last glacial-interglacial transition at the Central Pyrenees (Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 402:113–124. <http://dx.doi.org/10.1016/j.palaeo.2014.03.015>.
- González-Sampérez, P., Valero-Garcés, B.L., Moreno, A., Jalut, G., García-Ruiz, J.M., Martí-Bono, C., Delgado-Huertas, A., Navas, A., Otto, T., Dedoubat, J.J., 2006. Climate variability in the Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. *Quat. Res.* 66, 38–52.
- Grosjean, M., van Leeuwen, J.F., van der Knaap, W., Geyh, M., Ammann, B., Tanner, W., Messerli, B., Núñez, L., Valero-Garcés, B., Veit, H., 2001. A 22,000 14C year BP sediment and pollen record of climate change from Laguna Miscanti (23°S), northern Chile. *Glob. Planet. Chang.* 28:35–51. [http://dx.doi.org/10.1016/S0921-8181\(00\)00063-1](http://dx.doi.org/10.1016/S0921-8181(00)00063-1).
- Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25:101–110. <http://dx.doi.org/10.1023/A:1008119611481>.
- Heiri, O., Lotter, A.F., Hausmann, S., Kienast, F., 2003. A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. *The Holocene* 13, 477–484.
- Jalut, G., Montserrat, J., Fortugne, M., Delibrias, G., Vilaplana, J.M., Julià, R., 1992. Glacial to interglacial vegetation changes in the northern and southern Pyrenees: deglaciation, vegetation cover and chronology. *Quat. Sci. Rev.* 11, 449–480.
- Jalut, G., Esteban Amat, A., Bonnet, L., Gauquelin, T., Fontugne, M., 2000. Holocene climatic changes in the Western Mediterranean, from south-east France to south-east Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 160:255–290. [http://dx.doi.org/10.1016/S0031-0182\(00\)00075-4](http://dx.doi.org/10.1016/S0031-0182(00)00075-4).
- Jalut, G., Dedoubat, J.J., Fontugne, M., Otto, T., 2009. Holocene circum-Mediterranean vegetation changes: climate forcing and human impact. *Quat. Int.* 200, 4–18.
- Jambrina-Enríquez, M., Rico, M., Moreno, A., Leira, M., Bernárdez, P., Prego, R., Recio, C., Valero-Garcés, B.L., 2014. Timing of deglaciation and postglacial environmental dynamics in NW Iberia: the Sanabria Lake record. *Quat. Sci. Rev.* 94, 136–158.
- Jankovská, V., Komárek, J., 2000. Indicative value of *Pediastrum* and other coccal green algae in palaeoecology. *Folia Geobot.* 35:59–82. <http://dx.doi.org/10.1007/BF02803087>.
- Jowsey, P.C., 1966. An improved peat sampler. *New Phytol.* 65, 245–248.
- Lasheras-Álvarez, L., Pérez Sanz, A., Gil Romera, G., González Sampérez, P., Sevilla Callejo, M., Valero Garcés, B.L., 2013. Historia del fuego y la vegetación en una secuencia holocena del Pirineo central: la Basa de la Mora. *Cuad. Investig. Geográfica*, (ISSN 0211-6820), Nº 39, 1, 2013, págs. 77–95.
- Last, W.M., Smol, P., 2001. *Tracking Environmental Change Using Lake Sediments, Volume 1: Basin Analysis, Coring, and Chronological Techniques*. Kluwer Academic Publishers, New York, Boston, Dordrecht, London, Moscow.
- López-Vila, J., Montoya, E., Cañellas-Boltà, N., Rull, V., 2014. Modern non-pollen palynomorphs sedimentation along an elevational gradient in the south-Central Pyrenees (southwestern Europe) as a tool for Holocene paleoecological reconstruction. *The Holocene* 24, 327–345.
- Luque Marín, J.A., 2003. *El Lago de Sanabria: un sensor de las oscilaciones climáticas del Atlántico Norte durante los últimos 6.000 años*. Doctoral thesis, Universitat de Barcelona.
