

Was the Ebro valley a glacial refugium for temperate trees?

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Resumen

¿Era el Valle del Ebro un refugio glacial de árboles templados?

Se presentan los resultados del análisis polínico de la Salada Mediana, una secuencia tardiglacial situada en el sector central del Valle del Ebro (NE de la Península Ibérica). El registro polínico muestra la abundancia de *Corylus avellana* y *Quercus perennifolia*, junto a la presencia de otras especies arbóreas. En vista de la importancia y rapidez de la colonización tardiglacial, se sugiere que, debido a la disponibilidad hídrica edáfica, el valle fue un refugio glacial para especies termófilas durante la última glaciación.

Palabras clave: Paleoecología, Palinología, Biogeografía, Refugios glaciales, España.

Abstract

We present pollen-analytical results from lateglacial Salada Mediana, a playa-lake in central Ebro Valley, semi-arid northeastern Spain. The pollen record shows abundant *Corylus avellana* and evergreen *Quercus*, together with the occurrence of other tree species. In view of the importance and rapidity of lateglacial colonisation, it is suggested that, due to local edaphic moisture availability, the valley was a glacial refugium for temperate trees during the last ice age.

Key words: Palaeoecology, Palynology, Biogeography, Glacial Refugia, Spain.

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Introduction

The location of glacial refugia of European temperate tree species has been a devoted subject of investigation over the last decades. Largely, this includes the production of Quaternary palaeoecological sequences (Bennett et al. 1991, Willis 1994, Leroy et al. 1996, Follieri et al. 1998, Allen & Huntley 2000, Tzedakis et al. 2002) and phylogeographical models based on genetic structure of current populations (Taberlet et al. 1998, Hewitt 1999, Petit et al. 2002).

More than ten years ago, Bennett et al. (1991) augured that, while the Iberian peninsula might have

not been such an important refugial area as the Italian and Balkan peninsulas, this situation could change as new data were acquired. Now, that we are gaining information, a new picture is emerging in which Iberia represents a crucial phytodiversity reservoir of mesothermophilous trees and shrubs during the last ice age (Carrión 2002, Olalde et al. 2002, Carrión et al. 2003).

Due to the scarcity of full-glacial palaeobotanical records, an useful approach to locate glacial refugia can be obtained by using lateglacial pollen records that show relatively rapid responses of vegetation to deglaciation. Lateglacial rather than postglacial colonisation was long ago recognizable in the

continental Andalusian site of Padul (Pons & Reille 1988), and has been now made clear in mid altitudes of the eastern Betic Mountains (Carrión 2002). However, this phenomenon is not exclusive from southern latitudes and, at least for *Corylus* and *Quercus*, can be perceived in continental pollen sequences of the Pyrenees (Jalut et al. 1992, Montserrat 1992), pre-Pyrenees (Pérez-Obiol & Julià 1994), Iberian system and Meseta (Peñalba 1994, Stevenson 2000).

Palynological findings join to studies of fossil macrocharcoal (Uzquiano 1992) and palaeontological data to support the idea by Peñalba (1994) that northern Iberia was covered by a patched network of tree populations during the last glacial age (Carrión et al. 2003). Although the hypothesis of long-distance migration of European taxa may be applicable for some species (Petit et al. 2002), it is yet possible that this picture have rather arisen from the fragmentary character of databases (Brewer et al. 2002) than from the exclusive maintenance of trees in the south.

Another crucial issue deals with altitudinal location. More or less explicitly, most commentators tend to accept Bennett et al. (1991)'s postulation that refugia would have occurred principally in mid-altitude mountain positions (Tzedakis 1994, Willis 1994, Tzedakis et al. 1997, 2002) and nearby the sea (Turner & Hannon 1988, Brewer et al. 2002, Carrión et al. 2003), especially where local topography permitted rapid altitudinal displacements as response to climatic changes. Given the physiography of Iberia, this may well be the case for most of the region, but we should keep the model open to new findings.

