Quaterly Science Reviews 278 (2022) 107373

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

# Landscape dynamics and fire regime since 17,550 cal yr BP in the Cantabrian region (La Molina peat bog, Puente Viesgo, Spain)

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## ARTICLE INFO

*Article history:*
Received 12 October 2021
Received in revised form
28 December 2021
Accepted 3 January 2022
Available online xxx

Handling Editor: Yan Zhao

*Keywords:*
Paleogeography
Vegetation dynamics
Last Glacial Period
Holocene
Palynology
Sedimentary charcoal
Western Europe
Iberian Peninsula
Biogeography
Environmental history

## ABSTRACT

Our aim with this paper is to provide insight into the landscape dynamics of the Cantabrian region (northern Iberian Peninsula) from the Last Glacial Period to the present. We present a multiproxy approach performed in a sedimentary record from La Molina peat bog, located at 484 m a. s. l. in Puente Viesgo, Cantabria (Latitude: 43.26° N; Longitude: 3.97° W), that covers the last c. 17,550 years. Analyses were performed on the organic matter, pollen and sedimentary charcoals, which have been used to characterise the fire regime at a local level. The results revealed a steppe-like formation from the basis of the sequence to the Bølling-Allerød chronozone, when the spread of woody species is detected. The dry and cold conditions of the Younger Dryas caused the decrease of mesophilous taxa until the onset of the Holocene. From that point onwards, a mixed deciduous formation composed of *Betula* and deciduous *Quercus* was established in the region. Besides, a series of biomass pulses was detected during the early Holocene, probably linked to intervals of increased rainfall. Fire episodes detected at the 9.3 and the 8.2 ka events created forest openings and probably favoured the establishment of *Corylus,* most likely also helped by a climate shift. There was a lack of fire activity until the Neolithic, when the fire signal increased probably linked to grazing and agricultural practices and triggered deeper changes in the Cantabrian plant landscape structure.

## 1. Introduction

The Cantabrian range (northern Iberian Peninsula) is a mountain system that runs parallel to the Cantabrian Sea. Due to its orography and climate features, the area is of particular environmental interest since it is a natural border between the Eurosiberian and Mediterranean biogeographical regions (Rivas-Martínez et al., 2017) and determines the distribution pattern of several terrestrial species. The northern slope of the mountain range, also known as the Cantabrian region, has proved to be an exceptional scenario for the study of palaeoecological dynamics. A large number of natural registers, such as caves, rocky shelters and sedimentary deposits, have allowed characterising the environmental and climate change over the last millennia as well as assessing the influence of the anthropic factor as a landscape-shaping agent.

Concerning the role of climate (Fig. 1), the northern Iberian Peninsula has been under the influence of regional climatic variability, such as the succession between Stadials and Interstadials (Dansgaard et al., 1982; Johnsen et al., 1992; Rasmussen et al., 2014; Seierstad et al., 2014), the Heinrich events (Heinrich, 1988; Bond et al., 1992; Hemming, 2004) and the Bond cycles (Bond et al., 1997; Bond et al., 2001; Mayewski et al., 2004; Wanner and Bütikofer, 2008; Isono et al., 2009; Wanner et al., 2011). Several studies have examined the impact that this climate variability has had on the Cantabrian region through isotopic analyses of cave speleothems (Domínguez-Villar et al., 2008, 2009, 2017; Moreno et al., 2010a; Baldini et al., 2015, 2019; Smith et al., 2016; Rossi et al., 2018). For example, Baldini et al. (2019) modelled the seasonal distribution of temperature and rainfall from the Younger Dryas, while Smith et al. (2016) revealed quasi-cyclical events of

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https://doi.org/10.1016/j.quascirev.2022.107373

**Abbreviations**

| | |
|---|---|
| LGP | Last Glacial Period |
| GS | Greenland Stadial |
| GI | Greenland Interstadial |
| PAR | pollen accumulation rate |
| CONISS | constrained cluster analysis by the method of incremental sum of squares |
| PAZ | pollen assemblage zones |
| CHAC | charcoal concentration |
| CHAR | charcoal accumulation rate |

wet-to-dry conditions during the Holocene in Cantabria.

The cultural heritage of Cantabria, located on the easternmost flank of the Cantabrian range, is rich in prehistoric anthropogenic evidence. Up to now El Castillo cave, at about 3–4 km from La Molina peat bog, has been the site with the oldest documented human presence, dated at 89,000 years BP (Bischoff et al., 1992). In a more recent period, populations grew up across the Cantabrian region (González-Sainz, 1989; González-Sainz and González-Urquijo, 2004; Chauvin, 2007; Chauvin et al., 2018; Fano et al., 2020) coinciding with the temperate climate of the Bølling-Allerød chronozone (GI-1; Iversen, 1953; Rasmussen et al., 2014). Human groups expanded towards mid-mountain areas (0–700 m a. s. l.) along the Upper Magdalenian and the first stages of the Azilian (Fig. 1), achieving an increasing control of landscape with important migration rates among sites (Fernández-Tresguerres, 2004; González-Sainz and González-Urquijo, 2004). During the Azilian (Fig. 1), the Epipalaeolithic culture developed in several eastern sites from the northern Cantabrian range among other European regions, human populations still based their economies on hunter-gatherer activities (Fernández-Tresguerres, 2004), and their presence was detected at high altitudes of the northern Cantabrian range (Barandiarán et al., 2006). The expansion of human groups continued during the Mesolithic with more than 250 documented sites in Cantabria, 30 of which are in the Pas Valley, the same as for La Molina peat bog (Pérez-Bartolomé, 2019). Further on, the onset of agricultural practices triggered the transition from hunter-gatherer to farmer societies (Arias, 1991) which took place at between 7700 and 6800 cal yr BP along the Cantabrian range (Fano et al., 2015). The expansion of human groups was evident across all the territory since approximately 1250 megaliths have been documented from sea level to more than 1800 m a. s. l. (Arias, 2005). The need to create forest openings was accompanied by important fire events detected in La Molina (Pérez-Obiol et al., 2016) and in higher altitude environments (Carracedo et al., 2018). Metal mining exploitation stands out as the most important impact on landscape during the following cultural phases (e.g. Mantecón, 2000; Arias, 2005; Blas-Cortina, 2014), while human society exhibited an increasing control of landscape until contemporary dates.

Reconstruction of the plant dynamics has also been possible thanks to the large number of palynological records made all over the Cantabrian range (Fig. 2). The characterisation of the Last Glacial Period (LGP) has otherwise only been possible above 1300 m a. s. l. From West to East, the sequences of Laguna de Lucenza (Aira-Rodríguez, 1986; Santos-Fidalgo et al., 1997; Muñoz-Sobrino et al., 2001), Villaseca de Laciana (Jalut et al., 2010), La Mata (Jalut et al., 2010), Lago de Ajo (Allen et al., 1996), Puerto de Tarna (Ruíz-Zapata et al., 2000) and Puertos de Ríofrio (Menéndez-Amor and Florschütz, 1963) revealed an open area with a large presence of xerophytes during some intervals of the LGP. A few more records from Burgos (north-eastern Castile and León), such as La Piedra (Ramil-Rego et al., 1998), San Mamés de Abar (Iriarte-Chiapusso et al., 2001) and La Nava (Menéndez-Amor, 1968), documented a higher presence of pines and birches, while the dominance of pines becomes more evident in the northern Iberian System as indicated

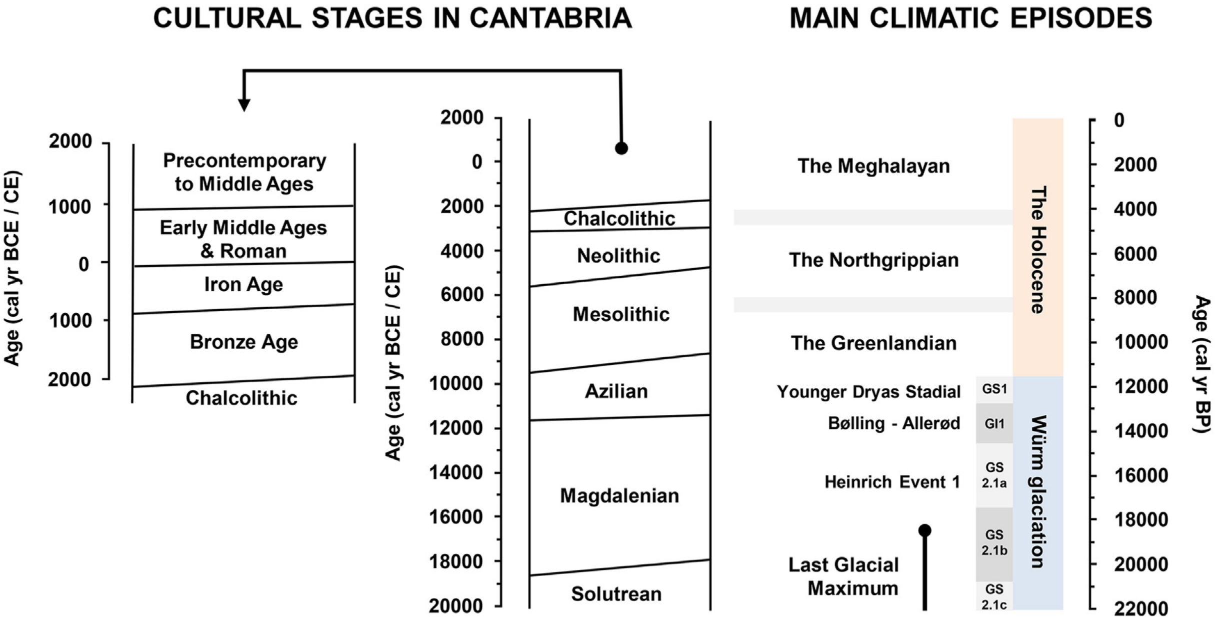

**Fig. 1.** Cultural stages in Cantabria from 22,000 cal yr BP to the present and the climatic characterisation of the sequence. Boundaries for the cultural stages have been drawn according to González-Sainz (1994), Rasilla-Vives and Straus (2004), González-Sainz and González-Urquijo (2004), Marín-Arroyo et al. (2018) and Straus (2018) for the Palaeolithic interval; to González-Sainz and González-Urquijo (2004), Alday-Ruiz (2009), Fano et al. (2015) and Straus (2018) for the Azilian, Mesolithic and Neolithic; Arias (1995), Ontañón (2003) and González-Rabanal et al. (2020) for the Chalcolithic; Marín-Suárez (2011) for the Bronze and Iron Ages; Costa-García (2018) for the onset of the Roman Period. Climate: Heinrich event 1 identified and discussed by Heinrich (1988), Bond et al. (1992) and Hemming (2004). The chronology for the Würm glaciation based on Greenland Stadials (GS) and Greenland Interstadials (GI) is shown (Rasmussen et al., 2014), and also the stages for the Holocene based on Walker et al. (2018, 2019).

