A continuous centennial Lateglacial-Early Holocene (15-10 cal kyr BP) palynological record from the Iberian Pyrenees and regional comparisons

Valentí Rull[1,2*], Arnau Blasco[3], Miguel Ángel Calero[4], Teresa Vegas-Vilarrúbia[3]

[1]Spanish National Research Council (CSIC), Botanic Institute of Barcelona, Pg. Migdia s/n, 08038 Barcelona, Spain
[2]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, C. Columnes ICTA-ICP Bld., 08193 Cerdanyola del Vallès, Barcelona, Spain
[3]Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain
[4]Department of Geography, Universitat de Barcelona, C. Montalegre 6, 08001 Barcelona, Spain

**Corresponding author. Email vrull@csic.es*

Abstract

This paper presents the first continuous (gap-free) Lateglacial-Early Holocene (LGEH) pollen record for the Iberian Pyrenees resolved at centennial resolution. The main aims are (i) to provide a standard chronostratigraphic correlation framework, (ii) to unravel the relationships between vegetation shifts, climatic changes and fire, and (iii) to obtain a regional picture of LGEH vegetation for the Pyrenees and the surrounding lowlands. Seven pollen assemblage zones were obtained and correlated with the stadial/interstadial phases of the Greenland ice cores that serve as a global reference. Several well-dated datums were also derived for keystone individual taxa that are useful for correlation purposes. Four vegetation types were identified, two of them corresponding to conifer and deciduous forests (Cf, Df) and two representing open vegetation types with no modern analogs (periglacial herbs, or PH, and *Saxifraga*-Cichorioideae, or SC). The first two forests dominated during interstadial phases (Bølling/Allerød and Early Holocene), and PH dominated during stadials (Oldest Dryas and Younger Dryas), with SC being important only in the first half of the Younger Dryas. The use of pollen-independent proxies for temperature (oxygen isotopes) and moisture (titanium) allowed the reconstruction of paleoclimatic trends and the responses of the four vegetation types defined. The most relevant observation in this sense was the finding of wet climates during the Younger Dryas, which challenges the traditional view of arid Pyrenean conditions for this phase on the basis of former pollen records. Fire incidence was low until the early Holocene, when regional fires were exacerbated, probably due to the combination of higher temperatures and forest biomass accumulation. These results are compared with the pollen records available for the whole Pyrenean range and the surrounding lowlands within the framework of elevational, climatic and biogeographical gradients. Some potential future developments are suggested on the basis of the obtained results, with an emphasis on the reconsideration of the LGEH spatiotemporal moisture patterns and the comparison of the Pyrenees with other European ranges from different climatic and biogeographical regions.

Keywords: Pyrenees, palynology, pollen stratigraphy, climate change, fire, vegetation response, Lateglacial, Early Holocene

1. Introduction

In the Iberian Peninsula (IP), the Lateglacial, or the Last Glacial Maximum (LGM)-Holocene transition, is an excellent time interval to study the response of vegetation to natural drivers of ecological change due to the occurrence of conspicuous climatic reversals and the lack of significant human pressure (Carrión et al., 2010). This is especially true for mountain ranges, where extensive landscape anthropization did not begin until the Late Holocene (Rull et al., 2021a, b). In the Iberian Pyrenees, anthropization initiated during the Bronze Age (~3.7 cal kyr BP) in the southern lowlands (González-Sampériz et al., 2017) and progressed northward following an altitudinal trend characterized by rates of 40 m elevation per century, on average (Rull & Vegas-Vilarrúbia, 2021). Therefore, climate was the major ecological forcing for Pyrenean vegetation during the LGM-Holocene transition.

Globally, the Lateglacial has been defined in Greenland ice cores by a stadial-interstadial succession that characterized the transition from the LGM to the Holocene. The classical sequence, which serves as a worldwide stratigraphic reference, includes the stadial GS-2.1a or Oldest Dryas (OD) (17,500-14,700 cal yr BP), the interstadial GI-1 or Bølling/Allerød (B/A) (14,700-12,900 cal yr BP) – which has been subdivided into minor events GI-1a to GI-1e – and the stadial GS-1 (12,900-11,700 cal yr BP) or Younger Dryas (YD), which was the last Pleistocene cooling reversal that preceded the Early Holocene (EH) warming (Rasmussen et al., 2014) (Fig. 1). This climatic sequence, with some minor variations, was identified in the Ostolo speleothem record (OST2) from the westernmost end of the Pyrenees (Bernal-Wormull et al., 2021), which is considered a regional paleoclimatic reference for the northern IP (Fig. 2). The main departures of this Pyrenean record with respect to the ice-core standards were a small offset at the end of GS-2.1a (i.e., the Bølling warming commenced a couple of centuries before in OST2) and the absence of minor GI-1d, GI-1c2 and GI-1b coolings, along with the occurrence of a cooling event during the GI-1c1 Greenland warming (Fig. 1). The remaining trends are in good agreement with the ice core records, including the GS-1 (YD) and the 11.4 cold event.

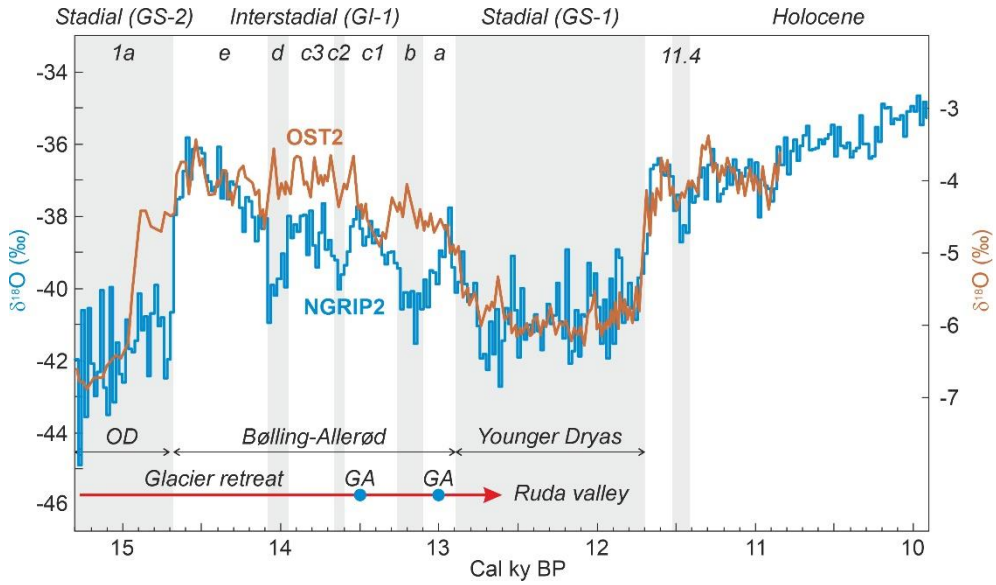

Figure 1. Lateglacial-Early Holocene stratigraphy based on Greenland ice core NGRIP2 (Rasmussen et al., 2014) compared with the speleothem record from Ostolo cave (OST2) on the westernmost Pyrenean end (Bernal-Wormull et al., 2021) (Fig. 2). The glacier dynamics, as reconstructed in the Ruda valley (parallel to the Aiguamòg valley, where the record analyzed in this study lies; Fig. 5), is indicated for reference (Fernandes et al., 2022). GA, glacier advance; OD, Oldest Dryas.

In the Pyrenees and surrounding lowlands, the Lateglacial-Early Holocene (LGEH) palynostratigraphic and paleovegetational trends are relatively well known on the northern side but largely unknown on the southern flank (Fig. 2). A first synthesis from the northern French slope (Jalut et al., 1992) reported that the Lateglacial began with the expansion of *Betula*, the decrease in Chenopodiaceae and the decrease/disappearance of *Ephedra* at the initial Bølling. In some localities, *Juniperus* and *Pinus* also increased. Open cold/dry steppe environments were represented by *Artemisia*, which remained relatively constant, and increasing amounts of Poaceae, Apiaceae and *Rumex*. In drier Mediterranean areas (eastern sector), steppe assemblages were dominated by *Artemisia*, whereas in wetter Atlantic areas (western sector), the dominant were the Poaceae. A manifest *Pinus* increase coeval with a *Juniperus* decrease was recorded at the B/A transition, when *Quercus* began to establish and *Corylus* was still absent. During the YD, steppe elements (*Juniperus*, *Artemisia*, Chenopodiaceae, *Ephedra*) expanded again, while forest trees (*Betula*, *Pinus*) declined. This YD vegetation opening was more pronounced in the Mediterranean area due to the occurrence of drier conditions. At the end of the YD, *Artemisia* declined and *Ephedra* disappeared due to the onset of Holocene warming, characterized by the massive colonization of the Pyrenees by deciduous forests (*Betula*, *Corylus*, *Quercus*).

Further high-resolution studies on some localities of the easternmost French Pyrenean side recorded an expansion of steppe elements (*Artemisia*, *Ephedra*, Poaceae, Apiaceae, Caryophyllaceae and others) and a decline in *Pinus* during the OD stadial (Reille & Lowe, 1993). The same studies documented a regional expansion of *Juniperus*, *Betula* and *Salix* during the initial B/A and a significant *Pinus* increase at the end of this interglacial. The YD stadial was characterized by a sudden decrease in *Pinus* and *Betula* and the expansion of steppe elements, especially *Artemisia*. The incoming warmer conditions during the Early Holocene were marked by a significant increase in *Betula* followed by *Quercus* and *Corylus*, which marked the initial colonization of the region by temperate forests. According to Reille & Lowe (1993), oscillations in *Pinus* during Lateglacial times would have been largely due to fluctuations in long-distance pollen transport from low elevations; however, the local presence of *Pinus* forests during the Early Holocene was supported by the presence of stomata of *Pinus uncinata*. In general, increases in pollen from forest trees are considered to be indicative of forest expansions from neighboring refugia, which would have survived the last glaciation on sites with particular microclimatic conditions. The studies refined the existing chronologies and allowed a more precise dating of significant events such as the maximum of *Artemisia* (18.1 cal kyr BP), the rise of *Betula* (14.7 cal kyr BP), *Quercus* (12.3 cal kyr BP) and *Corylus* (11.5 cal kyr BP), or the first decline of *Betula* (12.8 cal kyr BP), among others (Reille & Andrieu, 1995).

A more recent study identified similar trends (Aubert et al., 2004), but the low resolution of the LGEH sequence and the existence of a single radiocarbon date in this interval prevent detailed correlations. A more recent multicentennial record identified the following succession: *Juniperus*-*Artemisia* (OD) – *Pinus*-*Betula*-Poaceae (B/A and YD) – *Pinus*-*Betula*-*Quercus*-*Corylus* (Early Holocene) (Rius et al., 2014). This work included charcoal analysis and documented no fire activity during the OD, low to medium fire incidence during the B/A and the YD, and a sudden fire increase during the Early Holocene. These patterns were explained in terms of climate-vegetation interactions, with the former as the main driver and the latter as a modulator of the amplitude of fire regimes. In this way, the abrupt fire increase at the beginning of the Holocene was linked to the expansion of temperate deciduous woodlands.

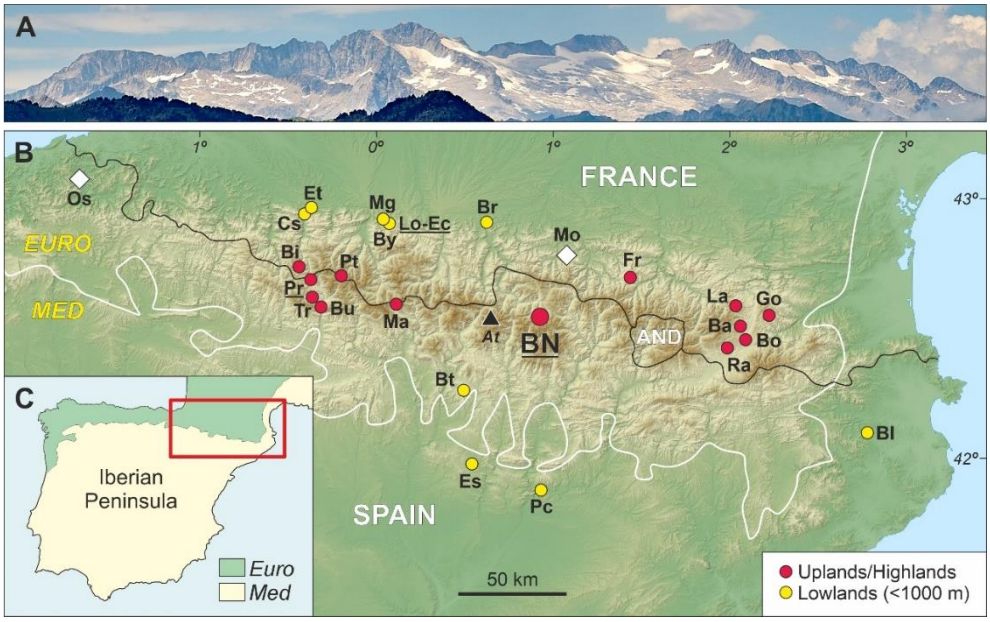

Figure 2. The Pyrenean range within the Iberian Peninsula. A) The Iberian Maladeta Massif, with the highest Pyrenean peak (Aneto; 3404 m) in the center, as seen from near the Bassa Nera (1890 m) coring site (Photo: V. Rull). B) Topographic map of the Pyrenees indicating the Bassa Nera coring site (BN) and other localities of the Pyrenees and the surrounding lowlands with Lateglacial pollen records. The locations of the Ostolo (Os) and Moulis (Mo) paleoclimatic records are indicated by white diamonds, and the highest peak of the Pyrenees (At, Aneto) is marked by a black triangle. The black line is the boundary between Spain and France, which represents the boundary between the northern and southern Pyrenean sides (AND, Andorra), and the white line is the boundary between the Eurosiberian and Mediterranean biogeographical regions. Lateglacial sites: Ba, Balcère; Bi, Bious; Bl, Banyoles; Bo, Borde; Br, Barbazan; Bt, Bentué; Bu, Búbal; By, Biscaye; Cs, Castet; Ec, Ech; Es, Estanya; Et, Estarrès; Fr, Freyxinède; Go, Gourg-Nègre; La, Laurenti; Lo, Lourdes; Ma, Marboré; Mg, Monge; Pc, Parco; Pr, Portalet; Pt, La Pouretère; Ra, Racou Tr, Tramacastilla (details and references in Appendix 1). Sites with charcoal records as fire proxies are underlined. C) Map of the Iberian Peninsula showing the location of the Pyrenees (red box). The Mediterranean (Med) and Eurosiberian (Euro) biogeographical regions are indicated by pale yellow and green areas, respectively.

On the southern Pyrenean side, only four LGEH palynological sequences are available, all of them on the western side (Fig. 2). Three of these records (Marboré, Búbal and Tramacastilla) are of multicentennial resolution, and the LGEH stadials/interstadials are not well defined palynostratigraphically. In addition, in the Búbal and Tramacastilla records, chronological correlations among similar palynological zones are problematic despite their proximity (barely 6 km), which was attributed to methodological dating issues (Montserrat Martí, 1992). The fourth record, Portalet, is well bracketed chronologically and of higher resolution but incomplete, as the YD is missing by a sedimentary gap, which was attributed to the permanent freezing of the Lateglacial paleolake (González-Sampériz et al., 2006). The lack of highland YD palynological records is the norm on the southern side, where this climatic reversal is represented only in the lowlands by cold-steppe elements (notably *Artemisia*, Poaceae, Chenopodiaceae and *Juniperus*) (review in García-Ruiz et al., 2016). Therefore, a chronologically well-bracketed complete and continuous LGEH palynological sequence of centennial or higher resolution for the Iberian Pyrenees is lacking.

In general, increases in pollen from forest trees (*Pinus*, *Betula*, *Corylus*, *Quercus*) similar to those documented for the northern Pyrenean slopes occurred during warming phases (B/A, EH). These increases are believed to reflect temperate forest expansions from nearby glacial refugia situated in the southern lowlands (<800 m) as part of a highly diverse mosaic landscape composed of conifer forests, mixed pine-oak forests, parklands, grasslands and xerophytic steppes (González-Sampériz et al., 2005, 2010). Similar to the northern side, LGEH Pyrenean

records from the Iberian side usually lack charcoal records as fire proxies, except for the Portalet sequence, where Lateglacial wildfire incidence was lower than in the Early-Mid Holocene, probably due to the combination of higher temperatures and increased biomass fuel due to the expansion of deciduous forests since 10 cal kyr BP (Gil-Romera et al., 2014). Other palynological parameters and proxies unusual on both northern and southern Pyrenean slopes are pollen accumulation rates (PAR), as a proxy for plant cover (Theuerkauf & Couwenberg, 2018), and non-pollen palynomorphs (NPP), which have demonstrated to be very useful for environmental reconstruction (Cook et al., 2011; Shumilovskikh & van Geel, 2020).

