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Vegetation and fire history since the last glacial maximum in an inland area of the western Mediterranean Basin (Northern Iberian Plateau, NW Spain)

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ABSTRACT

We reconstructed vegetation responses to climate oscillations, fire and human activities since the last glacial maximum in inland NW Iberia, where previous paleoecological research is scarce. Extremely sparse and open vegetation composed of steppic grasslands and heathlands with scattered pioneer trees suggests very cold and dry conditions during the Oldest Dryas, unsuitable for tree survival in the surroundings of the study site. Slight woodland expansion during the Bølling/Allerød was interrupted by the Younger Dryas cooling. Pinewoods dominated for most of the early Holocene, when a marked increase in fire activity occurred. Deciduous trees expanded later reaching their maximum representation during the mid-Holocene. Enhanced fire activity and the presence of coprophilous fungi around 6400–6000 cal yr BP suggest an early human occupation around the site. However, extensive deforestation only started at 4500 cal yr BP, when fire was used to clear the tree canopy. Final replacement of woodlands with heathlands, grasslands and cereal crops occurred from 2700 cal yr BP onwards due to land-use intensification. Our paleoecological record can help efforts aimed at restoring the natural vegetation by indicating which communities were dominant at the onset of heavy human impact, thus promoting the recovery of currently rare oak and alder stands.

Introduction

The Iberian Peninsula is currently one of the most biodiverse areas in the Mediterranean Basin (Médail and Quézel, 1997), which is in turn one of the main hotspots in the world for biodiversity conservation (Myers et al., 2000). A long history of human disturbance has shaped current floristic and vegetation patterns, often modifying the original ecosystems in a drastic way (Blondel, 2006; Carrión et al., 2007; Colombaroli et al., 2008) and, thus, making it difficult to imagine what the natural landscape would look like. In this sense, the plateaus of inland Iberia represent one of the most extreme cases of natural ecosystem disruption by human activities, as they currently show an almost completely deforested landscape dominated by crops. Deciphering the appearance of the natural vegetation is therefore a formidable task.

Paleoecological study of sedimentary sequences allows for the reconstruction of vegetation history, disturbance regimes and their interactions. Thus, pollen analysis is employed as a proxy for vegetation composition and biome type, anthropogenic pollen indicators (Behre, 1981; Brun, 2011) and dung fungal spores (van Geel et al., 2003; Baker et al., 2013) are related to agriculture and grazing, and microscopic charcoal particles are linked to regional fire activity (Tinner et al., 1998). The Northern Iberian Plateau constitutes a perfect study area for tracking human impacts through the last millennia, as it was strongly disturbed by anthropogenic activities. However, in relatively dry and continental environments such as inland Iberia, suitable sites for paleoecological research (e.g., lakes, mires) are fairly rare. In addition to this, many attempts aiming at paleoenvironmental reconstruction from this region have been unsuccessful due to poor preservation of pollen and other biological indicators in the available sedimentary archives (Carrión et al., 2009). As a consequence, most of the Iberian paleoecological sites are located in mountain and coastal areas (Postigo-Mijarra et al., 2010), and Holocene paleoenvironmental data at mid-altitudes in north-central Iberia are scarce.

Nevertheless, there are several paleoecological sequences from inner lowland areas of northern Iberia that provide valuable information on the past vegetation development over these territories: slope deposits in the Minho Basin (e.g., van Mourik, 1986), saline lakes of the central Ebro Basin (e.g., Valero-Garcés et al., 2000; Davis and Stevenson, 2007; González-Sampériz et al., 2008) and mires and marshlands in the Duero Basin (e.g., Allen et al., 1996; Muñoz Sobrino, 2001; Muñoz Sobrino et al., 2004). Focusing on the Northern Iberian Plateau, most of the existing sequences spanning the Holocene are located in its eastern half (García-Antón et al., 1995; Muñoz Sobrino et al., 1996; Franco-

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Múgica et al., 2001; Iriarte et al., 2001; Iriarte-Chiapusso et al., 2003; Franco-Múgica et al., 2005; García-Antón et al., 2011), while almost no paleoecological information is available from the western sector (López Sáez, 2012; Morales-Molino et al., 2013). Furthermore, some of these sites record only part of the Holocene or lack an accurate chronology, reinforcing the importance of obtaining new paleoecological data with a well-established chronological framework.

The late glacial period is a crucial period for understanding the subsequent ecosystem dynamics during the Holocene, and it has been studied profusely in the Northwestern Iberian Mountains (summarized in Muñoz Sobrino et al., 2007) and other mountainous areas of Iberia (e.g., Pons and Reille, 1988; Peñalba et al., 1997; van der Knaap and van Leeuwen, 1997; González-Sampériz et al., 2006). However, studies dealing with late glacial vegetation dynamics in inland Iberia are quite rare (Carrión et al., 2010), with no data from the Northern Iberian Plateau. Consequently, the response of vegetation to the abrupt climatic oscillations reconstructed for this period (Moreno et al., 2012; Muñoz Sobrino et al., 2013) remains unknown over vast areas of inland Iberia. It is important to determine whether there were rapid biotic responses to these climatic changes in inland Spain, similar to those recorded in central and northern Europe (Birks and Ammann, 2000; Ammann et al., 2000, 2012). Finally, fire history remains poorly studied in the westernmost sector of the Mediterranean Basin (e.g., Morales-Molino et al., 2011, 2013; Vannière et al., 2011; Connor et al., 2012), despite the enormous importance that fire has in the functioning of Mediterranean ecosystems (Pausas et al., 2008; Colombaroli et al., 2009; Gil-Romera et al., 2010).

In this paper we present a new paleoecological sequence (pollen, microscopic charcoal, dung fungal spores) from a mire located in the northwestern sector of the Northern Iberian Plateau. Our main aims were: i) reconstructing late glacial and Holocene vegetation history in the surroundings of the study site; ii) identifying the responses of inland Iberian ecosystems to the climatic oscillations occurred since the last glacial maximum (LGM); iii) reconstructing the fire history around the study site since the LGM and its relationship to vegetation dynamics; and iv) assessing human impact on the natural vegetation and determining which activities have led the landscape to be in its current state.

Study area

The Ayoó de Vidriales site (called Ayoó onwards) is a small mire (≈2 ha) situated on the northwestern fringe of the Northern Iberian Plateau (42°7.57′N, 6°4.22′W, 780 m asl; Fig. 1). It occupies a small hollow that lies on Pleistocene sediments, approximately 400 m from the town of Ayoó de Vidriales (Zamora province). Wet grassland dominated by *Molinia caerulea*, *Nardus stricta* and *Carex* spp., with some sparse shrubs (*Genista anglica*, *Calluna vulgaris*, *Erica tetralix*), covers most of the studied mire. The landscape surrounding the site is hilly and defined by the broad valleys of the River Esla tributaries, all of which are included in the River Duero Basin.

The regional climate is Mediterranean with some continental features. The mean annual temperature is approximately 10°C and annual precipitation averages approximately 500 mm, with a summer drought period that is approximately three months long (SIGA; sig.marm.es/siga). At a nearby weather station at Castrocontrigo (920 m asl), the mean temperature of the coldest month is 3.8°C and the mean temperature of the hottest month is 19°C. With regards to lithology, siliceous rocks are dominant and consist mainly of Ordovician phyllites, schists and