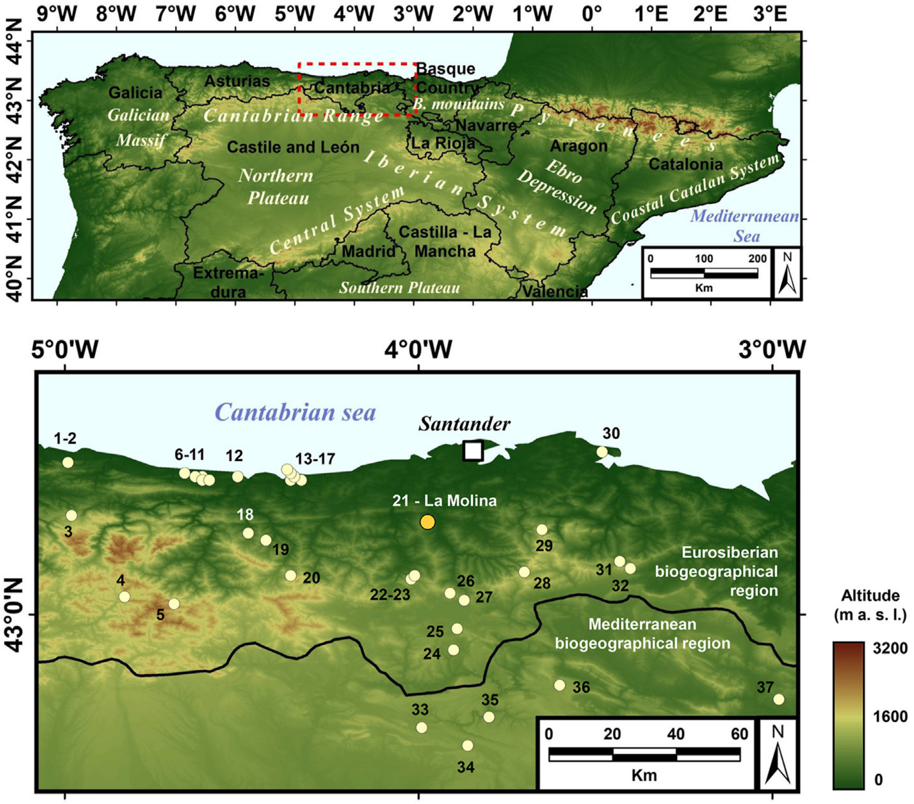

**Fig. 2. Top:** geographical map of the northern Iberian Peninsula. **Bottom:** palaeoecological records studied in the western sector of the Cantabrian range. The location of La Molina peat bog is highlighted as a yellow dot. **Legend: 1:** Enol lake (Menéndez-Amor, 1975; López-Merino, 2009; Moreno et al., 2010b, 2011) **2:** Ercina lake (Menéndez-Amor, 1975) **3:** Comella/Comeya (Ruiz-Zapata et al., 2001; Jiménez-Sánchez et al., 2003) **4:** Esla (Sánchez-Hernando et al., 1999) **5:** Puertos de Ríofrio (Menéndez-Amor and Florschütz, 1963) **6:** Vidiago (Menéndez-Amor, 1950a, 1950b) **7:** Llano de Mesa (Menéndez-Amor, 1950a, 1950b) **8:** Pendueles (Menéndez-Amor, 1950a, 1950b; López-Días et al., 2013a) **9:** Buelna (Menéndez-Amor, 1950a, 1950b; Menéndez-Amor and Florschütz, 1961; López-Días et al., 2013a) **10:** Borbolla (García-Amorena et al., 2008; López-Días et al., 2013a) **11:** Llano Roñanzas (Menéndez-Amor, 1950a, 1950b; Ortiz et al., 2008, 2010; Moreno et al., 2009; Gallego et al., 2013; López-Días et al., 2013a, 2013b) **12:** Las Arenas – Tina Mayor (Mary et al., 1975) **13:** Río Bederna (Mary et al., 1975) **14:** Jerra I (Mary et al., 1975) **15:** Jerra II (Mary et al., 1975) **16:** Merón (Mary, 1990; García-Amorena et al., 2008) **17:** Oyambre (Mary, 1990; García-Amorena et al., 2008) **18:** Culazón (González-Pellejero et al., 2014) **19:** Pico Sertal (Mariscal, 1986; Carracedo et al., 2018) **20:** El Cueto de la Avellanosa (Mariscal, 1983; Carracedo et al., 2018; Nuñez, 2018) **21:** La Molina (Pérez-Obiol et al., 2016; Carracedo et al., 2018; this paper) **22:** Pico Ano (Salas, 1993) **23:** Alsa (Mariscal, 1993) **24:** Santa Gadea (Iriarte-Chiapusso et al., 2003) **25:** La Nava (Menéndez-Amor, 1968) **26:** El Cueto de la Espina (Rodríguez-Coterón, unpublished PhD; Sánchez-Morales, unpublished PhD) **27:** Puerto del Escudo (Muñoz-Sobrino, 2001) **28:** Estacas de Trueba (Mariscal, 1987, 1989) **29:** Sotombo (Pérez-Díaz et al., 2016a) **30:** Noja (García-Amorena et al., 2008) **31:** Los Tornos (Peñalba, 1994; Muñoz-Sobrino et al., 2005) **32:** Zalama (Pérez-Díaz et al., 2016b; Souto et al., 2016; Souto, 2018) **33:** San Mamés de Abar (Iriarte-Chiapusso et al., 2001, 2016; Muñoz-Sobrino, 2001) **34:** La Piedra (Ramil-Rego et al., 1998) **35:** Tubilla del Agua (Moreno-Amat et al., 2009; García-Amorena et al., 2011) **36:** Huidobro (Iriarte-Chiapusso et al., 2003) **37:** Arreo Lake (Corella et al., 2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

by the papers on Hoyos de Iregua (Gil-García et al., 2002), Laguna del Hornillo (Gómez-Lobo et al., 1996), Laguna Negra (Von EngerIbrechten, 1998), Lago Las Pardillas (Sánchez-Goñi and Hannon, 1999), Quintanar de la Sierra (Peñalba, 1994; Peñalba et al., 1997) and Laguna Grande (Ruiz-Zapata et al., 2002).

On the northern slope of the Cantabrian range, several palynological records have been used to characterise the plant dynamics throughout the Holocene (Fig. 2), mainly dominated by mixed deciduous formations. In Asturias, the papers on El Alto de la Espina (López-Merino, 2009), Las Dueñas (López-Merino et al., 2006), El Monte Areo peat bogs (López-Merino, 2009; López-Merino et al., 2010) and the Enol lake (López-Merino, 2009) characterised the landscape from the early Holocene to the present and stand out as the most relevant. In Cantabria, located in the eastern sector of the mountain system (Fig. 1), the main sequences, covering from the Mid-Holocene to the present, are the obtained from the peat bogs of Culazón (González-Pellejero et al., 2014), Pico Sertal (Mariscal, 1986; Carracedo et al., 2018), El Cueto de la Avellanosa (Mariscal, 1983; Nuñez, 2018), Pico Ano (Salas, 1993), Alsa (Mariscal, 1993), Puerto del Escudo (Muñoz-Sobrino, 2001), Estacas de Trueba (Mariscal, 1987, 1989), Sotombo (Pérez-Díaz et al., 2016a), Los Tornos (Peñalba, 1994; Muñoz-Sobrino et al., 2005) and La Molina (Pérez-Obiol et al., 2016).

Among all the mentioned sites, however, only a few studies considered the role of fire in the reconstruction of the landscape. This may lead to partial interpretations, since fire is an important factor in the complex scenario between vegetation, climate and anthropic pressure (Harrison et al., 2010; Whitlock et al., 2010; Krawchuk and Moritz, 2011). On the one hand, biomass burnings seem to have been strongly influenced by climate variability during certain glacial and postglacial intervals (Power et al., 2008; Daniau et al., 2010, 2012; Marlon et al., 2016). In this line, several papers have examined the influence of both the climate and anthropic factors on determining the frequency and intensity of the fire regime over the Holocene, especially from the Neolithic period onwards (e.g., Vannière et al., 2008; Rius et al., 2009; Mercuri and Sadori, 2014; Gil-Romera et al., 2014; Sadori et al., 2015; Beffa et al., 2016). The sedimentary charcoal records performed in El Sertal, El Cueto de la Avellanosa (Carracedo et al., 2018) and La Molina (Pérez-Obiol et al., 2016), all located in the eastern sector of the Cantabrian range, indicated intense use of fire from c. 7000 cal yr BP coinciding with the onset of agricultural practices and the need to create forest openings, thus revealing an anthropic origin. Nevertheless, the lack of research on the role of fire has made it difficult to determine how long fire activity has been present in the Cantabrian region.

Here we present a multiproxy approach performed in a sedimentary record from La Molina peat bog (Cantabria) from c. 6740 to 17,550 cal yr BP. Since Pérez-Obiol et al. (2016) studied the most recent 6740 years, we obtained palynological, charcoal and organic matter records spanning from the LGP to the present. In this respect, the sequence of La Molina covers an unstudied interval of the LGP in the northern Cantabrian range, from the GS-2.1a onwards. The appropriate chronological resolution also provides added value to the sequence. Thus, the main objective of this study was to characterise the vegetation dynamics and fire regime of the north-eastern Cantabrian range since c. 17,550 cal yr BP. We sought to assess how the plant landscape changed during the different climatic and cultural phases and also determine whether the northern slope of the mountain system was a glacial refuge for certain plant species. We aimed to discern the source of landscape changes by interpreting whether they are linked to climatic features, anthropic pressure or to a combination of both. Besides, we hoped to determine from when there have been fires in the study area and from what point they have played a significant role in the configuration of the plant landscape.

### 1.1. Study setting

La Molina is an acidic peat bog in the municipality of Puente Viesgo (Cantabria), approximately 25 km south of Santander (Latitude: 43.26° N; Longitude: 3.97° W; Altitude: 484 m a. s. l.). The site is in the northern foothills of the Cantabrian range in the Pas valley close to the Pas-Besaya water-divide. The surrounding terrain consists of sandstones, silts and clays, and there are some other minerotrophic peat bogs nearby which are smaller than La Molina.

The orography of the Cantabrian range has important implications in the climate configuration of the northern Iberian Peninsula. Moisture-laden oceanic winds usually condense on the northern slope leading to annual precipitations ranging from 1000 to 1800 mm (climate Cfb according to the Köppen-Geiger classification: Beck et al., 2018), reaching over 2000 mm at the highest altitudes (Ancell and Célis-Díaz, 2012).

Accordingly, the principal plant formations along the Cantabrian low valleys and mid-mountain areas are subatlantic and submediterranean broad leaved mixed forests (Costa-Tenorio et al., 2005). In particular *Fagus sylvatica, Quercus robur* and *Quercus petraea*, all of them with a Eurosiberian distribution, are the forest species with the largest presence on the northern slope of the Cantabrian range. *Fagus sylvatica* is well adapted to both siliceous and calcareous lithology and has a greater presence on the eastern side of the Cantabrian range. In terms of oak trees, *Quercus robur* is the most common in the Cantabrian sector (Amigo et al., 2017) and is dominant on the siliceous basal plains (Costa-Tenorio et al., 2005). *Quercus petraea*, however, is less resistant to cold winters and is therefore found at a higher altitude range to avoid thermal inversion and also in some points on the southern mountain slope (Costa-Tenorio et al., 2005). On the other hand, recent plantations of *Pinus radiata*, *P. sylvestris*, *P. pinaster*, *P. nigra* and *Eucalyptus* spp. constitute important components of the current landscape composition.

Communities dominated by *Quercus ilex* subsp. *ilex* and *Laurus nobilis* are a common formation on the Cantabrian littoral, while *Quercus ilex* subsp. *rotundifolia* (= *Quercus rotundifolia*) develop at higher stages on poorly developed mountain soils (Costa-Tenorio et al., 2005; Sainz-Ollero et al., 2010; Amigo et al., 2017).

Brushwood groves also develop and cover large extensions on mid-mountain areas. They are favoured by openings generated by anthropogenic activities such as grazing and recurring fires, which can be replicated over centuries or millennia (Pérez-Obiol et al., 2016; Carracedo et al., 2018). The most recurrent species are *Rhamnus cathartica, Prunus spinosa, Calluna vulgaris, Daboecia cantabrica, Erica vagans, Erica mackaiana, Erica ciliaris, Ulex europaeus* and *Ulex gallii.*

In the mountain environment, birchwoods of *Betula pubescens* (= *Betula alba*) appear on nutrient-poor siliceous soils and steep slopes. These communities hold a scattered presence of *Sorbus aria, Sorbus aucuparia*, *Quercus petraea, Fagus sylvatica, Taxus baccata* and *Ilex aquifolium.* Also, there is a great variety of grasslands in cryorotemperate and supra-orotemperate environments (Díaz-González and Penas, 2017).

In contrast to the Atlantic façade, the southern slope presents colder winters, a water deficit in summer and less than 800 mm of annual precipitation (Csb, according to the Köppen-Geiger classification: Beck et al., 2018). Accordingly, the tree layer of the continental slope is mainly composed of marcescent and evergreen oaks (Penas et al., 2017).

Pérez-Obiol et al. (2016) described the vegetation of the peat bog. They identified *Molinia caerulea, Rhynchospora alba, Erica tetralix, Drosera rotundifolia* and *Eriophorum angustifolium* among other hygrophilous taxa and peat mosses of the genus *Sphagnum.* Besides, there are a few individuals of *Betula pubescens* and *Salix* spp. on the edge of the peat bog, while in the surrounding area the potential formations are composed of *Quercus robur* and *Fraxinus excelsior* (Rivas-Martínez et al., 1987). Although there are some patches of deciduous communities, shrublands are the principal formations, mainly composed of *Ulex* spp., *Pteridium aquilinum* and *Erica* spp. and are accompanied by several plantations of *Pinus* spp. and *Eucalyptus* spp. (Fig. 3). Approximately 3 km north of the peat bog, El Monte Castillo (355 m a. s. l.) stands out as a limestone formation that hosts a forest of *Quercus ilex* subsp. *ilex* on the southern slope while there is a plantation of *Eucalyptus* spp. in the northern area (Fig. 3).

## 2. Materials and methods

### 2.1. Sampling

In 2013, a sampling campaign was conducted in La Molina peat bog by Pérez-Obiol et al. (2016). A continuous sedimentary record (MOL2) was retrieved from the top to 260 cm depth by using a PVC tube, 11 cm in diameter. Analyses on the organic matter, sedimentary charcoals (>150 μm), pollen and metal analyses (titanium and aluminium) enabled the reconstruction of the environmental geohistory of the region for the last 6740 cal yr BP. Another record (MOL4 m1, from 367 to 467 cm depth) was also sampled in 2013 to estimate the bottom age of the peat bog, with a basal age of c. 18,840 cal yr BP at 467 cm depth (Table 1).

Due to the long chronology and optimum preservation of the MOL2 sediment, a second sampling campaign was performed in 2016 to sample the oldest sediments from La Molina. Ten sedimentary cores were sampled using a Russian peat corer with a total length of 499 cm. Under laboratory conditions, the colour of the sediment was determined with a Munsell colour chart. The MOL6 records were then kept in a fridge (4 °C) until they were cut into a total of 654 samples around 1 cm (Table 1).

### 2.2. Chronology

Pérez-Obiol et al. (2016) established an age-depth chronological model for the MOL2 record of La Molina peat bog using radiocarbon

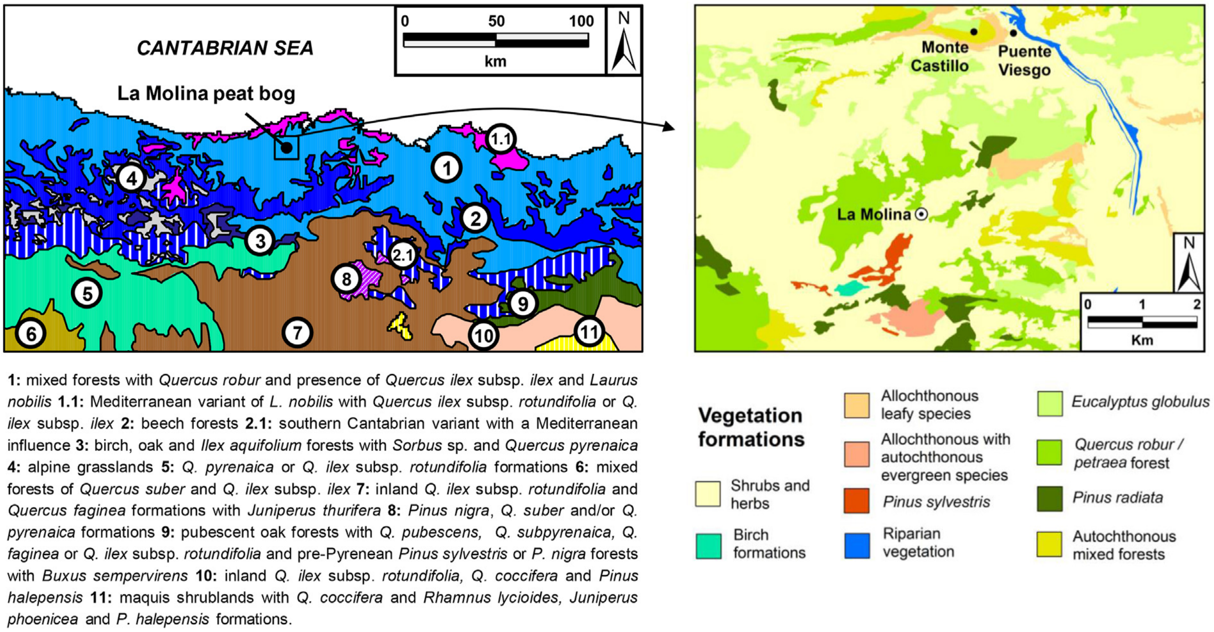

**Fig. 3. Left:** Potential vegetal map, modified from Sainz-Ollero et al. (2010) **Right:** Vegetation formations surrounding La Molina peat bog. Modified from Mapa forestal de España 1:25,000 (Miteco, 2014).

