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Glacial and Lateglacial vegetation in northeastern Spain: New data and a review

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Abstract

Though usually under-represented in palaeobiogeographical models, northeastern Spain is one of the regions of southern Europe with the greatest biodiversity. Strong climatic and geographic gradients and topographic contrasts have contributed to the marked physiographic heterogeneity of the region. Pollen sites from the Ebro River Basin (northeastern Spain) have been insufficiently studied, perhaps because of the scarcity of suitable sites for conventional pollen analyses (i.e. lakes, peatbogs) and the characteristic mosaic vegetation patterns. Glacial and Lateglacial pollen records from a variety of archives located along a N–S transect: Glacial lakes, periglacial screes, peatbogs, hyena coprolites and archaeological sites were analyzed.

The reconstruction of full and Lateglacial landscapes in the Ebro River valley provides new insights into the vegetational history of the region: (i) the abundance of steppe formations with *Artemisia*, Poaceae, Chenopodiaceae, *Ephedra*, Asteraceae during the most intensive cold-arid episodes in both the non-glaciated mountains and the lowlands, (ii) the continuous occurrence of woody taxa even at high areas, (iii) the expansion of these woody taxa during Lateglacial climatic ameliorations, (iv) the survival of mesothermophytes in small refuge areas during full-glacial stages. There was great vegetation diversity in the northeastern Iberian landscapes during the Last Glacial and Lateglacial stages, suggesting patches of vegetation with steppic areas, Mediterranean shrubs, coniferous forest and refuges of mesothermophilous taxa.

1. Introduction

The study of continental pollen records along geographical transects may help to improve our understanding of environmental change in regions with marked physiographic heterogeneity. This is the case of the Ebro River Valley in Northeastern Spain, which embraces, from the Pyrenees to the Mediterranean Sea, a broad spectrum of vegetation landscapes, namely boreal-alpine coniferous forests, mixed deciduous forests, Mediterranean evergreen and mixed forest and scrub, and semi-arid treeless formations (Blanco et al., 1997). These landscapes occur in the context of strong topographic contrast between the highest Pyrenees peaks (up to 3404 m a.s.l.) and the lowlands of the Central Ebro Depression, at about 200 m a.s.l.

In this paper, several new pollen records along this transect are discussed and compared with all the available sequences. In recent decades, geomorphological and palynological studies in both the Pyrenees and the Ebro Depression have supplied information on glacial and periglacial stages and landforms, as well as hill-slope erosion and sedimentation and mass movements, including the chronology of some of the most important palaeoenvironmental events (Montserrat, 1992; García-Ruiz et al., 2001, 2003; González-Sampériz, 2004; Peña-Monné et al., 2004). Due to the scarcity of

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suitable sites for conventional analysis (i.e. lakes, peatbogs), many archives in the area contain few layers that are fertile in palynological terms. For this reason, a general perspective is needed to analyse the temporal and spatial interactions between all the records of this area that comprises ecotones from the Euro-Siberian and Mediterranean biogeographical regions within a short distance of each other.

This study includes all available (published and unpublished), full- and Lateglacial pollen records from a variety of sedimentary archives: saline lakes, small peatbogs, stratified screes and cave and rock shelter infills from archaeological sites. These palaeorecords are compared with regional and extra-regional palaeoecological sequences. Our goals are (i) to illustrate the composition of Glacial and Lateglacial flora in poorly known areas, (ii) to document and locate possible areas of Glacial refugia for temperate and Mediterranean woods in northeastern Spain, and (iii) to evaluate the spatial variation of vegetation responses to deglaciation.

2. Physical setting

In northeastern Spain, as in other regions of the Iberian Peninsula, altitude and orography frequently override latitudinal climatic changes, bringing moisture to southern microclimates and warmth to northern ones. A north–south transect will therefore show abrupt vegetation and climate gradients over short distances (200 km), e.g. from forested high mountains with around 2000 mm yr^{-1} of rainfall to steppes receiving less than 350 mm yr^{-1}.

The Ebro River drains a large depression surrounded by the Pyrenees to the north (Aneto: 3404 m a.s.l.), the Iberian Cordillera to the southwest (Moncayo: 2315 m a.s.l.) and the Catalonian mountains to the east (Montseny: 1700 m a.s.l.) (Fig. 1). The climate in the Pyrenean regions displays an oceanic influence in the west, becoming more Mediterranean toward the east. Cold winters, mild summers and high rainfall throughout the year sustain forest landscapes dominated by conifers (*Pinus, Abies, Juniperus*) or broad-leaf angiosperms (deciduous *Quercus, Fagus, Corylus*, *Betula, Acer, Tilia, Sorbus*). Foothills are covered by Mediterranean pine and oak forests (*Quercus ilex-rotundifolia, Q. faginea, Q. pubescens*), with dense shrub land (*Rhamnus, Pistacia, Arbutus*, *Prunus, Cornus, Buxus, Genisteae, Cistaceae,* etc.) and *Corylus avellana* and other phreatophytes such as *Salix, Fraxinus* or *Ulmus* in the riverine soils (Peinado-Lorca and Rivas-Martínez, 1987). In most of the Central Spanish Pyrenees, sub-Alpine forest was replaced by grasslands during the Middle Ages (Montserrat, 1992), with *Carex curvula* and *Festuca scoparia*. Given the long history of human activity, it is not easy to distinguish cultural and natural landscapes.

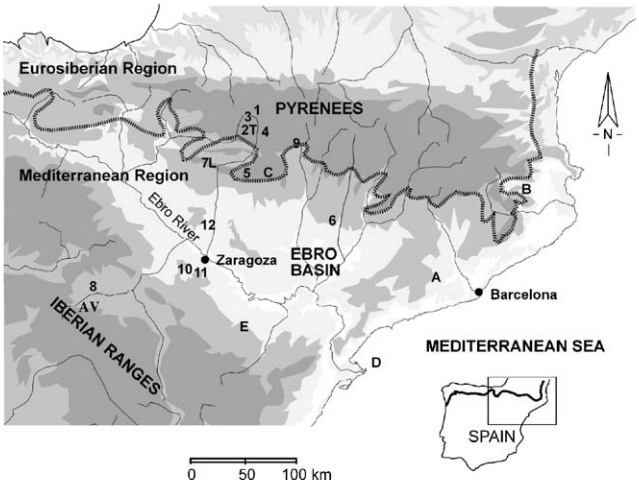

Fig. 1. Location map: (i) description, altitude and selected dates of each new deposit type presented in this paper (number 1–12): 1–Portalet peatbog, 1980 m a.s.l., 28,300 ± 370 BP (NSRL-11969); 2–Tramacastilla palaeolake, 1640 m a.s.l., 20,600 ± 170 BP (AZ-35870); 3–Formigal palaeolake, 1585 m a.s.l., 20,120 ± 150 BP (AZ-35867); 4–Linás de Broto palaeolake, 1250 m a.s.l., 30,380 ± 400 BP (AZ-35868); 5–Bentué de Rasal stratified scree, 1000 m a.s.l., 13,770 ± 100 BP (AZ-33221); 6–Gabasa hyena coprolites, 780 m a.s.l., >39,900/>51,900 BP (OxA-5671/5674); 7–Peña 14 archaeological site, 760 m a.s.l., 10,160 BP/10,630 BP (GrN-25096/26000); 8–Peña del Diablo archaeological site, 720 m a.s.l., 10,760 ± 140 BP (GrN-21014); 9–Devotas stratified scree, 700 m a.s.l., 22,800 ± 200 BP (AZ-35865); 10–Valmadrid stratified scree, 570 m a.s.l., 17,100 ± 85 BP (NSRL-12148); 11–Salada Mediana playa-lake, 350 m a.s.l., 11,250 ± 60 BP (NSRL-10589); 12–San Juan de Mozarrifar palaeopeatbog, 220 m a.s.l., >28,000 BP (UZ-1778). (ii) Other published pollen and macrofaunal sites referred to in the text: A–Abric Romaní (Burjachs and Julià, 1994); AV–Abrigo Vergara site (Utrilla et al., 2000) B–Bañolas lake (Pérez-Obiol and Julià, 1994); C–Chaves cave (Castaños, 1993); D–Ebro Delta record (Yll and Pérez-Obiol, 1992); E–Eudoviges site (Montes, 1988); L–Legunova site; T–Tramacastilla lake (Montserrat, 1992).

Further south, the central Ebro basin is under a continental Mediterranean climate, with low rainfall (300–350 mm/yr), high insolation and evapotranspiration (1000–1500 mm/yr), and the prevalence of strong, dry north-westerly winds (Cuadrat, 1999). The Ebro Basin is currently widely used for agriculture, leaving small patches of open parkland dominated by *Pinus halepensis, Q. coccifera* and *Juniperus thurifera*, and/or a dense shrubland with *Rhamnus lycioides, Rosmarinus officinalis, Globularia alypum, Ephedra nebrodensis, E. fragilis, Thymelaea tinctoria, Pistacia lentiscus, Phillyrea angustifolia,* and *Brachypodium ramosum*, depending on topography and soil. Mesophytes are here restricted to particularly humid canyons, as in the Sierra de Alcubierre near Zaragoza (Villar et al., 1997). Nitrophylous and gypsophylous plants are abundant: *Salsola vermiculata, Atriplex alimus, Artemisia herba-alba, Peganum harmala, Ferula communis, Malcomia africana*, *Marrubium alysoon*, *Ononis tridentata, Gypsophila hispanica, Helianthemum squamatum,* and *Cistus clusii*

(Braun Blanquet and de Bolos, 1957; Peinado-Lorca and Rivas-Martínez, 1987).