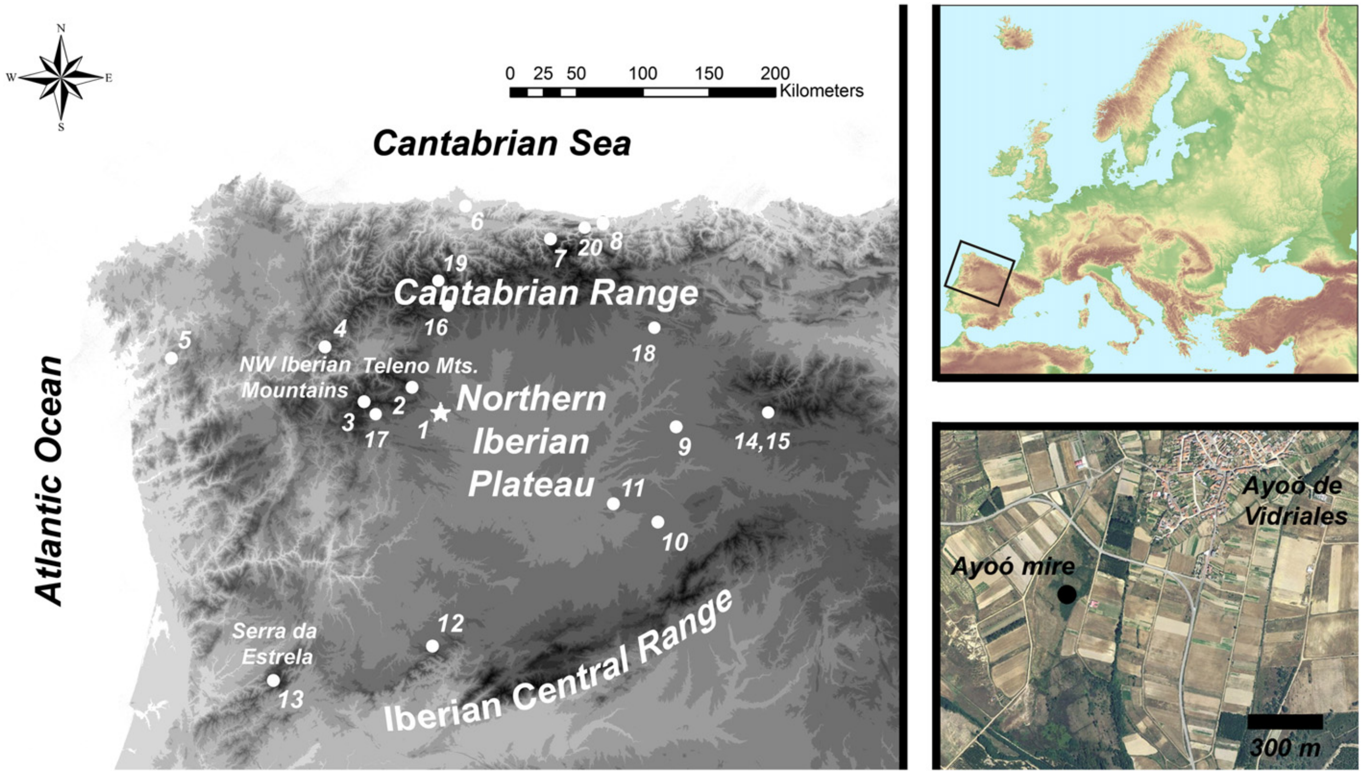

Figure 1. Location of the study site and the main paleoecological and paleoclimatic records discussed in the text. 1. Ayoó (this study), 2. Xan de Llamas (Morales-Molino et al., 2011), 3. La Roya (Allen et al., 1996; Muñoz Sobrino et al., 2013), 4. Lagoa de Lucenza (Muñoz Sobrino et al., 2001), 5. Campo Lameiro (Carrión-Marco et al., 2010; López-Merino et al., 2012), 6. Monte Areo (López-Merino et al., 2010), 7. Lago Enol (Moreno et al., 2011), 8. Pindal Cave (Moreno et al., 2010), 9. Espinosa de Cerrato (Franco-Múgica et al., 2001), 10. El Carrizal (Franco-Múgica et al., 2005), 11. Camporredondo (García-Antón et al., 2011), 12. El Maíllo (Morales-Molino et al., 2013), 13. Charco da Candieira (van der Knaap and van Leeuwen, 1995, 1997; Connor et al., 2012), 14 Quintanar de la Sierra (Peñalba et al., 1997), 15 Laguna Grande (Ruiz Zapata et al., 2002), 16 Laguillín (García-Rovés, 2007), 17 Lleguna, Laguna de las Sanguijuelas (Muñoz Sobrino et al., 2004), 18 La Piedra, San Mamés de Abar (Muñoz Sobrino et al., 1996; Iriarte et al., 2001), 19 La Mata (Jalut et al., 2010), 20 Roñanzas peat bog (Ortiz et al., 2010). At the bottom right is an aerial photograph of the study site, very close to Ayoó de Vidriales town and surrounded predominantly by cereal crops.

quartzites, Miocene, Plio-Pleistocene and Pleistocene conglomerates, and Holocene alluvial and colluvial sediments.

The Northern Iberian Plateau is mainly characterized by extensive deforested areas mainly covered with crops, cereals and vineyards. In the northwestern corner (where Ayoó is located), sparse and small patches of woodland, in particular deciduous (*Quercus pyrenaica*) and sclerophyllous oaks (*Quercus ilex*), are interspersed with croplands; these patches are probably remnants of more extensive forests. In contrast, shrublands dominated by brooms (*Genista*, *Cytisus*), heaths (*Erica*, *Calluna*) and rockroses (*Cistus*, *Halimium*) are the most widespread vegetation communities; in some places scattered oaks (*Quercus pyrenaica*, *Q. faginea*, *Q. ilex*) are also found.

In a regional context, deciduous *Quercus pyrenaica*-dominated forests are common and widespread between 700 and 1200 m asl, and mainly grow on siliceous soils in mountainous areas with a higher amount of rainfall. In drier areas, *Q. pyrenaica.* stands are often replaced by sclerophyllous *Q. ilex*-dominated forests, and mixed stands are quite common. Furthermore, birch (*Betula pubescens*) stands are quite common above 1200 m asl in the mountain ranges nearby, and usually growing on scree, steep slopes, mires or in riparian corridors. The most typical riparian forests are dominated by *Alnus glutinosa*, *Betula pubescens, Frangula alnus* and *Salix atrocinerea* or almost exclusively by willows (*Salix* spp.). Lastly, there are some natural *Pinus pinaster* stands in areas with poor soils and a high fire recurrence at the foothills of the Teleno Mountains.

Material and methods

Coring

A 174-cm-long core was extracted from a weakly disturbed area of the Ayoó mire in March 2009 using a 5-cm-diameter Russian corer. Core sections were stored in plastic drainpipes, wrapped in cling film and kept at 4°C in the dark until subsampling was performed.

Radiocarbon dating and age–depth model

Fifteen AMS radiocarbon dates from macrofossils, peat and bulk sediment were obtained to establish the chronology of the studied sedimentary sequence. ^{14}C ages were converted to calendar years using the program CALIB 6.0.1 (Stuiver and Reimer, 1993) coupled with the INTCAL09 calibration curve (Reimer et al., 2009).

The relationship between the sediment depth and its estimated age was modeled by fitting weighted cubic spline functions to confidence intervals calculated using Monte Carlo methods with the program MCAgeDepth (Higuera et al., 2009; code.google.com/p/mcagedepth). For the topmost section of the record, a linear interpolation through the median has been used (Telford et al., 2004) to avoid negative sedimentation rates. We also used a more conservative approach to account for the possible existence of hiatuses associated to certain abrupt lithological changes present along the core. Thus, we used a generalized mixed-effect regression model (Heegard et al., 2005), which provides relatively large confidence intervals for the estimated ages.

Pollen, dung fungal spores and microscopic charcoal analyses

A total of 79 samples with volumes of 0.4–1.1 cm^3 were treated according to the method of Faegri and Iversen (1989) to concentrate the fossil pollen preserved in the sediments. Sediment slices 0.5 cm thick were taken from the core at a sampling interval which varied along the core (every 1 to 4 cm) depending on the sedimentation rate, looking for a relatively constant resolution throughout the sequence. *Lycopodium* tablets with a known concentration were added at the beginning of the treatment for estimating the pollen concentration (Stockmarr, 1971). The pollen sum, excluding spores and pollen from aquatic plants, was almost always above 300 grains (mean = 396, standard deviation = 46). For the identification of pollen and spores we used the reference collection of the *Palynology Laboratory* at the *Autonomous University of Madrid*, along with identification keys by Punt et al. (1976–2009) and Moore et al. (1991) and photographic atlases by Reille (1992, 1995).

The programs PSIMPOLL 4.27 and PSCOMB 1.03 (Bennett, 2009) were used to plot the pollen diagrams and conduct the statistical analyses. Several divisive and agglomerative techniques were applied for the zonation of the palynological sequence, with similar results. Then, local pollen assemblage zones (LPAZs, termed AYOÓ) were delimited using the CONISS method, an agglomeration method that uses constrained cluster analysis (Grimm, 1987), taking into account the ecological meaning of the obtained zones. The number of statistically significant zones was determined by means of the broken stick model (Bennett, 1996). In addition to those, some subzones were also defined by considering their paleoenviromental relevance.

The rate of change was calculated to measure the dissimilarity between adjacent pairs of samples and then relate it to the temporal difference between the samples (Bennett et al., 1992); it can be considered a proxy of the rate of change of the ecosystem (Seppä and Bennett, 2003). Several coefficients were calculated to measure the dissimilarity between adjacent samples, with similar results. Finally, we chose the χ^2-2 dissimilarity coefficient (Bennett and Humphry, 1995). Palynological richness, a proxy for plant species diversity, was estimated applying rarefaction analysis to a constant pollen sum of 297 pollen grains, the minimum pollen count in the whole sequence (Birks and Line, 1992).

We quantified fungal spores belonging to the *Sporormiella*-, *Podospora*- and *Sordaria*-types to assess the grazing intensity by large herbivores. These spores are usually present in areas with high densities of wild and domestic ungulates and are produced by obligate coprophilous fungi (Baker et al., 2013). We also looked for *Apiosordaria*-type, another fungal spore type usually linked to grazing (e.g., van Geel et al., 2003), but unsuccessfully. On the contrary, we identified *Cercophora*-type in some samples, but as there are several *Cercophora* species that are not coprophilous (Baker et al., 2013) we decided not to represent its curves in the diagrams. The descriptions and photographs in van Geel et al. (2003) were used for their identification. The abundance of dung fungal spores is expressed as percentages of the pollen sum, excluding the pollen from aquatic plants and spores, and also as accumulation rates.

Microscopic charcoal particles longer than 10 μm were counted in the same slides used for the pollen analysis at 200× magnification following the recommendations of Tinner and Hu (2003) and Finsinger and Tinner (2005). Charcoal concentrations and charcoal accumulation rates (CHAR), which are well-correlated with regional fire activity (Tinner et al., 1998), were estimated using the same approach as for the pollen.

Results

Lithology

Figures 2, 3 and 4 show the main lithostratigraphic units of the Ayoó sedimentary sequence. At the bottom, the sediment mostly consists of highly inorganic sandy clay (173–162 cm), overlain by a level of organic detritus (162–149 cm). From 149-cm depth upwards, the dominant sediment is well-humified dark peat up to 45 cm, with the exception of two thin layers of sandy clay (130–127 cm) and organic detritus (120–110 cm). The top section of the sequence (45 cm to the surface) is composed of fibrous dark peat rich in rootlets. Abrupt sediment shifts at 162, 149 and 45 cm could be associated to sedimentary hiatuses, so paleoecological data in these sections of the sequence must be interpreted cautiously.