This paper presents the Bassa Nera record, which is the first well-dated complete and continuous (gap-free) Lateglacial-Early Holocene (15,200-10,000 cal yr BP) palynological record of vegetation change at centennial resolution from the central Iberian Pyrenees, including PAR, charcoal and NPP analyses. The main Holocene trends (10 cal kyr BP onward) in the development of the Bassa Nera vegetation have already been studied (López-Vila et al., 2014 a, b; Garcés Pastor et al., 2016, 2017), but the LGEH ecological history remains unknown. The main aims of this study are (i) to provide a standard LGEH palynological sequence for the central Pyrenees, which may serve correlation and dating purposes; (ii) to characterize the response of vegetation to local and regional climatic shifts in the absence of human disturbance, which may be useful to disentangle natural and anthropogenic drivers of ecological change; (iii) to document the fire regime history and its potential climatic and vegetational drivers; and (iv) to situate the results obtained in a regional context by comparing them with former studies on the northern and southern Pyrenean sides, including the surrounding lowlands. In addition to providing clues on the origin of ecosystems and their sensitivity to natural forcings, knowing the responses of preanthropic vegetation to climate changes is useful to anticipate the potential responses of natural communities to future climatic change.

2. Study area

2.1. Present conditions

Bassa Nera is a small pond (ca. 100 m long, 60 m wide and 5 m deep) located in a small depression known as Pletiu dera Muntanheta, situated in the headwaters of the Aiguamòg valley (upper Garona basin), at 42° 38’ 17” N - 0° 55’ 27” E and 1890 m elevation (Fig. 3). Although it belongs to Spain (Val d’Aran), the site is located on the northern Pyrenean slope, near the Pyrenean ridge. In some maps, the pond is also called Estanh dera Muntanheta, but we prefer to use Bassa Nera because this is the most utilized name in recent botanical and paleoecological publications. The pond is in its later infilling stages and is surrounded by a mire. The site is situated in the peripheral protection zone of the National Park “Aigüestortes i Estany de Sant Maurici” (PNAESM). The Pletiu dera Muntanheta is of glacial origin and is excavated on the granodioritic bedrock that is part of the Carboniferous-Permian Maladeta batholith (Delgado & Soler, 2010; Casas et al., 2019). The climate is alpine with oceanic influence, and the regional 0 °C isotherm is estimated to be at 2950 m elevation (López-Moreno et al., 2019). The nearest meteorological station is Port de la Bonaigua, situated approximately 6 km NE and 2072 m elevation, 182 m above Bassa Nera. The annual average temperature for the 1990-2020 period is 3.34 °C, and the total annual precipitation is 1218 mm. Minimum temperatures (-2.9 to -3.2 °C) are recorded in January and February, and maxima (11.6 °C) correspond to July and August. Total precipitation shows a bimodal pattern with maxima (131-137 mm) in May and November and minima (70-79 mm) in February and July (Fig. 4).

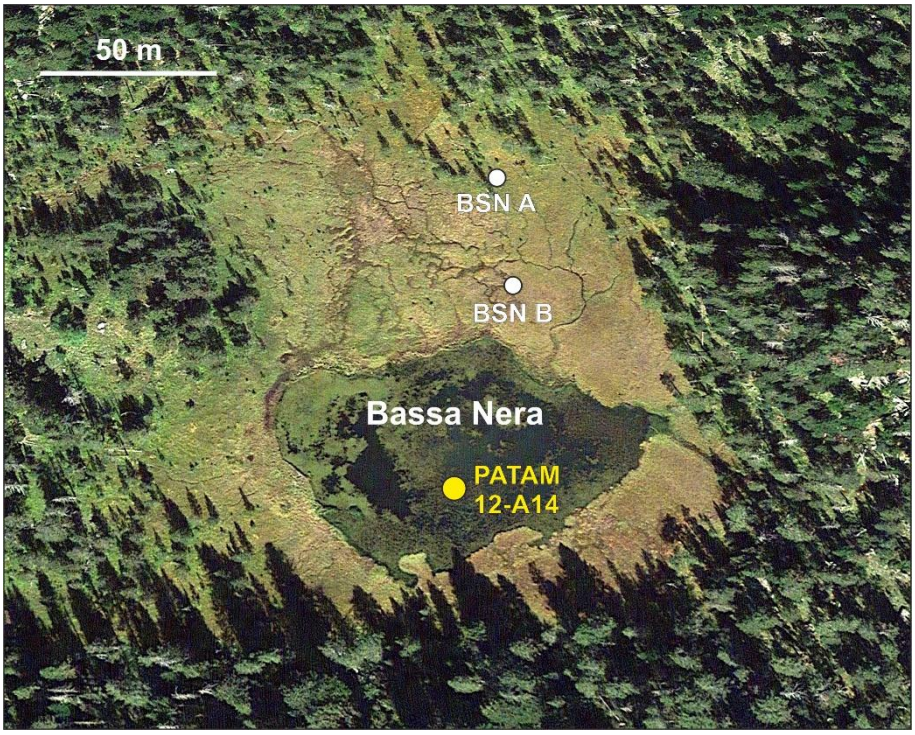

Figure 3. Google Earth image of the Pletiu dera Muntanheta with the Bassa Nera and the surrounding mire. The yellow dot indicates the location of the core analyzed in this work, and white dots mark the position of Holocene cores analyzed previously (Garcés-Pastor et al., 2016, 2017).

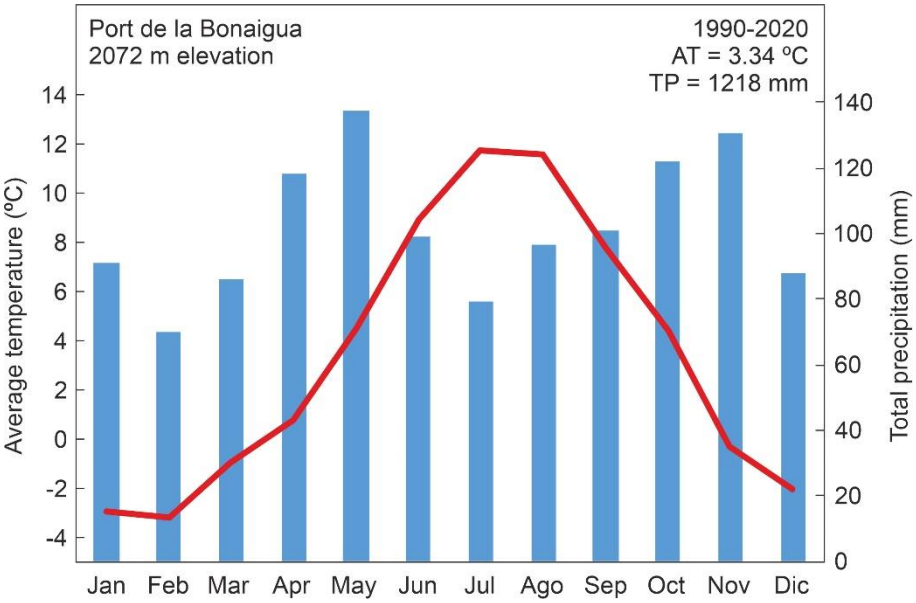

Figure 4. Climogram for the meteorological station of Port de la Bonaigua (9656) corresponding to the period 1990-2020 (31 years). Temperature trends are represented by a red line, and precipitation values are depicted as blue bars.

Biogeographically, the Bassa Nera is located in the southern margin of the Eurosiberian region, characterized by wet temperate Atlantic macrobioclimates and dominated by plant species distributed across central and northern Europe. This contrasts with the Mediterranean biogeographic region, under the influence of Mediterranean climates with at least two consecutive arid months during the warmest season (summer). The Mediterranean biome

dominates most of the Iberian Peninsula (Fig. 2) and is characterized by plant species distributed across southern Europe and northern Africa (Rivas-Martínez et al., 2017).

A study of plant communities along the Aiguamòg valley ranging between approximately 1300 m and 2600 m elevation, which included the Pletiu dera Muntanheta, recognized the following vegetation stages (Figure 6): mixed forests of *Pinus sylvestris* and *Betula* (1300-1600 m); conifer forests of *Pinus mugo* and *Abies* (1600-2000 m); mosaic vegetation of *Pinus mugo*, *Rhododendron* and *Nardus* (2000-2250 m); and alpine meadows/bogs with *Festuca*, *Nardus*, *Carex*, *Luzula* and *Juncus* (Cañellas-Boltà et al., 2009). In this transect, the Bassa Nera lies within the *Pinus-Abies* forest belt, ~350 m below the treeline, which is situated at 2250 m (Fig. 6). A further study specifically of the Pletiu dera Muntanheta identified seven plant associations (Pérez-Hasse & Ninot, 2017). The pond margins are characterized by *Sphagnum* peats, *Carex-Potentilla* associations, or *Sphagnum-Carex* carpets, depending on the local features. The surrounding areas are covered by marshes and grasslands dominated by *Carex*, *Scirpus* or *Succisa*, with scattered *Sphagnum* hummocks. *Pinus-Abies* forests with a *Rhododendron*-dominated understory grow on encircling slopes. The same study highlighted the uniqueness of the site in terms of plant richness in comparison with other Pyrenean mires and attributed this fact to the combination of hydrological and water chemistry variability.

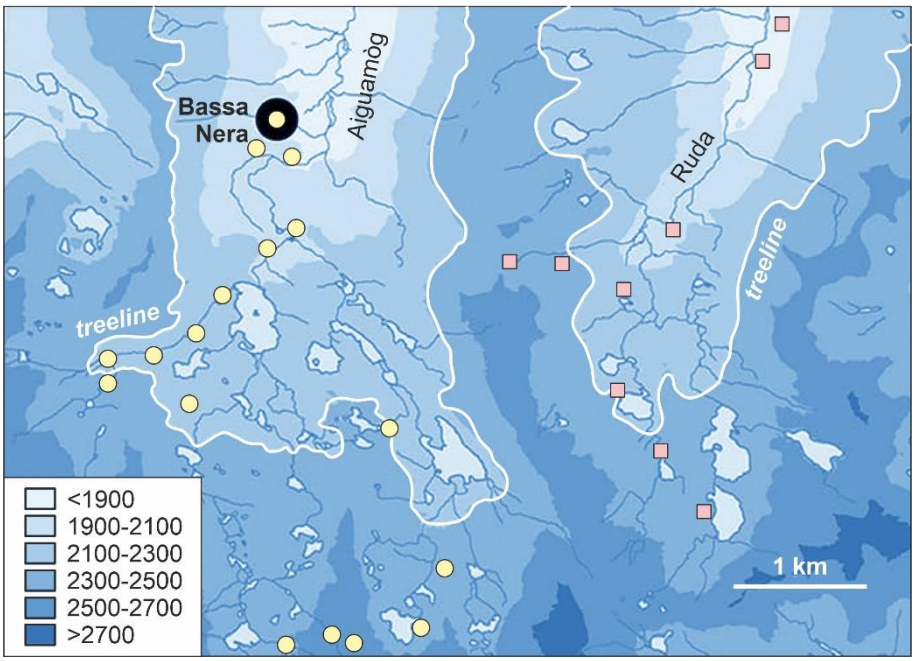

Figure 5. Topographic map of the study site. Blue tones indicate the elevation in meters (see legend). The approximate position of the treeline is indicated by a white line. Yellow dots in the Aiguamòg valley indicate superficial samples used in the previous study on modern pollen sedimentation, corresponding to the subalpine and alpine vegetation belts (Cañellas-Boltà et al., 2009). Pink boxes in the Ruda valley are samples for ^{10}Be exposure dating (Fernandes et al., 2022).

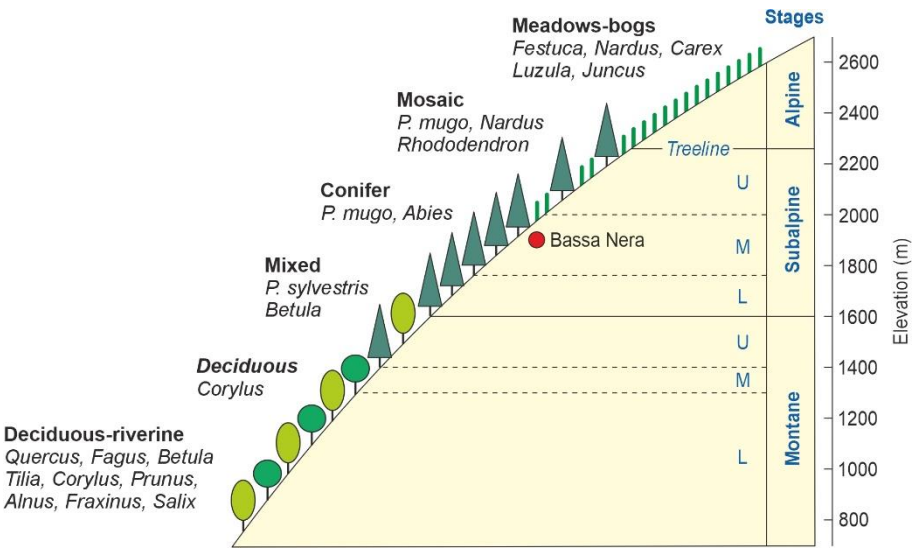

Figure 6. Elevational vegetation transect along the Aiguamòg valley and below (Cañellas-Boltà et al., 2009), indicating the location of the Bassa Nera coring site (red dot). U, upper; M, middle; L, lower.

2.2. Previous studies

The Pletiu dera Muntanheta was included in a modern-analog study developed on an altitudinal transect (ca. 870-2600 m elevation) along the Aiguamòg valley. This survey was aimed at establishing qualitative and quantitative relationships between extant vegetation patterns and modern pollen sedimentation, which may be useful for the interpretation of past pollen records in terms of vegetation change (Cañellas-Boltà et al., 2009). The lower montane vegetation belt (800-1300 m) was characterized by *Alnus*, *Betula*, deciduous *Quercus*, *Fraxinus* and *Salix* pollen, which is absent in the upper levels (Fig. 7). In the middle and upper montane levels (1300-1600 m), the pollen assemblages were almost exclusively composed of *Pinus*, with lower amounts of *Corylus*. The subalpine belt (1600-2300 m; below the treeline) was absolutely dominated by *Pinus*, with low percentages of grass and sedge pollen, whereas the pollen of deciduous trees from montane belts was virtually absent. The situation was similar in the alpine belt (2300-2600 m; above the treeline) but with higher amounts of herbaceous plants, which may be locally more abundant than *Pinus*. The best altitudinal indicators were found in *Fraxinus* and *Salix*, whose pollen is restricted to the montane and subalpine belts, respectively. *Betula* and *Corylus* pollen was restricted to the montane belt, together with deciduous *Quercus*, *Tilia*, *Alnus*, *Buxus* and Brassicaceae. Pollen types almost restricted to the alpine belt were *Plantago*, *Calluna*, Poaceae, Asteraceae and Cyperaceae, which may serve as treeline indicators. Interestingly, the pollen of *Olea* and evergreen *Quercus* have their maxima in the subalpine belt, although their parent plants are characteristic of lowlands and were not found in the vegetation gradient analyzed, suggesting efficient upward wind dispersal. In the same transect, the modern sedimentation of NPP was studied to unravel their potential as paleoecological indicators (López-Vila et al. 2014a). These authors found that NPP assemblages are influenced not only by elevation but also by local moisture conditions, landscape openness and human pressure, especially grazing.