Here we bring new data to this debate. The Salada Mediana pollen record shows abundant *Corylus avellana* and evergreen *Quercus*, together with the occurrence of other tree species during the Lateglacial and Early Holocene. The significance of these findings rely on the geographic, topographic, and climatic features of the study site. The Salada Mediana lies within the central Ebro Valley in the northeastern plain of Iberia under a semi-arid climatic regime. From a neontological perspective, a region indeed hardly conceivable as suitable refugium for mesophilous woods.

Physical Setting

The Salada Mediana (41° 30' 10" N, 0° 44' W, 350 m a.s.l.) is a playa-lake lying in the Ebro River Basin (Fig. 1), within the northernmost European region with semi-arid climate. The basin is surrounded by the Pyrenees to the north, the Iberian Range to the southwest and the Catalanian Ranges to the east

(Gutiérrez & Peña 1994). The climate is continental Mediterranean with hot summers, cold dry winters, low annual rainfall (ca. 300 mm) and mean temperatures of 24.2°C and 6.4°C in July (warmest month) and January (coldest month) respectively (Cuadrat 1999).

Climatic aridity and local endorheism have favoured the development of small saline lakes like Salada Mediana. Most are ephemeral playa-lake systems associated to karstic or aeolian processes on Tertiary evaporitic units. Locally, the margins of Salada Mediana playa-lake are covered by halophytic plant communities. Regional landscape is steppic, with vegetation cover below 50% (Braun-Blanquet & de Bolòs 1957), although it has been traditionally cultivated. Open forest stands of *Pinus halepensis*, *Quercus coccifera* and *Juniperus thurifera* interrupt this steppic landscape, while deciduous trees are mainly restricted to inaccessible gorges. Relictic *Corylus* can be only found in the north-western but not in the central areas of the Ebro Valley (Blanco et al. 1997).

Methods

Two 165-cm long sediment cores were raised with a modified Livingstone corer in the summer of 1996 when the playa-lake was dry. Sedimentary facies were identified based on colour, lithology and sedimentological structures. One long core was photographed, described and sampled for pollen analysis, organic matter and carbonate content. Isotopic composition of cyanobacterial mats and halophytic plants have been studied previously (Valero-Garcés et al. 2000a, b).

Pollen grains and spores were extracted in the laboratory by the classic chemical method (Moore et al. 1991) using Thoulet liquid for palynomorph concentration (Dupré 1992) and *Lycopodium clavatum* spore tablets (Stockmarr 1971) to calculate pollen concentration. A pollen diagram was constructed using Tilia, TiliaGraph and CorelDraw software. Chronological control is based on six AMS ¹⁴C dates (Table 1) from pollen concentrates (Valero-Garcés et al. 2000a).

Results and Discussion

In spite of the caveats of the Salada Mediana chronology, it is clear that most of the sequence below 25 cm depth is of lateglacial age (Middle and Lower sections of the core). A combination of several factors may account for the age inversions. The $\delta^{13}\text{C}$ values (around -25‰ PDB) do not indicate any significant