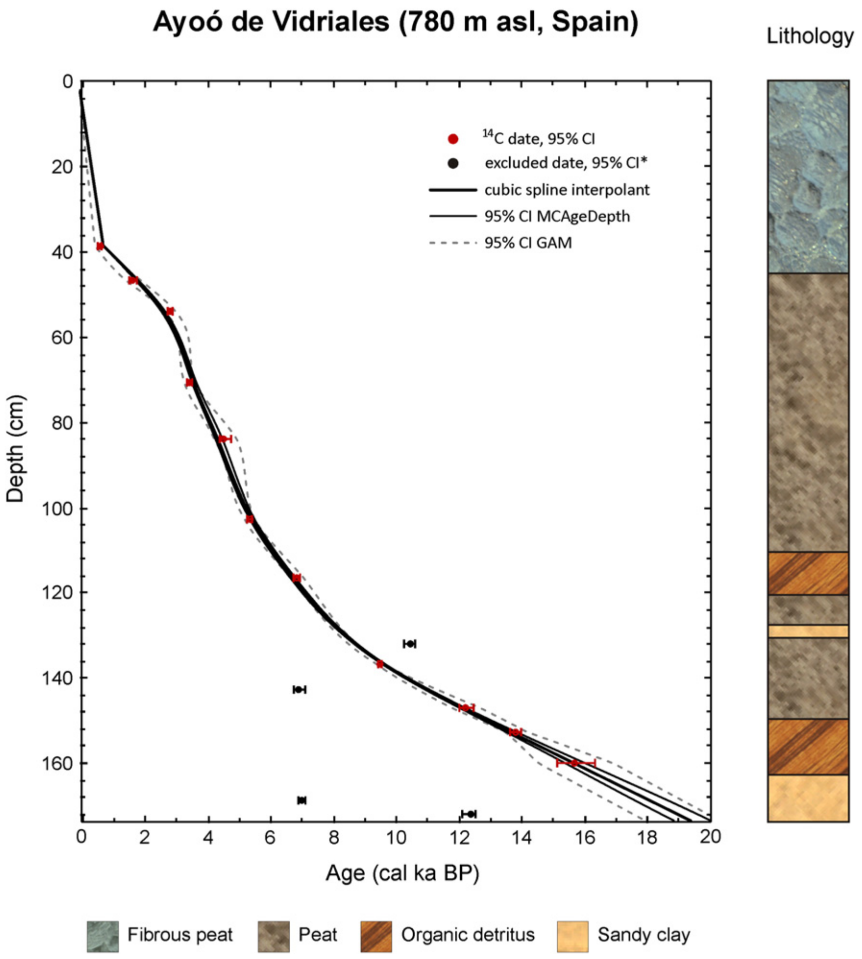

Figure 2. Age–depth model for the sedimentary sequence of Ayoó with a schematic representation of the main lithological units present in the sedimentary sequence. 'Cubic spline interpolant' curve and the '95% CI MCAgeDepth' envelope has been obtained using the MCAgeDepth model (Higuera et al., 2009), while the '95% CI GAM' envelope has been calculated following the Heegard et al. (2005) approach.

Chronology

The list of radiocarbon dates is shown in Table 1. Most of them have been used to construct the age–depth model and establish the chronology. However, four radiocarbon dates have been rejected because they were inconsistent with the rest of the series and incompatible with the biostratigraphy. Samples Beta-258143 and Beta-258144 probably correspond to fragments of roots of *Betula*, a tree that typically grows on mires and fens (Costa et al., 1997). Regarding sample UBA-19748 (woody charcoal), it has been shown that these types of macrofossils usually have older ages than those of the sediment where they are embedded due to their long terrestrial residence time and/or the inbuilt age of woody remains (Oswald et al., 2005). Finally, Beta-330977 may have experienced some contamination from recent carbon, as this sample was taken from the bottom of the sequence. The resulting age–depth model is shown in Figure 2, together with the error estimates calculated using Monte Carlo methods (Higuera et al., 2009) and GAM (Heegard et al., 2005).

With these conditions and the lithology in mind, the resulting chronology for the late glacial period shows several constraints that lead to consider with caution the timing of the different processes occurred during this period. First, estimated ages below 161 cm depth have been obtained by extrapolation, which makes them not very reliable. Second, we cannot rule out that the age reconstructed from the radiocarbon dates is older than the actual age, due to the inwash of older organic matter from the slopes of the catchment. The complete absence of carbonate rocks from the studied catchment led us to disregard the occurrence of the hard-water error. Lastly, it is likely that there are some sedimentary hiatuses corresponding to the sharp lithological changes detected at 162 and 149 cm depth, which could affect age estimates for this section of the sequence. The rate-of change curve (Fig. 5) supports the existence of these possible hiatuses, as it shows relative maxima at these sedimentary transitions.

On the contrary, the chronology for the Holocene seems to be quite robust overall, and rate-of-change maxima do not parallel the minor sedimentary changes of this part of the sequence. Nevertheless, there is an exception at approximately 45 cm in depth, where there is a marked change in the sediment, from well-humified dark peat to brown fibrous peat, coupled with an important maximum in the rate-of-change curve. This situation suggests the presence of another interruption of the sediment accumulation at this point in the core. A rise in *Pinus* representation is usually observed in the topmost samples of several palynological sequences from northwestern Iberia (e.g., van der Knaap and van Leeuwen, 1995; Muñoz Sobrino et al., 1997; Morales-Molino et al., 2013) linked to pine afforestations during the 20th century AD. In Ayoó there is no noticeable rise in pine pollen representation at the top of sequence but it remains quite constant. On one hand, the absence of that *Pinus* increase could be explained either by the absence of the topmost centimeters of the sequence or, more likely, by the fact that recent pine afforestations are not extensive at all in the surroundings of the studied mire. On the other hand, the relatively constant representation of *Pinus* throughout the late Holocene could be related to the regional pollen signal from natural *Pinus pinaster*

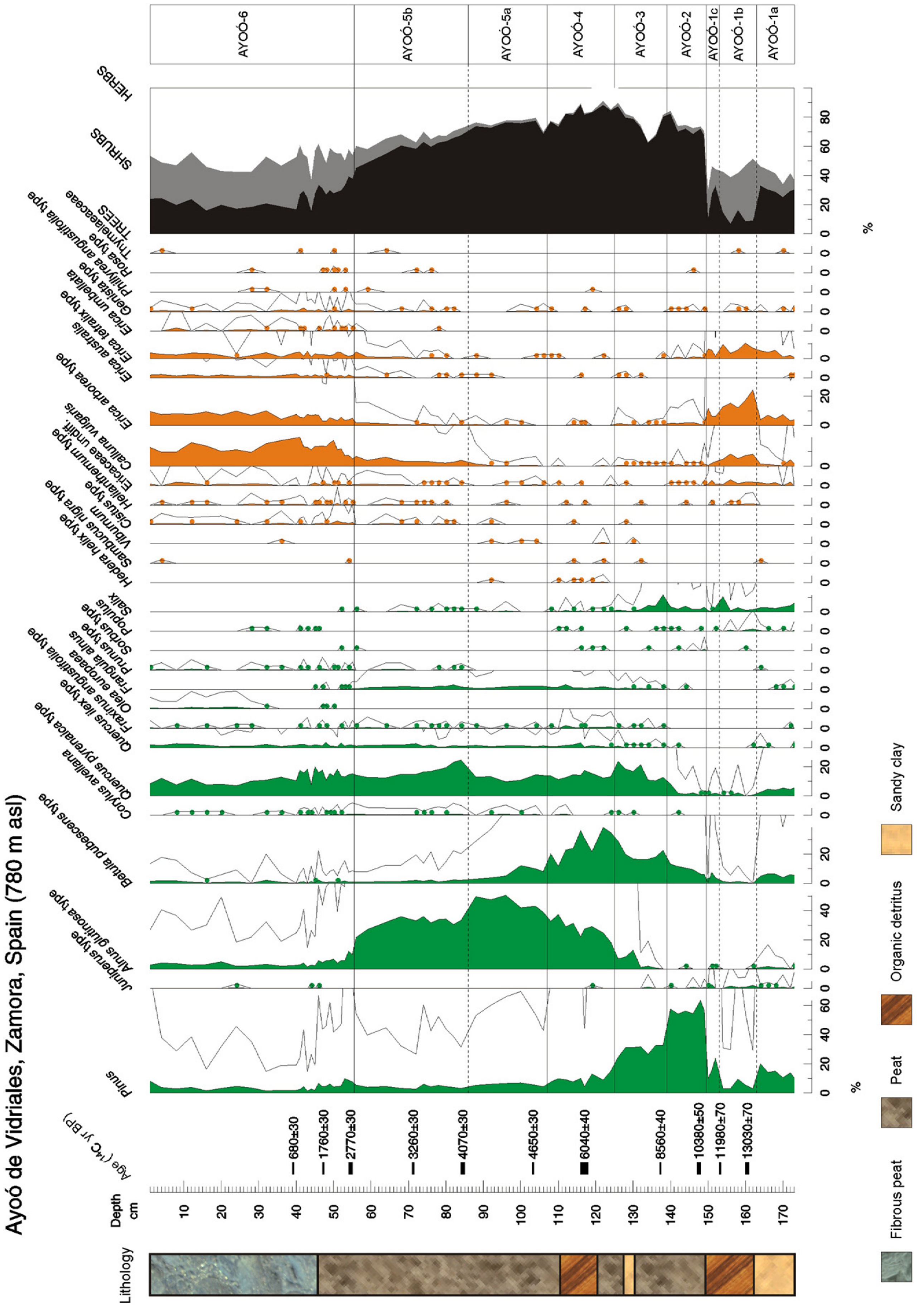

Figure 3. Percentage pollen diagram of Ayoó: trees and shrubs (selected pollen types). Dots represent percentages below 0.5%. Empty curves are exaggerated ten-fold. Main lithological units are represented schematically. Pollen analyst: C. Morales-Molino.