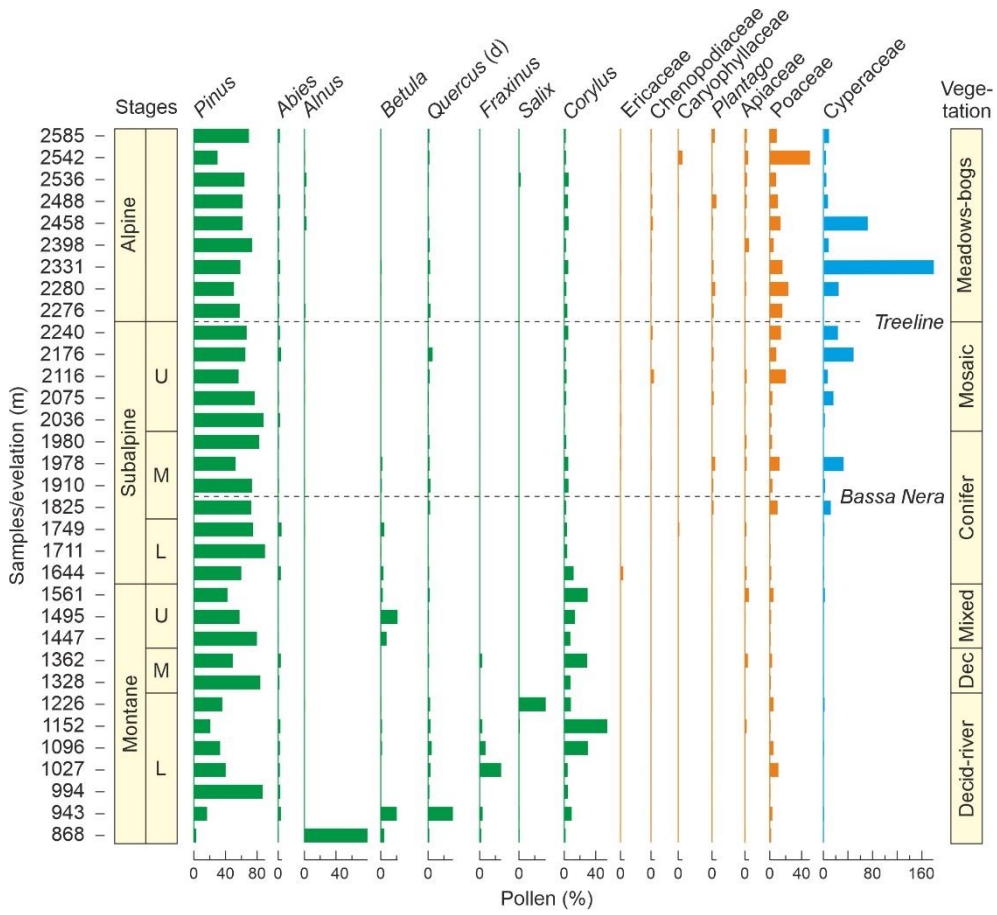

Figure 7. Modern pollen spectra along an elevational transect including the Bassa Nera coring site (Cañellas-Boltà et al., 2009). Only major components (>2% of the total) are shown. Forest trees are in green, and shrubs/herbs are in orange. Cyperaceae (blue) were not included in the pollen sum. Stages and vegetation types as in Fig. 6.

Previous studies in the Pletiu dera Muntanheta based on cores retrieved in the mire surrounding Bassa Nera recorded the vegetation shifts of the last ~10,000 years. This Holocene sequence was subdivided into seven vegetation phases (Garcés-Pastor et al., 2017): phase I (10,210-10,070 cal yr BP), transition from steppe-like grasslands to deciduous birch forests; phase II (10,070-7340 cal yr BP), shift from *Betula* woodland to *Betula-Corylus* forests; phase III (7340-5830 cal yr BP), mixed *Corylus*-deciduous *Quercus* woodland; phase IV (5830-3910 cal yr BP), transition from deciduous to conifer forests; phase V (3910-790 cal yr BP), conifer *Abies-Pinus* forests with some deciduous representatives (*Quercus*, *Betula Fagus*); phase VI (790-390 cal yr BP), conifer forests and meadow/fire increase indicating forest clearance for agropastoral activities (appearance of *Secale* and other cereals); phase VII (390 cal yr BP to present), conifer forests and grass meadows with dominance of pastoralism. These changes were interpreted in terms of responses to changes in North Atlantic climates related to Bond cycles, especially in the case of montane deciduous forests.

Human pressure was low until the Late Bronze Age, when agricultural landscapes were established around Bassa Nera, after forest clearance. The first evidence of grazing dates to 7300 cal yr BP, and the oldest cereal records were found at 5190 cal yr BP, but general landscape anthropization did not occur until 3150-2650 cal yr BP (Garcés-Pastor et al., 2017). No archaeological evidence of human occupation of the PNAESM prior to the Holocene is available, and Neolithization began by 7250 cal yr BP at lower elevations (<1600 m) and 5350 cal yr BP at higher elevations (Gassiot et al., 2017), which is consistent with the above palynological evidence from Bassa Nera. Landscape anthropization accelerated in the Middle

Ages (800 cal yr BP). The last millennium was subdivided into five phases (Garcés-Pastor et al., 2016): phase I (800-1300 CE), montane forests under warm MCA climates; phase II (1300-1490 CE), mixed forests (downward vegetation shift) during the MCA-LIA transition; phase III (1490-1620 CE), maintained downward shift under LIA colder conditions; phase IV (1620-1820 CE), conifer forests during the second stage of the LIA; phase V (1820 CE-present), recovery of mixed forests (upward migration) due to the recent warming. Crops and pastures were continuous around Bassa Nera until the LIA (1500 CE), when human activities significantly decreased due to harsh climates and only grazing activities remained active. Farming activities ceased in the mid-20th century, when the National Park was created (1955 CE).

A complementary NPP study encompassing the last two millennia identified an abrupt change from aquatic (algae, crustaceans) to terrestrial (fungi) indicators at 1500 CE, which was interpreted in terms of a relevant shift from lacustrine to mire environments. Further increases in spores from coprophilous fungi (notably *Sporormiella*) indicated an intensification of grazing activities until 1950 CE, when these indicators disappeared and were replaced by forest proxies. This coincided with the massive migration of the Pyrenean population to industrialized cities and the creation of the National Park around the site, which regulated human activities (López-Vila et al., 2014b).

No paleoecological studies are available for the LGEH, but a recent glaciological survey near Bassa Nera provides the paleoclimatic context for the interpretation of the palynological studies presented in this paper. LGEH chronology and paleoclimatology were resolved in detail in the adjacent Ruda valley (Fig. 5) using ^{10}Be cosmic-ray exposure dating of moraine boulders and polished surfaces, combined with glacier equilibrium-line altitude calculations (Fernandes et al., 2022). After the LGM, a general glacier retreat occurred that exposed areas at elevations of approximately 1860-1900 m between 15 and 14 cal kyr BP. The Bassa Nera lies within this elevational range; thus, it can be inferred that the Pletiu dera Muntanheta was covered by glaciers until ~15 cal kyr BP, when our pollen record begins (Fig. 1). Therefore, this record may be the oldest possible to be retrieved in the Bassa Nera sediments and represent periglacial environments. The deglaciation trend continued until the YD and the Holocene but was interrupted by two glacier advances/stillstands at 13.5 and 13.0 cal kyr BP, represented by moraine systems situated at 2080 m and 2190 m elevation, which means that the glacier fronts were 190 m and 300 m above Bassa Nera, respectively. The deglacial trend exposed the surface of the highest cirque floors of the Ruda valley (2300-2500 m elevation) by 12.7-12.6 cal kyr BP, at the onset of the YD (Fernandes et al., 2022).

3. Methods

3.1. Coring and dating

The Bassa Nera core used in this study (PATAM12-A14) was retrieved in July 2014 with a 50-mm diameter Linvingstone corer. This core consisted of 10 drives (D1 to D10) for a total length of 845 cm (1102 cm once corrected for compression). This study is focused on the basal sequence (drives D7 to D9), which contains the LGEH interval. Eight samples for radiocarbon dating were taken in this interval and submitted to acid/base digestion (KOH, HCl, HF) to remove the rejuvenating effect of eventual incorporation of younger plant material and/or humic acids percolating through the peat profile (Vandergoes, 2003). AMS radiocarbon dating was performed at the Radiochronology Lab of the University Laval (Canada). Calibration was performed with *CALIB 8.2* and *IntCal 20* (Reimer et al., 2020). The age-depth model was built by interpolation using *clamR* (Blaauw, 2010).

3.2. Palynological analysis

In the same interval, 51 samples (2 cm^3) were taken with a volumetric syringe at regular intervals of approximately 100 years once the age-depth model was known (Fig. 1). These samples were digested with NaOH for disaggregation, HCl for carbonate removal and HF for silicate removal and submitted to centrifugation with Thoulet solution (density 2 g/cm^3) for mineral separation (Bennett & Willis, 2001). Two tables of *Lycopodium* spores (Batch 280521 291; 13,761±448 spores/tablet) were added to each sample before processing (Stockmarr, 1971). Processing was performed at the Archaeobotany Lab of the Catalan Institute of Human Paleoecology and Social Evolution (IPHES). Pollen/spore identification was based on Moore et al. (1991), Reille (1992) and the author's (VR) own reference collection, which contains over 700 species/subspecies from the Iberian flora. NPP identification followed López-Vila et al. (2014a, b) and the NPP Image Database (https://non-pollen-palynomorphs.uni-goettingen.de/); last visited 3 May 2023). Fungal spores were not identified, but special attention was placed on those considered to be indicators of herbivory and therefore of human impact, such as *Sporormiella* and *Sordiaria* (Lee et al., 2022).

Counting was conducted until a minimum pollen sum of 300 grains, stabilization of confidence intervals and saturation of diversity (Rull, 1987). In a number of samples, *Pinus* was superabundant, and its counts were stopped at 100-150 grains and further extrapolated using *Lycopodium* spores. In those cases, the above statistical criteria were applied to the remaining pollen types. The pollen sum included all pollen types with the exception of aquatic and semiaquatic plants (Cyperaceae, *Typha*, *Ludwigia*). Paleoecological interpretation was based on the available modern-analog studies for both pollen/spores and NPP developed on the elevational transect that includes the study site (Cañellas-Boltà et al., 2009; López-Vila et al., 2014a). Pollen accumulation rates (PAR) are used as a proxy for vegetation cover (Theuerkauf & Couwenberg, 2018). It is important to stress that pollen is not used as a climatic proxy, as usual in most Pyrenean literature. This is due to the lack of sufficient taxonomic resolution (usually at the genus or family level) and to the fact that such a procedure may lead to circularity when analyzing the response of vegetation to changing climates. Paleoclimatic trends were inferred from pollen-independent proxies such as the OST2 speleothem record (temperature) and the titanium content of the studied core (moisture), obtained by X-ray fluorescence (XRF) scanning. Charcoal particles above 5 μm were also recorded and used as fire proxies. Two size classes of these particles were considered, above and below 150 μm, as proxies for fires around the coring site and regional fires, respectively (Whitlock & Larsen, 2001).

Zonation of pollen diagrams was performed using the optimal splitting by information content (OSIC) and broken-stick methods (Bennett, 1996). Cluster analysis used the Pearson linear correlation coefficient (r) and the unweighted pair-group average (UPGMA) clustering algorithm (Sokal & Michener, 1958). Plotting and zonation were performed with *Psimpoll 4.27* (Bennett, 1992), and statistical analyses were carried out with *MVSP 3.22* (Kovach, 1999) and *Past 4.12* (Hammer et al., 2001).

4. Results

4.1. Lithology and Chronology

The full core was subdivided into five sedimentary units, of which three (U3 to U5) were present in the LGEH interval studied here. These units are characterized by intercalated clay, silt and sand layers of varied appearance and composition. U3 was composed of gray clays and fine sands with plant macroremains, whereas in U4, the alternating laminae consisted of

brown clays and ochre silts/sands with low organic matter content, and U5 was dominated by brown greenish clay layers with no apparent organic matter and occasional gravel and silt/sand beds (Fig. 8). Radiocarbon dating (Table 1) showed that the interval studied contained a complete and continuous (i.e., free from sedimentary gaps) LGEH sequence that lasted approximately 4800 years, from 15.2 to 10.0 cal kyr BP, and included the OD stadial, the BA interstadial, the YD stadial and the EH warming (Fig. 1). The average sedimentation rate (r) was 0.63 mm yr^{-1}, but it was far from homogeneous, showing minimum to intermediate values (0.35-0.76 mm yr^{-1}) in U3 and U5 and maximum values (1.33-2.07 mm yr^{-1}) in U4. This U4 sedimentation acceleration event occurred in the first part of the YD (12.8-12.3 cal kyr BP) and is abbreviated here as YDsa (Fig. 8).

Table 1. Radiocarbon dates of the basal part of core PATAM12-A14 using pollen residues (Vandergoes, 2003). Dating: Radiochronology Lab, University Laval, Canada (ULA). Calibration: *CALIB 8.2* and *IntCal 20* (Reimer et al., 2020). Sedimentation rates (r) refer to the intervals after the corresponding age values; for example, 0.35 mm yr^{-1} corresponds to the interval 15,167-13,549 cal yr BP (see also Fig. 8). ND, no data.

Lab code	Drive	Sample	Depth (cm)	^{14}C yr BP	Cal yr BP (2σ)	Median	r (mm yr^{-1})
ULA-10114	D7	63-64	799	9260±20	10,300-10,557	10,442	ND
ULA-10115	D7	104-105	849	9785±20	11,191-11,241	11,216	0.65
ULA-10116	D8	19-20	869	10,040±20	11,358-11,727	11,542	0.61
ULA-10117	D8	51-52	907	10,410±20	12,102-12,482	12,290	0.51
ULA-10118	D8	94-95	959	10,635±20	12,621-12,716	12,682	1.33
ULA-10119	D9	32-33	984	10,915±20	12,757-12,882	12,803	2.07
ULA-10120	D9	76-77	1041	11,710±20	13,493-13,602	13,549	0.76
ULA-10121	D9	119-120	1097	12,715±20	15,049-15,281	15,167	0.35

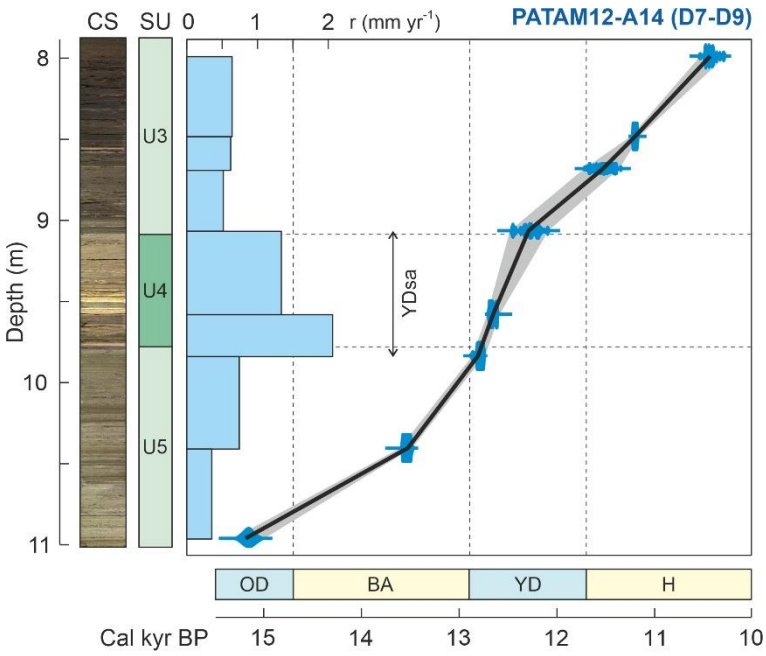

Figure 8. Lithology (CS, core scan; SU, sedimentary units) and age-depth model of the basal part of core PATAM12-A14 (drives D7 to D9) using the dates of Table 1 and the interpolation age-depth modeling method with the software *clamR* (Blaauw, 2010). Sedimentation rates (r) between dated samples are represented as blue bars using the above scale in mm yr^{-1} (YDsa, Younger Dryas sedimentation acceleration). The standard stadial/interstadial succession (Fig. 1) is also represented for reference (OD, Oldest Dryas; BA, Bølling/Allerød; YD, Younger Dryas; H, Holocene). Dotted lines represent the boundaries of stratigraphic units (horizontal) and stadial/interstadial phases (vertical).

4.2. Palynology

Globally, a total of 56 palynomorph types (33 pollen, 8 pteridophyte spores and 15 NPP) were identified. Total counts averaged 914 (804 pollen, 18 pteridophyte spores and 92 NPP), and the average pollen sum was 792. The pollen diagram was subdivided into six pollen zones, which are described in chronological order (Figs. 9 and 10). Ages, in cal kyr BP, were interpolated using the age-depth model (Fig. 8). The most abundant NPP are depicted in Plates 1, 2 and 3.

Zone BN1 (15.2 to 14.1 cal yr BP; GS-2 to GI-1e). Zone dominated by *Pinus* (>40%), followed by *Artemisia* and Poaceae (15-20% each), all other elements absent or below 1% of the pollen sum. Codominance of arboreal (Cf) and nonarboreal elements. Minimum PAR (pollen accumulation rates) values (<2000 grains cm^{-2} y^{-1}). Low percentages of fungal spores (~5%). Algae dominated by *Pediastrum* and Type BN-II as the main animal remains. Minimum charcoal influx (<100 particles cm^{-2} y^{-1}).