**Table 1**
Sampling year, code, depth and number of samples of each record from La Molina peat bog.

| Sampling year | Code of the record | Depth (cm) | Samples |
|---|---|---|---|
| 2013 | MOL2 | 0–260 | 302 |
| 2013 | MOL4 m1 | 367–467 | – |
| 2016 | MOL6 m1 | 0–50 | 48 |
| | MOL6 m2 | 50–100 | 50 |
| | MOL6 m3 | 100–150 | 56 |
| | MOL6 m4 | 150–200 | 55 |
| | MOL6 m5 | 200–250 | 62 |
| | MOL6 m6 | 250–300 | 61 |
| | MOL6 m7 | 300–350 | 63 |
| | MOL6 m8 | 350–400 | 64 |
| | MOL6 m9 | 400–450 | 92 |
| | MOL6 m10 | 450–499 | 103 |

dates (n = 5) and one documental datum related to *Pinus* spp. and *Eucalyptus* spp. plantations that occurred at 1950 years AD (at 14 cm depth). For the chronological model used in this work, ten $^{14}$C AMS dates (Beta Analytic Inc.) from the MOL6 record were added to the initial model. Both the $^{14}$C ages from MOL2 and MOL6 were calibrated using the IntCal20 Northern Hemisphere radiocarbon age calibration curve (Reimer et al., 2020). In addition, the chronology from the most superficial sediments of MOL2 was established by measuring the $^{210}$Pb specific activity of ten samples from 0 to 20 cm depth. Measurements of $^{210}$Pb were performed applying a constant rate of supply model (Appleby and Oldfield, 1978). The documental datum included in the chronological model used in Pérez-Obiol et al. (2016) was not considered since we had the new $^{210}$Pb-based surface age model. A $^{14}$C date from MOL2 was also rejected because it did not fit into the 95% confidence interval of the chronological model (Table 2). Considering this data set, the MOL2/MOL6 age-depth model was performed using the open-source environment RStudio for R (RStudio, 2020), the Clam package (Blaauw, 2010) and smoothing spline interpolation (Fig. 5).

### 2.3. *Organic matter*

Analyses of the organic matter content were carried out on 383 samples from MOL6 (499 - 250 cm depth; c. 17,550–6190 cal yr BP) using 1 g of wet sample. The samples were put in an oven for 24 h at 60 °C and after this process dry weight was measured. Organic content was determined by the weight loss after ignition according to standard procedures (4 h, 550 °C; modified from Dean, 1974; Heiri et al., 2001). A single organic matter sequence (MOL2/MOL6) was obtained by the combination of 287 samples from the top 250 cm of MOL2, analysed in Pérez-Obiol et al. (2016), and 383 samples of the interval from 250 to 499 cm of MOL6, obtaining a mean annual resolution of 26.19 years per sample.

### 2.4. *Pollen*

A total of 251 samples from MOL6 (499 - 250 cm depth; c. 17,550–6190 cal yr BP) were treated for palynological analyses following standard chemical procedures. One gram of each sample was weighed and sieved through a 300 μm mesh. A tablet of *Lycopodium* spores was added to estimate the pollen concentration (Stockmarr, 1971). The chemical procedure included washes with HCl (10%), HF (70%), KOH (10%) and acetolysis, followed by glycerol mounting (Faegri and Iversen, 1989; Moore et al., 1991; Bennett and Willis, 2001).

The counting and identification were carried out under an optical microscope using reference collections from the Universitat Autònoma de Barcelona, visual atlases (e.g., Reille, 1992, 1998; van Geel and Aptroot, 2006) and morphological identification keys (e.g., Faegri and Iversen, 1989; Moore et al., 1991).

Pollen percentages were calculated as a percentage of the total terrestrial pollen, thus excluding hygrophytes, aquatic plants and non-pollen palynomorphs. Also, the total pollen concentration of the terrestrial pollen (arboreal and non-arboreal grains cm$^{-3}$) and the pollen influx (palynomorph cm$^{-2}$ yr$^{-1}$; Bennet and Willis, 2001), also known as the pollen accumulation rate (PAR), were calculated and included in the diagrams.

**Table 2**
Chronological data and calibrated ages for La Molina cores (MOL2 and MOL6). Radiocarbon dates were calibrated using the IntCal20 Northern Hemisphere radiocarbon age calibration curve (Reimer et al., 2020).

| Core | Laboratory code | Depth (cm) | Material dated | Dating technique | $^{13}C/^{12}C$ (‰) | Conventional radiocarbon age (yr BP) | Calibrated age (2σ) (cal yr BP) | Median probability age, used for chronological model (cal yr BP) |
|---|---|---|---|---|---|---|---|---|
| MOL2 | Surface | 0 | peat | – | – | – | – | −63 |
| MOL2 | – | 1.02 | peat | $^{210}$Pb | – | – | – | −63 |
| MOL2 | – | 3.07 | peat | $^{210}$Pb | – | – | – | −61 |
| MOL2 | – | 5.11 | peat | $^{210}$Pb | – | – | – | −55 |
| MOL2 | – | 7.16 | peat | $^{210}$Pb | – | – | – | −47 |
| MOL2 | – | 9.2 | peat | $^{210}$Pb | – | – | – | −38 |
| MOL2 | – | 11.25 | peat | $^{210}$Pb | – | – | – | −30 |
| MOL2 | – | 13.29 | peat | $^{210}$Pb | – | – | – | −23 |
| MOL2 | – | 15.34 | peat | $^{210}$Pb | – | – | – | −19 |
| MOL2 | – | 17.38 | peat | $^{210}$Pb | – | – | – | −6 |
| MOL2 | – | 20.71 | peat | $^{210}$Pb | – | – | – | 22 |
| MOL2 | Beta-371859 | 40 | peat | $^{14}$C | −27.5 | 650 ± 30 | 555–605 | 600 |
| MOL2 | Beta-385973 | 68 | peat | $^{14}$C | −27.3 | 3340 ± 30 | – | Rejected |
| MOL2 | Beta-371860 | 113 | peat | $^{14}$C | −25.9 | 3480 ± 30 | 3687–3836 | 3757 |
| MOL2 | Beta-371861 | 186 | peat | $^{14}$C | −26.6 | 4130 ± 30 | 4567–4729 | 4676 |
| MOL6 | Beta-490941 | 252 | peat | $^{14}$C | −27.4 | 5280 ± 30 | 5988–6122 | 6079 |
| MOL2 | Beta-360118 | 260 | peat | $^{14}$C | −27.7 | 5910 ± 30 | 6661–6795 | 6726 |
| MOL6 | Beta-490942 | 299 | peat | $^{14}$C | −28.1 | 8060 ± 40 | 8846–9032 | 8972 |
| MOL6 | Beta-480943 | 302 | peat | $^{14}$C | −27.8 | 7840 ± 30 | 8543–8656 | 8616 |
| MOL6 | Beta-480942 | 348 | peat | $^{14}$C | −29 | 9180 ± 30 | 10,244–10,420 | 10,329 |
| MOL6 | Beta-475549 | 352 | peat | $^{14}$C | −29.8 | 9380 ± 30 | 10,510–10,691 | 10,611 |
| MOL6 | Beta-475548 | 399 | peat | $^{14}$C | −28.5 | 11,940 ± 30 | 13,751–13,871 | 13,806 |
| MOL6 | Beta-475547 | 401 | peat | $^{14}$C | −28.2 | 12,270 ± 30 | 14,076–14,324 | 14,178 |
| MOL6 | Beta-475546 | 449 | peat | $^{14}$C | −27.3 | 13,800 ± 30 | 16,581–16,929 | 16,749 |
| MOL6 | Beta-468818 | 450 | peat | $^{14}$C | −29.5 | 12,830 ± 60 | 15,137–15,552 | 15,323 |
| MOL6 | Beta-468819 | 499 | peat | $^{14}$C | −27.1 | 14,400 ± 40 | 17,368–17,802 | 17,552 |

The palynological diagrams (MOL2/MOL6) included 144 pollen samples counted in the MOL2 record (0–250 cm depth, previously analysed in Pérez-Obiol et al., 2016) and 251 pollen samples counted in the MOL6 record (250–499 cm depth). The mean annual resolution of the MOL2/MOL6 record was of 44.4 years per sample.

Pollen diagrams were constructed using the Tilia and Tiliagraph software (Grimm, 1991). Pollen assemblage zones (PAZ) were determined through a constrained cluster analysis by the method of incremental sum of squares (CONISS; Grimm, 1987). PAZ were identified with La Molina acronym (MOL) followed by an identification number and a letter in the case of the subzones (e.g., MOL/1a).

### 2.5. Sedimentary charcoals

Sedimentary charcoals (>150 μm) were analysed on 193 samples from the MOL6 record (499 - 250 cm depth; c. 17,550–6190 cal yr BP). The chemical procedure broadly followed the protocol described in Carcaillet et al. (2001, 2007). One $cm^3$ of sample was treated with a solution of NaClO (15%) and KOH (5%) (Finsinger et al., 2014). Samples were heated at 70 °C during 90 min with a magnet inside the beaker that moved following an electromagnetic field to facilitate the reaction. When cooled, samples were sieved through a 150 μm mesh under a water jet.

The remaining charcoal particles (>150 μm) were counted using a stereomicroscope at a magnification of 40x. The surface area of each charcoal was measured with an ocular grid of 100 squares, each 0.0625 $mm^2$ (Rhodes, 1998; Carcaillet et al., 2001). The charcoal particles were classified into size-classes that increased exponentially.

In a similar way to the organic matter and palynological sequences, a single charcoal sequence (MOL2/MOL6) was obtained by joining 288 charcoal samples analysed in Pérez-Obiol et al. (2016) from the MOL2 record (from 0 to 250 cm depth) and 193 charcoal samples analysed from the MOL6 record (from 250 to 499 cm depth), obtaining a mean annual resolution of 36.5 years per sample. Charcoal counts were divided by the sample volume and then by the sedimentation rate to obtain the charcoal concentration (CHAC, particles $cm^{-3}$) and the charcoal accumulation rate (CHAR, particles $cm^{-2}$ $yr^{-1}$), respectively. Also, charcoal peaks were determined by a Gaussian mixture model for each window of 500 years, with a threshold of the 95% of modelled noise distribution. The signal-to-noise index was calculated to quantify the suitability of the charcoal record for peak analysis (Kelly et al., 2011). A peak analysis was performed to identify the main charcoal peaks and the peak's magnitude (pieces $cm^{-2}$ $peak^{-1}$). All the analyses were performed using the CharAnalysis v1.1 software (Higuera et al., 2009).

The fire regime interpreted from the charcoal record must have had a local origin (within the watershed) since charcoal particles larger than 150 μm are known to be deposited in an area close from their source (Patterson et al., 1987; Whitlock and Larsen, 2001). Additionally, the CHAR of sedimentary charcoals larger than 0.25 $mm^2$ was also plotted to better distinguish the local fire signal (Whitlock and Larsen, 2001; Finsinger et al., 2014), as was previously done by Pérez-Obiol et al. (2016).

## 3. Results

### 3.1. Sedimentary description

Pérez-Obiol et al. (2016) described three stratigraphic phases in the MOL2 record for the interval between 0 and 260 cm (Fig. 4). The shallowest layer (0–40 cm) was described as the acrotelm. It was composed of light brown material (10 YR – 3/6, according to the Munsell colour chart), containing living *Sphagnum* spp. in the upper

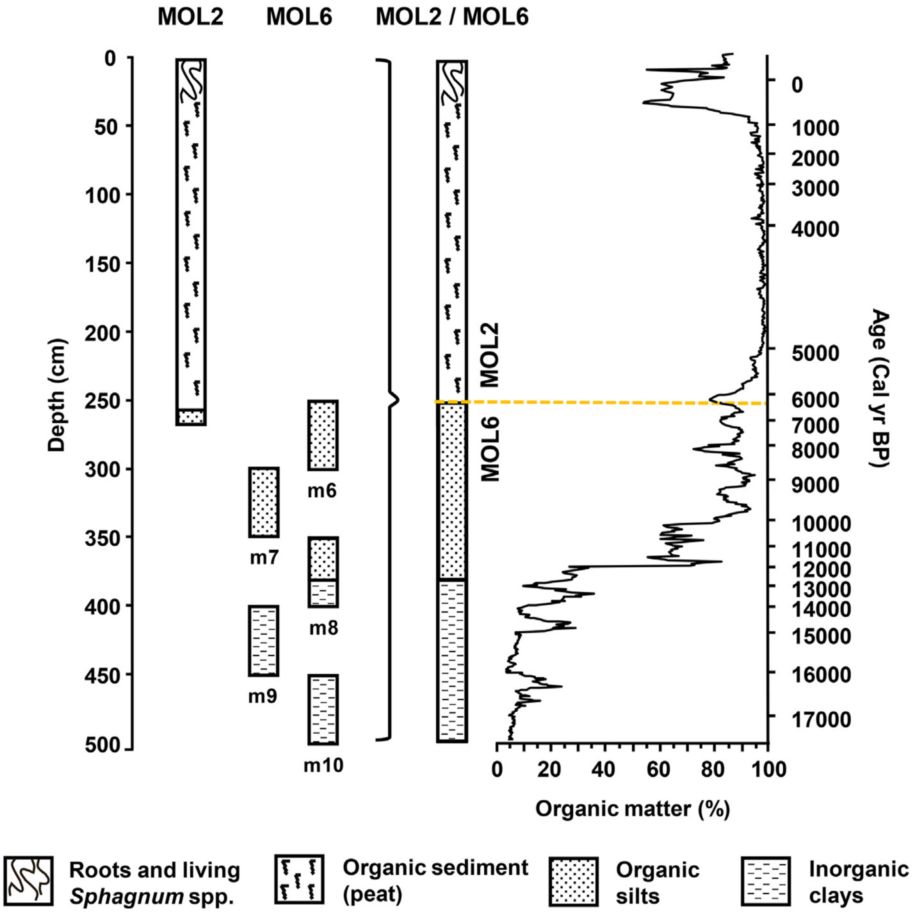

**Fig. 4.** Lithological structure of the MOL2 and MOL6 records and organic matter content of the MOL2/MOL6 record from La Molina peat bog. The MOL2/MOL6 record (on the right) was obtained by the combination of the top 250 cm of the MOL2 record, analysed in Pérez-Obiol et al. (2016), and the interval from 250 to 499 cm of the MOL6 record.