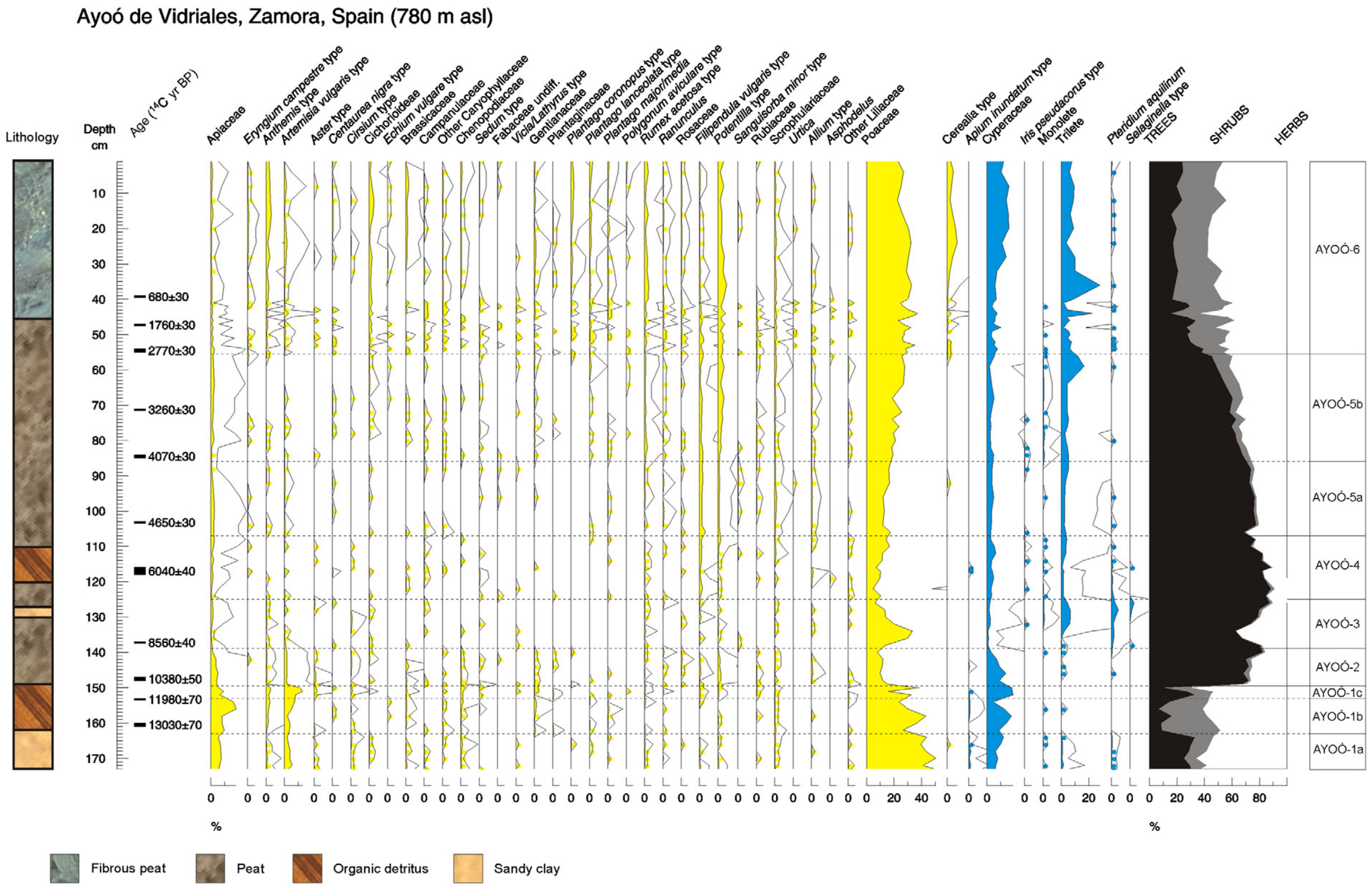

Figure 4. Percentage pollen diagram of Ayoó: herbs, aquatics and spores (selected types). Dots represent percentages below 0.5%. Empty curves are exaggerated ten-fold. Main lithological units are represented schematically. Pollen analyst: C. Morales-Molino.

Table 1
Radiocarbon dates from Ayoó mire.

Laboratory number	Depth (cm)	Material	^{14}C age (yr BP)	Median age (cal yr BP)[a]	Confidence interval (2σ, p = 0.954) (cal yr BP)[a]
CNA-778	39–39.5	Peat	680 ± 30	650	560–680
Beta-330974	47–47.5	Peat	1760 ± 30	1660	1570–1730
UBA-19745	54–55	Peat	2770 ± 30	2860	2790–2950
CNA-779	71–71.5	Peat	3260 ± 30	3480	3400–3560
UBA-19746	84–85	Peat	4070 ± 30	4560	4440–4800
CNA-780	103–103.5	Peat	4650 ± 30	5410	5310–5470
UBA-19747	116–118	Wood/bark	6040 ± 40	6890	6760–7000
UBA-19748	132–133	Charcoal	9300 ± 50	Rejected	Rejected
Beta-330975	137–137.5	Bulk sediment	8560 ± 40	9530	9490–9550
Beta-258143	143–143.5	*Betula* wood	6080 ± 40	Rejected	Rejected
Beta-340996	147–148	Bulk sediment	10,380 ± 50	12,250	12,050–12,510
Beta-330976	153–153.5	Bulk sediment	11,980 ± 70	13,840	13,730-13,970
UBA-19749	160–161	Bulk sediment	13,030 ± 70	15,710	15,160–16,380
Beta-258144	168.5–170	*Betula* wood	6140 ± 40	Rejected	Rejected
Beta-330977	172–173	Bulk sediment	10,470 ± 50	Rejected	Rejected

[a] Calibrated ages were obtained using CALIB 6.0 software (Stuiver and Reimer, 1993) with the calibration dataset INTCAL09 (Reimer et al., 2009).

forests located at the foothills of the Teleno Mountains, which dates back at least to the Roman Times (Domergue and Herail, 1978).

Pollen, coprophilous fungi and microscopic charcoal

The palynological record from Ayoó is very diverse, with 155 different pollen and spore types identified. The main pollen and spore types are shown in the pollen diagrams in Figures 3–4. Figure 5 displays a summary pollen diagram where the results of dung fungal spore and microscopic charcoal analyses are represented along with the rate-of-change, palynological richness and main pollen curves. Figure 6 shows pollen concentrations of selected pollen types, charcoal concentration and dung fungal spores accumulation rates throughout the record.

Six statistically significant LPAZs have been delimited mainly on the basis of shifts in the relative proportions of *Pinus*, *Alnus glutinosa*-t., *Betula pubescens*-t., *Quercus pyrenaica*-t., several Ericaceae pollen types, Apiaceae, *Artemisia vulgaris*-t. and other Asteraceae, several *Plantago* types, *Potentilla*-t., Poaceae and Cerealia-t. Zones AYOÓ-1 and AYOÓ-5 have in turn been divided in three and two subzones, respectively. Although these subzones are not statistically significant, they are relevant when reconstructing paleoenvironmental conditions. In the following paragraphs a brief description of all the zones and subzones is provided as well as the inferred vegetation history.

AYOÓ-1 (173–149.5 cm depth; ca. 19,000–12,680 cal yr BP)

Subzone AYOÓ-1a (173–163 cm depth; ca. 19,000–16,380 cal yr BP) reflects an open landscape dominated by steppic grasslands (dominance of Poaceae and steppic plants) in the surroundings of Ayoó. Trees (pines, birches and perhaps oaks) would have been scattered over the territory, or would have formed small woods dispersed over the steppic landscape. Ericaceae, Cyperaceae and *Apium* would have developed in close proximity to the sedimentary basin, which could have been a pool during this period taking into account the type of sediment (mostly clay) and the relative abundance of *Apium inundatum*-type. During subzone AYOÓ-1b (163–153 cm depth; ca. 16,380–13640 cal yr BP), vegetation suddenly became sparser (very low pollen concentrations) and Ericaceae, Poaceae, and a number of xerophytic plants typical of steppic areas (mainly *Artemisia* and *Helianthemum*) became dominant, whereas trees almost disappeared (minimum tree pollen percentages). Considering the pollen concentrations (Fig. 6), the apparent expansion of heathlands during this period could be due to the drop in the pollen concentrations of trees and grasses, leading to an overrepresentation of pollen from Ericaceae and other plants growing on the mire. Later, AYOÓ-1c (153–149.5 cm depth; ca. 13,640–12,680 cal yr BP) shows a slight woodland recovery led by *Pinus* and *Betula*. But around 12,800 cal yr BP, open woodlands were suddenly replaced with sparse herbaceous vegetation (Poaceae, steppic plants), presence of *Juniperus* and low representation of Ericaceae, in marked contrast with the previous subzone.