Zone BN2 (14.1 to 13.0 cal yr BP; GI-1d to GI-1a). Increase in the abundance of *Pinus* (60-80%) and decline in *Artemisia* and Poaceae (<10%). Arboreal elements (Cf) are dominant (70-80%). Increasing PAR and charcoal values (up to 4000 grains and 100 particles cm^{-2} y^{-1}, respectively). Fungi spores remained low (<5%). General decrease of all algae and animal types.

Zone BN3 (13.0 cal yr to 12.7 cal yr BP; GI-1a to GS-1). Transitional zone representing a gradual reversal to values similar to BN1, except for PAR, which showed a maintained increase and peaked at the end of the zone. First significant percentages of Chenopodiaceae (~5%). Fungi also increasing. Increase in *Zygnema* and *Pediastrum* and decrease in *Botryococcus*. Charcoal values also increasing peaking at the end of the zone (~200 particles cm^{-2} y^{-1}).

Zone BN4 (12.7 to 12.5 cal yr BP; GS-1). Slight decrease in *Pinus*, *Artemisia*, Poaceae and Chenopodiaceae and a distinct increase in Cichorioideae, Cyperaceae and *Saxifraga*, followed by other Asteraceae, Caryophyllaceae and Apiaceae. Dominance of nonarboreal elements (~70%) and significant decline in PAR values after the BN3 peak. Conspicuous fungi increased (up to 15%), and minimum values of all algae and animal remains, which almost disappeared. Charcoal values remained relatively high, as in the top of BN3, and then declined to values similar to BN2.

Zone BN5 (12.5 12.0 cal yr BP; GS-1). Another transitional zone showing trends opposite to BN3, that is, increasing arboreal and decreasing nonarboreal pollen. First significant appearance of *Betula* at the middle of the zone and further increase. Nonarboreal elements recovered the situation of BN3 due to the strong decline of Cichorioideae, Cyperaceae, *Saxifraga*, other Asteraceae, Caryophyllaceae and Apiaceae. PAR values remained low, with minor increases. Fungi decline to former values, and all algae underwent significant increases, especially *Zygnema*, which dominated the assemblage. Among animal remains, only Type BN-II increased to values similar to BN1. Charcoal also declined to intermediate values (up to 100 particles cm^{-2} y^{-1}).

Zone BN6 (12.0 to 11.1 cal yr BP; GS-1 to Early Holocene). Dominance of Pinus (~60%) and Betula (~20%), with a significant decline in *Artemisia*, Poaceae and all other nonarboreal taxa, which almost disappeared. Evergreen *Quercus* began to appear in a consistent fashion, and the first appearances of deciduous *Quercus* and *Corylus* were recorded at the end of the zone. PAR

values showed a gradual increase up to ~6000 grains cm^{-2} y^{-1}. Algae declined again, especially *Zygnema*. Among animals remains, Type BN-II remained as in the former zone, and Cladocera showed relevant abundances for the first time. Charcoal increased to maximum values of 400 particles cm^{-2} y^{-1}.

Zone BN7 (11.1 to 10.0 cal yr BP; Early Holocene). Zone characterized by the full dominance of arboreal pollen types (*Pinus*, *Betula*, *Corylus* and both *Quercus*), which reached values over 95%. Nonarboreal taxa were negligible, and only Poaceae attained values of ~1%. PAR values were maximum (up to 12,000 grains cm^{-2} y^{-1}). All algae types declined to negligible values except *Cosmarium*, which slightly increased to its maximum, although low (~1%), values. Animal remains did not show significant changes, and *Pinus* stomata attained significant values throughout the zone. Charcoal influx remained high but highly fluctuating, and particles above 150 μm showed maximum values.

Individually, the first significant increases in some important elements, such as *Betula* (12.2 cal kyr BP), deciduous *Quercus* (11.3 cal yr BP), *Corylus* (11.1 cal kyr BP) and *Ulmus* (10.8 cal yr BP), are worth noting. Also important are the last significant appearances of relevant elements such as *Saxifraga* and Cichoridoideae (12.5 cal kyr BP), Chenopodiaceae (12.3 cal kyr BP), and *Artemisia* and Poaceae (11.1 cal kyr BP).

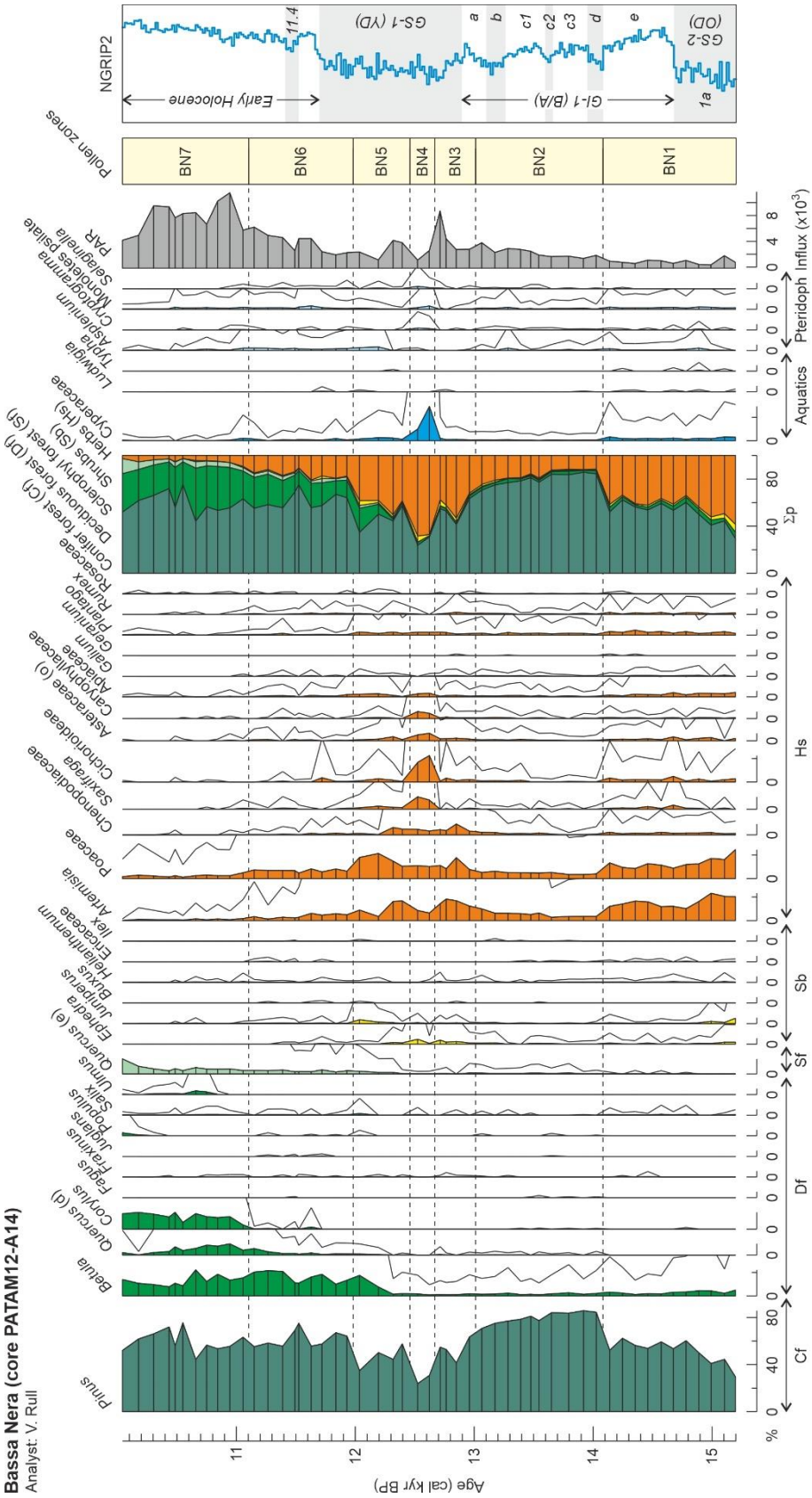

Figure 9. Percentage diagram of pollen and pteridophyte spores showing the pollen zones (BN1 to BN7) established using the OSIC and broken stick methods (Bennett, 1996). Solid lines are x10 exaggeration. Arboreal pollen is subdivided into conifer forest (Cf), deciduous forest (Df) and sclerophyll forest (Sf) elements; nonarboreal pollen is subdivided into shrubs (Sb) and herbs (Hs). PAR, pollen accumulation rates in pollen grains cm^{-2} yr^{-1}. Σp, pollen sum.

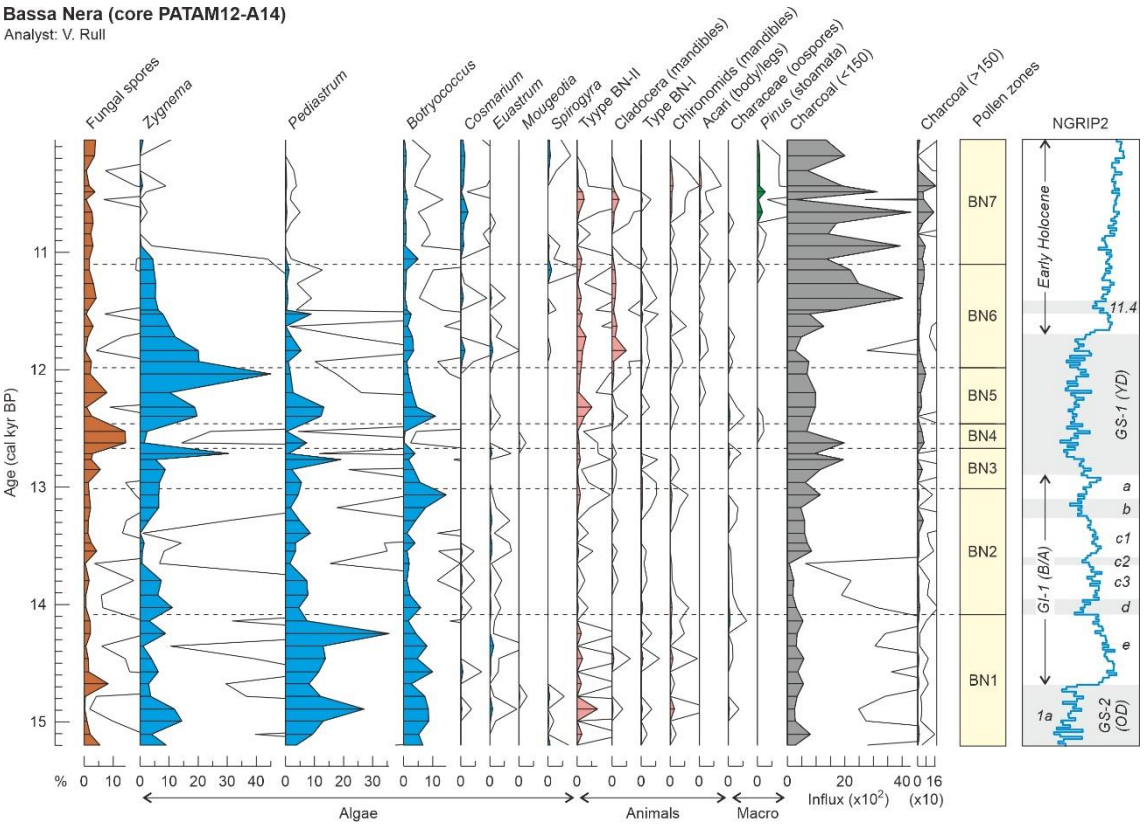

Figure 10. Percentage diagram of non-pollen palynomorphs (NPP) using the pollen zones defined in Fig. 9. Charcoal particles are represented as influx (particles cm^{-2} y^{-1}). Macro, plant macroremains. The most abundant NPP are depicted in plates 1, 2 and 3.

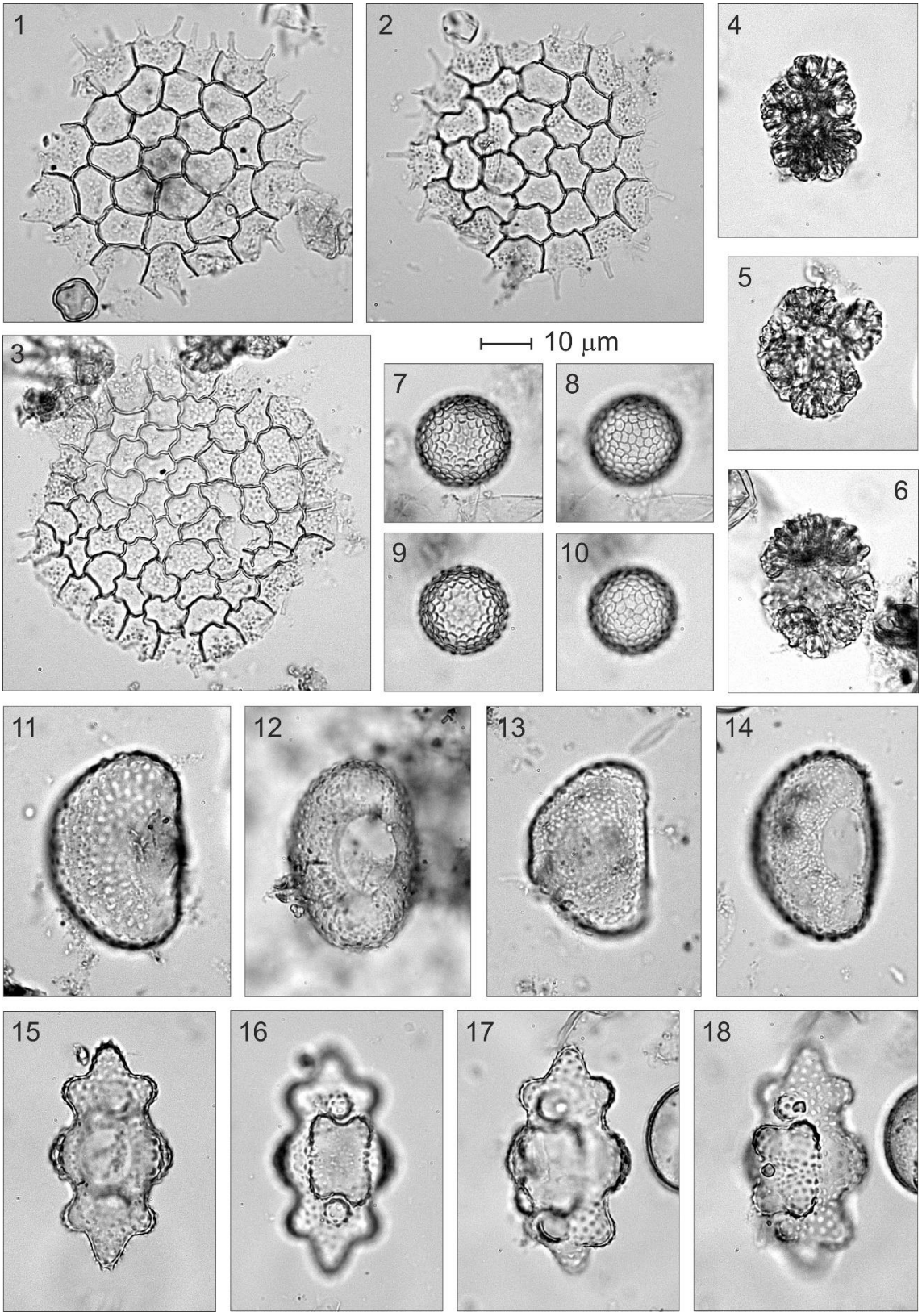

Plate 1. Algae remains. 1-3, *Pediastrum*; 4-6, *Botryococcus*; 7-10, *Zygnema*; 11-14, *Cosmarium*; 15-18, *Euastrum*.