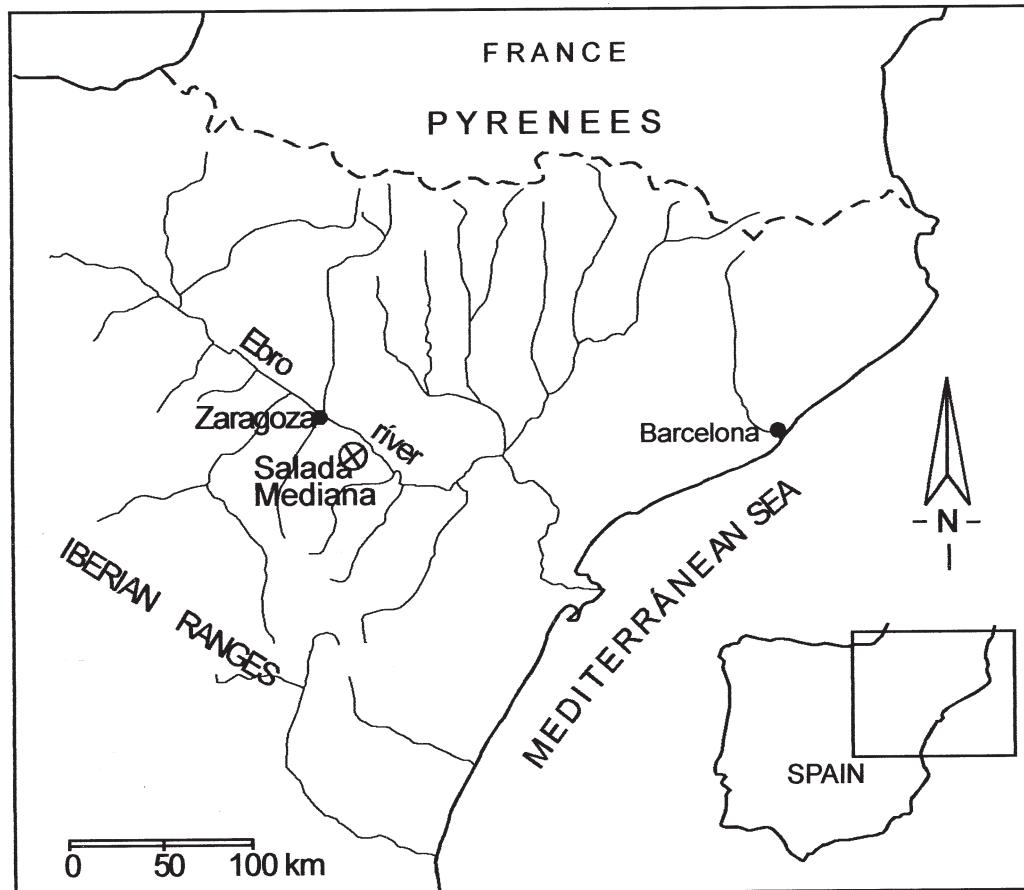


Figure 1. Location map of Salada Mediana in northeastern Spain (Ebro Basin).

Depth (cm)	Material	Weight (mg)	^{14}C yr B.P.	Lab number
4.5-5.5	Pollen	27.23	1710 ± 35	OS-16717
28-29.5	Pollen	0.97	$12,400 \pm 110$	NSRL-10586
50-51	Pollen	3.3	$10,850 \pm 200$	OS-14932
89.5-91	Pollen	0.64	$10,350 \pm 65$	OS-22658
132-135.5	Pollen	0.94	$17,300 \pm 130$	NRSL-10588
146.5-148	Pollen	0.89	$11,250 \pm 60$	NRSL-10589

Table 1. AMS ^{14}C dates of Salada Mediana sediment core (Valero-Garcés et al. 2000a).

presence of lacustrine organic matter in the dated samples and pollen and sedimentological data do not suggest significant reworking and contamination by old detrital carbon in these levels. However, a reservoir effect cannot be ruled out completely in some samples (Valero-Garcés et al. 2000a). The reservoir effect is not constant for a specific lake, and it depends on water level (Geyh et al. 1998). The date of $17,300 \pm 130$ ^{14}C yr B.P. at 132-135.5 cm depth

could be affected by hard-water effect due to the presence of aquatic pollen (*Myriophyllum*) in the sample. In spite of the chronological uncertainties, the study suggest a Lateglacial sequence and a historic section (up to 25 cm depth) with a long hiatus between (Valero-Garcés et al. 2000a).

A striking feature of the Salada Mediana pollen diagram is the relatively high AP values (Fig. 2), at least if the reconstructed vegetation is compared with