5 cm. The organic values ranged from 55 to 87%. A deeper level (40–250 cm), identified as the catotelm, was composed of dark brown gyttja (10 YR – 2/2 and 10 YR – 2/1), yielding high organic values ranging from 78 to 95%. Within the deepest part of MOL2 (250–260 cm), a progressive decrease in organic matter was detected with a greater presence of silts, followed by an organic pulse. This oscillation was also captured by the MOL6 record, which was followed by a series of pulses until 373 cm depth. Peaks of inorganic material were detected at 6230, 7090, 8210 and 9350 cal yr BP. In particular, from 342 to 369.5 cm depth (from 10,130 to 11,760 cal yr BP) the organic content was notably lower and ranged between 76 and 55%. An organic increase was detected from 369.5 to 373 cm (from 11,760 to 12,010 cal yr BP), prior to the transition towards a lacustrine material. Along this deepest phase, the colour progressively changed from dark brown (10 YR – 2/1) to grey (10 YR – 4/1) tones.

At 373 cm depth (12,010 cal yr BP) an abrupt lithological change in a short interval was detected. The organic content sharply decreased and remained at low values until the bottom of the core, even though some organic pulses were registered with values ranging from 4 to 36%. The organic peaks were detected at 13,410, 14,870, 16,320 and 16,650 cal yr BP. The material was essentially made up of lacustrine grey clays (10 YR – 4/1) until the end of the record, exhibiting a more flexible and plastic structure than the peat material from shallower layers.

### 3.2. *Chronological model*

The age-depth chronological model spans the last c. 17,550 cal yr BP and supports continuous sedimentation (Fig. 5). The $^{210}$Pb profile indicated that the top 20 cm of the peat bog was not altered. The sedimentary accumulation rate, with a mean value of 0.028 cm yr$^{-1}$, revealed two sectors with the highest chronological resolution (the 20th century and the period comprised between the Neolithic and the Chalcolithic, the latter registering a maximum at 4590 cal yr BP), with peaks of 0.5 and 0.15 cm yr$^{-1}$, respectively.

### 3.3. *Pollen*

The diagrams of pollen percentages and pollen accumulation rate (PAR) obtained from the MOL2/MOL6 record of La Molina peat bog (Figs. 6 and 7) permitted the landscape reconstruction of the area for the last c. 17,550 cal yr BP. According to the CONISS, four pollen assemblage zones (PAZ) and seven subzones were identified.

From 17,550 to 16,070 cal yr BP (MOL/1a), non-arboreal pollen values moved around 85–90% (Fig. 6), while the PAR were minimal (Figs. 7 and 9). Poaceae clearly dominated the landscape, registering a PAR between 300 and 700 grains cm$^{-2}$ yr$^{-1}$ and percentages around 50%. There was also presence of xerophytes such as *Artemisia* (7–18%), Amaranthaceae (<5%) and *Ephedra* (<5%), while other herbs and shrubs registered low values: *Calluna vulgaris*,

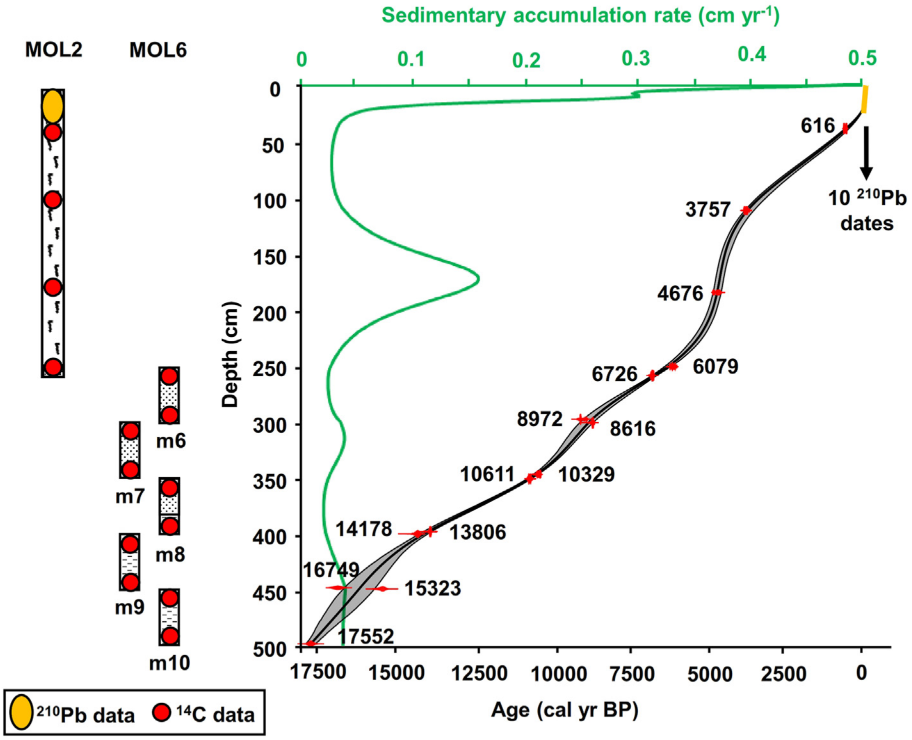

**Fig. 5.** Dates, smoothed age-depth chronological model and sedimentary accumulation rate of La Molina peat bog. The age-depth model included radicarbon dates (n = 4) analysed in the MOL2 record by Pérez-Obiol et al. (2016) and radiocarbon dates (n = 10) analysed in the MOL6 record in this paper, all of them calibrated using the IntCal20 Northern Hemisphere radiocarbon age calibration curve (Reimer et al., 2020). Measurements of $^{210}$Pb were performed from 0 to 20 cm depth applying a constant rate of supply model (Appleby and Oldfield, 1978).

Asteroideae, Cichorioideae, *Plantago*, Rubiaceae, *Helianthemum* and *Centaurea*. *Pinus* (5–10%), Ericaceae (<5%) and *Juniperus* (<5%) stood out over the woody species which appeared interruptedly. Concerning the local vegetation, there was a great presence of hydrophytes, hygrophytes (*Myriophyllum alterniflorum, Potamogeton*, Ranunculaceae, Cyperaceae, Apiaceae, *Potentilla*-type and *Typha/Sparganium*) and algae (*Botryococcus*). Ranunculaceae, probably an aquatic buttercup, were the best represented among the excluded taxa, with a 50–70% over the total taxa until 16,250 cal yr BP when their PAR sharply decreased to be surpassed by Cyperaceae percentages.

The period from 16,070 to 13,700 cal yr BP (MOL/1b) started with a progressive Poaceae increase reaching a PAR greater than 1000 grains cm$^{-2}$ yr$^{-1}$ at 14,900 cal yr BP, representing 85% of the terrestrial pollen. Following the opposite trend, *Artemisia* decreased from 20 to 15% to less than 5% and *Juniperus* values became minimal. After 14,900 cal yr BP, a series of pollen fluctuations was detected. Poaceae oscillated in accordance with organic matter pulses while *Juniperus* recovered its minimal presence between 14,700 and 13,960 cal yr BP. In addition, particularly noteworthy were also the peaks of *Sanguisorba officinalis* at 14,550 cal yr BP (23%) and Ericaceae at 13,900 cal yr BP (51%). Overall, the arboreal pollen was still low (10%), with similar values of *Pinus* and a slight increase in deciduous *Quercus*. At a local scale, a *Sordaria* pulsation (25%) was registered between 16,070 and 14,600 cal yr BP. The presence of aquatic taxa decreased during MOL/1b.

Between 13,700 and 11,900 cal yr BP (MOL/2a), corresponding to the end of the Würm glaciation, *Betula* percentages sharply increased and represent 81% of pollen at 13,400 cal yr BP. The *Salix* signal increased during this PAZ too, with values close to 10% around 13,000 cal yr BP. It is also worth stressing the increase of the *Pinus* influx up to 1050 grains cm$^{-2}$ yr$^{-1}$, even though its percentage did not vary due to the great quantity of *Betula* pollen. In this line, *Betula* signal represented the greatest portion of the arboreal pollen percentages, which revealed an interval of sharp fluctuations along the Bølling-Allerød chronozone (GI-1) and the Younger Dryas (GS-1). The great quantity of *Betula* also triggered the first significant peak of pollen influx, detected at 13,260 cal yr BP (Figs. 7 and 9). After this period, *Betula* progressively decreased down to 12% during the last stages of the LGP (13,370–11,900 cal yr BP), resulting in an increase of *Pinus* (20%) and non-arboreal percentages (65%). Also particularly significant were the short-duration pulses of Poaceae (39%), Cichorioideae (28%), Asteroideae (10%), *Centaurea* (8%) and *Filipendula* cf. *F. ulmaria* (10%) registered prior to the onset of the Holocene.

During the first millennia of the Holocene (MOL/2b), peaks of terrestrial PAR were detected at 11,600, 11,200, 10,130 and 9600 cal yr BP, the latter being the greatest of all the sequence (up to 60,000 grains cm$^{-2}$ yr$^{-1}$; Fig. 9). The pollen influx of *Pinus, Betula*, evergreen *Quercus*, deciduous *Quercus* and *Salix* increased, and the values of *Betula* (>32,000 grains cm$^{-2}$ yr$^{-1}$) and deciduous *Quercus* (>14,000 grains cm$^{-2}$ yr$^{-1}$) were significantly relevant. *Betula* registered mean percentages between 50 and 70%, deciduous *Quercus* between 20 and 40% and *Pinus* around 5%, yielding arboreal pollen percentages above 90%. The terrestrial pollen concentration was also the greatest detected in all the sequence, with peaks up to $2 \cdot 10^6$ grains cm$^{-3}$. *Pteridium*-type also stood out during the first stages of the Holocene, with values around 56% at 11,900 cal yr BP. Later on, the beginning of the *Corylus* continuous signal was detected at 10,680 cal yr BP, which increased progressively to reach more than 10% at 9720 cal yr BP. A decrease of *Betula* percentages in favour of deciduous *Quercus* was also identified between 10,100 and 9850 cal yr BP.

PAZ MOL/3 (9300–4860 cal yr BP) started with a sharp decrease of *Betula* at 9300 cal yr BP. Apart from a pulsation of 25% at 9100 cal yr BP, *Betula* stood at around 10% throughout the period.

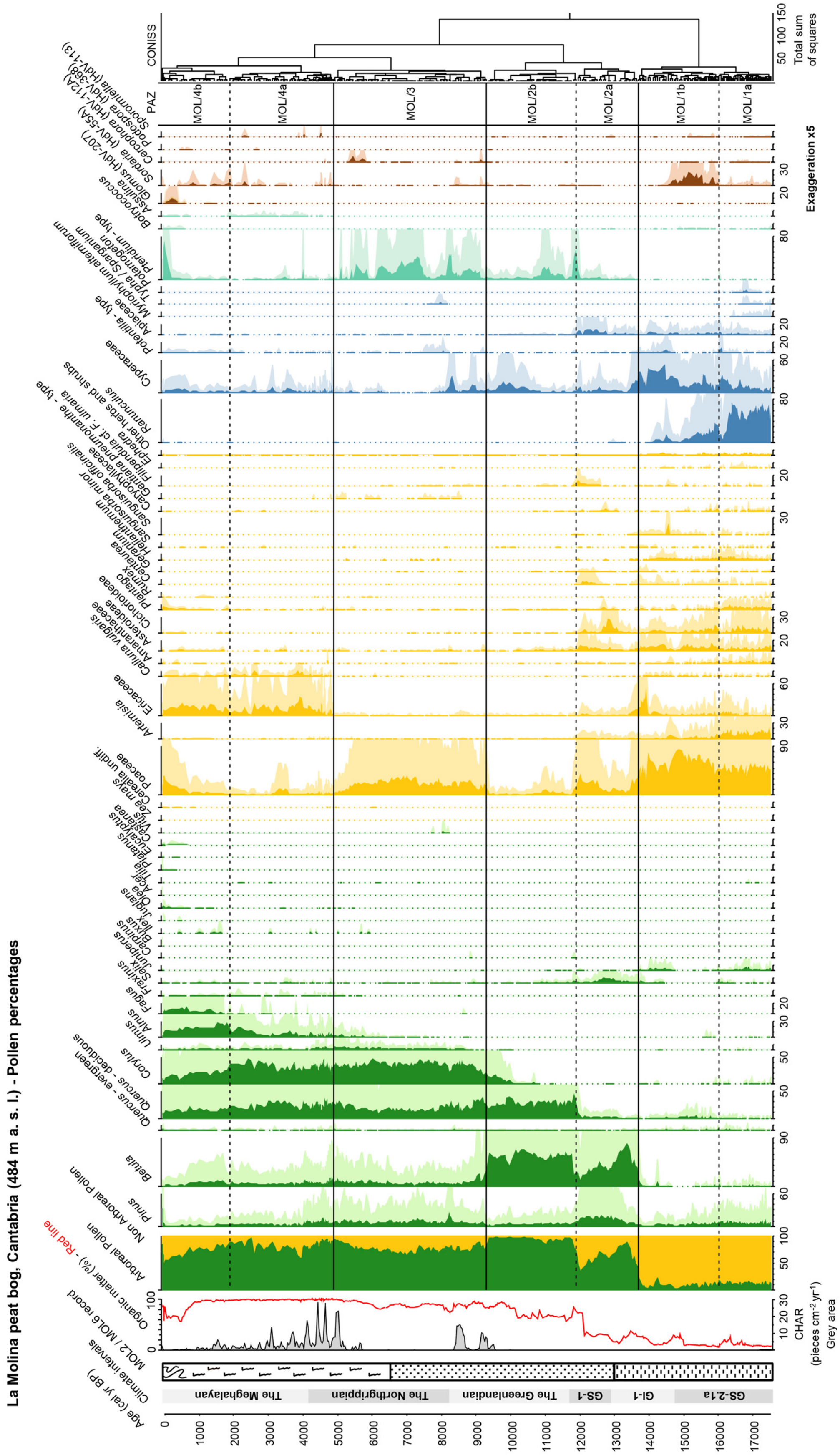

**Fig. 6.** Diagram of pollen percentages of La Molina peat bog (MOL2/MOL6 record). Light silhouettes indicate x5 exaggeration. The organic matter content (%) is shown as a red line and the charcoal accumulation rate (CHAR, pieces cm$^{-2}$ yr$^{-1}$) of charcoal particles >150 μm is shown as a grey area. Pollen assemblage zones (PAZ) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