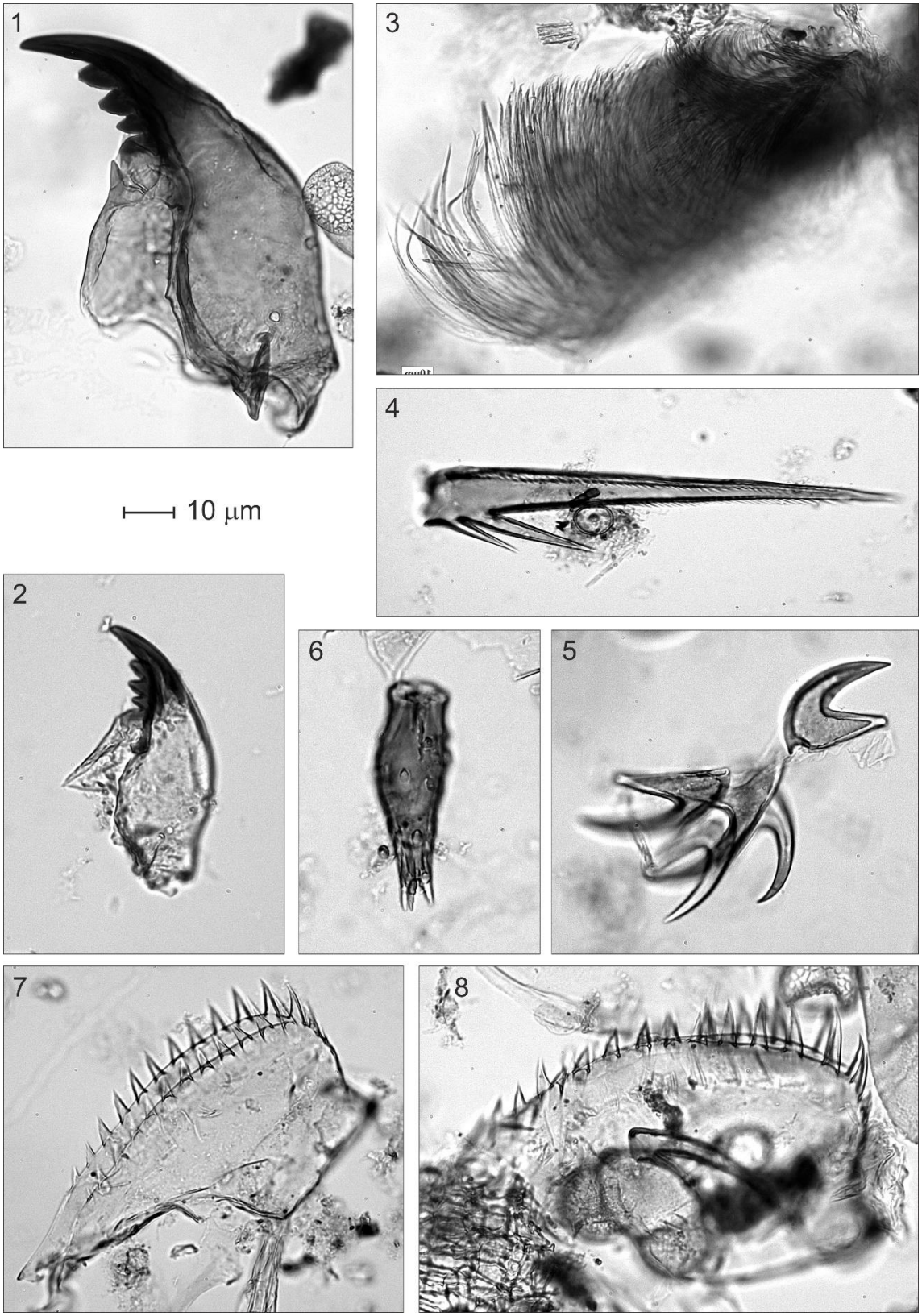

Plate 2. Animal remains. 1-2, Chironomids (mandibles); 3, Type BN-I; 4, Type BN-IIa; 5, Type BN-IIb; 6, Acari (legs); Cladocera (mandibles).

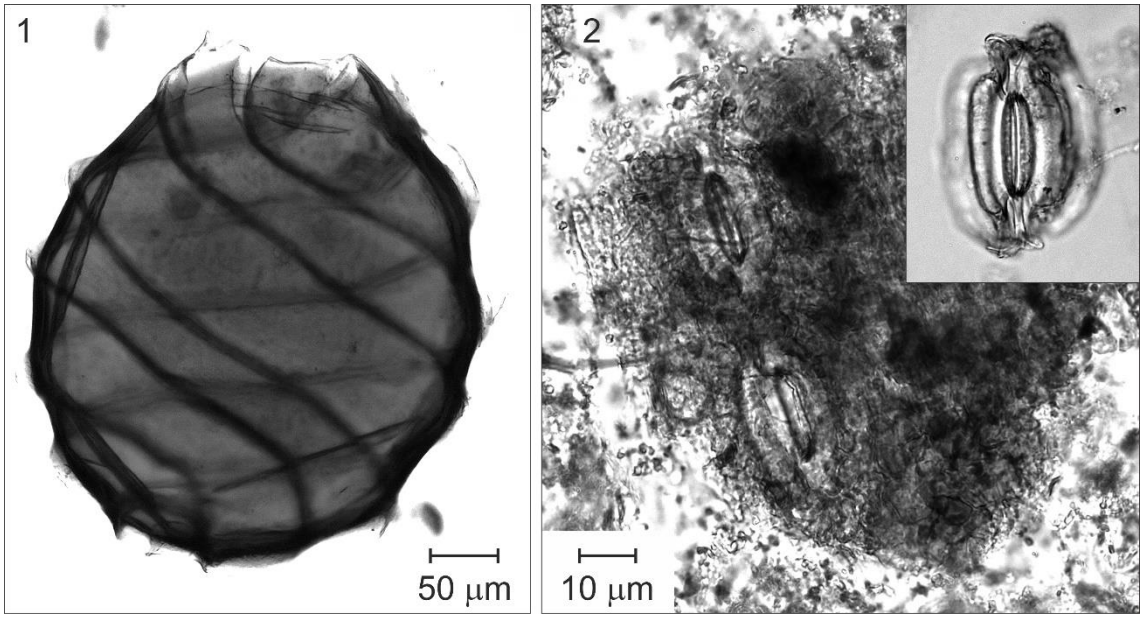

Plate 3. Plant macroremains. 1, Characeae (oospore); 2, Fragment of epidermis of a pine leaf with stomata and an isolated stoma (upper right corner).

To leave open the possibility of LGEH plant associations different from present ones, a cluster analysis was performed on pollen taxa, avoiding scarce components with only sporadic occurrences. Four assemblages were identified, two representing open (nonforested) associations (O1 and O2) and two representing forests (F1 and F2) (Fig. 11). O1 was dominated by *Artemisia* and Poaceae, and O2 was dominated by *Saxifraga* and Cichoroideae. Forest associations showed patterns similar to the present: F1 was dominated by deciduous trees (notably *Betula* and *Corylus*) and coincided with Df, whereas F2 had a single component, *Pinus*, thus coinciding with Cf. The stratigraphical distribution of the assemblages defined is shown in Fig. 12, where the following succession of dominant assemblages can be seen (%): F1-O1 (BN1), F1 (BN2), F1-O1 (BN3), O1-O2 (BN4), F1-O1 (BN5), and F1-F2 (BN6 and BN7). PAR values show a slightly different pattern, with very low values for all assemblages in BN1. The high percentages of F1 in BN2 were not due to high PAR values for this assemblages but to the still low amounts of the other assemblages. The decrease in F1 in BN3 to BN5 was due to a slight PAR decline of this assemblage combined with a significant increase in the same parameter for O1 and O2. Further percentage increases in F1 and F2, and declines in O1 and O2, were due to actual PAR increases and decreases in the same elements.

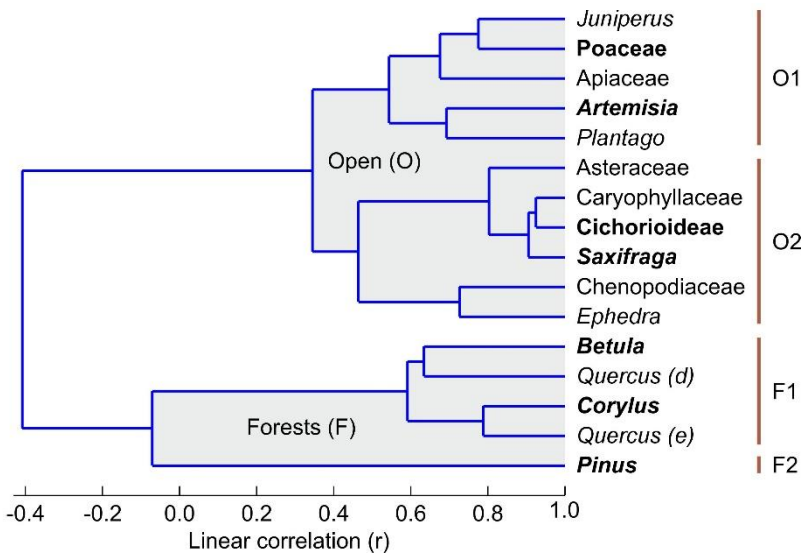

Figure 11. Cluster analysis using pollen taxa above 0.5% of the total. Dominant taxa of each association are in bold.

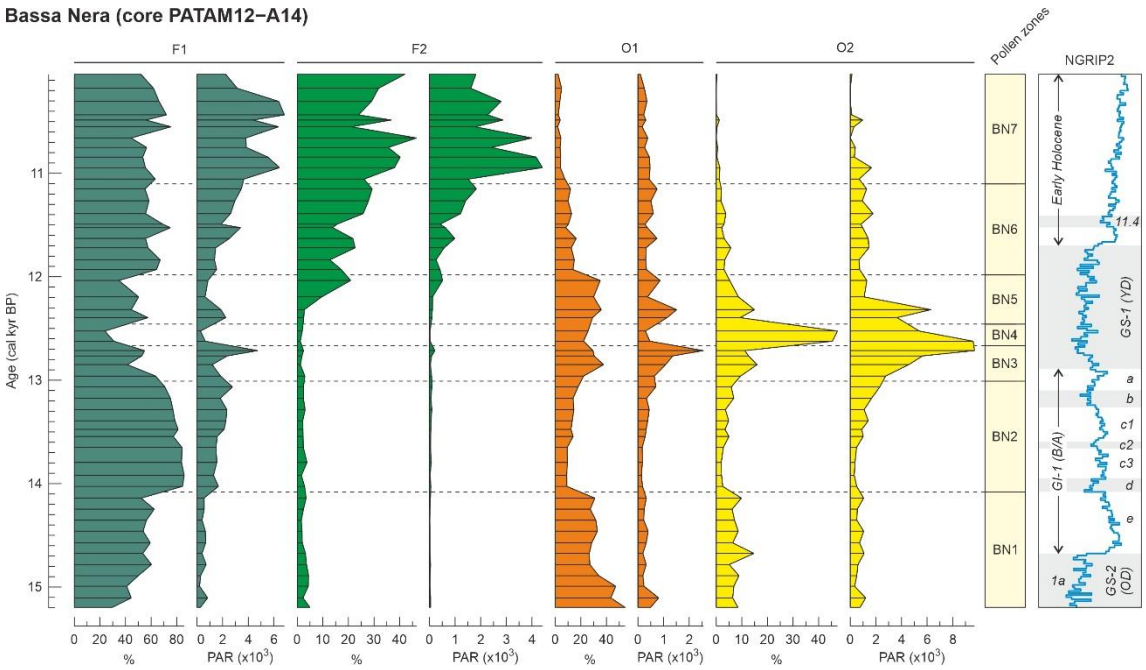

Figure 12. Stratigraphic arrangement of pollen assemblages defined by cluster analysis (Fig. 10) in percentage and influx units (PAR; grains cm^{-2} y^{-1}).

5. Discussion

This section is aimed at interpreting the above results in terms of vegetation dynamics and the potential influence of climatic drivers, notably temperature and moisture. The account is subdivided into two subsections: the first aims to identify the vegetation types that could have produced the pollen assemblages found, and the second aims to reconstruct the temporal trends of these vegetation types in relation to paleoclimatic shifts and fire.

5.1. Vegetation types

Modern pollen spectra around Bassa Nera are dominated by *Pinus* (~80%) with small percentages of grasses (<10%), *Corylus* and deciduous *Quercus* (<1%) (Fig. 7). A similar assemblage has not been found in our pollen sequence, which indicates that the LGEH vegetation was significantly different from the present. This is not surprising, as previous glaciological studies demonstrated that the site was near the snowline during the Lateglacial (Fernandes et al., 2022). However, no modern pollen analogs exist on the uppermost sites close to the present snowline (~2800 m), which indicates that Lateglacial vegetation was also different from the present, even at the highest vegetation belts. The main difference was the Lateglacial abundance of O1 and O2 taxa, especially *Artemisia*, *Saxifraga* and Cichorioideae (but also Chenopodiaceae, other Asteraceae, Caryophyllaceae, *Ephedra*, Apiaceae and Plantago), which is unparalleled in modern pollen assemblages and deserves further consideration.

In the Mediterranean region, the indicator character of *Artemisia* pollen in past records has long been debated, which is linked to the difficulty of identifying the species involved using only pollen morphology. The pollen of this genus has traditionally been used to characterize glacial and other cold climatic phases, but according to Subally & Quétzel (2002), the approximately 30 extant species of *Artemisia* living in the Mediterranean region bear a wide range of environmental conditions, and a strictly glacial character cannot be guaranteed, which is supported by increases in this pollen during interglacial and other warming phases. In addition, the concurrence of *Artemisia*, Chenopodiaceae and *Plantago* pollen has been considered strong evidence for regional grazing in the Pyrenees, whereas Cichorioideae has been linked to local grazing activities (Mazier et al., 2006). In our case, however, the absence of archaeological and paleoecological evidence for human impact during the period of study, along with the lack of fungal spores from coprophilous fungi as indicators of grazing activities, strongly argues against this possibility in the Bassa Nera Lateglacial.

In the Pyrenees, Lateglacial pollen assemblages dominated by *Artemisia*, Poaceae and Chenopodiaceae have traditionally been interpreted in terms of cold and arid steppe-like vegetation on the basis of similarities with modern pollen spectra from this vegetation type in eastern Europe (Jalut, 1992; Montserrat Martí, 1992). This interpretation was further extended to the adjacent Pyrenean lowlands (Pérez-Obiol & Julià, 1994) and the whole Iberian Peninsula (González-Sampériz et al., 2010; García-Ruiz et al., 2016), regardless of elevation. In some cases, however, steppe vegetation is not mentioned, and the association *Artemisia*-Chenopodiaceae (along with several Caryophyllaceae and Cichorioideae, among others) is considered to be characteristic of pioneering vegetation on open mineral soils, whereas Poaceae is considered to be dominant in closed herb vegetation (van der Knaap & van der Leeuwen, 1997). Notably, these associations are similar to our O1 and O2 assemblages, but in our case, no modern analogs for these pollen assemblages have been found (Fig. 7). O1 differs from alpine meadow assemblages by the abundance of *Artemisia* and the presence of *Juniperus*, whereas O2 is lacking at all.

Assemblage O1 could represent herbaceous vegetation with *Artemisia* species characteristic of periglacial climates. Presently, two species of this genus, *A. eriantha* and *A. gabriellae*, occur at the highest elevations of the Pyrenean alpine belt; however, they are restricted to rocky habitats and do not occur on alpine meadows (Vigo, 2009). The shrubby *Juniperus* is represented in the alpine and subalpine stages by *J. communis* subsp. *nana* and *J. sabina*, respectively, both typical of relatively warm and humid environments. It seems unlikely that the same *Artemisia* and *Juniperus* species were present in extremely cold Lateglacial conditions. In addition to Poaceae, *Plantago*, represented by three species (*P. alpina*, *P. media*

and *P. monosperma*), is the only component of this assemblage commonly growing on alpine meadows. Apiaceae pollen could not be identified, but it is mostly of the *Eryngium* type, which is represented in the high mountain meadows by *E. alpinum*, *E. bourgatii* and *E. campestre*. In summary, this pollen assemblage might be representative of uppermost alpine meadows with scattered shrubs with no modern analogs, probably of steppic nature due to the presence and abundance of unknown *Artemisia* and *Juniperus* species. With the available evidence, however, it is not possible to know whether this vegetation type is similar to the modern eastern European steppes because of the lack of sufficient taxonomic resolution (genera or families, at most). Therefore, this pollen assemblage will be considered to represent periglacial herbaceous vegetation (PH) with no further biogeographical considerations.

Assemblage O2 is even more difficult to interpret. One of the dominant taxa, *Saxifraga*, is represented in the Pyrenean highlands by numerous species, many of them living in rocky environments close to the snowline, situated at ~2800 m elevation (Vigo, 2009). The codominant Cichorioideae could correspond to several genera with different ecological requirements, which is also true for other Asteraceae and Caryophyllaceae. The Chenopodiaceae are represented mainly by *Chenopodium bonus-henricus*, a nitrophilous megaphorb growing on forest clearings and ruderal sites. *Ephedra* is mostly represented by the *E. distachya* type, which is absent from the Pyrenean highlands and occurs mainly on southern dry lowland steppes. The lack of sufficient taxonomic resolution and the fact that a similar association has not been documented in extant plant communities or pollen assemblages (Cañellas-Boltà et al., 2009) makes O2 difficult to interpret in terms of vegetation type. A number of O2 elements (notably Cichorioideae, Caryophyllaceae, Chenopodiaceae and *Ephedra*) have been considered in the Pyrenean and Iberian Lateglacial literature as characteristic of cold/dry Eurasian steppes and interpreted in combination with the O1 elements. However, the clear separation of O1 and O2 assemblages in our Bassa Nera record could have some paleoecological significance that remains unknown. Therefore, this pollen assemblage is considered here to represent an unknown high mountain plant association with no modern analogs tentatively called the *Saxifraga*-Cichorioideae association (SC).