3. Methodology

Eleven sites with different sedimentary archives, situated between 220 and 1980 m a.s.l. were selected to evaluate the variability of palaeovegetation landscapes across the transect (Fig. 1). Sampling methods differ according to the sites investigated. In outcrops, the samples were taken in a vertical profile except at the San Juan de Mozarrifar palaeopeat-bog, from which samples were taken at different stratigraphical levels. At Linás de Broto, Tramacastilla and Formigal palaeolakes, clay-rich layers were sampled because of the poor preservation and low pollen concentration of sandy sediments. In Bentué de Rasal, Las Devotas and Valmadrid stratified screes, matrix-supported layers and palaeosols were sampled, as at archaeological sites, excluding the clast-supported layers where percolation could occur. Hyena coprolites from Gabasa cave were selected by weight (the 12 largest were used for pollen analyses). Finally, the Portalet peatbog and the Salada Mediana saline lake were cored with a modified Livingstone corer obtained from the Pyrenean Institute of Ecology (CSIC).

The laboratory preparation techniques included HF, HCl, and KOH digestion followed by mineral separation (Thoulet dense liquid: Dupré, 1992). *Lycopodium clavatum* spore tablets (Stockmarr, 1971) were added to each sample to facilitate concentration calculations (grains per gram dry weight). All slides were mounted in silicone oil. Samples were identified and counted with light microscopy aided by the pollen reference collection of the Pyrenean Institute of Ecology in Zaragoza. TILIA, TILIAGRAPH and CORELDRAW were used for plotting pollen diagrams.

Terrestrial macrofossils were very scarce and pollen concentrates were used to establish a chronological framework based on AMS ^{14}C dates. The samples for dating were obtained by the same chemical method used to prepare palynological samples (Valero-Garcés et al., 2000; González-Sampériz, 2004).

4. Results

4.1. Portalet, Tramacastilla and Formigal

The bases of the Portalet peatbog (González-Sampériz et al., 2001 (Fig. 1, number 1) and Tramacastilla lake (Montserrat, 1992) (Fig. 1, letter T) in the Central Spanish Pyrenees show geomorphological and sedimentological evidence of an early glacier retreat. As the moraines formed by the maximum extent of the ice during the last glaciation are 100 m above Tramacastilla lake (Montserrat, 1992), the maximum advance of glaciers must have taken place before 30,000 yr BP (base of the lake sequence) (García-Ruiz et al., 2003). The base of Portalet peatbog is also dated >28,000 yr BP, indicating that glacial ice had already retreated from the headwaters of the Gállego valley. This early retreat of the Pyrenean glaciers is also supported by: (i) ^{14}C dating of correlative sites at Linás de Broto, Formigal, Tramacastilla palaeolake, and Las Devotas (García-Ruiz et al., 2001, 2003; Martí-Bono et al., 2002) (Fig. 1, numbers 4, 3, 2 and 9 respectively), and (ii) recent OSL dates (Sancho et al., 2003; Peña-Monné et al., 2004) showing that the maximum glacier advances in the Pyrenees occurred at about 85,000 and 35,000 yr BP.

A 6 m-long core was collected in the Portalet peatbog (1980 m a.s.l., 42° 48′ 00″ N, 0° 23′ 52″ W) in autumn 1999 with a Livingstone corer. Palynological, sedimentological and stable isotope data reflect the climate evolution and vegetation changes for the last 30,000 yr BP. The pollen diagram shows a stadial pollen assemblage during the deposition of blue clays and carbonate-poor grey silts (Fig. 2). This is characterized by relatively high percentages of *Artemisia* (>30%), and other herbaceous elements (Chenopodiaceae, *Ephedra*, Poaceae, *Plantago*, *Helianthemum*, Caryophyllaceae, and Asteraceae). Arboreal pollen (AP) is dominated by *Pinus* and *Juniperus* (reaching 20% in the base and 60–70% during the Lateglacial) and with the minor but continuous presence of mesothermophilous taxa (evergreen *Quercus*, deciduous *Quercus, Ulmus, Fraxinus, Salix, Corylus*). The pollen record suggests, therefore, generally arid climate during Oxygen Isotopic Stage 3 (OIS3) with unstable periods identified by the *Artemisia* oscillations and isotopic value fluctuations in authigenic carbonates (González-Sampériz et al., 2004).

A minor glacial readvance is indicated by an abrupt decrease in pine after 24,170+240 yr BP (Fig. 2) and a sedimentary hiatus. It is plausible that this event defines the global LGM, synchronous in the Gállego valley with general glacial readvances, as was shown for the Tramacastilla area by García-Ruiz et al. (2003). Angiosperm forest developments were observed above 450 cm depth, starting with *Betula,* then *Corylus* and deciduous *Quercus*, which attain their highest values around 8600 yr BP. On both Pyrenean slopes, the dominance of mesophytes occurs during the Early Holocene, after a Lateglacial expansion of some deciduous taxa such as *Betula* (Jalut, 1976, 1990; Jalut et al., 1982, 1985, 1988, 1992; Mardones, 1982; Jalut and Mardones, 1983; Andrieu, 1989; Reille, 1990; Reille and Duplessy, 1990; Montserrat, 1992; Reille and Lowe, 1993; Reille and Andrieu, 1995).

The Tramacastilla (1640 m a.s.l., 42° 43′ 53″ N, 0° 23′ 51″ W) and Formigal palaeolakes (1585 m a.s.l., 42° 47′ 14″ N, 0° 23′ 42″ W) are located at lower altitude than

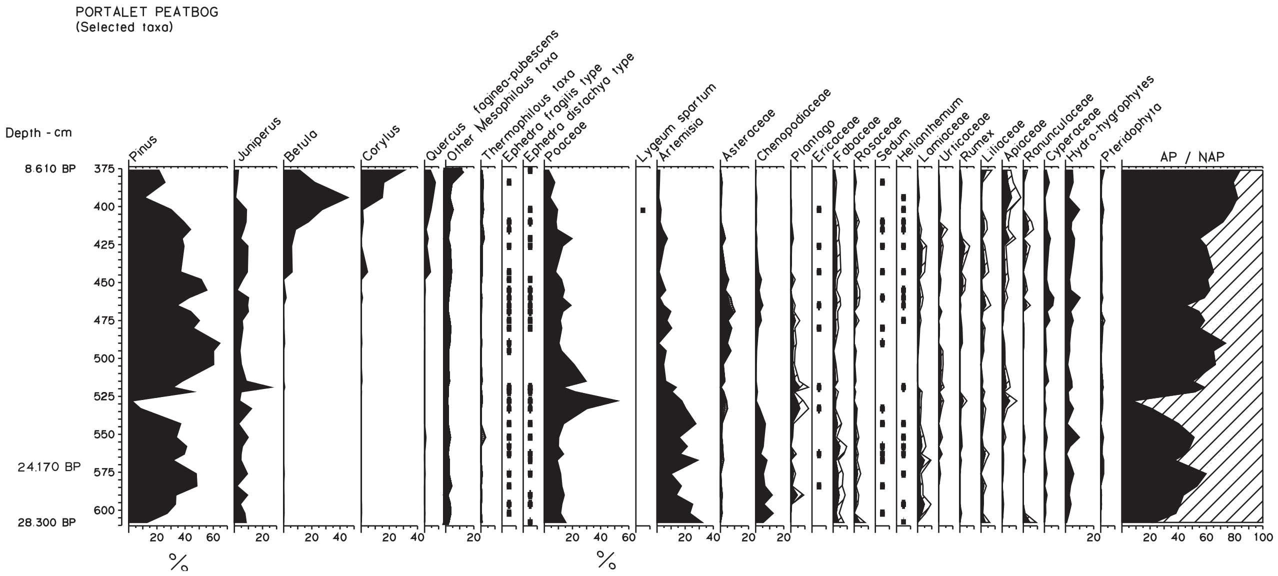

Fig. 2. Pollen diagram of selected taxa in Portalet peatbog.

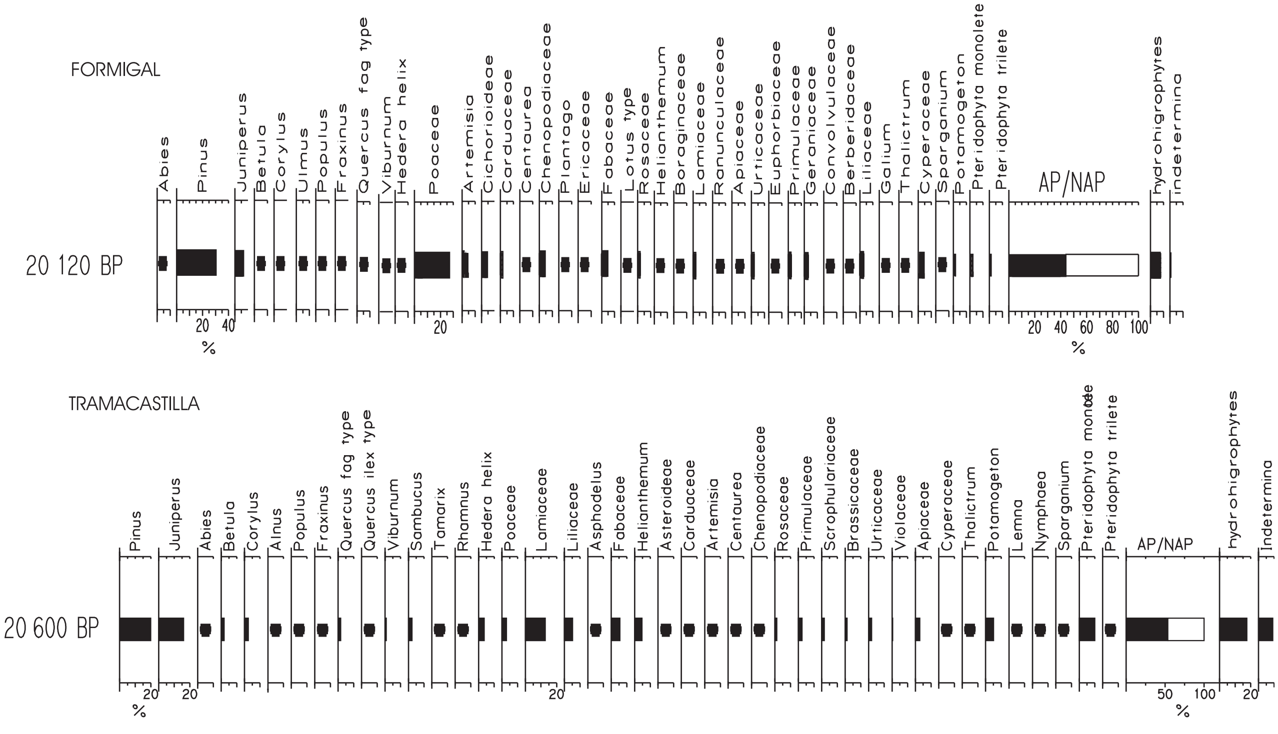

Fig. 3. Pollen histogram of Formigal and Tramacastilla palaeolakes.