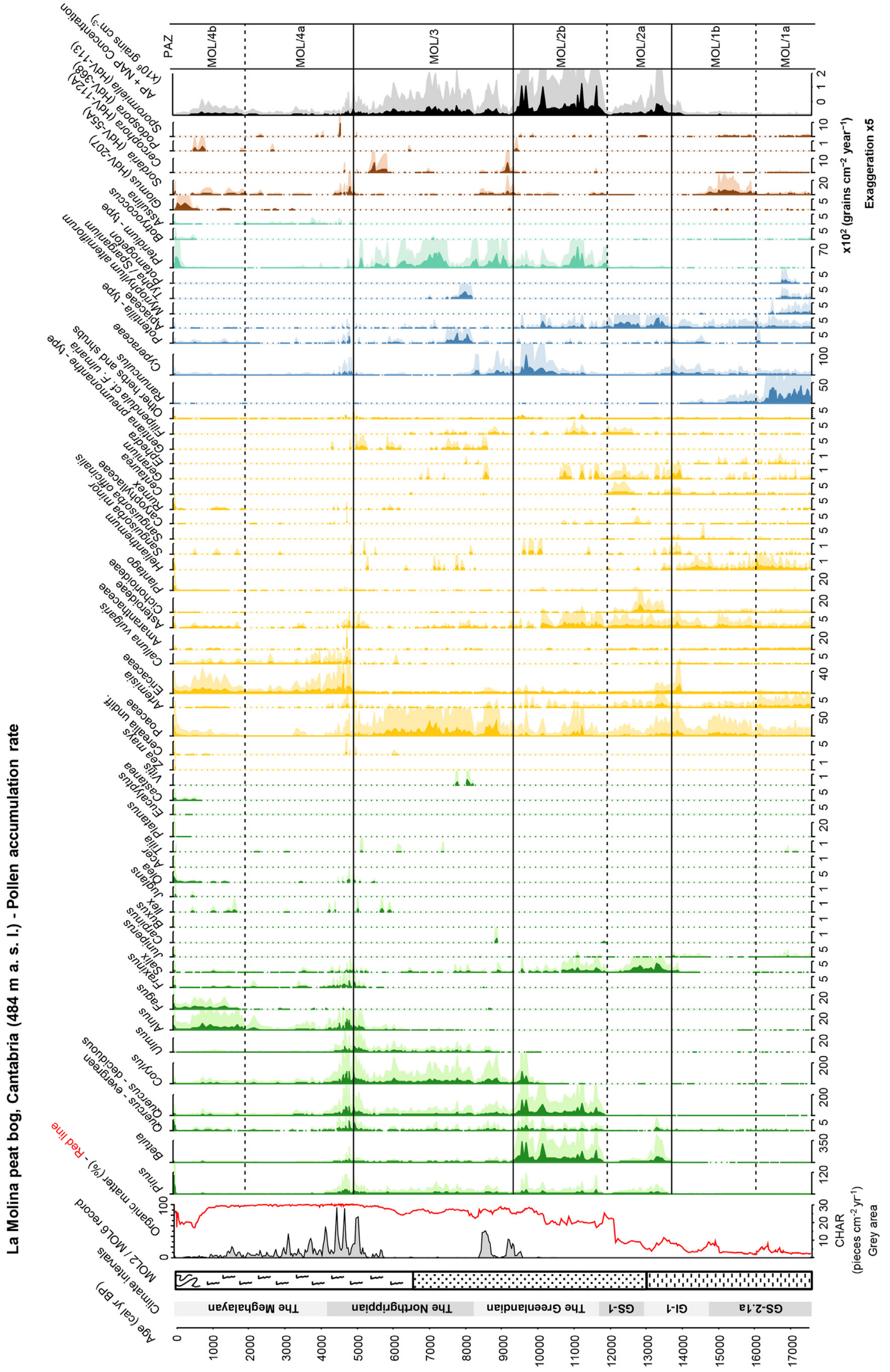

**Fig. 7.** Diagram of pollen accumulation rates (grains cm$^{-2}$ yr$^{-1}$) of La Molina peat bog (MOL2/MOL6 record). Light silhouettes indicate x5 exaggeration. The organic matter content (%) is shown as a red line and the charcoal accumulation rate (CHAR, pieces cm$^{-2}$ yr$^{-1}$) of charcoal particles >150 μm is shown as a grey area. Pollen assemblage zones (PAZ) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Deciduous *Quercus* also registered a lower PAR than in MOL/2b, despite not being reflected in the percentage diagram mainly due to *Betula*'s significant decline. Both decreases, however, led to the greatest percentages of *Corylus* along all the sequence, varying between 35 and 45%. Between 8330 and 8180 cal yr BP, an important decrease in the *Corylus* and deciduous *Quercus* influx led to a *Pinus* increase up to 27%. Also, the beginning of the *Ulmus, Alnus* and *Fraxinus* continuous curves was found at 8800, 7200 and 5000 cal yr BP, respectively. A low pulsation of *Vitis* was detected between 8180 and 8040 cal yr BP and the first appearances of Cerealia and *Olea* were estimated at around 6660 cal yr BP. Especially significant is the detection of a single instance of *Fagus* pollen at 8620 cal yr BP and another of *Carpinus* at 8840 cal yr BP. Equally, the non-arboreal spectra expanded due to the Poaceae increase (25–35%) as the main taxon of the local openings. *Pteridium*-type and *Gentiana pneumonanthe* signal also increased mainly within this PAZ.

Between 5270 and 4100 cal yr BP, corresponding to the late stages of MOL/3 and the first centuries of MOL/4a, the greatest values of arboreal pollen influx were registered, particularly for *Pinus, Betula,* evergreen *Quercus*, deciduous *Quercus, Corylus, Ulmus, Alnus, Fraxinus* and *Salix*. As indicated by Pérez-Obiol et al. (2016), during the time period encompassed by MOL/4a (4860–1900 cal yr BP), *Corylus* and deciduous *Quercus* continued to express high values. However, the non-arboreal composition shifted as Poaceae decreased in benefit of Ericaceae. At the same time, the signal of *Pteridium*-type also became minimal. Low values of *Assulina*, a testate amoeba, were registered from 4560 cal yr BP together with an intermittent but continuous signal of coprophilous fungi, mainly *Sordaria* and *Sporormiella*.

From 1900 to −63 cal yr BP (MOL/4b) a falling arboreal pollen trend was observed until the onset of the 20th century. *Alnus* and *Fagus* stood out among the tree species, coinciding with the decrease of *Corylus* and deciduous *Quercus* percentages. According to the updated chronological model, *Alnus* reached the highest percentages at 1820 cal yr BP, and the onset of the continuous signal of *Fagus* is estimated at 1680 cal yr BP.

The decline of *Corylus* and deciduous *Quercus* coincided with high values of Poaceae and Ericaceae PAR, leading to increased non-arboreal pollen percentages. An important peak of *Pteridium*-type was also recorded coinciding with the greatest non-arboreal percentages. During the 20th century, however, the decreasing arboreal trend shifted as a result of a significant *Pinus* influx increase. In addition, *Olea, Platanus, Eucalyptus* and *Castanea* reached a continuous signal, yielding lower percentages of deciduous *Quercus, Corylus, Fagus* and *Alnus* while maintaining a similar pollen influx. The coprophilous signal was similar to the preceding PAZ, now with pulsations of *Sordaria* and *Podospora* instead of *Sporormiella.* An increase in *Botryococcus* and *Assulina* was detected among the aquatic taxa from 500 cal yr BP onwards.

### 3.4. Sedimentary charcoals (>150 μm)

The interpretation of the fire dynamics was based on the same pollen assemblage zones identified within the pollen diagrams. The charcoal signal displayed low values from 17,550 to 13,700 cal yr BP (MOL/1), with charcoal peaks with less than 10 pieces $\text{cm}^{-2}\ \text{yr}^{-1}$ (Figs. 8 and 9). Between 13,700 and 9300 cal yr BP (MOL/2), the fire evidence was still low, even though the first particles larger than 0.25 $\text{mm}^2$ were detected. The first significant charcoal peaks occurred at 9300 cal yr BP (206 pieces $\text{cm}^{-2}\ \text{peak}^{-1}$) and 8650 cal yr BP (128 pieces $\text{cm}^{-2}\ \text{peak}^{-1}$). The local component of the two fire events is supported by the presence of charcoal particles larger than 0.25 $\text{mm}^2$. Additionally, most charcoal peaks coincide with a singal-to-noise index above or close to 3 from that point onwards, suggesting that charcoal peaks were confidently separated from noise (Kelly et al., 2011). From 8400 to 5700 cal yr BP, the charcoal frequency decreased with a mean CHAR value at around 0.1 pieces $\text{cm}^{-2}\ \text{yr}^{-1}$. The CHAR value started increasing again at 5700 cal yr BP and was followed by the greatest fire peak of all the sequence registered at 5020 cal yr BP (834 pieces $\text{cm}^{-2}\ \text{yr}^{-1}$). Subsequently, the CHAR value stood at up to 28 pieces $\text{cm}^{-2}\ \text{yr}^{-1}$ between 4650 and 4430 cal yr BP. Also, the charcoal influx of particles larger than 0.25 $\text{mm}^2$ reached 0.85 pieces $\text{cm}^{-2}\ \text{yr}^{-1}$ within these peaks. After the event of 4430 cal yr BP, however, the charcoal values and the peak magnitude started to decline, registering the last significant fire episode at around 990 cal yr BP. The charcoal curves displayed a low signal during the most recent period (MOL/4b, from 1900 to −63 cal yr BP), with peaks below 65 pieces $\text{cm}^{-2}\ \text{peak}^{-1}$ that were not well separated from noise in agreement with the signal-to-noise index (Kelly et al., 2011).

## 4. Discussion

To date, there have been few studies examining what the plant landscape of the Cantabrian region was like during the Last Glacial Period (LGP). The multiproxy approach performed in La Molina (484 m a. s. l.) is the oldest chronology studied on the northern slope of the Cantabrian range and made it possible to determine the succession of different landscape units over the last c. 17,550 cal yr BP.

### 4.1. An open landscape after the Last Glacial Maximum

A steppe-like formation with scarce tree cover is deduced from the pollen spectra during the Greenland Stadial 2.1a (from 17,550 to 14,700 cal yr BP; Rasmussen et al., 2014). This phase, which also encompasses the Heinrich event 1 (Heinrich, 1988; Bond et al., 1992; Hemming, 2004), was characterised on the northern slope of the Cantabrian range by cold and dry climate features until 15,500 cal yr BP, inferred through isotopic analyses on a speleothem from the nearby Asiul cave (Moreno et al., 2010a). Accordingly, the plant landscape fully reflects the climatic severity of that time with limited water availability which did not allow either the tree or shrub cover to develop. The dominance of Poaceae over *Artemisia* and other xerophytes is consistent with the plant composition documented in the littoral and coastal mountain sites from the north-western Iberian Peninsula in Portugal (Gómez-Orellana et al., 2001, 2013), Galicia (Saa-Otero and Víaz-Fierros, 1988; Gómez-Orellana et al., 1998, 2001; López-Merino et al., 2012; García-Moreiras et al., 2019) and Asturias (López-Merino, 2009). From analyses of modern surface samples (mosses), it can be deduced that the open landscape could be equivalent to the current alpine grasslands located above the treeline in the European Alps (≥2360 m a. s. l.), which are communities that are certainly well-adapted to water scarcity and cold temperatures (Furlanetto et al., 2019). A greater proportion of Mediterranean xerophytes has been detected in Iberian sites with a greater Mediterranean influence during the LGP (e.g., Pantaléon-Cano et al., 2003; Camuera et al., 2019), suggesting drier climate features than in the Eurosiberian biogeographical region.

At 15,500 cal yr BP, a shift to warmer and wetter conditions is detected in the Cantabrian region (Moreno et al., 2010a). This climate change ties in well with the decrease of xerophyte taxa from 16,000 cal yr BP onwards. At a local scale, the loss of lacustrine features and the transition to an early stage of a peat bog has also been noted, as indicated by the decrease of hydrophytes, hygrophytes and algae. Here the *Sordaria* pulsation detected between 16,070 and 14,600 cal yr BP might indicate a higher amount of decaying organic matter.