5.2. Climate changes, vegetation shifts and fire

The relationship between the identified pollen assemblages and the independent paleoclimatic records is shown in Fig. 13, using the OST2 oxygen isotopic record as a regional temperature proxy for the Pyrenees (Bernal-Wormull et al., 2021) and a local paleotemperature reconstruction from the Ech paleolake (Fig. 2) based on chironomids (Millet et al., 2021). Notably, the Ech curve matches well with the OST2 reconstruction, especially in the B/A warming, which began a few centuries before than in the NGRIP2 ice core. In addition to disparities in temporal resolution, the main difference is that the YD cold reversal is less pronounced in the Ech than in the OST2 reconstruction. Titanium content is used as a pollen-independent proxy for moisture availability. Detrital titanium (Ti) has been demonstrated to be a reliable proxy for continental runoff and precipitation (e.g., Haug et al., 2001, 2003; Metcalfe et al., 2010; Thevenon et al., 2012). The only source for this element in aquatic sediments is catchment rocks, and its compounds are insoluble and not affected by redox conditions that may lead to the formation of soluble compounds in other metals, such as Fe (Mason & Moore, 1982). Therefore, all the Ti released by weathering and carried by superficial runoff is finally sedimented in the corresponding waterbodies. This element has successfully been used as a precipitation proxy in the Lateglacial of high-mountain periglacial environments similar to those studied here (Rull et al., 2010).

The first Lateglacial sediments of Bassa Nera began to be deposited at the end of the GS-2 (OD) stadial (15.2-14.7 cal kyr BP), when both temperature and moisture were rising (Fig. 13). This

trend was followed by an increase in conifer forests and a decline in PH, whereas other vegetation types were still absent. This trend occurred before the abrupt warming recorded in the NGRIP2 ice core, indicating that the Bassa Nera warming and the corresponding upward vegetation displacement took place some centuries before the onset of the GI-1 (B/A) interstadial. PH and SC vegetation possibly grew on the coring site, although its cover was very low, as indicated by PAR values. *Pinus* percentages were typical of montane stages situated >1500 m below the snowline (Fig. 7); therefore, these forests were probably situated in the surrounding lowlands. The absence of conifer forests on the site and its surroundings is supported by the low PAR values. During GI-1 (B/A), temperatures stabilized at relatively high values, and moisture availability was low to medium with minor oscillations. Cf and PH/CS percentages stabilized until ~14 cal kyr BP (i.e., the boundary between pollen zones BN1 and BN2), when the former abruptly increased and the latter declined, coinciding with a moisture decrease. However, PAR values remained low to medium, indicating that forests were still absent and most of their pollen was wind-transported. This shift occurred during the global GI-1d cold event, which was not evident in the OST2 regional temperature reconstruction. The *Pinus* increase situated this pollen at values that today are characteristic of subalpine stages (Fig. 7), situated 800-1000 m below the snowline, suggesting a >500 m upward shift of the treeline.

After this event, temperatures started to decrease slowly until the beginning of the GS-1 (YD) interstadial (BN2/BN3 boundary), with no evident moisture variations. This trend was paralleled by a similar decline in conifer forests and a coeval increase in open vegetation (PH/SC), which showed a significant PAR increase. Notably, the two glacier readvances recorded in the adjacent Ruda valley at 13.5 and 13.0 cal kyr BP (Fernandes et al., 2022) occurred during this phase. The onset of GS-1 (YD) was marked by a distinct temperature decline and a major moisture increase (occurred during the YD sedimentation acceleration; Fig. 8) coeval with a downward shift of conifer forests to levels similar to GS-2 (OD) and a densification of the local PH/SC vegetation, indicated by an abrupt PAR increase (~12.7 cal kyr BP). A further sudden moisture decline – as recorded by the Ti curve and the virtual disappearance of algae remains and other NPP from aquatic organisms (e.g., cladocera, rotifers, chironomids, midge and other invertebrates – with no significant temperature change coincided with a sudden decrease in Cf and PH and an equally abrupt increase in SC vegetation between 12.7 and 12.5 cal kyr BP (BN4). Therefore, this vegetation type, for which no modern analog has been identified, was characteristic of cold and dry climates, whereas the PH vegetation occurred under both wet and dry conditions before (BN3) and after (BN5) the SC peak. Also noteworthy was the increase in fire incidence during the peak of vegetation cover, suggesting that fuel availability would be important for fire occurrence during this interval. It is also worth noting that *Betula* significantly increased toward the middle of the GS-1 (YD) interstadial, coinciding with a gentle warming trend and a phase of local aridity (12.2-11.7 cal kyr BP), when the vegetation around the coring site was scattered.

The abrupt temperature increase at the onset of the Holocene was not marked by a synchronous vegetation shift, as both conifer forests and *Betula* were already increasing, and PH/SC decreasing, since the middle of GS-1 (YD). Another major but short (decadal) moisture increase occurred during the 11.4 cold event without a clear manifestation of vegetation features. Fire also showed a conspicuous increase at the same time. The most significant vegetation change took place by ~11 cal kyr BP (BN6/BN7 boundary), when other components of deciduous forests (*Quercus*, *Corylus*, *Ulmus*) began to increase, which was coeval with a significant increase in vegetation cover and coincided with two short (decadal or less) moisture peaks. The occurrence of evergreen *Quercus* within the Df assemblage is not anomalous, as mixed deciduous and evergreen oak forests are common in the montane stage, which is reflected in modern pollen assemblages (Cañella-Boltà et al., 2009). In this case, the closest

(but still different) modern analogs are found in the montane stage, situated 500-1000 m below Bassa Nera (Fig. 7), but a potential upward shift of this magnitude would imply average temperatures 3-6 °C warmer than today, which is incompatible with the available paleoclimatic information (Fig. 13). However, it is difficult to escape the idea that deciduous forests were closer to Bassa Nera than they are today, which is also supported by the relatively high PAR values. A possible explanation is that deciduous forests expanded from nearby small refugia with suitable microclimatic conditions –, i.e., microrefugia (Rull, 2009) – as formerly proposed for the northern Pyrenean slope (Jalut et al., 1992; Reille & Lowe, 1993). A number of these microrefugia for forest trees within Pleistocene glacial and periglacial environments have been documented in SW France using edaphic charcoal analysis (de Lafontaine et al., 2023). In the case of evergreen *Quercus*, this explanation is unlikely, as its climatic habitat lies ~2000 below the snowline. However, the upward dispersion of its pollen is noteworthy, as demonstrated by the modern-analog study in the Aiguamog valley, where evergreen oaks are absent but their pollen occurs along the whole transect up to 2600 m elevation (Cañellas-Boltà et al., 2009).

Regarding *Pinus*, the well-known high dispersion power of its pollen prevents us from knowing whether conifer forests dominated by this tree grew on the coring site during the LGEH. Indeed, no significant differences were found in pine pollen percentages at elevations with conifer forests and above the treeline (Fig. 7). In this case, the presence of *Pinus* stomata can provide support, as they are deposited mostly locally and are morphologically distinct (García Álvarez et al., 2009). These stomata were absent until pollen zone BN7, except for a couple of single occurrences in BN4/BN5 (Fig. 10), which suggests that conifer forests were not present in the coring site until the Early Holocene, since ~11 cal yr BP onward. High PAR values also support this interpretation.

A general observation is that even in the case of abrupt temperature and/or moisture shifts, the responses of vegetation are usually gradual, likely due to the response lag characteristic of plant communities, especially when long-lived organisms such as trees are involved (Rull, 2020). These lags could also be responsible for the lack of vegetation responses to decadal moisture shifts, such as those of the early Holocene. The lack of correspondence between some temperature/moisture changes and vegetation shifts suggests that other climatic parameters and/or different environmental drivers (edaphic, sedimentological, etc.) may be involved in biotic responses. A study on a wide range of physico-chemical and biological proxies is in progress for a more comprehensive view. A relevant observation is that Lateglacial pollen assemblages dominated by *Artemisia* and Poaceae, which are usually considered to represent dry steppes, grow well under wet conditions, as occurred in Bassa Nera during the GS-2 (OD) and the GS-1 (YD) stadials, which challenges traditional paleoenvironmental interpretations. The occurrence of wet climates during the YD was also documented in one of the few studies that used pollen-independent proxies for Lateglacial paleoclimatic reconstruction, as is the speleothem record from the French Moulis cave (Fig. 2) (Perrin et al., 2022).

The already discussed lack of sufficient taxonomic resolution for *Artemisia* pollen records, along with the wide arrangement of environments where the species of this genus may live, hinders specific paleoenvironmental inferences such as those attempted traditionally (Subally & Quézel, 2002). In addition, in periglacial environments, wet climates and water stress can coexist, as moisture availability may be reduced by permanent freezing (permafrost) rather than by decreases in the hydrological balance (precipitation/evaporation ratio) characteristic of arid climates. The vegetation of these environments is known as periglacial desert and occurs on highland tundra-like biomes (Ponel et al., 2001; Bertran et al., 2013). Care must be taken when assigning well-defined vegetational terms to unknown past vegetation types. In the case of the Pyrenees, the use of the term “steppe” for the Glacial and Lateglacial open

vegetation may induce implicitly accepting the existence of specific climatic, ecological and biogeographical conditions that are not necessarily supported by the available evidence. In the long run, these terms and the associated environmental features may be consolidated by repetition and become established as paradigms in the scientific literature. In this way, unwarranted paleoenvironmental reconstructions may become axiomatic and foster circular interpretations when analyzing the response of vegetation to LGEH climatic shifts.

Also noteworthy is that total vegetation cover, as inferred from PAR, and fire, as deduced from charcoal influx, showed good statistical agreement ($r = 0.629$; $p<0.001$), suggesting that fuel availability was a major driver for fire incidence during the period studied, as previously noted in other localities from the northern and southern Pyrenean sides. Indeed, the Bassa Nera record follows similar trends of reduced fire activity during the Lateglacial and enhanced incidence since the beginning of the Holocene, when the combination of higher temperatures and increasing biomass accumulation by forest expansion led to the exacerbation of regional fires (Rius et al., 2004; Gil-Romera et al., 2014). It should be noted that the main bulk of charcoal particles found in this study were below the boundary for regional vs. local fire events (150 μm), and therefore, they record mostly regional fires, likely by burning of lower elevation forests. Charcoal particles larger than 150 μm were comparatively scarce and only increased in zone BN7, coinciding with the appearance of *Pinus* stomata (Fig. 10), which suggests that the burning of in situ pine forests did not occur before those dates.

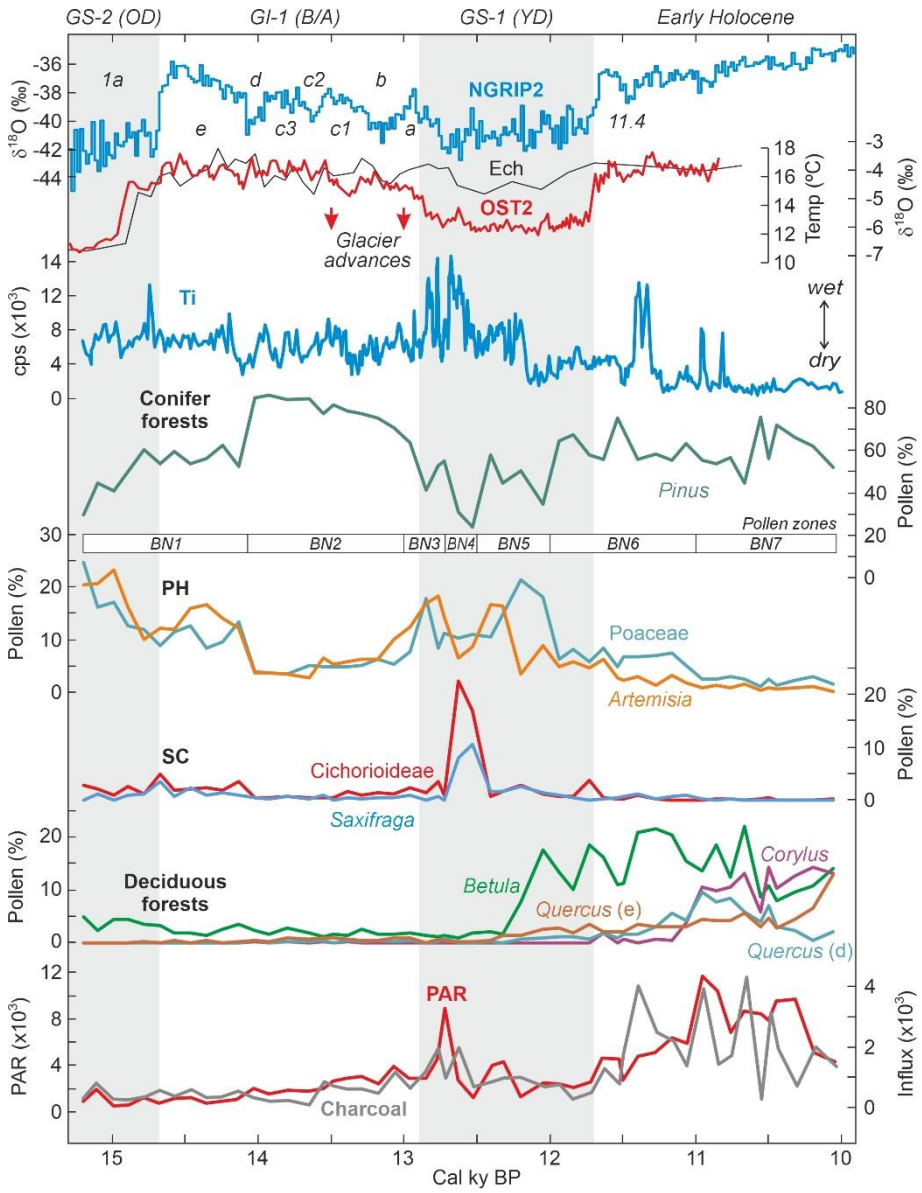

Figure 13. Comparison of climate changes, vegetation shifts and fire incidence. Temperature proxies are oxygen isotopes from the NGRIP2 ice core (Rasmussen et al., 2014), OST2 speleothem (Bernal-Wormull et al., 2021), and Ech chironomid redord (Millet et al., 2021). The other proxies are from this study, namely, pollen for vegetation, titanium (Ti) for moisture and charcoal for fire incidence.

6. Regional comparisons

Pyrenean-wide comparisons among pollen assemblages were carried out for each LGEH stadial/intestadial considering general climatic (wet Atlantic vs. dry Mediterranean), biogeographical (Eurosiberian vs. Mediterranean) and elevational (highlands vs. lowland) gradients (Fig. 14). Independent paleoclimatic reconstructions are scarce in surveyed localities, and most paleoenvironmental inferences are based on the same palynological proxies used for vegetation reconstruction, which hinders detailed comparisons of vegetation responses to past climatic changes. To homogenize nomenclature, we used the classical terminology (Oldest Dryas, Bølling/Allerød, Younger Dryas), as the updated terminology (GS-2, GI-1, GS-1) was unavailable in former studies. Sites with dating problems and/or poorly defined LGEH phases (Appendix 1) were not considered in this comparison.

6.1. Oldest Dryas

During this stadial, our record (BN) shows an intermediate situation between the Atlantic (western) and Mediterranean (eastern) sides. Indeed, open BN landscapes were codominated by Poaceae and *Artemisia*, the first being more abundant in the western open formations and the second being more important in nonforested areas from the eastern sector. Forest communities did not show significant differences and were dominated by *Pinus* on both sides. In the lowlands, the situation was also intermediate but open predominate over forested formations, except for a northern locality (Br), where *Pinus* was dominant. Sites from the Mediterranean biome did not show significant departures from Eurosiberian localities and were more consistent with the east–west gradient. The general impression is of relatively open landscapes dominated by Poaceae and *Artemisia* – with *Juniperus* in the west and Chenopodiaceae in the east – intermingled with conifer forests everywhere.

6.2. Bølling/Allerød

During this interstadial, BN was fully dominated by pine pollen, which strongly contrasts with eastern-western Pyrenean sides and with lowlands, which were covered by mosaic vegetation. In general, the former Poaceae-*Artemisia* dipole was less pronounced and the forest cover increased, but at that time *Betula* was as important as *Pinus* everywhere, except in the southern and eastern lowlands, where *Betula* was not an important element of the vegetation. Also noteworthy is the increase in *Juniperus* in the northern and southern lowlands from the central and western sectors. In general, during the B/A, major differences were recorded between the northern and southern Pyrenean sides, rather than on the east–west, highland-lowland or Eurosiberian-Mediterranean gradients.