AYOÓ-2 (149.5–139 cm depth; ca. 12,680–10,020 cal yr BP)

Approximately 12,500 cal yr BP, an abrupt tree expansion (mainly *Pinus*, but also *Betula*) is detected, which replaced heathlands and xerophytic/steppic grasslands. Nevertheless, steppic plants continued to be important in the understory of the pinewoods. These boreal-mountain forests were quite stable until ca. 10,000 cal yr BP.

AYOÓ-3 (139–125 cm depth; ca. 10,020–7670 cal yr BP)

At the onset of this zone deciduous *Quercus* gained importance in the landscape at the expense of pines. *Betula* also increased its representation during this period. This partial replacement or enrichment of the pine forests with birches and oaks was progressive, as is indicated by the low rate-of-change values. Simultaneously, sclerophyllous *Quercus* began to have a limited but continuous regional presence.

Forests composed mainly of *Pinus*, *Betula* and deciduous *Quercus* dominated until ca. 7700 cal yr BP. Between ca. 9800 and 8500 cal yr BP, tree pollen percentages dropped while those of Poaceae and *Pteridium aquilinum* rose. This situation could be interpreted at once as a deforestation episode. However, concentrations of the main arboreal pollen types and total tree pollen followed increased during this zone instead of decreasing, a process that would have occurred during a deforestation process. Consequently, the most plausible explanation would be a local expansion of Poaceae and *Pteridium aquilinum* on and around the study site, replacing former dominant Cyperaceae (whose concentration decreased in this zone). Later, approximately 8700 yr ago, the representation of *Alnus* increased, although it was more sustained from ca. 7700 cal yr BP onwards.

AYOÓ-4 (125–107 cm depth; ca. 7670–5780 cal yr BP)

During this zone forests around Ayoó reached their maximum development. Pines became rare in the forests, which were then dominated by deciduous trees such as *Betula*, *Alnus*, deciduous *Quercus* and other mesophytes (e.g., *Fraxinus*, *Frangula*, *Hedera*, *Sambucus*, *Viburnum*), whereas *Q. ilex* type remained poorly represented. Palynological richness values were minima during this zone, probably linked to the dominance of closed forests with shady understory.

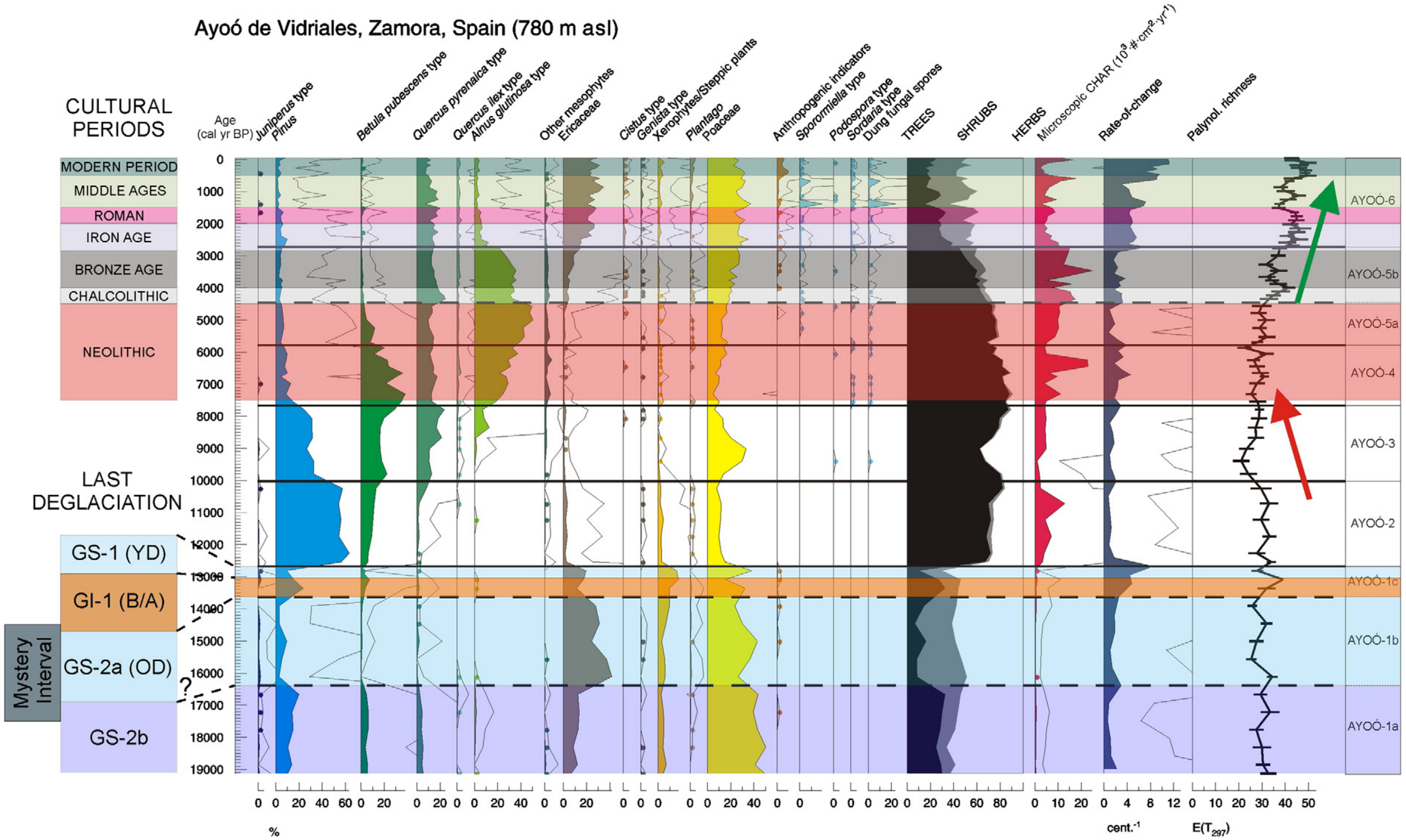

Figure 5. Diagram summarizing the main results of the Ayoó paleoecological record: pollen, charcoal and dung fungal spores. 'Other mesophytes' curve includes *Acer, Ilex, Corylus, Fraxinus, Frangula, Prunus, Sorbus, Ulmus, Hedera, Lonicera, Sambucus, Viburnum, Ligustrum* and *Crataegus*. 'Ericaceae' comprises all the *Erica.* pollen types and *Calluna*. 'Xerophytes/Steppic plants' curve includes *Artemisia, Ephedra distachya*-t., Chenopodiaceae, Caryophyllaceae (excluding *Scleranthus*-t.), Brassicaceae and *Helianthemum*-t. '*Plantago*' represents the sum of the pollen types included in this genus. 'Anthropogenic indicators' comprises *Scleranthus*-t., Cerealia-t., *Erodium, Spergula*-t., *Papaver, Chelidonium, Echium, Urtica, Polygonum aviculare*-t., *Olea, Vitis, Juglans*. 'Dung fungal spores' represents the sum of obligate coprophilous fungi. Black dots represent percentages below 0.5%. Empty curves are exaggerated ten-fold. Chronology of the main late glacial periods according to Lowe et al. (2008) is shown, as well as the main regional cultural periods. Pollen, charcoal and fungal spores analyst: C. Morales-Molino.