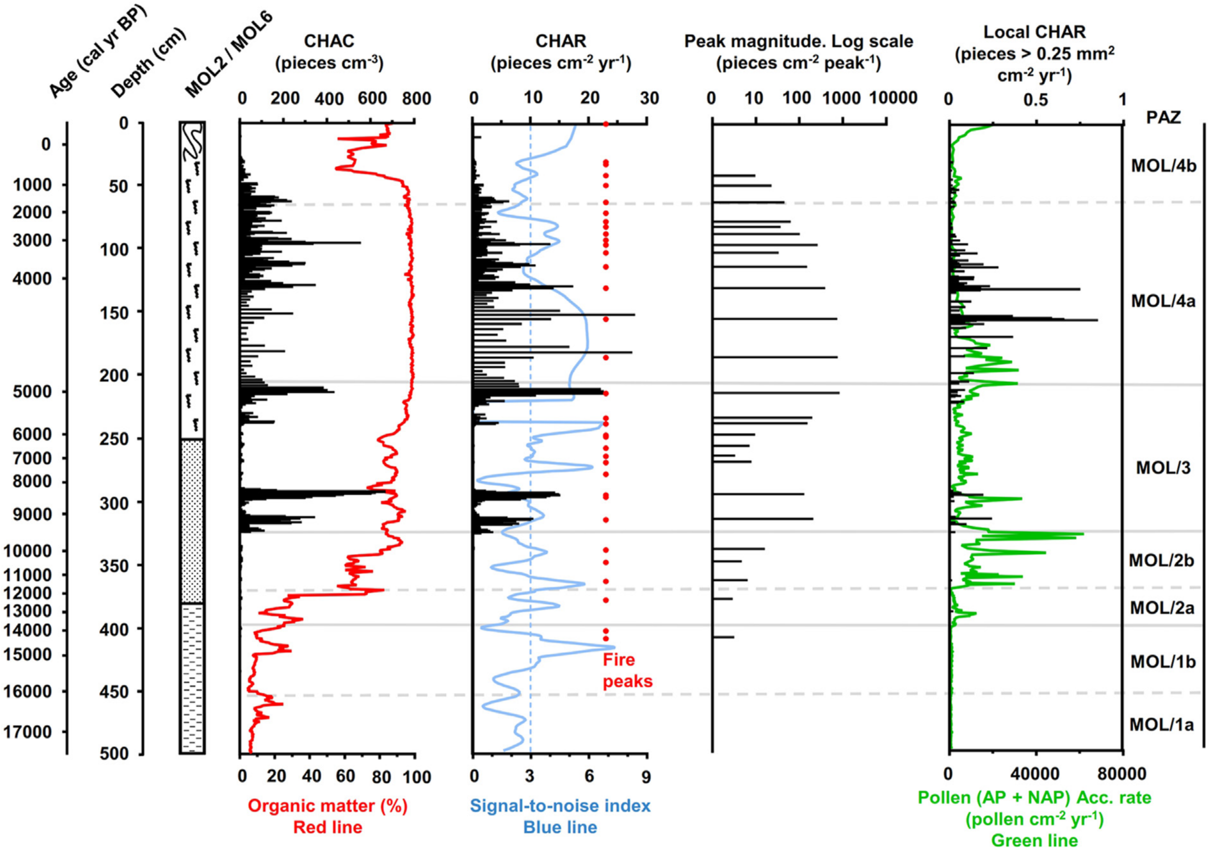

**Fig. 8.** Diagram of the charcoal concentration (CHAC), charcoal accumulation rate (CHAR), fire peaks as red dots, fire peak magnitude and charcoal accumulation rate of charcoal particles larger than 0.25 mm$^2$ of La Molina peat bog (MOL2/MOL6 record). The organic matter is shown as a red line, the pollen accumulation rate (arboreal: AP + non arboreal: NAP) as a green line and the signal-to-noise index (SNI) as a blue line. The cutoff value of SNI = 3 (Kelly et al., 2011) is indicated as a blue dashed line. Pollen assemblage zones (PAZ) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

At a regional scale, the landscape described on the northern slope differs from what has been documented in other sectors of the Cantabrian range, which seems to have played a significant role in the geographical distribution of certain species. On the one hand, glaciers expanded from 22,500 to 18,000 cal yr BP at higher altitude areas of the mountain system (Frochoso et al., 2013; Ruiz-Fernández et al., 2016). Accordingly, the vegetation community within this altitudinal range appears to have been sensitive to more arid and colder conditions, since steppe-like taxa displayed greater values than on the Atlantic façade from the Last Glacial Maximum (from 26,500 to 19,000 cal yr BP), both on the westernmost flank (Aira-Rodríguez, 1986; Santos-Fidalgo et al., 1997; Muñoz-Sobrino et al., 2001) and also in the central sector (Ruíz-Zapata et al., 2000; Jiménez-Sánchez et al., 2003). The community composition did not change during the immediately preceding millennia in the mountain environment as recorded, from West to East, in Laguna de Lucenza (Aira-Rodríguez, 1986; Santos-Fidalgo et al., 1997; Muñoz-Sobrino et al., 2001), Villaseca de Laciana (Jalut et al., 2010), La Mata (Jalut et al., 2010), Lago de Ajo (Allen et al., 1996) and, closer to La Molina, in Puertos de Ríofrio (1700 m a. s. l.), which displays 30% of *Artemisia* during the Late Glacial (Menéndez-Amor and Florschütz, 1963). In the latter site, although only a few pollen samples were analysed from the Late Glacial, the significant presence of *Artemisia* may indicate that the arid conditions were maintained in the upper reaches of the mountain system for a longer period of time than in La Molina.

On the other hand, the situation was very different on the southern slope. In northern Burgos, there was a greater presence of trees, mainly *Pinus* and *Betula*, in La Piedra (Ramil-Rego et al., 1998) and San Mamés de Abar (Iriarte-Chiapusso et al., 2001), in what is likely to be the last stages of the GS-2.1a (Rasmussen et al., 2014). Unfortunately, the absence of a robust chronology did not allow accurate identification the climate episodes, though it is possible to recognise different behaviour from the Cantabrian oceanic slope. Moreover, the dominance of *Pinus* becomes more evident if we look further south. It is the case of the northern Iberian System, where several sites reveal vegetation communities with a great presence of pines at certain stages of the LGP (Peñalba, 1994; Gómez-Lobo et al., 1996; Peñalba et al., 1997; Von EngerIbrechten, 1998; Sánchez-Goñi and Hannon, 1999; Gil-García et al., 2002), reaching pollen values up to 70–90% in Laguna Grande (Ruiz-Zapata et al., 2002). These forest communities contrast with the open grasslands from the Atlantic coastal region. It is likely that the continental conditions of the southern slope, which implies higher maximum temperatures or at least more water availability, may have facilitated the development of the tree cover in the inland region. On the northern slope, anthracological analyses performed in caves reported high abundance of pine macroremains during the Upper Pleistocene (Baena et al., 2005). However, there is no evidence of large extensions of pinewoods in the region around La Molina, at least from the Magdalenian to the present. The pine values are not only far below the documented percentages in southern areas, but also modern pollen rain calibration attributed more than 50–60% of *Pinus* to pinewoods in the Central System (López-Sáez et al., 2013), which is substantially higher than the *Pinus* signal documented in La Molina. The lack of large extensions

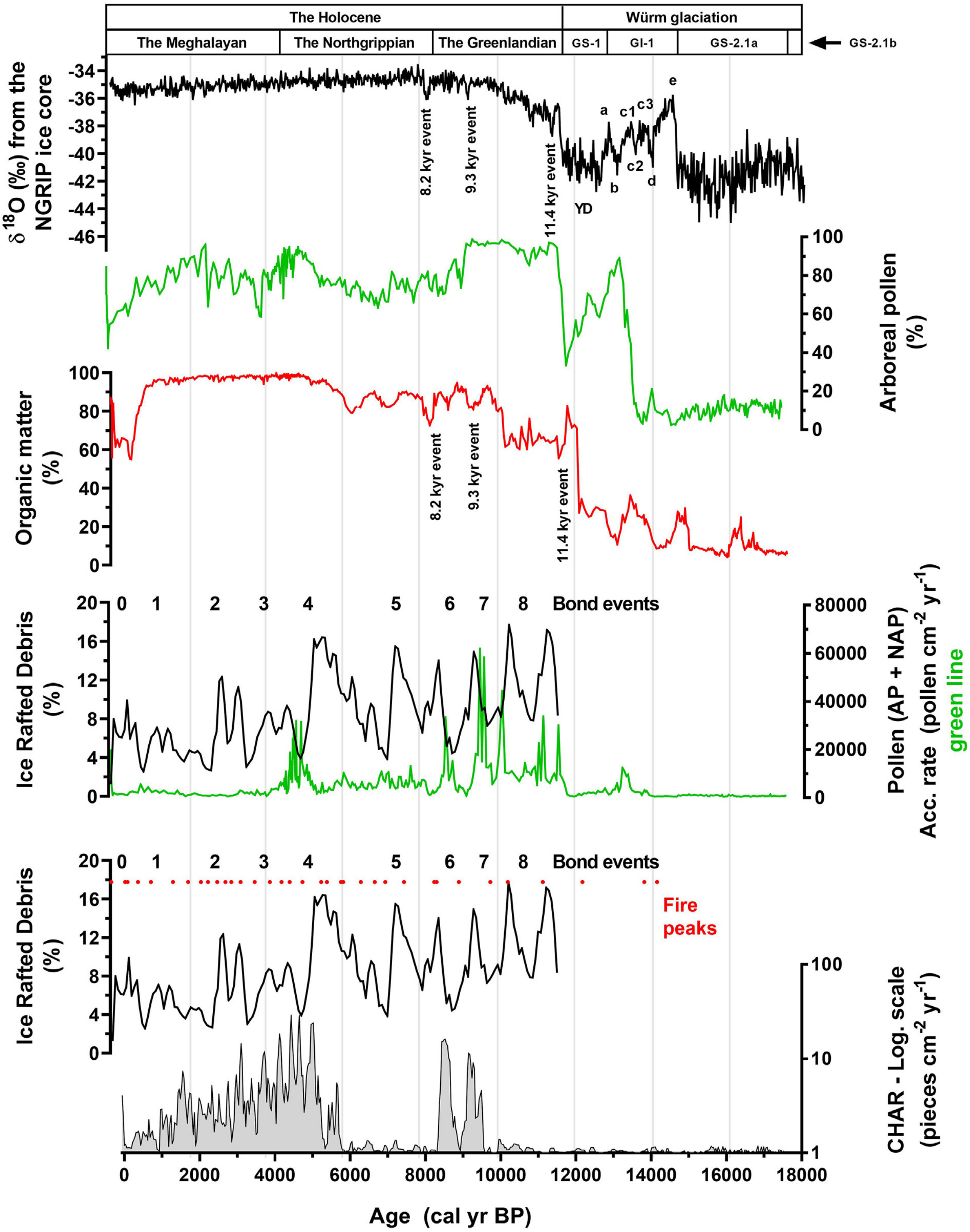

**Fig. 9.** Comparison of CHAR, Ice Rafted Debris (IRD) index: Stack of MC52-V29191 + MC21-GGC22 (Bond et al., 2001), pollen accumulation rate (arboreal: AP + non arboreal: NAP), organic matter and $\delta^{18}O$ from the NGRIP ice core, adapted from Rasmussen et al. (2014). At the top of the figure, the chronology for the Würm glaciation based on Greenland Stadials (GS) and Greenland Interstadials (GI) is shown (Rasmussen et al., 2014), and also the stages for the Holocene based on Walker et al. (2018, 2019). The Younger Dryas Stadial (YD) and the substages of the Greenland Interstadial 1 (a—e) are indicated.

of pines is also supported by the low pollen values recorded in the vast majority of Holocene pollen records along the Cantabrian littoral (e.g., Mariscal, 1993; Peñalba, 1994; García-Antón et al., 2006; Iriarte-Chiapusso et al., 2006; López-Merino et al., 2006, 2010; López-Merino, 2009; González-Pellejero et al., 2014). Without ruling out the possible existence of scattered pine individuals, the origin of the low but continuous *Pinus* signal recorded in La Molina could be explained by the recognised large pollen dispersal of this species (Poska and Pidek, 2010) and the long transport from southern regions where *Pinus* populations were more consolidated.

Concerning the role of fire, the lack of woody species went hand in hand with the absence of significant fire events during the Palaeolithic section of the record. The lack of charcoal particles larger than 0.25 mm$^2$ during that period also reinforces the idea that no significant fires occurred at a local level, since a larger size would indicate a closer origin (Whitlock and Larsen, 2001; Finsinger et al., 2014). We need to look beyond the Cantabrian region to compare La Molina's fire regime during the LGP, since the available charcoal records only cover the period up to c. 7000 cal yr BP (Carracedo et al., 2018). Thus, the lack of fires registered in La Molina before the Holocene is in line with other Iberian sites with an Eurosiberian distribution, such as Charco da Candieira (Portugal; Connor et al., 2012), El Portalet (Central Pyrenees; Gil-Romera et al., 2014) and also in the Mediterranean site of Siles (Andalucía; Carrión, 2002) where the fire signal was weak during the LGP. The low intensity of fires meant it was not possible to explore any possible connexion with an environmental signal during that period (e.g., the $\delta^{18}$O curve from Greenland ice cores: Dansgaard et al., 1982; Johnsen et al., 1992; Rasmussen et al., 2014; Seierstad et al., 2014).