6.3. Younger Dryas

During this stadial, open vegetation became more dominant, and the east–west gradient accentuated due to the reinforcement of the Poaceae-*Artemisia* dipole (which was even more pronounced than in the OD) and to the newly emerged contrast between western and eastern forests due to the importance of *Betula* in the former and its absence in the latter. In this case, the BN record was intermediate regarding open formations but more similar to the eastern sector because of the absence of *Betula* as an important component. In addition, our record differed from all other Pyrenean localities in the presence of the Sc (*Saxifraga*-Cichorioideae) assemblage. No evident differences between highlands and lowlands or between sites from Eurosiberian and Mediterranean regions were observed.

6.4. Early Holocene

A major regional vegetation shift took place at the onset of the Holocene due to the full dominance of forest formations, except for a southern locality (Es), where stadial-like open landscapes remained. This general forest increase was due to the influx of *Betula*, *Corylus* and *Quercus* rather than to an expansion of conifer forests. In this case, BN experienced the same general replacement of open vegetation by newly arrived forests, which showed similar patterns across the east–west, highland-lowland and Eurosiberian-Mediterranean gradients, except for a few western lowland sites where grasslands were still important. Some minor differences between western and eastern forests were the importance of *Corylus* in the former and *Betula* in the latter, with BN in an intermediate position.

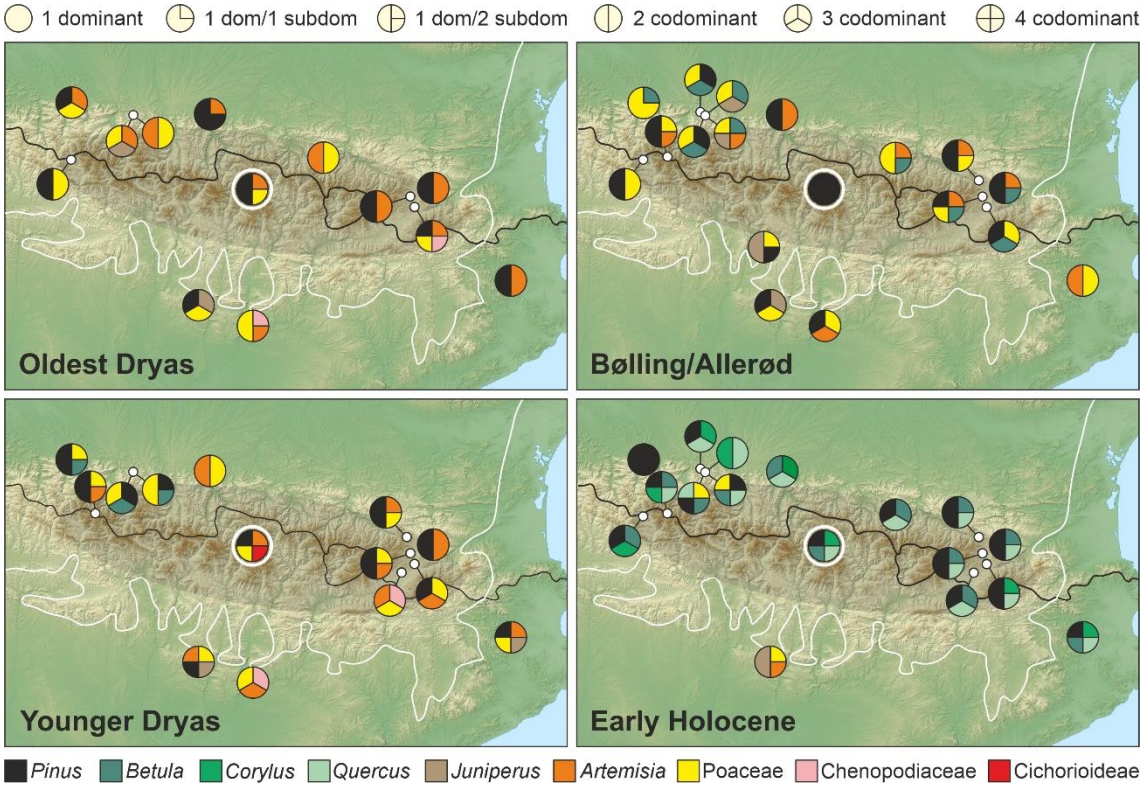

Figure 14. Sketch map with the main components of pollen assemblages from the LGEH stadials/interstadials in the different Pyrenean and lowland sites analyzed (see Fig. 2 and Appendix 1 for details). The Bassa Nera record is encircled by a white circle for easier location. As in Fig. 2, the black line is the border between France (northern Pyrenean slope) and Spain (southern Pyrenean slope), and the white line marks the boundary between Eurosiberian and Mediterranean biogeographical regions. Localities outside the shadow area are lowland records. Forest taxa are in black (Cf) and tones of green (Df and Sf) for better appreciation.

7. Conclusions and final remarks

The Bassa Nera pollen record allowed the identification of seven pollen zones that may be useful for chronostratigraphic correlation in the central Pyrenees and beyond (Table 2). Several additional correlation points were identified on the basis of individual pollen types. In three of these datums, the rise of *Betula*, *Quercus* and *Corylus* occurred slightly later in Bassa Nera than in the eastern Pyrenean side (Reille & Andrieu, 1995). The geographical ambit of this correlation framework should be established by further studies.

Table 2. Pollen zones identified in the Bassa Nera LGEH record indicating the ages in cal kyr BP and the correlation with the global chronostratigraphy from the NGRIP2 ice core. Significant individual datums are also indicated.

Zone	Age	NGRIP2	Classical phases	Individual datums
BN7	11.1-10.0	Holocene	Early Holocene	*Ulmus* rise (10.8)
BN6	12.0-11.1	GS-1 to Holocene	Younger Dryas-Early Holocene	*Quercus* rise (11.3) *Corylus* rise (11.1) *Artemisia*-Poaceae drop (11.1)
BN5	12.5-12.0	GS-1	Younger Dryas	*Saxifraga*-Cichorioideae drop (12.5) *Betula* rise (12.2) Chenopodiaceae drop (12.3)
BN4	12.7-12.5	GS-1	Younger Dryas	
BN3	13.0-12.7	GI-1a to GS-1	Bølling/Allerød-Younger Dryas	
BN2	14.1-13.0	GI-1d to GI-1a	Bølling/Allerød	
BN1	15.2-14.1	GS-2.1a to GI-1e	Oldest Dryas-Bølling/Allerød	

Four main pollen assemblages representing the same number of vegetation types were defined on the basis of pollen abundances. Two of these assemblages (F1, F2) represented known communities, such as conifer and deciduous forests (Cf, Df), whereas the other two (O1, O2) represented open communities with no modern analogs. O1 was tentatively called periglacial herbaceous (PH) community, and O2 was named *Saxifraga*-Cichorioideae (SC) community. The temporal trends of these assemblages were related to temperature changes, as deduced from a regional speleothem record, and moisture shifts, inferred from the titanium (Ti) content of the Bassa Nera sediments. Climate was the main driver of vegetation dynamics during the interval studied, as no evidence for human activities was detected. PH was dominant during the Oldest Dryas stadial, characterized by rising temperature and moisture trends, and Cf dominated the warmer and drier Bølling/Allerød interstadial. The Younger Dryas stadial was characterized by cold/wet climates during the first half and cold/dry conditions during the second half. The dominant vegetation was PH again but was replaced by SC during a short phase in the wet–dry transition. The early Holocene was characterized by warmer and drier climates, spiked by short-lived moisture increases, which favored the expansion and diversification of forests, especially the Df. Fire incidence was low until the Early Holocene, except for a small local peak at the beginning of the Younger Dryas, and abruptly increased at the beginning of the Holocene. These trends matched well with vegetation cover, suggesting that early Holocene warming and the accumulation of forest biomass were the main drivers of fire incidence.

The identification of wet Younger Dryas conditions using pollen-independent proxies (Ti) is noteworthy and challenges the traditional view of dry conditions during this phase on the basis of pollen assemblages dominated by *Artemisia*-Poaceae, usually interpreted as evidence for the occurrence of Eurasian-like cold/dry steppes. This finding and others similar –i.e., wet conditions during the Younger Dryas using speleothem records (Perrin et al., 2022) – call for a reconsideration of Lateglacial moisture trends on the Pyrenees using paleoclimatic proxies other than pollen. This would not only provide more realistic and straightforward paleoclimatic reconstructions but also prevent circularity when studying the vegetation responses to climatic shifts.

Finally, the results obtained in this work were analyzed under a regional perspective considering the available Lateglacial records for the Pyrenees and the surrounding lowlands in the context of the general east–west climatic gradient and the Eurosiberian-Mediterranean biogeographical regions. During the Oldest Dryas, the Pyrenean landscapes were relatively open and dominated by Poaceae and *Artemisia*, the former more abundant in the west and the latter in the east, as formerly proposed for the French side (Jalut et al., 1992). In Bølling/Allerød, the vegetation was dominated by conifer forests, and the Poaceae-*Artemisia* dipole was less pronounced, with the main differences being between the northern and southern sides. During the Younger Dryas, open vegetation returned, and the Poaceae-*Artemisia* dipole was more pronounced than in the OD. An additional contrast was the importance of *Betula* in the west and its absence in the east. A general forest increase took place in the early Holocene that led to regional homogenization, with no evident differences within the elevational, climatic and biogeographical gradients considered. It would be interesting to extend these regional comparisons to the continental ambit for a better appraisal of the influence of climatic, biogeographical and anthropogenic (when present) factors on the composition and temporal trends of LGEH montane vegetation across Europe. The use of the European Pollen Database (https://epdweblog.org/) would be especially useful in this sense but should be complemented with more regional compilations similar to those existing for the Iberian Peninsula (Carrión et al., 2022), which have been demonstrated to be much more exhaustive and useful than the available global databases for this type of reconstruction (e.g., Rull et al., 2023).

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References

Aubert, S., Belet, J.-M., Bouchette, A., Otto, T., Dedobat, J.-J., Fontugne, M., et al. 2004. Dynamique tardiglaciaire et holocène de la végétation à l'étage montagnard dans les Pyrénées centrales. Comptes Rendus Biologies 327, 381-388.

Bennett, K.D. 1992. Psimpoll – a quickbasic program that generates postcript page description of pollen diagrams. INQUA Newsletter 8, 11-12.

Bennett, K.D. 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytologist 132, 155-170.

Bennett, K.D., Willis, K.D. 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds.), Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal and Siliceous Indicators. Kluwer, New York, pp. 5-32.

Bergadà, M., Burjachs, F., Fullola, J.M. 1999. Évolution paléoenvironnemental du 14.500 au 10.000 BP dans le Prépyrénées catalans: La Grotte du Parco (Alòs de Balaguer, Lleida, Espagne). L'Anthropologie 103, 249-264.

Bernal-Wormull, J.L., Moreno, A., Pérez-Mejías, C., Bartolomé, M., Aranburu, A., Arrioalbegoa, M., et al. 2021. Immediate temperature response in northern Iberia to last deglacial changes in the North Atlantic. Geology 49, 999-1003.

Bertran, P., Sitzia, L., Banks, W.E., Bateman, M.D., Demars, P.-Y., Hernandez, :, et al. 2013. The Landes de Gascogne (southwest France): periglacial desert and cultural frontier during the Paleolithic. Journal of Archaeological Science 40, 2274-2285.

Blaauw, M. 2010. Methods and code for 'classical' age-modeling of radiocarbon sequences. Quaternary Geochronology 5, 512-518.

Cañellas-Boltà, N., Rull, V., Vigo, J., Mercadé, A. 2009. Modern pollen-vegetation relationships along an altitudinal transect in the central Pyerenees (southwestern Europe). Holocene 19, 1185-1200.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., et al. 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Review of Palaeobotany and Palynology 162, 458-475.

Carrión, J.S., Ochando, J., Munuera, M., Casas-Gallego, M., González-Sampériz, P., López-Sáez, J.A., et al. 2022. Paleoflora y Paleovegetación Ibérica II: Pleistoceno. Ministerio de Ciencia e Innovación/Fundación Séneca, Murcia.

Casas, J.M., Álvaro, J.J., Clausen, S., Padel, M., Puddu, C., Sanz-López, J., et al. 2019. Palaeozoic basement of the Pyrenees. In: Quesada, C., Oliveira, J.T. (eds), The Geology of Iberia: a Geodynamic Approach. Springer Nature, Cham, pp. 229-259.

Cook, E.J., van Geel, B., van der Kaars, S., van Arkel, J. 2011. A review of the use of non-pollen palynomorphs in palaeoecology with examples from Australia. Palynology 35, 155-178.

de Lafontaine, G. Amasifuen, C.A., Ducousso, A., Petit, R.J. 2014. Cryptic no more: soil macrofossils uncover Pleistocene forest microrefugia within a periglacial desert. New Phytologist 204, 715-729.

Delgado, J., Soler, A. 2010. Ilvaite stability in skarns from the northern contact of the Maladeta batholith, Central Pyrenees (Spain). European Journal of Mineralogy 22, 363-380.

Fernandes, M., Oliva, M., Vieira, G., Palacios, D., Fernández-Hernández, J.M., Garcia-Oteyza, J., et al. 2022. Glacial oscillations during the Bølling-Allerød Interstadial-Younger Dryas transition in the Ruda Valley, Central Pyrenees. Journal of Quaternary Science 37, 42-58.

García Álvarez, S., Morla juaristi, C., Solana Gutiérrez, J., García-Amorena, I. 2009. Taxonomic differences between *Pinus sylvestris* and *P. uncinata* revealed in the stomata and cutilce characters for use in the study of fossil material. Review of Palaeobotany and Palynology 155, 61-68.

Gassiot, E., Mazzucco, N., Clemente, I., Rodríguez, D., Obea, L., Quesada, M., et al. 2017. The beginning of high mountain occupations in the Pyrenees. Human settlements and mobility from 18,000 cal BC to 2000 cal BC. In: Catalan, J., Ninot, J.M., Aniz, M. (Eds.), High Mountain Conservation in a Changing World. Springer Nature, Cham, pp. 75-105.

Garcés-Pastor, S., Cañellas-Boltà, N., Clavaguera, A., Calero, M.A., Vegas-Vilarrúbia, T. 2016. Vegetation shifts, human impact and peat bog development in Bassa Nera pond (Central Pyrenees) during the last millennium. Holocene 27, 553-565.

Garcés-Pastor, S., Cañellas-Boltà, N., Pèlachs, A., Soriano, J.-M., Pérez-Obiol, R., Pérez-Haase, A., et al. 2017. Environmental history and vegetation dynamics in response to climate variations and human pressure during the Holocene in Bassa Nera, Central Pyrenees. Palaeogeography, Palaeoclimatology, Palaeoecology 479, 48-60.

García-Ruiz, J.M., Palacios, D., González-Sampériz, P., de Andrés, N., Moreno, A., Valero-Garcés, B., Gómez—Villar, A. 2016. Mountain glacier evolution in the Iberian Peninsula during the Younger Dryas. Quaternary Science Reviews 138, 16-30.

Gil-Romera, G., González-Sampériz, P., Lasheras-Álvarez, L., Sevilla-Callejo, M., Moreno, A., Valero-Garcés, B., et al. 2014. Biomass-modulated fire dynamics during the Last Glacial-Interglacial transition at the Central Pyrenees (Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 402, 113-124.

González-Sampériz, P., Valero-Garcés, B., Carrión, J.S., Peña-Monné, J.L., García-Ruiz, J.M., Martí-Bono, C. 2005. Glacial and lateglacial vegetation in northern Spain: new data and a review. Quat. Int. 140-141, 4-20.

González-Sampériz, P., Valero-Garcés, B., Moreno, A., Jalut, G., García-Ruiz, J.M., Martí-Bono, C., et al. 2006. Climate variability in the Spanis Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. Quaternary Research 66, 38-52.

González-Sampériz, P., Leroy, S.A.G., Carrión, J.S., Fernández, S., García-Antón, M., Gil-García, M.J., et al. 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. Review of Palaeobotany and Palynology 162, 427-457.

González-Sampériz, P., Aranbarri, J., Pérez-Sanz, A., Gil-Romera, G., Moreno, A., Leunda, M., et al. 2017. Environmental and climate change in the Southern Cen-tral Pyrenees since the Last Glacial Maximum: A view from the lake records. Catena 149, 668-688.