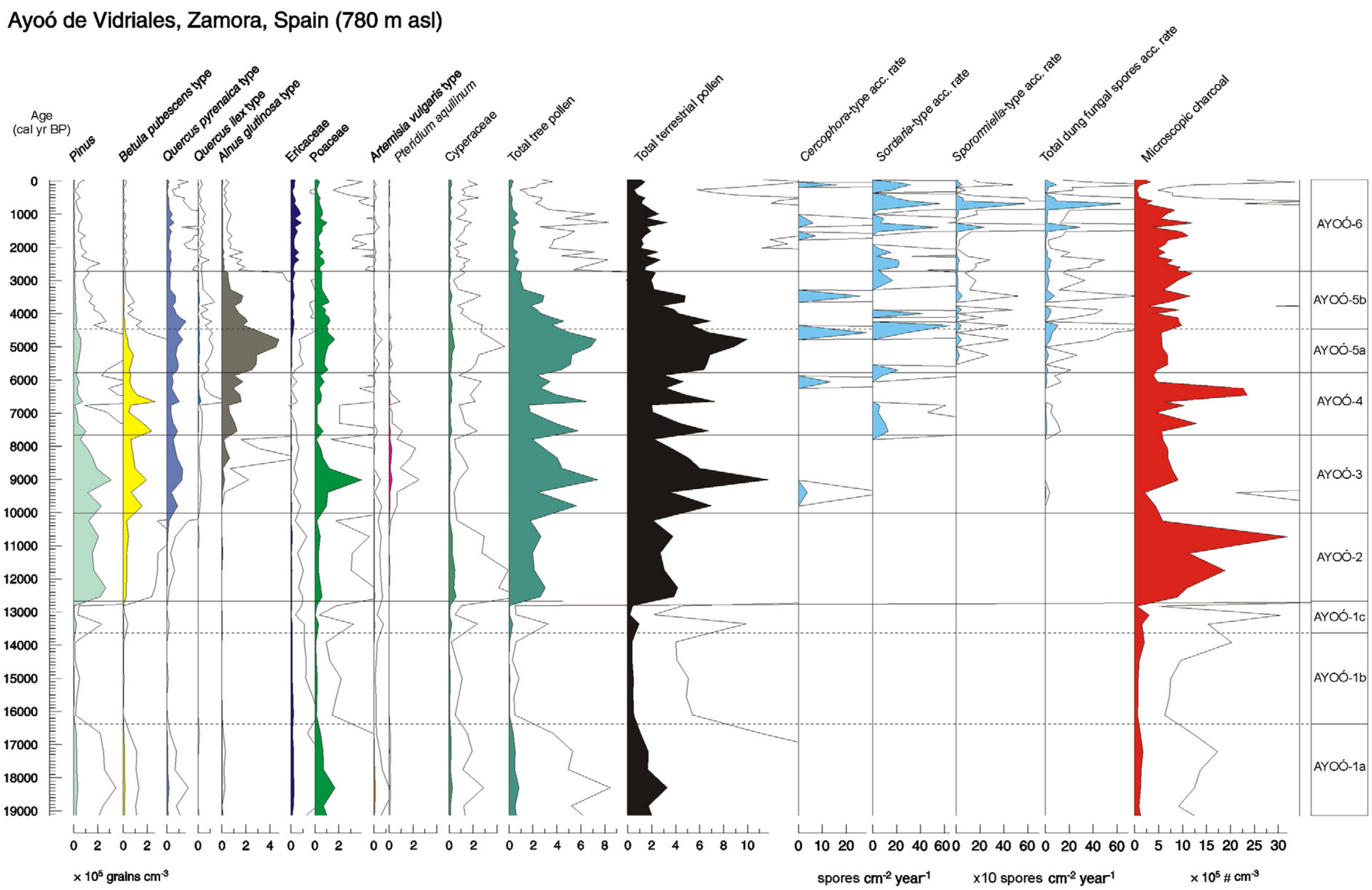

Figure 6. Concentration diagram of some selected pollen and spore types, and charcoal. Dung fungal spores data are expressed as accumulation rates following the recommendations of Baker et al. (2013). Empty curves are exaggerated ten-fold.

AYOÓ-5 (107–55.5 cm depth; ca. 5780–2720 cal yr BP)

During the subzone AYOÓ-5a (107–86 cm depth; ca. 5780–4460 cal yr BP) *Alnus* became dominant in the surroundings of the mire, probably also covering the alluvial environments of the adjacent valleys, whereas birches almost disappeared. *Quercus* maintained their representation in the landscape and probably dominated the nearby slopes. An important variety of mesophytic trees and shrubs, including a higher abundance of *Corylus*, continued providing diversity to these forests. Continuous representation of certain grazing indicators such as *Plantago* and dung fungal spores began ca. 5900–6000 cal yr BP, although the presence of *Sordaria*-type spores had already been recorded between ca. 7500 and 6800 cal yr BP.

Next subzone, AYOÓ-5b (86–55.5 cm depth; ca. 4460–2720 cal yr BP) shows a decreasing trend in tree pollen percentages indicative of progressive deforestation, mainly affecting *Alnus*-dominated stands concurrent with a spread of shrublands (Ericaceae, Cistaceae, *Genista*-type) and grasslands. The rise in the curve of coprophilous fungi ca. 3500 cal yr BP suggests an intensification of grazing close to the mire, taking into account that the long-distance dispersal of these spores is quite limited (Parker and Williams, 2012). Simultaneously, the curve of anthropogenic pollen indicators (*Echium vulgare*-type, *Polygonum aviculare*-type) became continuous. Palynological richness followed a general trend towards higher values coupled with increasing landscape opening during the last ca. 5000–4500 cal yr BP.

AYOÓ-6 (55.5–0 cm depth; ca. 2720 cal yr BP-present)

Abrupt vegetation changes characterized this zone, as shown by the highest values of rate of change. First, the remaining *Alnus*-dominated stands in valley bottoms were replaced with shrublands, grasslands and cereal crops (the Cerealia curve became continuous at ca. 2800 cal yr BP). Some of these heath species, such as *E. umbellata* and *E. australis*, are highly tolerant to frequent and/or severe disturbances and expanded greatly during this phase. The only forests that remained significant in the landscape were those dominated by oaks, both deciduous and sclerophyllous types, although they experienced certain oscillations due to human activities in the forests during the late Holocene. Human activities greatly intensified during this period, as shown by the record of pollen indicators of anthropogenic activities and disturbances (e.g., Cerealia, *Plantago*, *Urtica*, *Asphodelus*) and by the marked increase in the percentages of dung fungal spores, mainly *Sporormiella*-type and *Sordaria*-type. Two maxima of coprophilous fungi spores were detected at around 1400 and 700 cal yr BP, and are probably linked to cowpats lying close to the study site (Sjögren et al., 2007).

Discussion

The landscapes of the Northern Iberian Plateau during the last deglaciation

At the beginning of the record, palynological data indicate that the landscape around Ayoó was dominated by steppic grasslands with some scattered trees, and heathlands. Our age-depth model suggests that this period lasted from ca. 19,000 to 16,400 cal yr BP. However, these age estimates must be taken cautiously as they are based on extrapolation beyond the deepest radiocarbon-dated sample. Further, broad error estimates provided by the mixed-effect model support the previous statement. In addition, both the abrupt shift in the lithology at the top of this subzone and the local maximum in the rate-of-change curve point to the existence of a hiatus at 163 cm depth, adding further complexity to the age–depth model. Taking into account all these possible sources of uncertainty with regards to the chronology, this period could correspond to the end of the LGM (GS-2b stadial following the nomenclature of the INTIMATE group; Lowe et al., 2008). This vegetation suggests moderately cold and dry climatic conditions, as pollen concentration did not reach the minimum values of the record and there is a certain representation of tree pollen. Similar climatic conditions by the end of the LGM (≈19,000–18,000 cal yr BP) have been inferred from the analysis of a speleothem from El Pindal Cave in northern Spain (Moreno et al., 2010), as well as from global syntheses (Clark et al., 2012). Other paleoecological records from mountainous areas of northwestern Iberia also show a steppic landscape, in some cases with a higher representation of tree pollen, such as those from Lagoa Lucenza in the Galician Mountains (Muñoz Sobrino et al., 2001) or Laguna Grande in the Northern Iberian Range (Ruiz Zapata et al., 2002).

Later, between ca. 16,400 and 13,600 cal yr BP according to our age–depth model, the landscapes of the northwestern Iberian Plateau became dominated by a sparse vegetation cover including heaths, steppic plants and some *Juniperus*. However, the chronology of this phase should be considered with caution because this section of the sedimentary sequence is delimited by two possible sedimentary hiatuses both at the top and the bottom, This vegetation suggests the establishment of a dry and cold climate and the most unfavorable conditions for plant growth in the whole sequence. This phase could correlate with the GS-2a stadial (16,900–14,700 cal yr BP, also known as Oldest Dryas; Fig. 5), which includes Heinrich Event 1 (H-1, 16,500–15,800 cal yr BP). Some paleoclimatic reconstructions from northern Iberia shows that the known as “Mystery Interval” (17,500–14,500 cal yr BP; Denton et al., 2006), which embraces GS-2a and H-1, was colder and drier than the LGM over this region (Morellón et al., 2009; Moreno et al., 2010, 2012), while chironomid-based quantitative reconstruction of July air temperatures from La Roya Lake shows that GS-2a was by far the coldest period of the last deglaciation (Muñoz Sobrino et al., 2013). Other paleoecological records from northern Iberia record an increase in steppic taxa during this period and landscapes clearly dominated by steppic communities (Allen et al., 1996; Peñalba et al., 1997; González-Sampériz et al., 2006; Muñoz Sobrino et al., 2007; Jalut et al., 2010; Muñoz Sobrino et al., 2013). Nevertheless, tree representation did not decrease in many records from these mountainous areas (Ruiz Zapata et al., 2002; García-Rovés, 2007; Muñoz Sobrino et al., 2007) to such low values as they did in Ayoó, which indicates that moisture conditions for tree growth must have been more limiting in the inland plateau than in the surrounding mountains. This almost completely treeless landscape suggests the occurrence of extremely dry conditions during this stadial, which would have prevented significant glacial refugia from occurring in inland northwestern Iberia; however, the existence of scattered cryptic refugia cannot be excluded. Thus, important glacial refugia in northwestern Iberia would have been mainly located at low altitudes on seaward slopes (Muñoz Sobrino et al., 2007). In marked contrast, the sequence of San Mamés de Abar, located on the NE fringe of the Northern Iberian Plateau, shows a quite forested landscape during this period (Iriarte et al., 2001), suggesting that the rain-shadow effect was less important in this sector of the plateau therefore allowing tree development.