- Magny, M., 2004. Holocene climate variability as reflected by mid-European lake-level fluctuations and its probable impact on prehistoric human settlements. *Quat. Int.* 113:65–79. [http://dx.doi.org/10.1016/S1040-6182\(03\)00080-6](http://dx.doi.org/10.1016/S1040-6182(03)00080-6).
- Magny, M., Guiot, J., Schoellammer, P., 2001. Quantitative reconstruction of Younger Dryas to mid-Holocene paleoclimates at Le Locle, Swiss Jura, using pollen and lake-level data. *Quat. Res.* 56:170–180. <http://dx.doi.org/10.1006/qres.2001.2257>.
- Magny, M., Combourieu-Nebout, N., Beaulieu, J.L. De, Bout-Roumazielles, V., Colombaroli, D., Desprat, S., Francke, A., Joannin, S., Peyron, O., Revel, M., Sadori, L., Siani, G., Sicre, M.A., Samartin, S., Simonneau, A., Tinner, W., Vannièrè, B., Wagner, B., Zanchetta, G., Anselmetti, F., Brugiapaglia, E., Chapron, E., Debret, M., Desmet, M., Didier, J., Essallami, L., Galop, D., Gilli, A., Haas, J.N., Kallel, N., Millet, L., Stock, A., Turon, J.L., Wirth, S., 2013. North-south palaeohydrological contrasts in the central Mediterranean during the Holocene: tentative synthesis and working hypotheses. *Clim. Past Discuss.* 9, 1901–1967 (IF 3,509).
- Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). *J. Biogeogr.* 35, 450–463.
- Matías, L., González-Díaz, P., Quero, J.L., Camarero, J.J., Lloret, F., Jump, A.S., 2016. Role of geographical provenance in the response of silver fir seedlings to experimental warming and drought. *Tree Physiol.* 36:1236–1246. <http://dx.doi.org/10.1093/treephys/tpw049>.
- Mäukilä, M., 1997. Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland. *Boreas* 26:1–14. <http://dx.doi.org/10.1111/j.1502-3885.1997.tb00647.x>.

- Mauquoy, D., Hughes, P., van Geel, B., 2010. A protocol for plant macrofossil analysis of peat deposits. *Mires Peat* 7.
- Miras, Y., Ejarque, A., Riera, S., Palet, J.M., Orengo, H., Euba, I., 2007. Holocene vegetation changes and land-use history in the Andorran Pyrenees since the Early Neolithic: the pollen record of Bosc dels Estanyons (2180 m a.s.l., Vall del Madriu, Andorra). *Dyn. holocène la végétation Occup. des Pyrénées andorranes depuis le Néolithique ancien, d'après l'analyse pollinique la tourbière Bosc dels Estanyons* (2180 m, Vall del Madriu, Andorre). 6:pp. 291–300. <http://dx.doi.org/10.1016/j.crpv.2007.02.005>.
- Montserrat-Martí, J., 1992. Evolución glaciaria y postglaciaria del clima y la vegetación en la vertiente sur del Pirineo: estudio palinológico. *Monogr. del Inst. Piren. Ecol.* 6, 145.
- Moore, P., Webb, J., Collison, M., 1991. *Pollen Analysis*. Hodder & Stoughton, Blackwell Science, London, etc.
- Moreno, A., López-Merino, L., Leira, M., Marco-Barba, J., González-Sampérez, P., Valero-Garcés, B.L., López-Sáez, J.A., Santos, L., Mata, P., Ito, E., 2011. Revealing the last 13,500 years of environmental history from the multiproxy record of a mountain lake (Lago Enol, northern Iberian Peninsula). *J. Paleolimnol.* 46, 327–349.