Portalet (Fig. 1, numbers 2 and 3, respectively). In both cases, the lakes developed as a consequence of large landslides, probably related to hill-slope relaxation after deglaciation (García-Ruiz et al., 2003). *Pinus* and *Juniperus* were the principal arboreal taxa, accounting for 30% around 20,000 yr BP (Fig. 3). The dominant grassland-steppe, in conjunction with the abundance of *Artemisia*, Chenopodiaceae and other heliophytes, suggests cold, arid continental climate during the end of the glacial and Lateglacial periods. This agrees with previous palynological research in the Gállego valley and elsewhere in the Pyrenees (Jalut et al., 1985, 1988, 1992; Jalut, 1990; Montserrat, 1992; Andrieu et al., 1993; de Beaulieu et al., 1994; Reille and Andrieu, 1995).

4.2. Linás de Broto

The sedimentology of this glaciolacustrine deposit (1250 m a.s.l., 42° 36′ 40″ N, 3° 32′ 10″ W) (Fig. 1, number 4), one of the thickest in the Pyrenees (c. 60 m), was studied in detail by Martí-Bono et al. (2002). Twelve clayey beds were selected for pollen analysis, but only the lowest one had acceptable pollen concentration for palaeovegetation reconstruction and AMS dating. Excluding pine, the pollen spectrum shows the abundance of NAP components such as *Artemisia*, grasses, chenopods, composites and *Ephedra* (Fig. 4). The abundance of *Pinus* could be related to the over-representation typical of environments close to glaciers (Jalut et al., 1992; Montserrat, 1992; Reille and Andrieu, 1995; Carrión and van Geel, 1999; Stevenson, 2000; González-Sampériz, 2004). To check this hypothesis, we would need models of pollen rain-vegetation relationships that are not available for the area. However, there was local presence of pines and junipers during glacial times according to palaeovegetation reconstruction in the Pyrenees (Jalut et al., 1988, 1992; Andrieu, 1989; Reille, 1990; Montserrat, 1992; Reille and Lowe, 1993) and other mountain areas of the Iberian Peninsula (Peñalba et al., 1997; Sánchez-Goñi and Hannon, 1999; Carrión, 2002).

4.3. Bentué de Rasal, Devotas and Valmadrid

These sites correspond to slope deposits from the Cinca valley in the Central Pyrenees (Devotas: 710 m a.s.l., 42° 34′ 42″ N, 5° 47′ 47″ W, Fig. 1 number 9), the Gállego valley in the Pre-Pyrenees (Bentué de Rasal: 1000 m a.s.l., 42° 20′ 11″ N, 0° 29′ 23″ W, Fig. 1 number 5), and the central Ebro Basin (Valmadrid: 580 m a.s.l., 41° 26′ 51″ N, 0° 53′ 41″ W, Fig. 1 number 10). The sedimentological features of these deposits suggest periglacial processes during Full-Glacial and Lateglacial times (García-Ruiz et al., 2001), even in the Central Ebro Depression. Certainly, continental climate influence and thermal contrast were higher than today.

The pollen spectrum from Bentúe de Rasal (Huesca) shows that *Juniperus* was very abundant (60%) in certain areas during the Lateglacial (Fig. 5). The high AP values (including *Pinus, Juniperus*, *Betula* and evergreen *Quercus*) may be related to Bölling-Alleröd climate amelioration (13,770 ± 100 yr BP). Juniper pollen is also a major component of Lateglacial vegetation in other Pyrenean pollen diagrams such as Portalet (Fig. 2), Tramacastilla and Bubal (Montserrat, 1992), La Borde (Jalut et al., 1992) and La Moulinasse (Reille and Lowe, 1993).

Las Devotas (Huesca) is located at the bottom of a deep non-glaciated canyon surrounded by high mountains. This upper glacial (22,800 ± 200 yr BP) pollen sample shows the importance of the steppe component (*Artemisia*, Chenopodiaceae, Cichorioideae, Poaceae and *Ephedra*), but also indicates the occurrence of woody taxa such as *Pinus, Juniperus, Alnus* and *Salix*, which reach 20% (Fig. 5).

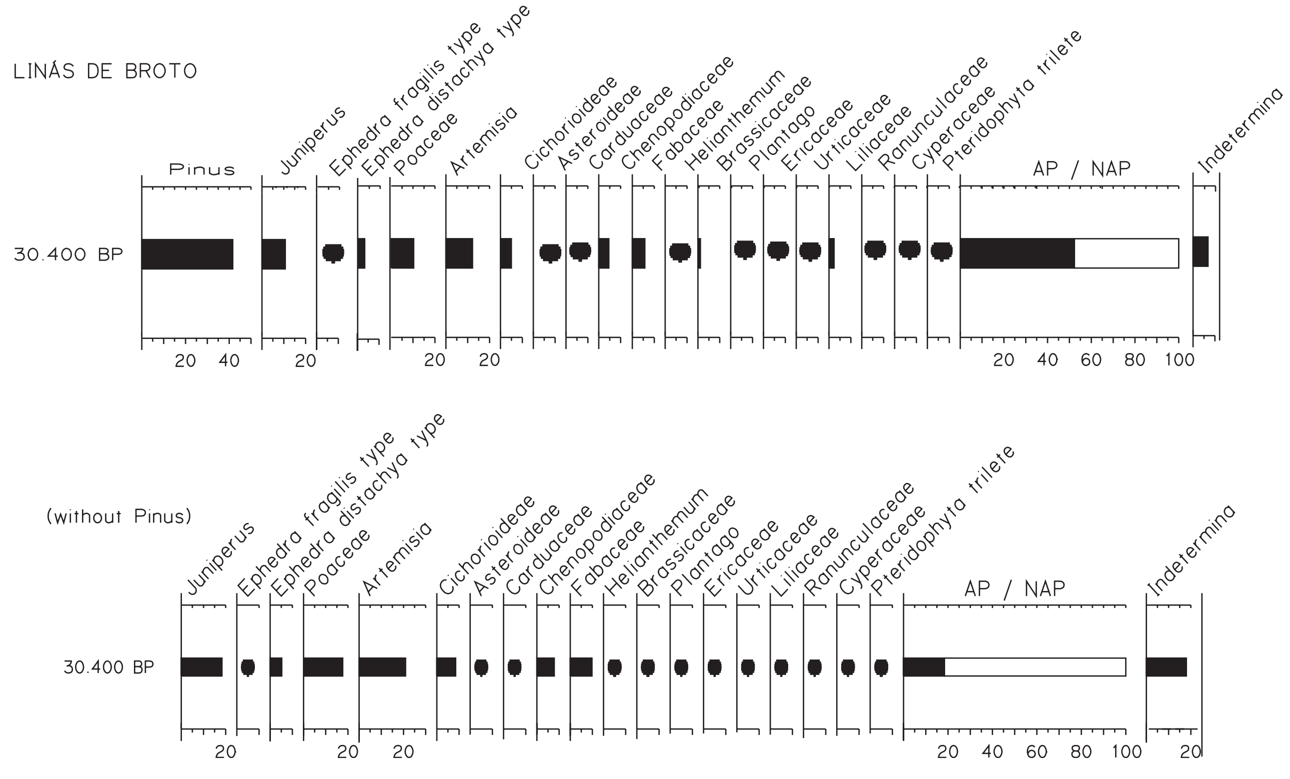

Fig. 4. Pollen histograms of the Linás de Broto palaeolake deposit: complete and without pine in the pollen sum.