Following this period, the interval of 13,600–12,800 cal yr BP featured slight tree colonization, with *Pinus* and *Betula* woods as the main types of vegetation. This suggests a climatic improvement, especially regarding precipitation, and late glacial forest development in northwestern Iberia seems to have taken place during this time (Peñalba et al., 1997; Ruiz Zapata et al., 2002; Muñoz Sobrino et al., 2004, 2007; Jalut et al., 2010). This phase could therefore be correlated with the late glacial interstadial GI-1 (Bølling-Allerød, 14,700–12,650 cal yr BP; Björck et al., 1998), which is characterized by a significant rise in temperature and precipitation (Clark et al., 2012). In northern Iberia, the speleothem record from El Pindal Cave indicates that this warming was gradual and precipitation only reached significant amounts near the end of the period (Moreno et al., 2010), while chironomid-based July air temperature from La Roya shows a rise of 2.5°C at the beginning of the interstadial and a decreasing trend afterwards (Muñoz Sobrino et al., 2013). The spread of pioneer trees detected in Ayoó was very slight and late compared to other records from the Northwestern Iberian Mountains, where pine and birch woodlands became well-developed, and an expansion of relatively thermophilous trees, such as oaks, took place (Maldonado, 1994; Allen et al., 1996; van der Knaap and van Leeuwen, 1997; Muñoz Sobrino et al., 2007). Palynological records from mid-altitude sites on the NW and NE borders of the Northern Iberian Plateau show a similar pattern of important boreal woodland spread (Muñoz Sobrino et al., 1996, 2004; Iriarte et al., 2001). It is likely that the rise in the amount of rainfall during the Bølling was not enough for tree establishment to occur in the northwestern area of the Northern Iberian Plateau due to the rain-shadow effect induced by the surrounding high mountains that could block the entrance of Atlantic humid air masses. On the contrary, a further increase in water availability during the Allerød could have triggered a threshold response of cold-tolerant and mesophilous trees. Another possibility that we cannot rule out is that significant glacial refugia were far away during stadial GS-2a (Oldest Dryas) and the trees could not rapidly reach the northwest part of the Plateau. Finally, it is necessary to stress that chronological uncertainty is important in this section of the core insofar as we cannot discard the existence of hiatuses.

Both charcoal concentration and CHAR indicate that fires were almost absent during the last deglaciation, as low fuel availability and cold and dry climatic conditions would have greatly limited the ignition and spread of fires. This situation was widespread over the entire Iberian Peninsula (Carrión and van Geel, 1999; Carrión, 2002; Connor et al., 2012) and the rest of Europe (Power et al., 2008).

The sudden replacement of steppes and open woodlands with very open, steppic vegetation containing some heaths suggests a return to cold and/or dry conditions at around 12,800 cal yr BP. This vegetation shift is typical of the stadial GS-1 (12,850–11,650 cal yr BP, Younger Dryas) in northwestern Iberian sites that have a certain oceanic influence (Allen et al., 1996; Peñalba et al., 1997; Muñoz Sobrino et al., 2007), but the dryness was probably exacerbated in Ayoó due to its lower altitude and more inland location. This inferred climatic change towards colder temperatures and aridity during the Younger Dryas is quite apparent in other climatic reconstructions from northern Iberia (Morellón et al., 2009; Moreno et al., 2010, 2011; Muñoz Sobrino et al., 2013).

Later, a rapid expansion of boreal forest (*Pinus*, *Betula*) is detected in the surroundings of Ayoó, dated at ca. 12,500 cal yr BP according to our chronology. It could be linked to warmer and wetter conditions towards the end of the Younger Dryas, and summer temperatures actually followed a steep increasing trend from approximately this date onwards in the nearby site of La Roya (Muñoz Sobrino et al., 2013). Moreover, pine forests were important in other areas of northwestern Iberia during this stadial (Muñoz Sobrino et al., 2007). However, considering age uncertainties in this section of the sedimentary sequence (apparent in the GAM error estimates shown in Fig. 2) and the possible presence of a sedimentary hiatus coincident with *Pinus* pollen sharp increase, we suggest that this afforestation could also correspond to the onset of the Holocene (≈11,600 cal yr BP; Hoek et al., 2008). Previous studies have shown a progressive tree colonization of the northwestern Iberian lowlands from glacial refugia located closer to the Atlantic Ocean, which would have involved pinewoods as one of the first stages of woodland recovery (Muñoz Sobrino et al., 2007).

Early Holocene: inertia and succession

The onset of the Holocene featured the dominance of boreal-mountain woodlands (*Pinus*, *Betula*) with a continuing significant representation of xerophytic/steppic plants; this points to relatively dry and continental climatic conditions. This scenario fits well with a marked seasonality at the beginning of the Holocene associated with the important differences between winter and summer insolation (Kutzbach and Webb, 1993). In other Mediterranean areas, a dry climate has been also reconstructed for the early Holocene (Reed et al., 2001; Carrión, 2002; Magny et al., 2012), probably due to the strengthening of the North Atlantic anticyclone that is linked to intensified Hadley circulation until ca. 8000–6000 cal yr BP (Tinner et al., 2009). The relative spread of deciduous *Quercus* in Ayoó was delayed until ca. 10,000 cal yr BP, quite a bit later than in the rest of northwestern Iberia (Maldonado, 1994; van der Knaap and van Leeuwen, 1995; Muñoz Sobrino et al., 2007). This delay in *Quercus* expansion and millennial dominance of pine-birch woodlands detected in Ayoó was also observed in other inland sites of northwestern Spain, such as the Sanabria area (Muñoz Sobrino et al., 2004, 2007) or the northeastern corner of the Northern Iberian Plateau (Muñoz Sobrino et al., 1996; Iriarte et al., 2001; Iriarte-Chiapusso et al., 2003). The strong seasonality at the beginning of the Holocene (Kutzbach and Webb, 1993), enhanced by the inland location of Ayoó, along with the inertia of a well-established forest community could have contributed to the persistence of pine forests as the dominant vegetation for several millennia during the early Holocene.

The Ayoó sequence contributes to show the importance of the oceanicity–continentality gradient in the Northern Iberian Plateau throughout the Holocene, with the most inland and eastern sites showing a longer persistence of pine forests linked to a marked continental climate and shallow soils (Franco-Múgica et al., 2001; Iriarte-Chiapusso et al., 2003; Franco-Múgica et al., 2005; García-Antón et al., 2011; Morales-Molino et al., 2012). This gradient has been also invoked as one of the main factors to explain Holocene vegetation dynamics in the Iberian Central Range (Franco-Múgica et al., 1998; Morales-Molino et al., 2013). Later, pine was replaced as the dominant tree by birch, then by oak, and finally by alder and other mesophytes, following the typical successional process in oceanic areas of western Iberia (Maldonado, 1994; van der Knaap and van Leeuwen, 1995; Allen et al., 1996; García-Rovés, 2007).

Fire, along with the discussed climatic oscillations, was an important ecological factor driving the different phases of the late glacial period and the Holocene. From the end of the late glacial period (ca. 12,800 cal yr BP), a moderate increase in CHAR values is noticeable, with two maxima at ca. 11,700 and 10,700 cal yr BP. Enhanced fire activity would have been a consequence of the increased fuel availability associated with woodland expansion within a warmer and still relatively dry climatic framework. In addition, those woodlands were dominated by pines, which are highly flammable. High summer insolation would have promoted the formation of thunderstorms and, consequently, the likelihood of lightning ignition, making the early Holocene a period of high fire occurrence in most of the western Mediterranean (Carrión, 2002; Vannière et al., 2008; Connor et al., 2012; Morales-Molino et al., 2013). 11.2 and 8.2 ka events, characterized by climatic cooling and enhanced dryness have been detected in other paleoecological records from northern Iberia (e.g., González-Sampériz et al., 2006; Muñoz Sobrino et al., 2013; Pérez-Sanz et al., 2013) but the resolution of the Ayoó sedimentary sequence did not allow to recognize these climatic reversals.

Mid-Holocene: maximum development of temperate forests

The maximum development of the deciduous forest was reached between ca. 7700 and 5800 cal yr BP, suggesting the prevalence of warm and humid conditions. The spread of temperate deciduous trees would have been favored by the generalized warming occurring in Europe during the Holocene Thermal Maximum between 8000 and 5000 cal yr BP (Renssen et al., 2009). With regards to rainfall, data from Ayoó suggests a climatic response similar to that recorded at southern Iberian sites and in Sicily with higher rainfall (Reed et al., 2001; Carrión, 2002; Tinner et al., 2009), and an opposite trend to the precipitation reconstructions from other northern sites of the western Mediterranean, which point to drier summers during the mid-Holocene (Moreno et al., 2011; Magny et al., 2012). The location of the northwestern sector of the Iberian Plateau, surrounded by high mountains that intercept the humid air masses that approach from the northwest (Atlantic Ocean and Cantabrian Sea), could cause that major precipitation amount was associated to Atlantic depressions arriving from the southwest. Thus, the climate in this region would have been similar to that affecting inland and southern Iberia, resembling what occurs today (Esteban-Parra et al., 1998).

The suggested increase in precipitation, along with the expansion of deciduous trees (which are less flammable than pines), led to low to moderate CHAR and charcoal concentration values between 10,500 and 6400 cal yr BP. Thus, there is another noticeable similarity between the Northern Iberian Plateau and the mountains of southeastern Iberia, where the mid-Holocene was also characterized by low fire activity (Carrión, 2002; Gil-Romera et al., 2010). On the contrary, fire activity remained almost unchanged in the more oceanic areas of western Iberia (Connor et al., 2012; Morales-Molino et al., 2013) or even increased in the southern Pyrenees (Pérez-Sanz et al., 2013). The dominance of closed deciduous forests could be the cause for minimum values of palynological richness during this period, as shady understory limits the development of herbs and shrubs.