Turning to the relationship between humans and the Cantabrian landscape, anthropic pressure does not seem to have been significant during the LGP. On the contrary, the plant formations could have affected the distribution of some animal species, the prey of the hunter-gatherer human groups that inhabited the Cantabrian range (e.g., Solórzano et al., 1999; González-Sainz and González-Urquijo, 2004) and other hunting animals. In particular, the Iberian ibex (*Capra pyrenaica*) was the principal prey documented in north-Iberian archaeological sites far from the current shoreline (>9 km) and above 200 m from the current sea level, as is the case of La Molina. On the other hand, remains of red deer (*Cervus elaphus*) were the most abundant fossils found close to the shoreline (Portero et al., 2019). Thus, the non-forested landscape inferred from La Molina's pollen spectra seems to have been a suitable habitat for the Iberian ibex, which is currently found in mountainous areas and has a diet mainly made up of herbaceous plants (Granados et al., 2001). The steppe-like formation was otherwise probably a limiting factor in the distribution of red deer, whose principal habitat is woodlands and open areas close to woody formations as they are often used as a refuge (Carranza, 2017). The red deer distribution might therefore suggest a more forested environment close to the coastline, which perhaps also occupied a wider area since the sea level was more than 100 m lower than at present (Lambeck et al., 2014; Spratt and Lisiecki, 2016). However, for now there is a lack of palynological records covering this period on the Cantabrian littoral plain to support this hypothesis.

### 4.2. *The spread of woody species over the Bølling-Allerød chronozone and their decline during the Younger Dryas*

The period from 14,690 to 12,900 cal yr BP (GI-1) is characterised by being an overall mild phase with a certain degree of climate variability (Rasmussen et al., 2014). Our results indicate several vegetation fluctuations for that period, very different from the little-disturbed landscape that remained after the LGM. A first vegetation shift occurred at the beginning of the Bølling-Allerød Interstadial in the form of *Juniperus* and Ericaceae pulses accompanied by a decrease of Poaceae in what can be interpreted as a weak vegetation response to the warmer climate features. Unfortunately, *Juniperus* and Ericaceae could not be identified to species level, but in both cases their presence reflects an environmental change from 13,900 cal yr BP onwards.

At the same time, *Betula* led the succession to a more forested environment. *Salix* exhibited a similar behaviour, although its signal is substantially lower than that of *Betula* perhaps because it has a certain degree of zoophily (Lara-Ruiz, 2019) and its pollen dispersal may be lower. In any case, the expansion of both taxa, which represented the first significant biomass pulsation of the sequence, is explained by a gradual humidity increase that took place in the region between 15,400 and 13,400 cal yr BP (Moreno et al., 2010a). *Betula* and *Salix* started increasing during that interval and *Betula* displayed its maximum values at 13,370 cal yr BP, having likely benefited from increased water availability. From that point onwards, *Betula* suffered a first decreasing pulse in what might have been a response to the cold spell registered from 13,310 to 13,100 cal yr BP in Greenland ice cores (GI-1b; Rasmussen et al., 2014). The decline of birches and willows was consolidated within the Younger Dryas, a dry and cold phase of regional extent (Rasmussen et al., 2014) well characterised in north-western Iberia (Moreno et al., 2010a; Muñoz-Sobrino et al., 2013; Baldini et al., 2015, 2019). In particular, at the onset of the Younger Dryas, a severe drop in temperatures of between 6 and 9 °C was inferred from La Garma cave (Baldini et al., 2015, 2019) at about 40 km from La Molina. The study also provided climatic models that revealed especially cold and dry winters for that period. The increasing influx of non-arboreal species, then dominated by Poaceae and accompanied by Asteroideae, Cichorioideae and *Centaurea,* is a good reflection of the tough conditions prior to the Holocene. *Pinus,* on the other hand, does not seem to have been significantly affected by the climatic fluctuations, exhibiting less variability than *Betula*.

*Betula*'s fluctuations were not an isolated dynamic detected in La Molina peat bog, as they were also captured in the western deposits of Laguna de Lucenza (Aira-Rodríguez, 1986; Santos-Fidalgo et al., 1997; Muñoz-Sobrino et al., 2001), Villaseca de Laciana and La Mata (Jalut et al., 2010), indicating a climatic response at a regional scale. Similarly, these oscillations have also been detected in the Pyrenees during the same period, although with a greater presence of *Pinus* (Reille and Lowe, 1993; Cunill et al., 2013; Gil-Romera et al., 2014).

The lack of taxonomical resolution does not allow interpreting which birch species undertook the woody colonisation. At present, *Betula pubescens* is the birch species present in the mountainous area, while *Betula pendula* is not so frequent in the Cantabrian range but has a wide distribution in north-eastern Iberian mountains (Pyrenees) and Europe. We cannot rule out these species having led the colonisation since they are recognised for their ability to colonise open areas, such as heathlands (Shaw et al., 2014a; Stritch et al., 2014). In this line, a significant exploitation of *Betula*'s wood has been documented in the littoral cave of La Pila during the late Magdalenian and early Azilian: from c. 12,500 to 11,700 yr BP (Bernaldo de Quirós et al., 1992; Uzquiano, 2014). Such a large amount of wood might suggest the presence of arboreal *Betula* species. Alternatively, shrubby birches such as *Betula nana* or *Betula humilis,* both widely distributed across Europe at present (Beck et al., 2016), could have also developed in the Cantabrian area. Considering their habitat, *Betula nana* is an arctic or high mountain plant of immature or peaty soils, found in alpine or subalpine environments (Stritch, 2014). *Betula humilis* can be found as part of different communities from the hill to the montane zone, both in acidic and wet forest soils and also close to wetlands (Shaw et al., 2014b). Thus, both the arboreal and shrub birch species mentioned above could fit well into the pre-Holocene Cantabrian landscape. In the case of *Salix*, it would be reasonable to think of low shrub or creeping dwarf willows. Future analyses on the vegetation macroremains or ancient DNA would help to identify

Ericaceae, *Salix* and *Betula* to a more specific level, thus shedding more light on how this succession occurred.

### *4.3. The establishment of mixed deciduous formations during the early Holocene*

The early Holocene was characterised by a general warming and humidity increase in the north-western Iberian Peninsula (Smith et al., 2016; Rossi et al., 2018; Morellón et al., 2018; Baldini et al., 2019), coinciding with the greatest Holocene values of summer insolation in the Northern Hemisphere (Berger and Loutre, 1991). Although most rainfall was concentrated during the winter months in the Cantabrian range (Baldini et al., 2019), the humidity increase was enough to support the rapid expansion of forests at the onset of the Holocene. Additionally, the presence of woody species during the Younger Dryas, mainly *Betula*, would have favoured soil development and is another important factor in explaining how fast the arboreal succession occurred. The sharp biomass increase suggests a different temperature threshold from higher altitude areas at the alpine Pyrenees, where colder temperatures postponed the increase of the PAR by a few millennia (Leunda et al., 2017).

During the Lateglacial-Holocene transition, Azilian human groups were settled at high altitudes of the Cantabrian range (Barandiarán et al., 2006). The Cantabrian landscape, however, seems to have remained little affected by anthropic pressure during that time. Plant biomass, mainly represented by tree species (>95%), exhibited the maximum values of the entire sequence, whereas human signals were not documented in the palynological record. Conversely, plant production seems to have been sensitive to a series of century-to-millennial scale environmental pulses triggered by changes in the North Atlantic Ocean circulation which have been well recorded in isotopic records on ice cores (Bond et al., 2001; Rasmussen et al., 2007, 2014). In the Cantabrian range, such climate variability entailed cyclical shifts of wetting and drying conditions, with a periodicity of 1290 years during the early Holocene (Smith et al., 2016). The frequency of biomass declines in La Molina was very similar to that of humidity shifts during that period, revealing a close relationship between climate conditions and vegetation growth with reduced productivity during the driest intervals.

Concerning the vegetation communities, the Cantabrian forests were mainly composed of *Betula,* deciduous *Quercus* and a scattered presence of *Salix, Pinus* and evergreen *Quercus*. The signal of deciduous *Quercus* might mainly correspond to *Quercus robur,* since it is the most common oak in the inner valleys of the current landscape. *Corylus*, on the other hand, started to expand some centuries later, in line with other montane and subalpine locations of the Cantabrian range (Menéndez-Amor and Florschütz, 1963; Menéndez-Amor, 1968; Allen et al., 1996; López-Merino, 2009; Jalut et al., 2010; Muñoz-Sobrino et al., 2012). This is also consistent with the hazel's dynamics in south European regions, where its expansion occurred later than the spread of other deciduous taxa (Finsinger et al., 2006; Giesecke et al., 2011), contrary to what happened in northern and central Europe (e.g., Huntley, 1993; Tinner and Lotter, 2001; Tallantire, 2002). Huntley (1993) suggests that high seasonality was an important factor in the development of hazel populations at high latitude regions, probably also linked to increased fire activity. Indeed, *Corylus* is a resprouting taxon well adapted to fire events (Delarze et al., 1992; Tinner et al., 1999). Finsinger et al. (2006) underlined similar reasons for the late spread of *Corylus* in the Southern Alps. In the Cantabrian region, the warm and humid climate conditions during the early Holocene (Smith et al., 2016; Rossi et al., 2018; Morellón et al., 2018; Baldini et al., 2019) and the lack of fire activity during that period may have prevented an earlier hazel expansion. The situation changed shortly afterwards due to an aridity increase detected in the region from 8.5 to 8.0 ka onwards (Rossi et al., 2018). This environmental shift, together with the local fire episodes registered during the 9.3 and 8.2 ka events, may have favoured *Corylus* expansion, thus coinciding with the hypothesis of Huntley (1993) and Finsinger et al. (2006).

The pollen record also revealed a very occasional presence of hornbeam and beech during the early Holocene. In regard to *Carpinus betulus*, an isolated pollen grain was detected at 8840 cal yr BP. Such minimal presence has also been documented during the early and mid-Holocene in nearby littoral sites (Mary et al., 1975; Iriarte-Chiapusso et al., 2006, 2016) and mountainous areas (Menéndez-Amor and Florschütz, 1963; Peñalba, 1989), while slightly more developed populations were settled along the western Galician coast (Muñoz-Sobrino et al., 2018). In several sites in northern Iberia, the scattered presence of hornbeam trees represented a vestige from a larger distribution achieved during the Würm glaciation (e.g., Sánchez-Goñi et al., 2005, 2008; Gómez-Orellana et al., 2007, 2013). However, *C. betulus* was not detected in the glacial interval of La Molina, probably due to the cold and arid conditions deduced from the steppe-like landscape, very far from the ecological requirements of this mesophyte species. In the aforementioned sites where it occupied a wider extension, the rise of the sea level, which flooded coastal regions where it was established, together with the post-glacial expansion of more competitive arboreal species in inland sites reduced its distribution area and relegated it to a very marginal role (Muñoz-Sobrino et al., 2018). Besides, landscape anthropisation did not benefit its populations which still have a very scattered presence in the Iberian Peninsula at present (Costa-Tenorio et al., 2005).

In regard to *Fagus*, an isolated pollen grain was detected at 8624 cal yr BP. This finding, although it cannot indicate the establishment of beech populations at a local level, is consistent with the discontinuous and low pollen curves detected in other sites from the eastern Cantabrian range and the Basque mountains during the early Holocene, such as La Nava (870 m a. s. l.; Menéndez-Amor, 1968), La Piedra (950 m a. s. l.; Ramil-Rego et al., 1998), Belate (825 m a. s. l.; Peñalba, 1994), Santa Gadea (837 m a. s. l.; Iriarte-Chiapusso et al., 2003), Puerto del Escudo (940 m a. s. l.; Muñoz-Sobrino, 2001) and Puerto de los Tornos (920 m a. s. l.; Peñalba, 1994; Muñoz-Sobrino et al., 2005), all of them located at a higher altitude than La Molina (484 m a. s. l.). Thus, a plausible hypothesis for the origin of the isolated beech pollen found in La Molina would be the long transport from higher altitude regions, where there was greater evidence of *Fagus*. Equally, it might also be held that small glacial refuges from the Cantabrian range (Magri et al., 2006) could have contributed to this pollen presence. The existence of these ancient refuges in the region is supported by the fossil evidence during the glacial period, which has been found in the form of pollen (Menéndez-Amor, 1968; Peñalba, 1989, 1994; Ramil-Rego et al., 1998; Iriarte-Chiapusso et al., 2016) and macroremains (Uzquiano, 1992). The sequence of La Molina, however, does not provide evidence of beech before the Holocene, since in the same way as with hornbeam the climatic conditions do not seem to have favoured *Fagus* development in the coastal mountains of the Cantabrian range. In a more recent period, *Fagus sylvatica* appeared in the area near La Molina at around c. 2800 cal yr BP. Pérez-Obiol et al. (2016) point out that fire could have facilitated its expansion along the Cantabrian range during the last millennium.

### *4.4. Implications of the 9.3 and 8.2 ka events on the Cantabrian landscape*

Apart from the decline in biomass production, the early Holocene climate pulses (Smith et al., 2016) were not accompanied by other significant ecological implications until the 9.3 and 8.2 ka events, when two fire episodes of high magnitude occurred. Both events are known to have had a regional scope (Rasmussen et al., 2007, 2014), coinciding closely with the Bond event 6 and the first peak of ice-rafted debris within the Bond event 5, respectively (Fig. 9; Bond et al., 2001). In the Cantabrian range, these climatic phases have been recorded as isotopic oscillations in cave speleothems (Domínguez-Villar et al., 2009; Moreno et al., 2010a; Smith et al., 2016; Rossi et al., 2018; Baldini et al., 2019). In a similar way, the organic matter record of La Molina, which has proved to be an efficient proxy to reflect environmental changes (Meyers and Lallier-Vergès, 1999), also captured these intervals in the form of falls in organic content.

The climate interpretation performed in Cantabria suggests a relatively humid phase between 9900 and 9700 cal yr BP (Rossi et al., 2018). Accordingly, the PAR exhibited the highest values of all the record, just before the first fire episode. During the 9.3 ka event, temperatures rose and summers became drier in the Cantabrian range (Baldini et al., 2019). The 8.2 ka event was also characterised as a dry interval close to La Molina (Domínguez-Villar et al., 2009; Smith et al., 2016; Rossi et al., 2018), even though it was one of the coldest pulses of the entire Holocene (Baldini et al., 2019). It has been shown that climate changes of this magnitude can cause major fires in a brief period of time (Daniau et al., 2019) since both temperature and humidity are acknowledged to be important factors in controlling biomass burning on a regional scale (Daniau et al., 2012). Additionally, Power et al. (2008) also point out that increased seasonality during the early Holocene could have regulated the fire regime in the Northern Hemisphere. Therefore, the climate pulses recorded during the 9.3 and 8.2 ka events in the Cantabrian range, together with the large fuel accumulation resulting from increased productivity, seem to have been key to the occurrence of the first major Holocene fire episodes.