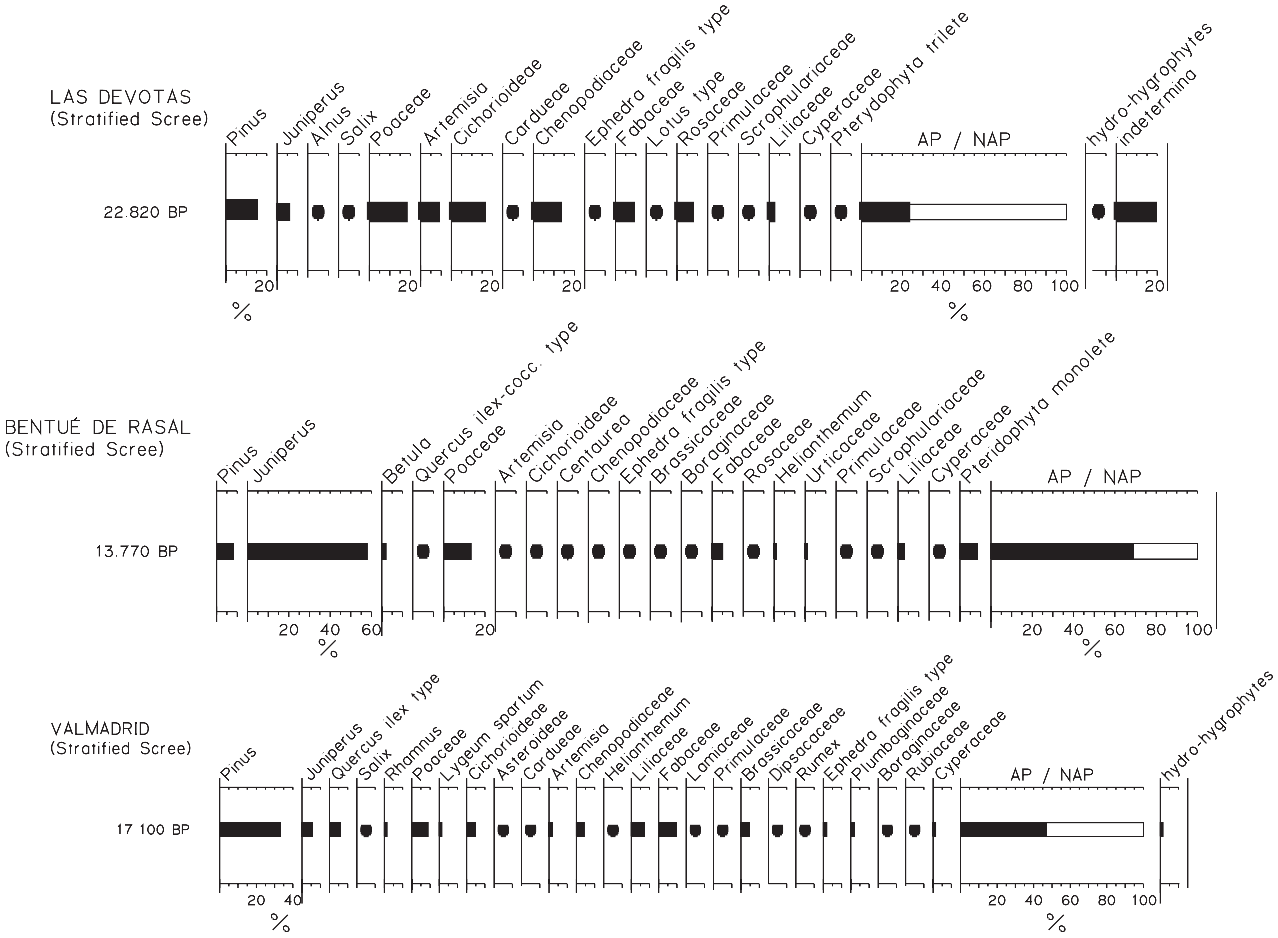

Fig. 5. Pollen diagrams of Las Devotas, Bentué de Rasal and Valmadrid stratified screes.

Valmadrid (Zaragoza) is situated in the lowlands at 580 m a.s.l. in a short canyon formed in Jurassic limestone. Compared with the Las Devotas site, this glacial (17,100 ± 85 yr BP) pollen spectrum shows higher incidence of temperate pollen, such as evergreen *Quercus*, while *Pinus* remains the dominant pollen. The herbaceous component is characterized by Poaceae, Compositae, *Artemisia, Ephedra*, Chenopodiaceae, *Rumex*, Fabaceae, Lamiaceae and *Lygeum spartum*.

4.4. Gabasa

In this Upper Pleistocene cave (780 m a.s.l., 42° 00′ 20″ N, 4° 06′ 20″ E, Fig. 1 number 6) spotted hyena (*Crocuta crocuta*) coprolites were analysed for pollen, because the sediment was palynologically sterile or there was evidence of percolation (González-Sampériz et al., 2003b). Pollen in hyena coprolites provides a regional perspective of the palaeoenvironment, since these animals travel long distances in search of food (Scott, 1995; Carrión et al., 2001a, b).

The sequence was dated between before ca 51,000 and 40,000 yr BP (Fig. 6). A mosaic glacial landscape was inferred from the pollen assemblages, with three coprolite samples clearly dominated by *Pinus*, one by Chenopodiaceae and another by Chenopodiaceae-Asteraceae. Other abundant pollen taxa are *Juniperus,* Poaceae and *Artemisia*. The occurrence of evergreen and deciduous *Quercus* and other mesophilous taxa (*Betula, Corylus, Ulmus, Fagus*) suggests the nearby location of refuges for temperate and Mediterranean vegetation.

4.5. Peña 14 and Peña del Diablo

Pollen spectra were obtained from rockshelter infills at two archaeological excavations (Utrilla et al., 2000; Montes, 2002): Peña 14 (Zaragoza: 760 m a.s.l., 42° 22′ 56″ N, 0° 56′ 18″ W) in the Pre-Pyrenean foothills, and Peña del Diablo (Zaragoza: 720 m a.s.l., 41° 20′ N, 1° 58′ E) in the Iberian Range (Fig. 1 numbers 7 and 8, respectively). The stratigraphic base of both sites have been dated around 11,000 yrs B.P. (Utrilla et al., 2000; Montes, 2002; González-Sampériz, 2004) with a pollen spectrum that shows a diversity of arboreal pollen types such as *Pinus, Juniperus, Abies, Betula, Corylus, Salix, Ulmus, Acer, Fraxinus, Juglans, Castanea, Quercus,* *Pistacia, Oleaceae, Hedera, Sambucus* and *Buxus*, among others (Fig. 7).

4.6. San juan de mozarrifar and Salada Mediana

Both sedimentological and geomorphological information suggest that, consistent with the current climatic gradient, temperatures were higher in the Central Ebro Basin than in the Pyrenees from the end of the OIS3 stage until the Lateglacial (González-Sampériz et al., 2003a; Valero-Garcés et al., 2004). However, aridity may still have been extensive in the lowlands, with moisture availability restricted to river valleys and ravines. This is confirmed by the stratigraphic sequences of the Salada Mediana playa-lake (350 m a.s.l., 41° 30′ 10″ N, 0° 44′ W, Fig. 1 number 11) (Valero-Garcés et al., 2000), the San Juan de Mozarrifar palaeopeatbog (220 m a.s.l., 41° 44′ 35″ N, 2° 51′ 50″ W, Fig. 1 number 12), and La Salineta (Valero-Garcés et al., 2004). These sites provide evidence for moisture fluctuations during

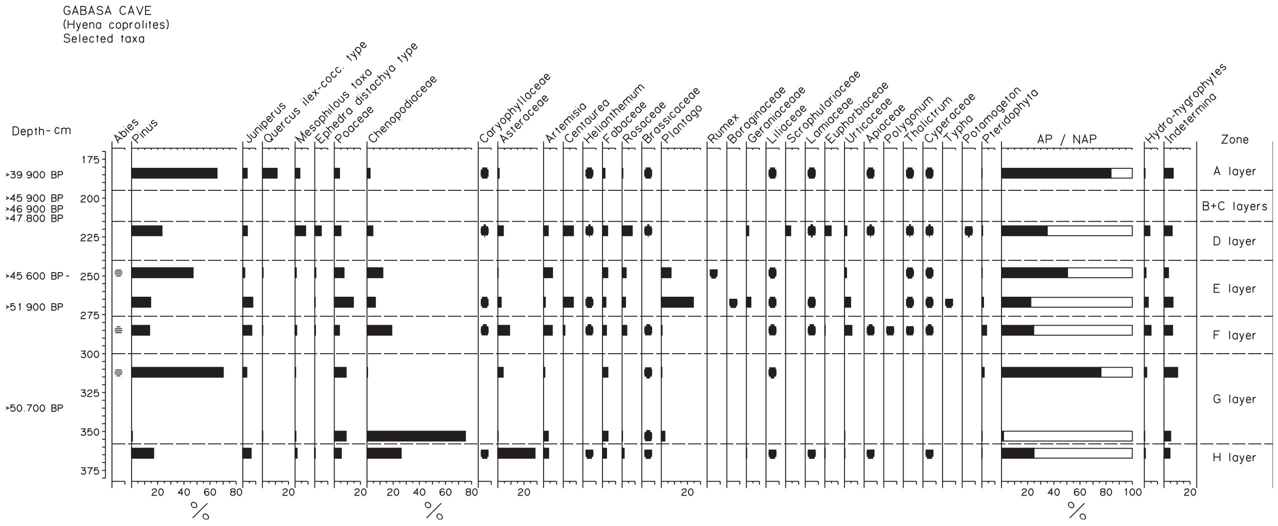

Fig. 6. Pollen diagram of hyena coprolites from the Mousterian cave of Gabasa. The absolute chronology of the cave sequence is somewhat imprecise (minimum age), since the dates are beyond the ^{14}C time scale.