Guiter, F., Andrieu-Ponel, V., Digerfeldt, G., Reille, M., de Beaulieu, J.L., Ponel, P. 2005. Vegetation history and lake-level changes from the Younger dryas to the present in Eastern Pyrenees (France): pollen, plant macrofossils and lithostratigraphy from Lake Racou (2000 m a.s.l.). Vegetation Histroy and Archaeobotany 14, 99-118.

Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. Past: paleontological statistics sofware package for education and data analysis. Palaeontologia Electronica 4, 4.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. Science 293, 1304-1308.

Haug, G.H., Günther, D., Peterson, L.C., Sigman, D.M., Hughen, K.A., Aeschlimann, B. 2003. Climate and the collapse of Maya civilization. Science 299, 1731-1735.
Jalut, G., Turu, V. 2008. Le dernier cycle glaciaire-interglaciaire dans les Pyrenees: englacement, climat, vegetation. In: Canérot, J., Coli, J.-P., Platel, J.-P., Bilotte, M. (Eds.), Pyrenees d'Hier et d'Aujourd'hui. Altantica, Biarritz, pp. 145-161.
Jalut, G., Delibrias, G., Dagnac, J., Mardonès, M., Bouhours, M. 1982. A palaeoecological approach to the last 21,000 years in the Pyrénées: the peat bog of Freychinède (alt. 1350 m, Ariège, South France). Palaeogeography, Palaeoclimatology, Palaeoecology 40, 321-359.
Jalut, G., Andrieu, V., Delibrias, G., Fortugne, M., Pagès, P. 1988. Palaeoenvironment of the valley of Ossau (western french Pyrénées) during the last 27000 years. Pollen Spores 30, 357-394.
Jalut, G., Montserrat Martí, J., Fontugne, M., Delubrias, G., Vilaplana, J.M., Julia, R. 1992. Glacial to interglacial vegetation changes in the northern and southern Pyrénées: deglaciation, vegetation cover and chronology. Quaternary Science Reviews 11, 449-480.
Kovack, W. 1999. MVSP – A Multivariate Statistical Package for Windows, Version 3.1. Kovach Computing Services, Pentraeth.
Lee, C.M., van Geel, B., Gosling, W.D. 2022. On the use of spores of coprohilous fungi preserved in sediments to indicate past herbivore presence. Quaternary 5, 30.
Leunda, M., González-Sampériz, P., Gil-Romera, G., Aranbarri, J., Moreno, A., Oliva-Urcia, B., Sevilla-Callejo, M., Valero-Garcés, B. 2017. The Late-Glacial and Holocene Marboré Lake sequence (2612 m a.s.l., Central Pyrenees, Spain): testing high-altitude sites sensitivity to millennial scale vegetation and climate variability. Global and Planetary Change 157, 214-231.
López-Moreno, J.I., Alonso-González, E., Montserrat, O., del Río, L.M., Otero, J., Lapazaran. J., et al. 2019. Ground-based remote-sensing techniques for diagnosis of the current state and recent evolution of the Monte Perdido Glacier, Spanish Pyrenees. Journal of Glaciology 65, 85-100.
López-Vila, J., Montoya, E., Cañellas-Boltà, N., Rull, V. 2014a. Modern non-pollen palynomorphs sedimentation along an elevational gradient in the south-central Pyrenees (southwestern Europe) as a tool for Holocene paleoecological reconstruction. Holocene 24, 327-345.
López-Vila, J., Montoya, E., Rull, V. 2014b. Non-pollen palynomorphs analysis of the last two millennia in the Bassa Nera peat bog record (South-Central Pyrenees, SW Europe). VI Workshop on Non-Pollen Palynomoprhs, Tallin, Estonia, 16-20 June 2014.
Mason, B., Moore, C.B. 1982. Principles of Geochemistry. Wiley, New York.
Mazier, F., Galop, D., Brun, C., Buttler, A. 2006. Modern pollen assemblages from grazed vegetation in western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. Holocene 16, 91-103.
Metcalfe, S.E., Jones, M.D., Davies, S.J., Noren, A., MacKenzie, A. 2010. Climate variability over the last two millennia in the North American mosoon region, recorded in laminated lake sediments from Laguna de Juanacatlán, Mexico. Holocene 20, 1195-1206.
Millet, L., Rius, D., Galop, D., Heiri, O., Brooks, S.J. 2012. Chironomid-based reconstruction of Lateglacial summer temperatures from the Ech paleolake record (French western Pyrenees). Palaeogeography, Palaeoclimatology, Palaeoecology 315-316, 86-99.
Montserrat Martí, J.M. 1992. Evolución glaciar y postglaciar del clima y la vegetación en la vetiente sur del Pirineo: estudio palinológico. Monografías del Instituto Pirenaico de Ecología 6, 1-147.
Moore, P.D., Webb, J.A., Collinson, M.E. 1991. Pollen Analysis. Blackwell, Oxford.
Pérez-Haase, A., Ninot, J.M. 2017. Hydrological heterogeneity rather than water chemistry explains the high plant diversity and uniqueness of a Pyrenean mixed mire. Folia Geobotanica 52, 143-160.

Pérez-Obiol, R., Julià, R. 1994. Climatic change on the Iberian Peninsula recorded in a 30,000-yr pollen record from Lake Banyoles. Quaternary Research 41, 91-98.
Perrin, C., Honiat, C., Prestimonaco, L. 2022. Deciphering paleohydrology from the petrography and microstratigraphy of stalagmites (MIS 5 – Holocene, Moulis Cave, Ariège, S. France). Sedimentary Geology 440, 106256.
Ponel, P., Parchoux, F., Andrieu-Ponel, V.Juhasz, V., de Beaulieu, J.-L. 2001. A late-glacial – Holocene fossil insect succession from Vallée des Merveilles, French Alps, and its paleoecological implications. Arctic, Antarctic and Alpine Research 33, 481-484.
Rassmussen S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchart, S.L., Clausen, H.B., et al. 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quaternary Science Reviews 106, 14-28.
Reille, M. 1992. Pollen et Spores d'Europe et d'Afrique du Nord. URA-CNRS, Marseille.
Reille, M., Lowe, J.J. 1993. A re-evaluationof the vegetation history of the eastern Pyrenees (France) from the end of the Last Glacial to the present. Quat. Sci. rev. 12, 47-77.
Reille, M., Andrieu, V. 1995. The late Pleistocene and Holocene in the Lourdes Basin, Western Pyrénées, France: new pollen analytical and chronological data. Veg. Hist. Archaeobot. 4, 1-21.
Reimer, P., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey C., et al. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0-55 cal kBP). Radiocarbon 62, 725-757.
Rius, D., Galop, D., Doyen, E., Millet, L., Vannière, B. 2014. Biomass burning response to high-amplitude climate and vegetation changes in Southwestern France from the Last Glacial to the early Holocene. Vegetation History and Archaeobotany 23, 729-742.
Rivas-Martínez, S., Penas, A., del Río, S., Díaz, T.E., Rivas-Sáenz, S. 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula. Springer Nature, Cham, pp. 29-80.
Rull, V. 1987. A note on pollen counting in palaeoecology. Pollen Spores 29, 471-480.
Rull, V. 2009. Microrefugia. Journal of Biogeography 36, 481-484.
Rull, V. 2020. Quaternary Ecology, Evolution and Biogeography. Elsevier/Academic Press, London.
Rull, V., Vegas-Vilarrúbia, T. 2021. A spatiotemporal gradient in the anthropization of Pyerenan landscapes. Preliminary report. Quaternary Science Reviews 258, 106909.
Rull, V., Stansell, N.D., Montoya, E., Bezada, M., Abbott, M.B. 2010. Palynological signal of the Younger Dryas in the tropical Venezuelan Andes. Quaternary Science Reviews 29, 3045-3056.
Rull, V., Vegas-Vilarrúbia, T., Corella, J.P., Valero-Garcés, B. 2021a. Bronze Age to Medieval vegetation dynamics and landscape anthropization in the southern-central Pyrenees. Palaeogeography, Palaeoclimatology, Palaeoecology 571, 110392.
Rull, V., Vegas-Vilarrúbia, T., Corella, J.P., Trapote, M.C., Montoya, E., Valero-Garcés, B. 2021b. A unique Pyrenean varved record provides a detailed reconstruction of Mediterranean vegetation and land-use dynamics over the last three millennia. Quaternary Science Reviews 268, 107128.
Rull, V., Burjachs, F., Carrión, J.S., Ejarque, A., Fernández, S., López-Sáez, J.A., et al. 2023. Historical biogeography of *Cannabis* in the Iberian Peninsula: a probabilistic aproach based on palynological evidence. Perspectives in Plant Ecology, Evolution and Systematics 58, 125704.
Shumilovskikh, L.S., van Geel, B. 2020. Non-pollen palynomorphs. In: Henry, A.G. (Ed.), Hanbook for the Analysis of icro-Particles in Archaeological Samples. Springer Nature, Cham, pp. 65-94.
Sokal, R.R., Michener, C.D. 1958. A statistical method for evaluating systematic relationships. University of Kansas Science Bulletin 38, 1409-1438.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615-621.
Subally, D., Quézel, P. 2002. Glacial or interglacial, a plant indicator with dual responses. Review of Palaeobotany and Palynology 120, 123-130.
Theuerkauf, M., Couwenberg, J. 2018. ROPES reveals past land cover and PPs from single pollen records. Frontiers in Earth Science 6, 14.
Thevenon, F., Adatte, T., Poté, J., Spangenberg, J.E. 2012. Recent human-induced trophic change in the large and deep perialpine Lake Lucerne (Switzerland) compared to historical geochemical variations. Palaeogeography, Palaeoclimatology, Palaeoecology 363-364, 37-47.
van der Knaap, W.O., van Leeuwen, J.F.N. 1997. Late Glacial and Early Holocene vegetation succession, altitudinal vegetation succession, and climatic change in the Serra da Estrela, Portugal. Review of Palaeobotany and Palynology 97, 239-285.
Vandergoes, M.J. 2003. AMS dating of pollen concentrates – a methodlological study of Late Quaternary sediments from South Westland, New Zealand. Radiocarbon 45, 479-491.
Whitlock, C., Larsen, C. 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.L. (eds), Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal and Siliceous Indicators. Kluwer, New York, pp. 75-97.
Vigo, J. 2009. L'Alta muntanya catalana: flora I vegetació. Institut d'Estudis Catalans, Barcelona.

Appendix 1. Details of the Lateglacial coring localities with published palynological records, sorted by elevation, including the major pollen taxa used to assemble Fig. ? listed in top-down dominance order. Palynological information has been taken directly from the pollen diagrams displayed in the cited references. NR, not recorded; ND, possibly present but not defined.

Site	Latitude N	Longitude	Elevation	Oldest Dryas	Bølling/Allerød	Younger Dryas	Early Holocene	Fire	References
Marboré	42°41'44"	2°00'30"E	2612	NR	*Pinus* *Corylus*	*Pinus* *Corylus*	*Pinus* *Corylus*		Leunda et al. (2017)
Gourg-Nègre	42°38"	02°13"E	2080	*Pinus* *Artemisia*	*Pinus* *Artemisia* *Betula*	*Artemisia* *Pinus*	*Pinus* *Betula* *Quercus*		Reille & Lowe (1993)
Racou	42°33'15"	0°02'24"E	2000	NR	NR	*Artemisia* Chenopodiaceae Poaceae	*Pinus* *Betula* *Quercus*		Guiter et al. (2005)
Bassettes*	42°39'30"	02°01"E	1900	NR	*Pinus* Poaceae	NR	*Pinus* *Corylus*		Reille & Lowe (1993)
Bassa Nera	42°38'17"	0°55'27"E	1890	*Pinus* *Artemisia* Poaceae	*Pinus*	*Pinus* *Artemisia* Poaceae Cichorioideae	*Pinus* *Betula* *Corylus* *Quercus*		This paper
Laurenti	42°40'30"	02°01'46"E	1860	NR	*Pinus* *Artemisia* Poaceae	*Pinus* *Artemisia* Poaceae	*Pinus* *Betula* *Quercus*		Reille & Lowe (1993)
Portalet	42°48"	00°23"W	1802	*Pinus* Poaceae *Artemisia* *Juniperus*	*Pinus* Poaceae *Artemisia* *Juniperus*	NR	*Pinus* *Betula* *Corylus*	+	González-Sampériz et al. (2006) Gil-Romera et al. (2014)
Balcère	42°35'27"	02°03'18"E	1764	*Pinus* *Artemisia*	*Pinus* *Artemisia* Poaceae *Betula*	*Pinus* Poaceae *Artemisia*	*Pinus* *Betula* *Quercus*		Reille & Lowe (1993)
Pouretère	42°48'40"	00°12'12"W	1720	NR	*Pinus* Poaceae *Artemisia*	*Pinus* Poaceae *Artemisia*	*Pinus* *Betula* *Quercus* *Corylus*		Aubert et al. (2004)
Sagnes*	42°35'27"	02°03'18"E	1670	NR	*Pinus* Poaceae	NR	*Pinus* *Betula*		Reille & Lowe (1993)
Tramacastilla**	42°43'27"	00°22'07"W	1668	*Pinus* Poaceae *Artemisia*	*Pinus* Poaceae *Artemisia*	*Pinus* Poaceae *Artemisia*	*Pinus* *Betula* *Quercus*		Montserrat Martí (1992)

Borde	42°32"	02°05"E	1660	*Artemisia* *Pinus* Poaceae Chenopodiaceae	*Pinus* Poaceae *Betula*	*Pinus* Poaceae *Artemisia*	*Pinus* *Corylus* *Quercus*		Reille & Lowe (1993)
Bious	42°50'	00°27'W	1550	ND	ND	ND	ND		Jalut et al. (1988)
Freychinède	42°48"	01°26'11"E	1350	*Artemisia* Poaceae *Pinus*	Poaceae *Artemisia* *Betula*	NR	*Pinus* *Betula* *Quercus*		Jalut et al. (1982)
Búbal**	42°40'58"	00°19'13"W	1115	*Pinus* *Betula* *Juniperus*	*Pinus* *Betula* *Juniperus*	*Pinus* *Betula* *Juniperus* *Artemisia* Poaceae	*Pinus* *Betula* *Corylus*		Montserrat Martí (1992)
Bentué	42°20'11"	00°29'23"W	1000	NR	*Juniperus* Poaceae *Pinus*	NR	NR		González-Sampériz et al. (2005)
Ech	43°02"	00°05"W	710	Poaceae *Juniperus* *Artemisia*	Poaceae *Pinus* *Betula*	Poaceae *Pinus* *Betula*	*Quercus* Poaceae *Pinus* *Betula*	+	Rius et al. (2014)
Estanya	42°02"	00°32"E	670	*Pinus* *Juniperus* Poaceae	*Pinus* *Juniperus* Poaceae	Steppe elem. Poaceae *Pinus* *Juniperus*	*Juniperus* Poaceae *Artemisia* *Pinus*		González-Sampériz et al. (2017)
Castet	43°02'	00°22'W	490	ND	ND	ND	ND		Jalut et al. (1988)
Barbazan	43°02'02"	00°37'28"E	480	*Pinus* *Artemisisa*	*Pinus* *Artemisisa*	*Artemisia* Poaceae	*Betula* *Corylus* *Quercus*		Andrieu (1991), in Jalut & Turu (2008)
Lourdes	43°02"	00°05"W	430	*Artemisia* Poaceae	Poaceae *Betula* *Juniperus*	NR	*Quercus* *Corylus*		Reille & Andrieu (1995)
Parco	41°54'48"	00°56'31"E	420	Poaceae Chenopodiaceae Asteraceae	Poaceae Asteraceae *Pinus*	Poaceae Chenopodiaceae Asteraceae	NR		Bergadà et al. (1999)
Biscaye	43°02"	00°04'15"E	410	*Artemisia* Poaceae	Poaceae *Betula* *Juniperus* *Artemisia*	Poaceae *Pinus* *Betula*	Poaceae *Pinus* *Betula* *Quercus*		Reille & Andrieu (1995)

Monge	43°03"	00°01'55"E	394	NR	Poaceae *Pinus* *Betula*	Poaceae *Pinus* *Betula*	*Quercus* *Corylus* *Pinus*	Reille & Andrieu (1995)
Estarrès	43°05'36"	00°22'45"W	356	*Pinus* *Artemisia* Poaceae	Poaceae *Betula*	*Pinus* Poaceae *Betula*	*Pinus* Poaceae	Jalut et al. (1992)
Banyoles	42°08'07"	02°45'23"E	175	*Pinus* *Artemisia*	*Artemisia* Poaceae	*Pinus* *Artemisia* Poaceae *Betula* *Juniperus*	*Pinus* *Betula* *Corylus* *Quercus*	Pérez-Obiol & Julià (1994)

*Localities with fragmentary Lateglacial palynological records very close to others with complete sequences.
**Dating issues.