Human impact on the vegetation of the northwestern corner of the Iberian Plateau

The first evidence of human activities around Ayoó was recorded between ca. 7500 and 6800 cal yr BP, where the regular presence of *Sordaria*-t. and an increase in fire activity indicate the occurrence of livestock husbandry. We cannot rule out, however, that the limited record of dung fungal spores is related to the presence of wild ungulates. Thus, our data suggest an earlier human presence in these inland areas of northwestern Spain than previously proposed, as evidence of Neolithic human settlement in this area was restricted to some megalithic monuments that date back to 6000–5000 cal yr BP (Fernández Manzano, 1986; Larrén, 2002). It is between 6000 and 5000 cal yr BP that grazing indicators (pollen, fungal spores) increased greatly following the rise in regional fire activity between 6400 and 6200 cal yr BP. Forest clearance by Neolithic people for establishing pastures could be the cause for the rise in fire activity beginning at ca. 5600 cal yr BP. Additionally, the trend towards increased aridity inferred for the Mediterranean area of Iberia since 6000–5000 cal yr BP (Reed et al., 2001; Carrión, 2002; Pérez-Sanz et al., 2013) would have promoted the spread of fire. The expansion of *Alnus glutinosa* during this period could be related to its positive response to fire (Tinner et al., 2000; Connor et al., 2012) or to changes in the local hydrological conditions. In any case, the absence of important deforestation processes around Ayoó suggests that human disturbances were weak during the Neolithic.

At ca. 4500 cal yr BP, an important forest replacement with shrublands and grasslands took place, concurrent with the arrival of the Chalcolithic to northwestern Iberia (Fernández Manzano, 1986; López Sáez, 2012). Fire would have played a role in this deforestation process, as high values of CHAR are detected throughout the interval between 4500 and 2700 cal yr BP (including important maxima at ca. 4300, 3900, 3500 and 2800 cal yr BP, which are also detected in the charcoal concentration curve). Arid climatic conditions reconstructed for this period from Lake Zoñar (4.0–2.9 cal ka BP; Martín-Puertas et al., 2008), Lake Siles (lake desiccation phases centered at 4.1 and 2.9 cal ka BP; Carrión, 2002), Lake Estanya (4.8–4.0 cal ka BP; Morellón et al., 2009) or the Roñanzas peat bog (4.5–3.0 cal ka BP; Ortiz et al., 2010) would have favored fire spread after human ignitions and consequently forest clearance. This forest clearance process would have increased plant diversity through increasing the variety of niches available and promoting disturbance-tolerant taxa. Increases in fire activity (Carrión, 2002; Carrión et al., 2007; Carrión-Marco et al., 2010) and forest declines (Fletcher et al., 2013) have been also linked to these dry spells in other Iberian regions. Around Ayoó, severe and recurrent fires favored the establishment of heathlands and grasslands, which are fire-tolerant communities (Morales-Molino et al., 2011; Connor et al., 2012). Land-use intensity remained unchanged during the Bronze Age, which constitutes an important difference with the nearby Teleno Mountains where metallurgical activities started by that time (Morales-Molino et al., 2011). The described increase in fire occurrence was almost simultaneous in subcoastal Galicia (López-Merino et al., 2012), and occurred later in Serra da Estrela (ca. 3500 cal yr BP; Connor et al., 2012). Furthermore, enhanced fire activity through the agency of humans was quite common from the Bronze Age onwards in the western Mediterranean Basin (Vannière et al., 2011).

The definitive replacement of alder-dominated forests with heathlands, grasslands and cereal crops took place around 2700 cal yr BP, at the beginning of the Iron Age (Lorrio and Ruiz Zapatero, 2005). This fits well with the discovery of numerous Iron Age hillforts close to the study site (Larrén, 2002) and the economic intensification typical of this period in the Northern Iberian Plateau (Blanco-González and López-Sáez, 2013) reflected in a significant rise of dung fungal spores. The spread of heathlands related to human activities is also a common feature of the late Holocene in northwestern Iberia (e.g., Maldonado, 1994; Muñoz Sobrino et al., 2001; Morales-Molino et al., 2011, 2013), occurring later in the Northwestern Iberian Mountains (e.g., Allen et al., 1996; Muñoz Sobrino et al., 2001; Jalut et al., 2010) than in the western Iberian Central Range (van der Knaap and van Leeuwen, 1995; Morales-Molino et al., 2013). Cereal cultivation seems to have begun by this time (ca. 2700 cal yr BP) as it is also recorded in other palynological sequences from the Northern Iberian Plateau (Franco-Múgica et al., 2001, 2005; García-Antón et al., 2011), quite later than in other northwestern Iberian areas where it started during the Neolithic (e.g., Ramil Rego and Aira Rodríguez, 1993; Zapata et al., 2004; López-Merino et al., 2010). Our data reveal that in the Ayoó area human populations began breeding livestock and only diversified their economy several millennia later with agricultural activities. Thus the lag between the onset of pastoral and agricultural activities was quite longer in Ayoó than in other areas of NW Iberia such as the Monte Areo, where cereal cultivation also started during the Neolithic (López-Merino et al., 2010). Further landscape transformations did not occur during the Roman period despite the significant occupation (Carretero, 1999). Perhaps the only land-use intensification occurred during the last centuries due to the human population increase. The decrease in fire activity detected between ca. 2700 and 1600 cal yr BP could correlate with the most humid period for the last 4000 years in Lake Zoñar, comprising the Iron Age-Iberian and Roman epochs (Martín-Puertas et al., 2008).

It is somewhat surprising that during the main stage of land-use intensification around Ayoó, CHAR and charcoal concentration values are generally lower, although there are several maxima at ca. 1650, 1260, 600 cal yr BP, with the final one occurring nearly at the present time. Charcoal maxima can be related to the arid period between 1.6 and 0.6 cal ka BP identified in Lake Zoñar (Martín-Puertas et al., 2008). It is around 1700 cal yr BP when local fire occurrence in Campo Lameiro caused the definitive establishment of shrublands around the study site (Carrión-Marco et al., 2010). The period with low fire activity could be due to better control of fire by humans but more probably to cooler and more humid climate during the Little Ice Age in Spain (Martín-Puertas et al., 2008; Morellón et al., 2011). Other relatively close sites show maximum fire activity for the last 2500–3000 years (Allen et al., 1996; Franco-Múgica et al., 2005; López-Merino et al., 2012), in marked contrast with Ayoó record.

Conclusions

Ayoó represents the first site in inland Spain recording vegetation and fire history since the last glacial maximum. In particular, it contributes greatly to improving our knowledge about the late glacial period in the western Mediterranean, where paleoecological records for this period are not abundant and are mainly located in mountainous areas. Thus, reconstructed landscapes from the northwestern Iberian Plateau would have been dominated by steppic grasslands with patches of heathland and sparse pioneer trees, suggesting a dominance of cold and especially dry conditions during most of the last deglaciation. Our data agree with previous paleoclimatic records from northern Iberia in indicating that the stadial GS-2a (Oldest Dryas) was the most limiting period for tree development (probably due to dryness). Dry conditions or/and the distance to important tree refugia were probably the causes for a late and weak spread of forests during the interstadial GI-1 (Bølling-Allerød), which was sharply interrupted by the GS-1 (Younger Dryas) climatic reversal. A cold and dry climate, and (above all) the low fuel loads could explain an extremely low fire occurrence over this entire period.

The Younger Dryas–Holocene transition was marked by a rapid spread of boreal woodlands around Ayoó, which persisted as the dominant vegetation for several millennia during the early Holocene prior to the spread of deciduous trees. Excluding the early Holocene inertial dominance of pine forests, forest recovery followed a successional trend similar to that in more oceanic areas of Iberia. The timing of pine forest replacement with temperate trees (delayed in the eastern sector) strongly supports the importance of the oceanicity–continentality gradient in the Northern Iberian Plateau. With regards to fire activity, the spread of forests along with a relatively dry and warm climate caused an increase in fire activity at the beginning of the Holocene.

The mid-Holocene was the period of maximum forest development, with the dominance of mesophilous trees, as also occurred in southern Spain. Vegetation dynamics suggest that the Holocene climate in northern inland Spain would have followed the trends detected in southern Spain more than those recorded in northern Iberian paleoclimatic sites facing the Atlantic Ocean or the Cantabrian Sea. The spread of less flammable vegetation (deciduous trees) and the onset of humid conditions led to an important decrease in fire occurrence during most of the early to mid-Holocene.

With regards to human impact, the record of dung fungal spores has contributed to the detection of human activities almost a millennium older than the oldest archeological sites currently known (dolmens of San Andrés, Las Peñezuelas, El Casetón de los Moros and El Tesoro, dated from the Neolithic ca. 6000–5000 cal yr BP; Fernández Manzano, 1986; Larrén, 2002). Human impact on the landscape was nevertheless weak until the Chalcolithic–Bronze Age, when forest clearance began around Ayoó; most of the impact was due to livestock husbandry. From the Iron Age onwards, land use intensified greatly, with an increase in livestock density and the establishment of cereal crops. This enhanced human disturbance produced extensive deforestation and contributed greatly to create the altered landscape currently dominant around Ayoó. Intensified land use superimposed on a possible aridification trend contributed to a marked rise in regional fire activity during the second half of the Holocene.

Paleoecological records, such as this one from inland northwestern Spain, can thus provide a good picture of natural ecosystems that were present prior to intensive land use. The record from Ayoó indicates that dense alder and oak stands that covered the surroundings of the site and heathlands were not at all widespread. Hereafter, we recommend the use of paleoecological records to guide efforts to pursue the restoration of natural ecosystems, especially in highly disturbed areas such as the Iberian Plateaus.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2013.10.010.

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