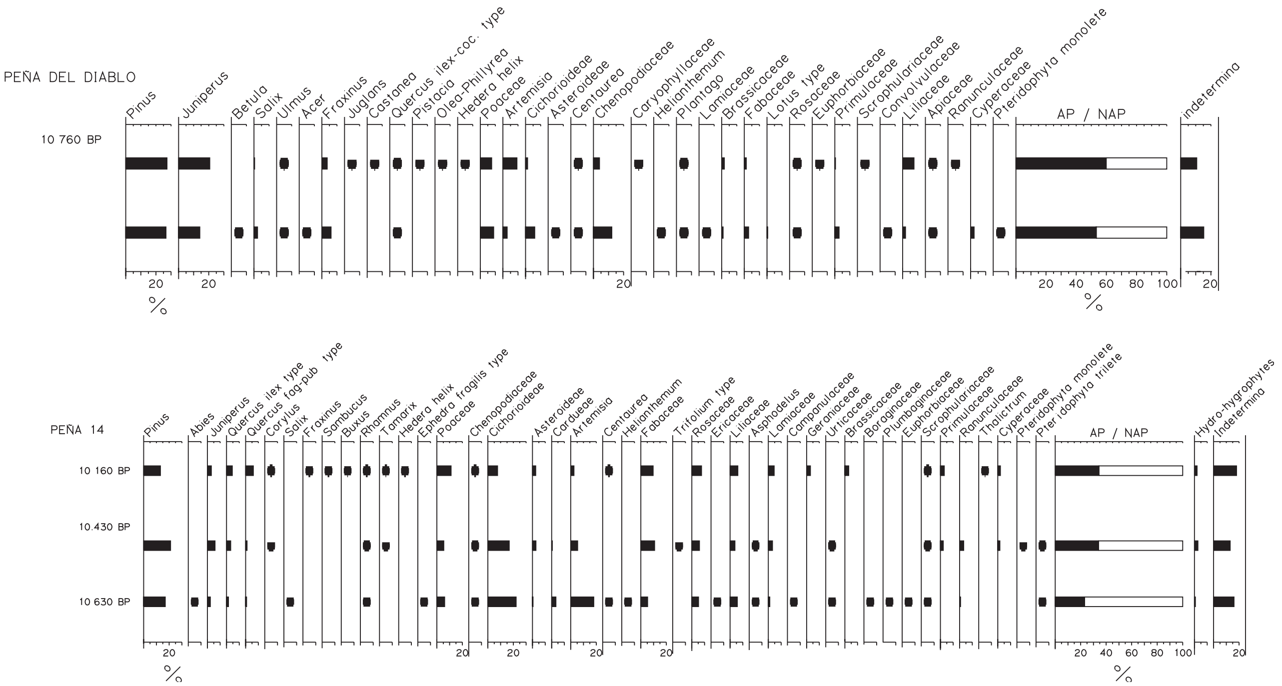

Fig. 7. Pollen diagram of the bases of Peña 14 and Peña del Diablo archaeological sites.

glacial times. Increased discharge of the Ebro River during meltwater pulses from mountain glaciers (González-Sampériz et al., 2003a; Sancho et al., 2003; González-Sampériz, 2004; Peña-Monné et al., 2004; Valero-Garcés et al., 2004) could have played a significant role in moisture availability in the lowlands, particularly in flooded areas such as San Juan de Mozarrifar, where the Gállego tributary flows into the Ebro River.

The glacial pollen spectra of San Juan de Mozarrifar reflect fluctuating hydrological regimes from before 28,000 yr BP (Fig. 8). This is seen in the fluctuations of aquatic and halophilous taxa. *Potamogeton* (hydro-hygrophytes) is present at high-water levels, probably related to deglaciation discharges and saline and xerophytic taxa (60% Chenopodiaceae) in desiccation episodes when the flooded areas became playa-lake formations. The records show 20–30% AP (*Pinus*, *Juniperus* and several mesothermophytes such as deciduous and evergreen *Quercus, Betula, Corylus, Alnus, Oleaceae, Pistacia, Buxus,…*) and a major steppic component (*Ephedra, Artemisia, Helianthemum*, Compositae, etc.), indicating an open landscape.

The pollen records from the Lateglacial site of Salada Mediana also support large moisture fluctuations (Fig. 9). Water availability and periods of relatively temperate climate conditions could explain the local abundance of *Corylus* (up to 40% if *Pinus* and

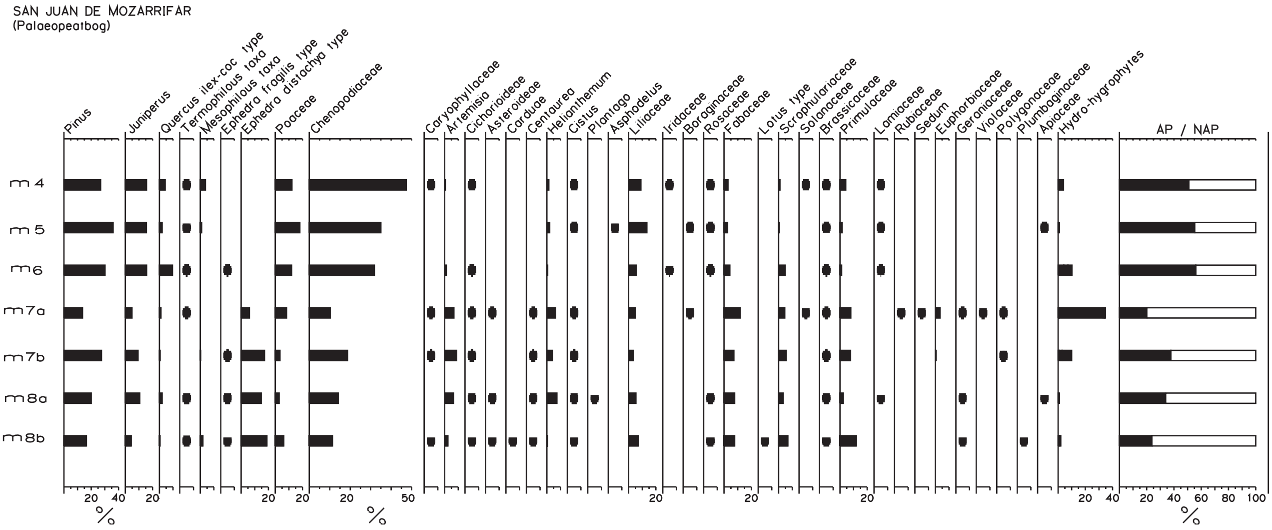

Fig. 8. Pollen diagram of the San Juan de Mozarrifar palaeo-peatbog.

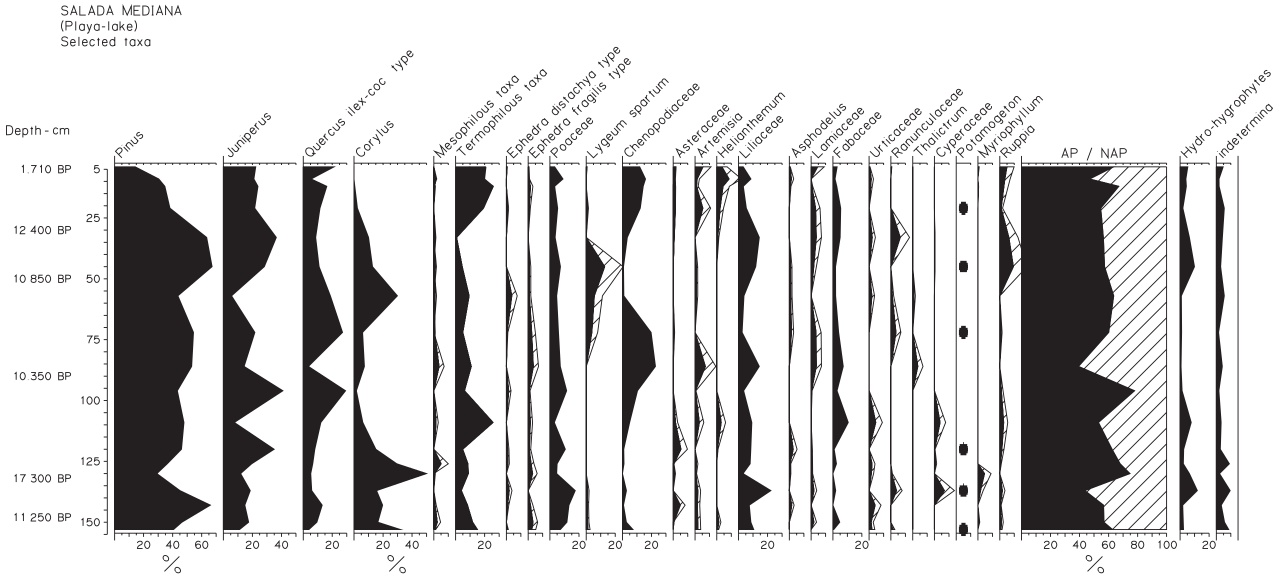

Fig. 9. Pollen diagram of selected taxa from Salada Mediana playa-lake.