- Nesje, A., Dahl, S.O., 2001. The Greenland 8200 cal. yr BP event detected in loss-on-ignition profiles in Norwegian lacustrine sediment sequences. *J. Quat. Sci.* 16:155–166. <http://dx.doi.org/10.1002/jqs.567>.
- Ninyerola, M., Pons, X., Roure, J.M., 2003. *Atlas Climàtic Digital de Catalunya* Universitat Autònoma de Barcelona.
- Pèlachs, A., Soriano, J.M., Nadal, J., Esteban, A., 2007. Holocene environmental history and human impact in the Pyrenees. *Contrib. to Sci.* 3:421–429. <http://dx.doi.org/10.2436/20.7010.01.19>.
- Pèlachs, A., Nadal, J., Soriano, J.M., Molina, D., Cunill, R., 2009a. Changes in pyrenean woodlands as a result of the intensity of human exploitation: 2,000 years of metallurgy in Vallferrera, northeast Iberian peninsula. *Veg. Hist. Archaeobotany* 18, 403–416.
- Pèlachs, A., Pérez-Obiol, R., Ninyerola, M., Nadal, J., 2009b. Landscape dynamics of *Abies* and *Fagus* in the southern Pyrenees during the last 2200 years as a result of anthropogenic impacts. *Rev. Palaeobot. Palynol.* 156, 337–349.
- Pèlachs, A., Julia, R., Pérez-Obiol, R., Soriano, J.M., Bal, M.-C., Cunill, R., Catalan, J., 2011. Potential influence of bond events on mid-Holocene climate and vegetation in southern Pyrenees as assessed from Burg lake LOI and pollen records. *The Holocene* 21, 95–104.
- Pèlachs, A., Pérez-Obiol, R., Soriano, J.M., Pérez-Haase, A., 2016. Dinàmica de la vegetació, contaminació ambiental i incendis durant els últims 10.000 anys a la Bassa Nera (Val d'Aran). In: de Catalunya, Generalitat (Ed.), *La investigació al Parc Nacional d'Aiguestortes i Estany de Sant Maurici*. Departament de Territori i Sostenibilitat, Espot, Generalitat de Catalunya.
- Pérez-Díaz, S., López-Sáez, J.A., Pontevedra-Pombal, X., Souto-Souto, M., Galop, D., 2016. 8000 years of vegetation history in the northern Iberian peninsula inferred from the palaeoenvironmental study of the Zalama ombrotrophic bog (Basque-Cantabrian Mountains, Spain). *Boreas* 45:658–672. <http://dx.doi.org/10.1111/bor.12182>.
- Pérez-Haase, A., Ninot Sugrañes, J., 2006. Caracterització florística i ecològica de les molles de la Nassa Nera (Aiguamòg). VII Jornades sobre Recer. al Parc Nat. d'Aiguestortes i St. Maurici.
- Pérez-Haase, A., Ninot Sugrañes, J., 2017. Hydrological heterogeneity rather than water chemistry explain high plant diversity and uniqueness of a Pyrenean mixed mire. *Folia Geobot.* <http://dx.doi.org/10.1007/s12224-017-9291-2> (in press).
- Pérez-Haase, A., Carrillo, E., Batriu, E., Ninot, J.M., 2012. Diversitat de comunitats vegetals a les molles de la Vall d'Aran (Pirineus centrals). *Acta Bot.* 61–112.
- Pérez-Obiol, R., Jalut, G., Julià, R., Pèlachs, A., Iriarte, M.J., Otto, T., Hernández-Beloqui, B., 2011. Mid-Holocene vegetation and climatic history of the Iberian peninsula. *The Holocene* 21:75–93. <http://dx.doi.org/10.1177/0959683610384161>.
- Pérez-Obiol, R., Bal, M.C., Pèlachs, A., Cunill, R., Soriano, J.M., 2012. Vegetation dynamics and anthropogenically forced changes in the Estanilles peat bog (southern Pyrenees) during the last seven millennia. *Veg. Hist. Archaeobotany* 21, 385–396.