At a regional scale, increased fire incidence has also been recorded around Europe during the early Holocene (e.g., Power et al., 2008; Daniau et al., 2012; Marlon et al., 2016). In the Iberian Peninsula, although not all charcoal records have detected particularly localised fire intensity during this interval (Carrión and Van Geel, 1999; Carrión et al., 2007; Miras et al., 2007; Anderson et al., 2011; Rius et al., 2011, 2012; Connor et al., 2012; Morales-Molino et al., 2013; Schneider et al., 2016; Garcés-Pastor et al., 2017; Leunda et al., 2020), there are some sites where fire activity was notable. For example, Carrion (2002) detected high intensity of fires between the onset of the Holocene and c. 8000 cal yr BP in the Siles lake, while Davis and Stevenson (2007) clearly identified macrocharcoal peaks in Hoya del Castillo at around 9500 cal yr BP. Fires specifically located during the 8.2 ka event have provided more evidence, in particular the charcoal peaks detected in El Portalet (Gil-Romera et al., 2014), Bassa de la Mora (Pérez-Sanz et al., 2013; Leunda et al., 2020) and Laguna Guallar (Davis and Stevenson, 2007). Therefore, the link between climate and fires seems to be confirmed. In any case, it should be considered that these fire episodes represented an opportunity to create open areas exploited by various Mesolithic groups. Furthermore, Mesolithic hunter-gatherers could have taken advantage of the arid conditions to start the fires, which would represent a shared strategy with other European regions.

Whether the origin of fires was climatic, as seems to be the case, anthropogenic, or resulted from the combination of both factors, the 9.3 and 8.2 ka fire episodes brought about a profund change in the Cantabrian landscape, representing a turning point towards a more open environment. Both episodes triggered one-off biomass declines affecting the vast majority of plant taxa, similar to the aforementioned early Holocene climate pulses of wetting and drying conditions. Pines were the least affected species, leading to a percentage increase especially well-recorded within the 8.2 ka event. Its lesser impact may be due to the fact that its pollen signal could have come from a regional area given its large pollen dispersion (Poska and Pidek, 2010), and thus being less affected by the local fires detected in La Molina. *Betula*, on the other hand, was seriously affected, and its presence became minimal after the 9.3 ka fire event. The fire episode created forest clearings dominated by grasses and *Pteridium*, and in this scenario hazels could colonise and develop well to become important components of mixed deciduous formations which have dominated the landscape until the present. Although *Corylus* is an important element in the secondary succession of many temperate forests (Hegi, 1981; Carreras et al., 2016), it should be noted that its expansion during the mid-Holocene did not merely represent a secondary colonisation after fire episodes, but rather the species was part of a stable community that remained in equilibrium for several millennia.

Although the species succession appears to have been logical, the arboreal biomass did not regain previous values during the Mesolithic or increase following climatic wetter pulses (Smith et al., 2016) as it did during the early Holocene. This situation leads us to believe that vegetation was no longer solely influenced by climate features, but rather the anthropic factor could have begun to contribute significantly to the configuration of the landscape during this period. Several Mesolithic groups were settled in the Cantabrian littoral and mid-mountain areas up to 750 m a. s. l., some of them documented in La Molina valley (Pérez-Bartolomé, 2019). It is known that *Corylus* was exploited by these Mesolithic groups, who used its wood for manufacturing tools and as fuel and hazelnuts as a source of food (Uzquiano, 2018). What is clear, however, is that fire was not employed to maintain this vegetation community, as indicated by the macrocharcoal curve. Also, the detection of coprophilous *Cercophora* might also indicate an increase in animal presence in La Molina's surroundings, which most likely benefited from the forest openings and may also have contributed to its maintenance by eating herbs and tree fresh buds. It is assumed that the coprophilous signal probably indicates an increase of wild animals rather than farming activities, since the oldest domesticated fauna remains date approximately from 6900 to 6500 cal yr BP in the Cantabrian region (Cubas and Fano, 2011). Taking everything into account, increased human pressure and animal presence in the Cantabrian region could have regulated the vegetation biomass, thus explaining the absence of pollen influx peaks from the 8.2 ka event onwards.

### *4.5. The creation and maintenance of open areas through the use of fire since the onset of agricultural practices*

Pérez-Obiol et al. (2016) attribute an age of 6735 - 6495 cal yr BP to the oldest cereal pollen. The study of deeper sediment in La Molina has not yielded older cereal evidence. Thus, according to the updated chronological model, an age of c. 6660 cal yr BP is estimated for the oldest cereal pollen in line with other locations from the northern Iberian Peninsula (Zapata, 2002; Zapata et al., 2004; Iriarte-Chiapusso et al., 2005; Peña-Chocarro et al., 2005; Iriarte-Chiapusso, 2009; López-Merino et al., 2010). Likewise, the domestication of animals for human consumption went hand in hand with the beginning of agriculture, with an estimated origin age between 6900 and 6500 cal yr BP (Cubas and Fano, 2011). In this regard, significant percentages of *Cercophora,* followed by *Sporormiella,* have been detected since the onset of the Neolithic, providing evidence of this grazing pressure. Agricultural practices brought with them the need to create forest openings and the use of fire became frequent from c. 5700 onwards, as indicated by the macrocharcoal record. In this case, the increase in the PAR detected between 5000 and 4000 cal yr BP, just before the beginning of fire activity, may not reflect a biomass increase as it did during the early Holocene climate pulses. An increase in the peat bog sedimentary accumulation rate (Fig. 5) is probably responsible for such high values of PAR, which therefore do not reflect any climate pulse.

Although the fire signal increased from 5700 cal yr BP onwards, it was not until 5000 cal yr BP when fires started exhibiting a more prominent magnitude. It seems that the maintenance of the continuous fire signal is likely due to anthropogenic causes, such as the need to preserve open spaces, yet a climatic relationship could be attributed to the main fire peaks linked to Bond cycles (Bond et al., 2001) as discussed in Pérez-Obiol et al. (2016). In this line, intervals of variable rainfall amount were detected in the Cantabrian range during the late Holocene (Domínguez-Villar et al., 2008). The palaeoclimate reconstruction performed in La Garma cave, at about 40 km from La Molina, determined that summers became progressively drier from 5900 cal yr BP onwards to reach pronounced summer aridity between 4500 and 4200 cal yr BP (Baldini et al., 2019), coinciding with Bond event 3 (Bond et al., 1997, 2001). Baldini et al. (2019) reported Mediterranean-like conditions in the northern Iberian Peninsula at that time. Consistent with this, the fire magnitude increased with local charcoal maximums around Bond event 3 (Fig. 9) which revealed a certain correlation with climate. Another significant fire episode is detected around Bond event 2 (c. 2800 cal yr BP). In this respect, it is plausible that the fire magnitude may have been particularly intense following climatic pulses.

Although the use of fire created forest openings, the arboreal composition does not seem to have been strongly influenced. It is observed that some trees, such as *Alnus* or *Fagus,* started to expand thereafter, as already discussed in Pérez-Obiol et al. (2016). On the other hand, the most notable change is found in the composition of non-arboreal species. The open areas were henceforth dominated by *Calluna vulgaris* and other Ericaceae instead of grasses and *Pteridium*. The germination of some heaths is stimulated by increased temperature, while most *Erica* spp. can resprout well after fire events (Iglesia-Rodríguez, 2010).

The vegetation dynamics from the Neolithic (c. 6740 cal yr BP) onwards in La Molina are extensively described in Pérez-Obiol et al. (2016). They showed the importance of human influence on the landscape related to fire activity during the main cultural phases studied: the Neolithic, Bronze Age, Iron Age, Roman period, and Middle Ages.

## 5. Conclusions

The multiproxy approach performed in La Molina peat bog (484 m a. s. l. Puente Viesgo, Cantabria) represents the oldest continuous chronology studied from the northern Cantabrian range, spanning the last 17,550 years.

The consideration of the pollen accumulation rate together with the pollen percentages has allowed a better interpretation of the dynamics of each plant species, as well as the detection of biomass pulses that may go unnoticed when only pollen percentages are available.

Concerning the role of fire, the study of sedimentary charcoals (>150 μm) has proved to be an efficient tool to detect local fire episodes and helped to understand some landscape changes during the early Holocene, while the organic matter fluctuations served to identify and delimit the main climate phases of a regional scope.

The multiproxy approach was a key to characterise the different plant landscape units and the fire regime of the north-eastern Cantabrian range since the LGP and determining the role played by both the climate and anthropic factors:

1) A weak local fire signal was detected from 17,550 to 13,700 cal yr BP that did not cause any significant change on the plant landscape. The landscape was mainly composed of non-arboreal species with a dominance of Poaceae accompanied by a lower proportion of other xerophyte taxa. The signal of arboreal pollen, consisting of *Pinus,* evergreen and deciduous *Quercus, Betula*, *Corylus* and the occasional presence of other mesophilous taxa, did not reach 20%. The onset of the Bølling-Allerød chronozone came together with *Juniperus* and Ericaceae pulses and a decrease of Poaceae values. The low signal of *Pinus* found through all the pollen spectra is indicative that the region has never had extensive pine forests in the last 17,550 years.
2) The woody colonisation was followed by the spread of *Betula* and *Salix* at 13,700 cal yr BP, coinciding with increased water availability in the Cantabrian region. *Betula* and *Salix* decreased in favour of Poaceae and other herbs with the appearance of tougher climate phases, first during the GI-1b and later within the Younger Dryas Stadial (GS-1).
3) A sharp increase in organic matter was detected at c. 12,000 cal yr BP, indicating an important change on climatic conditions. Shortly afterwards, a mixed deciduous formation with *Betula* and deciduous *Quercus* (>95% of arboreal pollen) dominated the landscape from 11,900 cal yr BP onwards. As a whole, a series of biomass fluctuations were detected at c. 11,600, 11,200, 10,130 and 9600 cal yr BP, probably related to century-to-millennial scale shifts of wetting and drying conditions.
4) The arid conditions triggered by the 9.3 and 8.2 ka events together with the fuel accumulation produced during the early Holocene were most likely responsible for the first significant fire episodes detected in the charcoal sequence. The fire episodes created forest openings, as indicated by the higher presence of Poaceae and *Pteridium. Betula* was severely affected and its signal sharply decreased, exhibiting minimal values from this point onwards. On the other hand, the establishment of *Corylus* was likely favoured by the fire episodes and a climate shift. *Corylus* became an important component of the mixed deciduous formations together with deciduous *Quercus* from that point onwards. The plant landscape underwent no further significant changes until the Neolithic without the presence of biomass fluctuations following climate pulses, contrary to what happened during the early Holocene. It cannot be ruled out that anthropic pressure favoured these landscapes during the Mesolithic, although it is clear that Mesolithic groups did not use fire to maintain them. The presence of coprophilous fungi likely indicates more animal presence, probably favoured by the increase in open areas.
5) The most recent 6600 years were characterised by a major anthropisation of the landscape. The updated chronological model indicated an age of c. 6657 cal yr BP for the first cereal pollen grain. Coprophilous fungi maintained stable values probably linked to grazing activites. The need to create open spaces went hand in hand with increased fire activity, which could no longer be easily related to the climate influence given the multitude of fire peaks. Some peaks of particular intensity could have been fostered by drier climate intervals, particularly during the Bond events 3 and 2 (c. 4200 and 2800 cal yr BP, respectively). The maintenance of fires involved a change in the non-arboreal composition, since *Calluna vulgaris* and other Ericaceae, well-adapted to fire, colonised the open areas where Poaceae was dominant.

## Funding

This work has been supported by coordinated project grants from Spain's Ministry of Economics and Competitiveness (MEC): “Geohistoria ambiental del fuego en el Holoceno. Patrones culturales y gestión territorial desde el inicio de la ganadería y la agricultura en la montaña Cantábrica y Pirineo” (CSO 2012-39680-C02-02); “Estudio biogeográfico histórico comparado (Montaña Cantabrica, Sistema Central y Pirineos): 18000 años de cambios climáticos y antrópicos sobre especies forestales indicadoras” (CSO 2015-65216-C2-1-P), awarded to the Department of Geography, Universitat Autónoma de Barcelona, which also awarded an FPI PhD grant (BES-2016-076641) within the project. In addition, the project was funded by the Catalan government's applied geography programme, “Grup de Geografia Aplicada” (AGAUR, Generalitat de Catalunya, 2014 SGR 1090 and 2017 SGR-00343).

## Author contributions

All the authors have made substantial contributions to the submission. In particular, Marc Sánchez Morales (Conceptualization; Methodology; Investigation; Writing - Original Draft; Visualization), Albert Pèlachs Mañosa (Conceptualization; Methodology; Resources; Writing - Review & Editing; Supervision; Project administration; Funding acquisition); Juan Carlos García Codrón (Conceptualization; Writing - Review & Editing), Virginia Carracedo (Conceptualization; Writing - Review & Editing) and Ramon Pérez Obiol (Conceptualization; Methodology; Resources; Writing - Review & Editing; Supervision; Project administration; Funding acquisition).

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

The authors gratefully acknowledge the Consejería de Desarrollo Rural, Ganadería, Pesca, Alimentación y Medio Ambiente, Gobierno de Cantabria, for the permissions granted to sample the sedimentary cores from La Molina peat bog.

The authors would also like to thank Dr. Jordi Garcia Orellana (Departament de Física, Universitat Autònoma de Barcelona) for his work on the chronological model and the special research assistance provided by multiple collaborators from the Departament de Geografia, Universitat Autònoma de Barcelona (Dr. Joan Manuel Soriano López, Dr. Jordi Nadal Tersa) and from the Departamento de Geografía, Urbanismo y Ordenación del Territorio, Universidad de Cantabria (Sara Rodríguez Coterón, PhD candidate).

The authors appreciate the English language review by Stephen Smith.

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