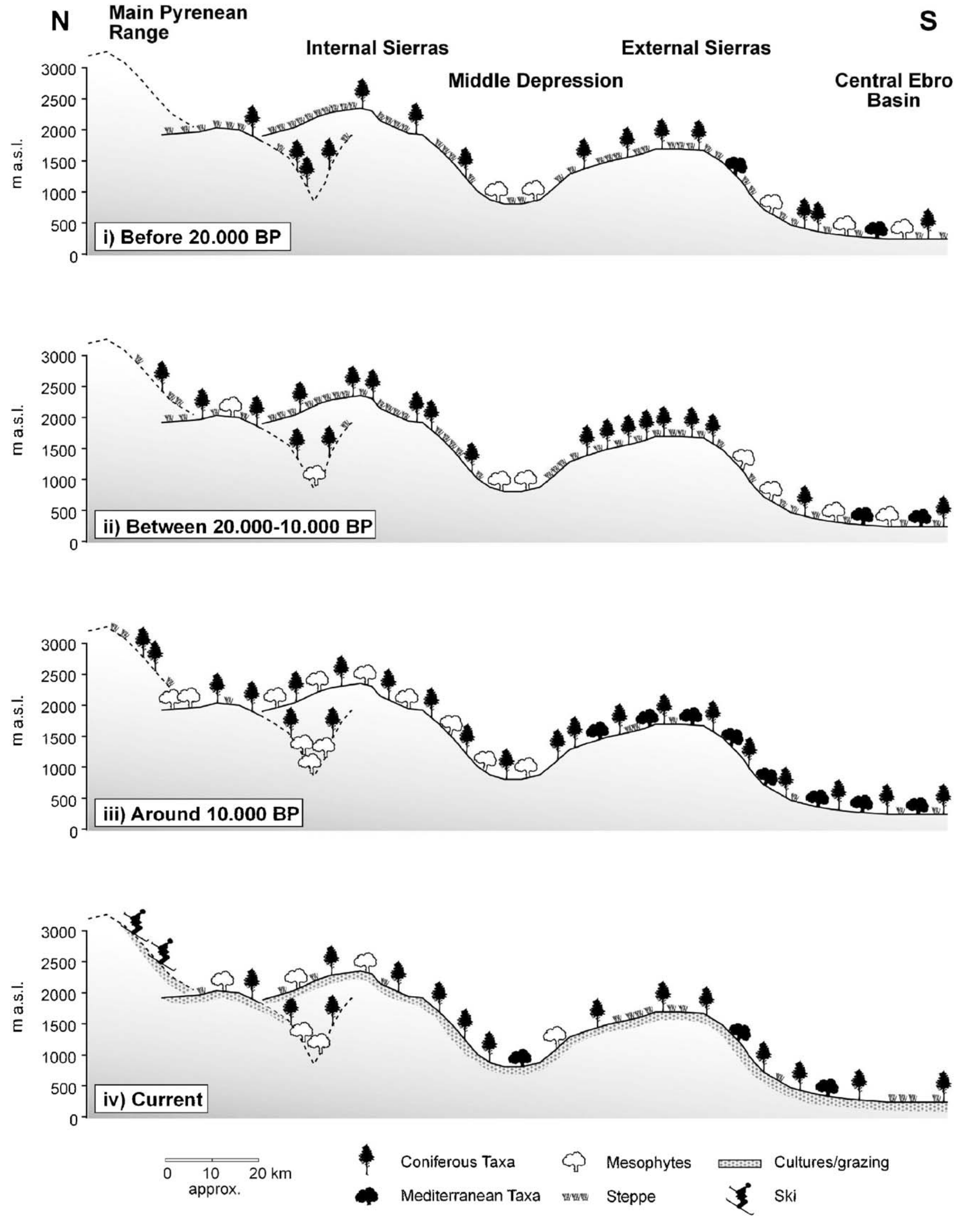

Fig. 10. Hypothetical reconstruction of a vegetation transect between the Pyrenees and the Central Ebro Valley: (i) before 20,000 yr BP, (ii) between 20,000–10,000 yr BP, (iii) around 10,000 yr BP and (iv) currently (present formations).

Chenopodiaceae are taken out of the total pollen sum), evergreen *Quercus* (25%) and other mesothermophilous taxa (20%). The overall aridity of the region is underlined by the abundance of conifers (*Pinus* 60%, *Juniperus* 30%), steppe herbaceous taxa and the fluctuating patterns of hydro-hygrophytes (*Potamogeton, Myriophyllum, Ruppia*) and chenopods (Fig. 9).

5. Discussion

The sequences described here provide new insights into several palaeoecological issues pertinent to glacial and Lateglacial vegetation history in northeastern Spain (Fig. 10). The palynological evidence supports the occurrence of Glacial refugia for temperate tree species in the Ebro Valley below 800 m a.s.l. Direct evidence for this comes from the records of *Abies, Pinus, Juniperus, Quercus* and other mesophilous taxa (*Betula, Corylus, Ulmus, Fagus*) in the coprolite pollen spectra of Gabasa Cave over ca 51,000–40,000 yr BP (Fig. 6). In addition, the mesophilous lowland site of Valmadrid shows the occurrence of evergreen *Quercus, Salix, Rhamnus, Juniperus* and *Pinus* around 17,100 yr BP (Fig. 5). The records at Gabasa are particularly useful because hyena coprolites can document the regional existence of species whose representation in pollen sequences from lacustrine basins is often obscured by over-representation of the local adjacent vegetation. This assertion is supported by taphonomical studies using pollen records from fresh hyena droppings in their modern vegetation context (Scott et al., 2003), and palaeoecological correlation of pollen spectra in hyena coprolites with reference pollen sequences from conventional sites (Carrión et al., 2001a).

The late Pleistocene records from Salada Mediana, Peña del Diablo, Peña 14, Bentué de Rasal and Linás de Broto provide further circumstantial evidence for the existence of local populations of evergreen and deciduous *Quercus, Betula, Salix, Ulmus, Acer, Fraxinus, Juglans, Castanea, Oleaceae, Buxus, Sambucus, Rhamnus* and *Ephedra fragilis* (Figs. 4, 5, 7 and 9). In spite of the caveats on its chronology (Valero-Garcés et al., 2000), it is clear that most of the Salada Mediana section below 25 cm-depth is from the Lateglacial age, if not older. The high frequencies of hazelnut pollen can be interpreted as the local existence of a gallery forest with prevailing *Corylus*, accompanied by other broadleaf

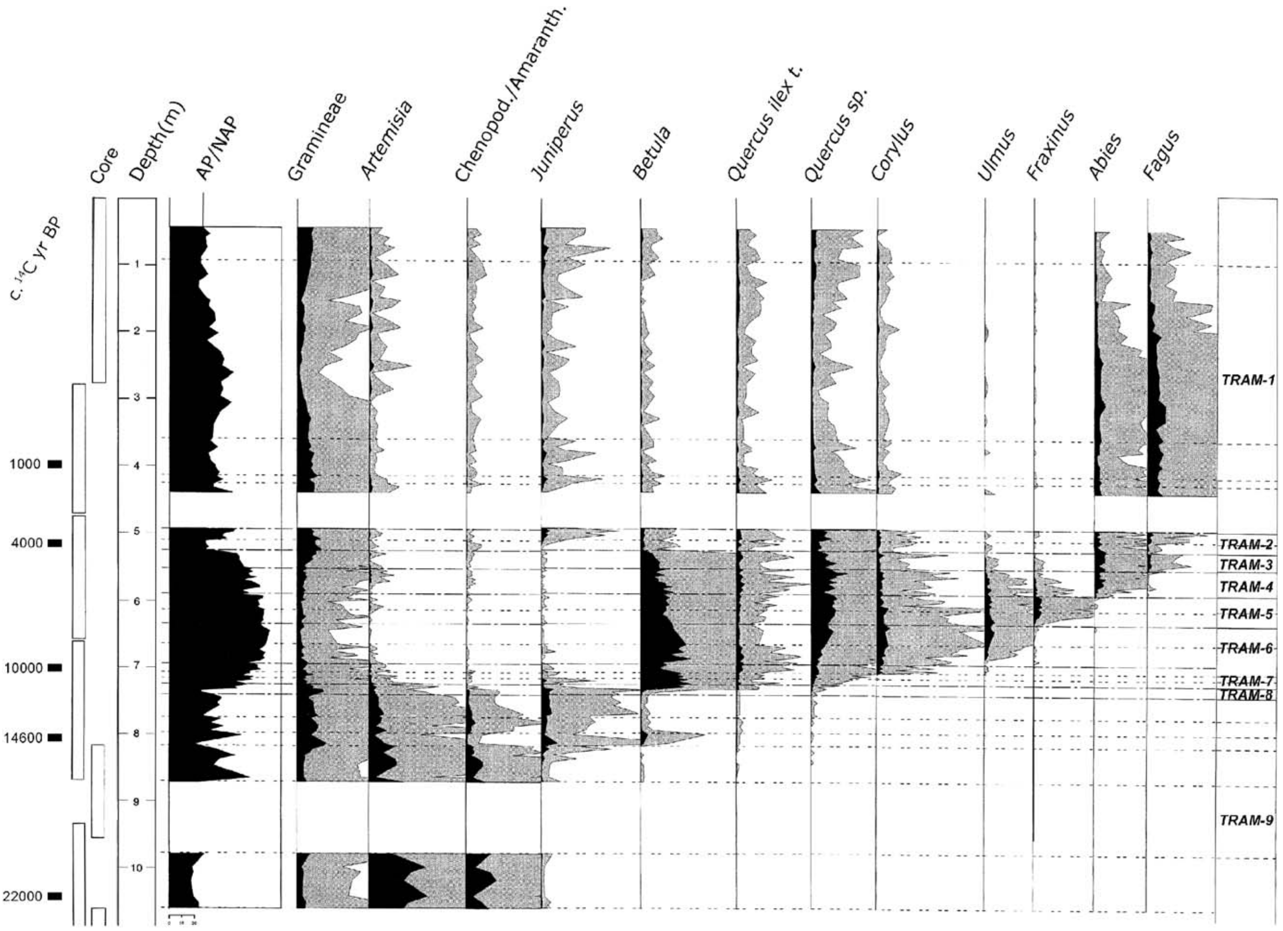

Fig. 11. Pollen diagram of Tramacastilla lake (Montserrat, 1992).

trees, which could have behaved as phreatophytes. The Ginel River and other tributaries of the Ebro basin provide a plausible scenario for tree survival under a regionally xeric climate.