- Pérez-Obiol, R., García-Codron, J.C., Pèlachs, A., Pérez-Haase, A., Soriano, J.M., 2016. Landscape dynamics and fire activity since 6740 cal yr BP in the Cantabrian region (La Molina peat bog, Puente Viesgo, Spain). *Quat. Sci. Rev.* 135, 65–78.
- Pérez-Sanz, A., González-Sampérez, P., Moreno, A., Valero-Garcés, B., Gil-Romera, G., Rieradevall, M., Tarrats, P., Lasheras-Álvarez, L., Morellón, M., Belmonte, A., Sancho, C., Sevilla-Callejo, M., Navas, A., 2013. Holocene climate variability, vegetation dynamics and fire regime in the Central Pyrenees: the Basa de la Mora sequence (NE Spain). *Quat. Sci. Rev.* 73, 149–169.
- Pla, S., Catalan, J., 2005. Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene. *Clim. Dyn.* 24, 263–278.
- Reille, M., 1992. Pollen et spores d'Europe et d'Afrique du Nord URA-CNRS.
- Reille, M., Lowe, J.J., 1993. A re-evaluation of the vegetation history of the eastern Pyrenees (France) from the end of the last glacial to the present. *Quat. Sci. Rev.* 12, 47–77.
- Reimer, P., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hafflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55: 1869–1887. http://dx.doi.org/10.2458/azu_js_rc.55.16947.
- Revelles, J., Cho, S., Iriarte, E., Burjachs, F., van Geel, B., Palomo, A., Piqué, R., Peña-Chocarro, L., Terradas, X., 2015. Mid-Holocene vegetation history and Neolithic land-use in the Lake Banyoles area (Girona, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 435:70–85. <http://dx.doi.org/10.1016/j.palaeo.2015.06.002>.
- Roca i Adrover, A., Miranda i Canals, J., Losantos, M., Berástegui, X., Ticó i Duran, I., 2010. *Atlas Geològic de Catalunya 1:50000*. Institut Geològic de Catalunya, Barcelona.
- Rohling, E.J., Pälike, H., 2005. Centennial-scale climate cooling with a sudden cold event around 8,200 years ago. *Nature* 434:975–979. <http://dx.doi.org/10.1038/nature03421>.
- Rull, V., 1987. A note on pollen counting in palaeoecology. *Pollen Spores* 29 (4), 471–480.
- Sanchez-Cabeza, J.A., Masqué, P., Ani-Ragolta, I., 1998. 210Pb and 210Po analysis in sediments and soils by microwave acid digestion. *J. Radioanal. Nucl. Chem.* 227:19–22. <http://dx.doi.org/10.1007/BF02386425>.
- Schnurrenberger, D., Russell, J., Kelts, K., 2003. Classification of lacustrine sediments based on sedimentary components. *J. Paleolimnol.* 29:141–154. <http://dx.doi.org/10.1023/A:1023270324800>.
- Simonneau, A., Chapron, E., Vannièr, B., Wirth, S.B., Gilli, A., Di Giovanni, C., Anselmetti, F.S., Desmet, M., Magny, M., 2013. Mass-movement and flood-induced deposits in Lake Ledro, southern alps, Italy: implications for Holocene palaeohydrology and natural hazards. *Clim. Past* 9:825–840. <http://dx.doi.org/10.5194/cp-9-825-2013>.
- Smith, A.J.E., Smith, R., 2004. *The Moss Flora of Britain and Ireland*. Second Edition.
- Van Geel, B., 2001. Non-pollen palynomorphs. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking environmental change using lake sediments*. Vol. 3: Terrestrial, algal, and siliceous indicators. Kluwer, Dordrecht, pp. 99–119.
- Walker, M.J.C., 1995. Climatic changes in Europe during the last glacial/interglacial transition. *Quat. Int.* 63–76.
- Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314, 1261–1265.