Another striking feature of the Salada Mediana pollen diagram is its relatively high AP values (Fig. 9), at least in the context of present-day xeromorphic vegetation. But it is well worth mentioning the abundance of evergreen *Quercus* (10–20%), *Corylus* (10–40%), *Pinus* (30–60%) and *Juniperus* (10–25%). It is likely that this Lateglacial composition is connected with local occurrences of the species during former glacial periods, as in other southern European regions. A good example of this behaviour of temperate tree taxa during the Lateglacial is given by Willis (1994) in a complete study of the vegetation history of central and eastern Europe (Willis and van Andel, 2004).

In the Central Pyrenees, *Corylus* show two maxima, starting at 9000 and 8000 yr BP, with rapid and substantial increases (Reille, 1990; Jalut et al., 1992; Reille and Andrieu, 1995; González-Sampériz et al., 2001), as we can observe in the Tramacastilla lake record (Fig. 1, letter T and Fig. 11) (Montserrat, 1992). The proximity of refugia could certainly permit this rapid development (González-Sampériz, 2004). A regional signal of early Lateglacial development of *Quercus* is also noticeable southwards in the Ebro Delta pollen sequence, from before 11,000 yr BP (Fig. 1, letter D and Fig. 12) (Yll and Pérez-Obiol, 1992).

A related issue concerns the existence of primary and secondary centres of dispersal/migration. Brewer et al. (2002) maintain that primary refugia for deciduous oaks were situated only in the extreme south of the continent in areas able to sustain mesophilous species even during the cold Glacial periods. Secondary refugia would have been formed during the climatic variations of the Lateglacial period (13–11 ky) in areas able to sustain temperate populations during some shorter climatically adverse periods (e.g. the Younger Dryas). It is perhaps worth stressing that macroscopic charcoal from continental central Europe indicates that trees were present during the coldest intervals, such as the Last Glacial Maximum and Heinrich events (Willis et al., 2000; Stewart, 2003; Willis and van Andel, 2004), and something similar can be asserted for southern Portugal (Figueiral and Terral, 2002).

This study confirms that one of the main features of Lateglacial pollen records from the Iberian Peninsula is the great spatial heterogeneity of the vegetational landscapes (Dupré, 1988; Pons and Reille, 1988; Jalut et al., 1992; Montserrat, 1992; Pérez-Obiol and Julià, 1994; Allen et al., 1996; Ramil-Rego et al., 1998; Carrión et al., 1999, 2001a, b; Sánchez-Goñi and Hannon, 1999; Stevenson, 2000; Valero-Garcés et al., 2000; González-Sampériz et al., 2001; Muñoz-Sobrino et al., 2001; Carrión, 2002). Lateglacial and/or post-glacial colonisation by angiosperms is frequently observed, but cannot be considered the rule, as exceptions are prominent in Eastern Spain (Carrión and van Geel, 1999; Pantaleón-Cano et al., 2003; Yll et al., 2003) and Central Spain (Franco et al., 1998; Carrión et al., 2001b). But generally they show the recurrence of tree and shrub pollen taxa, thus favouring the idea of a complex network of Pleistocene refugia, even if these involved small-sized populations that eventually became clonal. It is likely that the general picture of long-distance migration may be due to the fragmentary character of databases rather than the exclusive maintenance of trees in the south.

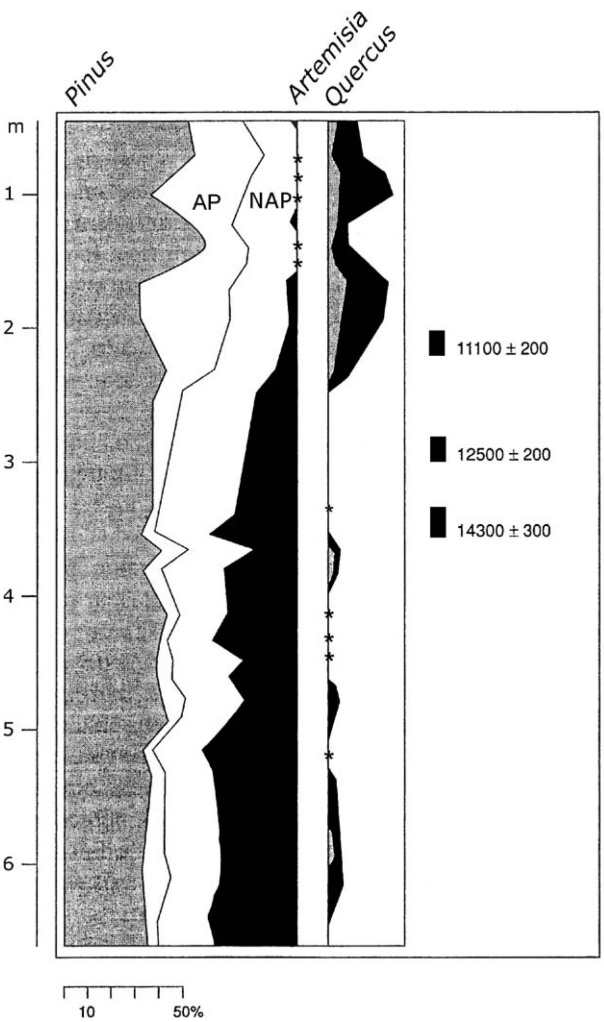

Fig. 12. Pollen diagram of Ebro Delta record (Yll and Pérez-Obiol, 1992).

This does not preclude the hypothesis of long-distance migration of European taxa being applicable to some species (Petit et al., 2002). Nor does it preclude that, in terms of both species diversity and population sizes, there were more Glacial refugia in southern latitudes of the Peninsula. So far, no single northern Iberian, Glacial or Lateglacial pollen site has shown the amounts and diversity of mesothermophilous pollen of meridional sites such as the mid-elevation Siles lake in the Segura Mountains (Carrión, 2002), the thermic sites of Perneras and Sima de las Palomas on the southeastern coast (Carrión et al., 1995, 2003), Cueva Negra, Cova Beneito and Navarrés in the inner meso-Mediterranean Levante (Carrión and Munuera, 1997; Carrión and van Geel, 1999; Carrión et al., 2003) or the well-known Padul pollen record in Granada (Pons and Reille, 1988). Tree taxa must have also survived more broadly along the northeastern coast of Spain during cold, Full-Glacial stages, as demonstrated by the Romaní pollen record near Barcelona (Fig. 1, letter A and Fig. 13), which shows tree pollen percentages of 40–60% between about 70,000 and 40,000 yr BP, with continuous presence of *Juniperus, Rhamnus, Quercus, Olea-Phillyrea, Alnus, Salix, Juglans, Betula, Fagus, Betula, Pistacia* and *Vitis* (Burjachs and Julià, 1994). This is also shown by the l'Arbreda pollen site in Girona, which shows a tree component dominated by pine and junipers with the presence of evergreen and deciduous *Quercus*, *Betula, Corylus, Alnus, Tilia, Buxus* and *Olea-Phillyrea* during Full-Glacial conditions (Burjachs, 1993). Finally, the Bañolas lake record (Fig. 1, letter B and Fig. 14) shows, as well as the nearby l'Arbreda site, a varied AP group formed by *Juniperus, Betula, Acer, Corylus,* deciduous and evergreen *Quercus, Tilia, Alnus, Ulmus, Salix, Olea, Buxus* and *Ephedra* among others in a pine-dominated pollen assemblage (Pérez-Obiol and Julià, 1994).

Although material from archaeological excavations and ongoing projects is available, there is no published charcoal analysis on Glacial or Lateglacial materials in the Ebro valley, unlike other regions (Cantabrian coast, Uzquiano, 1992).

All available data from the Ebro Valley (Davis, 1994; Burjachs et al., 1996; Valero-Garcés et al., 2000, 2004; González-Sampériz et al., 2003a), Cataluña (Yll and Pérez-Obiol, 1992; Burjachs and Julià, 1994; Pérez-Obiol and Julià, 1994) and the Pyrenees (Montserrat, 1992) show that northeastern Iberian landscapes were quite diverse during the Last Glacial and Lateglacial stages and included *Pinus* forests with or without junipers, *Juniperus*-dominated formations, mixed pine-oak forests, parklands, grasslands and xerophytic steppes. Studies on the spatial genetic structure of authochtonous pines (Agúndez et al., 1997; Salvador et al., 2000; Burban and Petit, 2003), oaks (Jiménez, 2000; Olalde et al., 2002; Petit et al., 2002), junipers

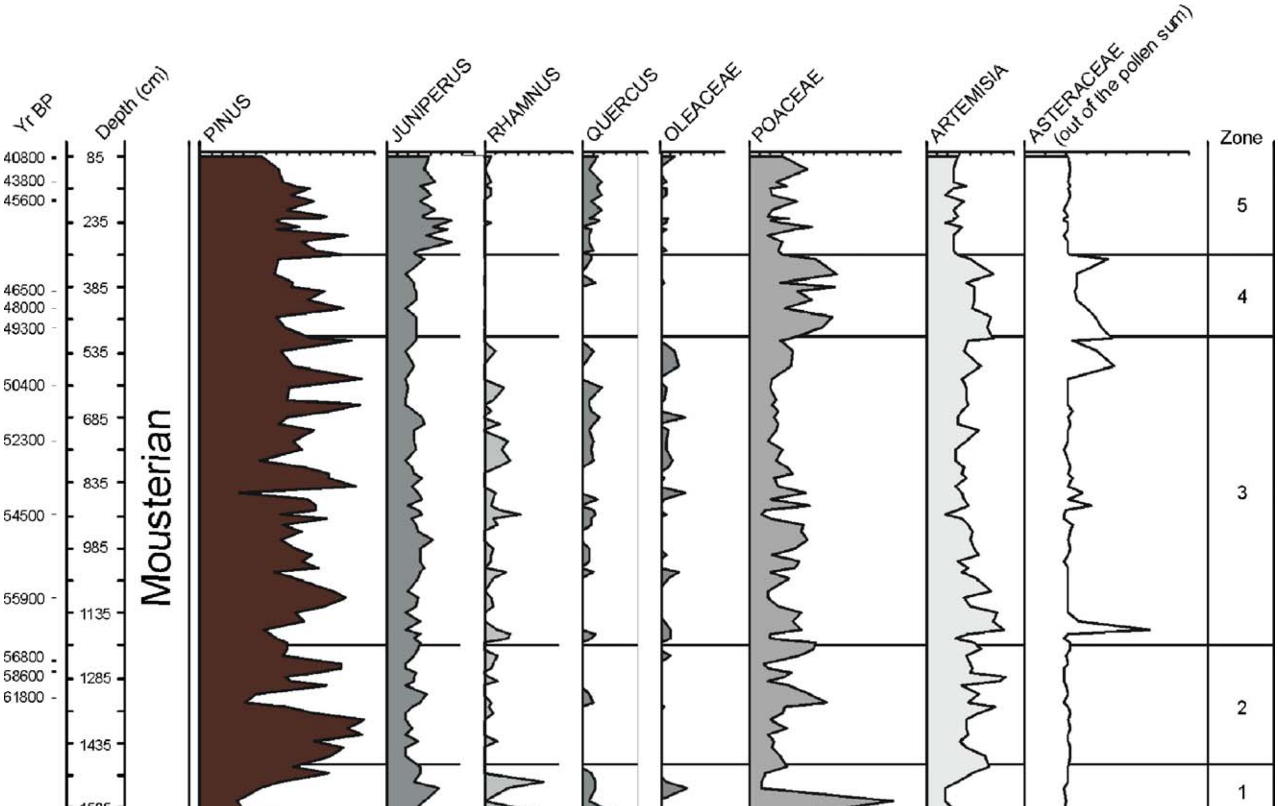

Fig. 13. Pollen diagram of Abric Romaní sequence (Burjachs and Julià, 1994).

(García et al., 1999; Jiménez et al., 2003) and other woody taxa (Besnard et al., 2002; Lumaret et al., 2004) further support this picture of biotope diversity during the Last Ice Age. This is also consistent with palaeoecological inferences from macrofaunal findings at several palaeontological sites (Table 1 and Fig. 1, letters AV, C, E and L and numbers 6 and 8).

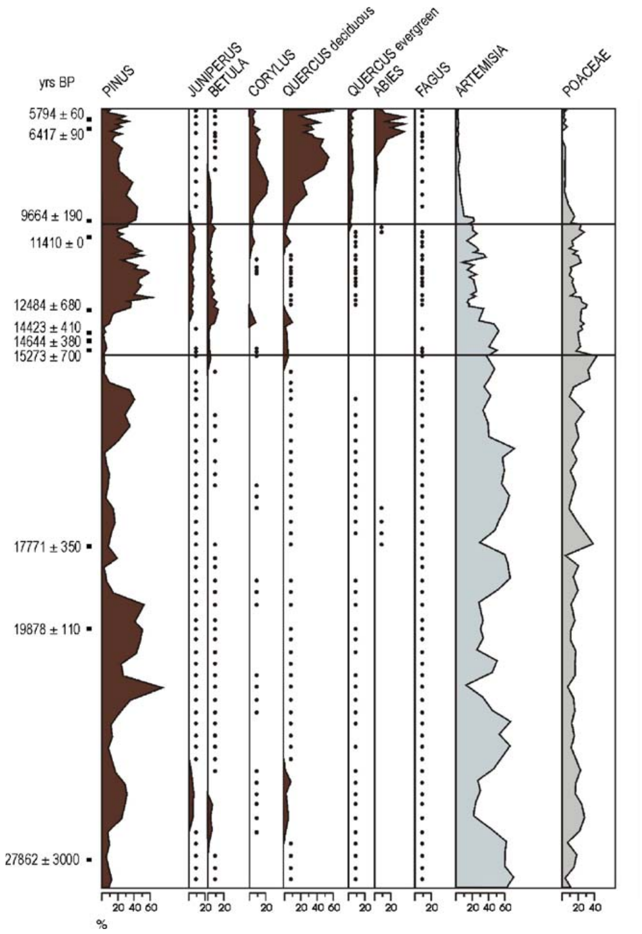

Fig. 14. Pollen diagram of Bañolas lake (Pérez-Obiol and Julià, 1994).

Apart from the well-known importance of *Pinus* forests in the Late Pleistocene and Holocene vegetation of continental and coastal Iberia (Peñalba, 1994; Sánchez-Goñi and Hannon, 1999; Jalut et al., 2000; Stevenson, 2000; Carrión, 2001, 2002; Carrión et al., 2001b; Franco-Múgica et al., 2001), the abundance of *Juniperus* at Glacial sites such as Portalet, Gabasa and Linás de Broto (Figs. 2, 4 and 6), and at the Lateglacial Salada Mediana, Peña del Diablo and Bentué de Rasal (Figs. 5, 7and 9) is worth stressing This extraordinary abundance could explain the origin of the modern *J. thurifera* populations in the Ebro Valley and adjacent highlands and plateaux (Blanco et al., 1997). Nevertheless, it is not unlikely that current distribution results partially from Late-Holocene expansions owing to aridification, as in the south-central (Carrión et al., 2001b) and south-eastern (Carrión et al., 2004a) plateaux of the Iberian Peninsula.

Finally, another topic of palaeoecological interest deals with the composition of herbaceous communities. It is generally accepted that, over the continent, most Glacial steppes were simply dominated by some sort of combination of a monotonous assemblage of Poaceae, *Artemisia*, Chenopodiaceae and *Ephedra,* with the eventual contribution of composites. However, Glacial pollen diagrams from this study and other sites in Mediterranean Spain (Dupré, 1988; Carrión, 1992a, b, 2002; Carrión and van Geel, 1999; Carrión et al., 2003; Pantaleón-Cano et al., 2003) indicate that Glacial flora were very diverse. The pollen records obtained from coprolites (Fig. 6) (Carrión et al., 2001a, 2004b;

Table 1
Macrofaunal remains of Ebro Valley Archaeological sites (NE Spain)

Site name	Macrofaunal remains	Palaeoenvironment
Gabasa mousterian cave (Blasco, 1995)	*Ursus spelaeus, Crocuta crocuta spelaea, Panthera pardus, spelaea* and *leo, Lynx spelaea, Dicerorhinus, Equus caballus* and *hydruntinus, Sus scropha, Cervus elaphus, Capreolus capreolus, Rupicapra rupicapra, Capra pyrenaica,* Bovidae, *Canis lupus, Vulpes vulpes, Cuon alpinus, Felis silvestris, Meles meles, Mustela putorius, Oryctolagus cuniculus* and *Lepus* sp.	Mosaic landscape with: grasslands woodlands shrubland-savanna steppes
Eudoviges mousterian rockshelter (Montes, 1988)	*E. caballus, Dicerorhinus* and *Dama dama*	Grasslands shrubland-savanna
Chaves magdalenian cave (Castaños, 1993)	*C. Pyrenaica, C. elaphus,* Bovidae, *R. rupicapra, S. scrofa, L. pardina, Lepus* sp. and *O. cuniculus*	Grasslands forested areas shrubland-savanna
Abrigo Vergara and Peña del Diablo magdalenian rockshelter (Utrilla et al., 2000)	*E. caballus* and *C. elaphus*	Grasslands forested areas
Legunova magdalenian rockshelter (Montes, pers.comm.)	*E. caballus*	Grasslands

González-Sampériz et al., 2003b) strongly support the broad biodiversity of Glacial steppes. A methodological limitation is that NAP types cannot normally be distinguished below the family level (e.g. Fabaceae, Caryophyllaceae, Campanulaceae, Liliaceae, Apiaceae, Lamiaceae, Dipsacaceae).

6. Final remarks

The complexity of Glacial and Lateglacial landscapes in the Ebro Basin can be explained by the geographic and climatic heterogeneity between the Pyrenean Range and the Ebro River Valley. The Ebro River valley was influenced from before 30,000 yr BP by meltwater discharge from the mountain areas (González-Sampériz et al., 2003a; Valero-Garcés et al., 2004). Early deglaciation in the Pyrenees provided, unlike present day conditions, more moisture availability in the Ebro valley and contributed to a complex palaeoenvironment mosaic with a big thermal contrast and large palaeohydrological fluctuations (González-Sampériz, 2004). The result was probably a patched landscape, with some treeless areas and other areas with Mediterranean shrubs, coniferous forests and refuges of mesophilous and thermophilous vegetation.

The palaeoenvironmental picture depicted by the network of pollen diagrams from Iberia for Glacial and Lateglacial times remains controversial as we gain information. This study confirms the variety of vegetational responses to climatic changes over a period that covers part of the last climatic cycle of the Quaternary. General features include (i) the abundance of steppe taxa (*Artemisia*, Poaceae, Chenopodiaceae, *Ephedra*, Asteraceae and many others) during cold, arid episodes, (ii) the continuous occurrence of a diversity of arboreal taxa even at high areas, (iii) their expansion during Lateglacial and Holocene ameliorations and (iv) the survival of mesothermophytes in small (northern and central Peninsula) and large (south, coast, intra-mountain valleys) areas. Finally, comparison of the pollen records shows the paramount importance of *Pinus* in the Glacial vegetation types of Iberia, regardless of altitude and latitude.

Acknowledgements

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