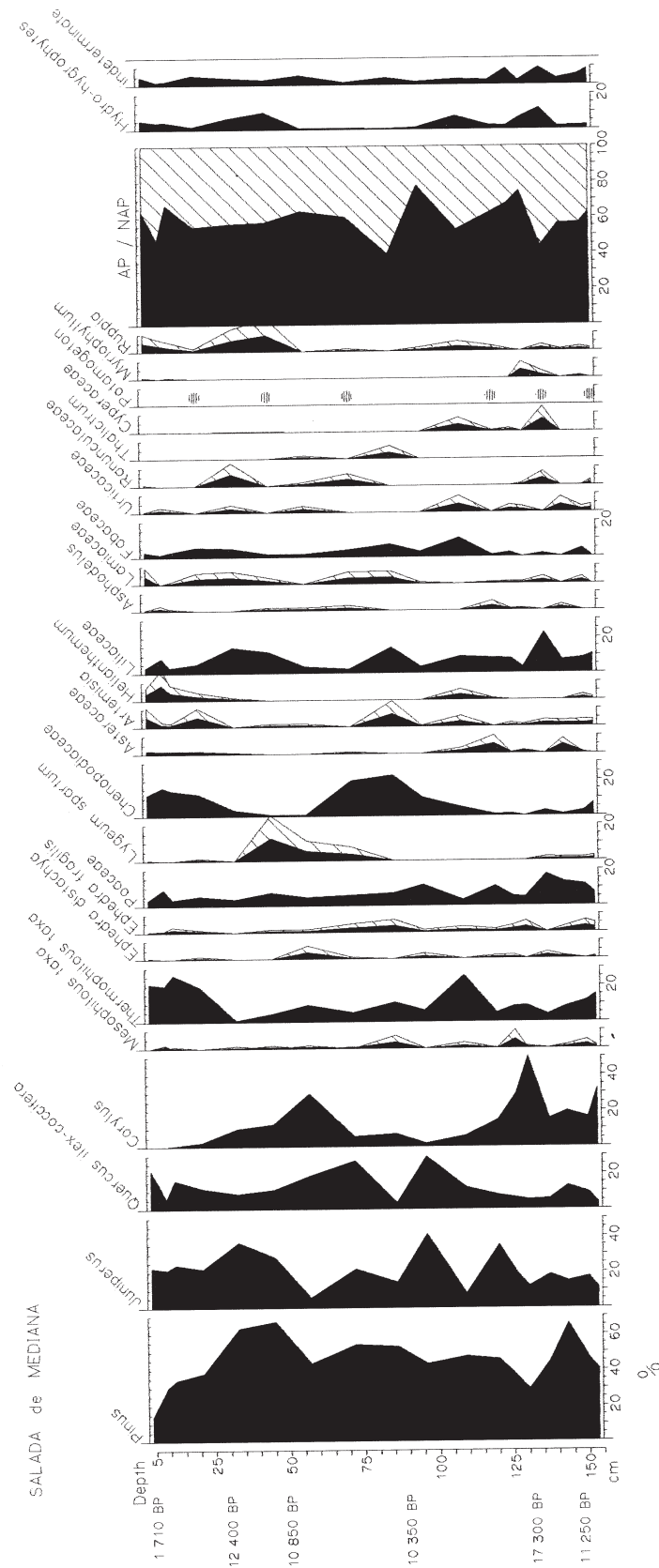


Figure 2. Pollen diagram of Salada Mediana with most representative taxa. *Pinus* and *Chenopodiaceae* have been excluded from the pollen sum and the calculation of the rest of taxa percentages. Mesophilous taxa are integrated by *Quercus faginea* type, *Betula*, *Alnus*, *Salix*, *Ulmus* and *Juglans*. Thermophilous taxa are integrated by *Olea-Phyllirea*, *Pistacia*, *Rhamnus*, *Myrtus*, *Cerantonia* and *Tamarix*.

the present-day steppic situation. In the diagram we can observe the percentages representation starting from a pollen sum without *Pinus* and Chenopodiaceae. It is particularly worth mentioning the abundance of evergreen *Quercus* (10-20%), *Corylus* (10-40%), *Pinus* (30-60%; out of pollen sum), and *Juniperus* (10-25%). An overall xeric continental vegetation can be envisaged from the abundance of pines and junipers, together with the xerophytes *Ephedra fragilis* type, *Ephedra distachya* type, *Artemisia* and *Lygeum spartum*, and the constant occurrence of Lamiaceae, Asteraceae and *Asphodelus*. The abundance of chenopod pollen may be rather related with the very halomorphic nature of study basin soils. In fact, fluctuations in Chenopodiaceae pollen correlate water level variations (Valero-Garcés et al. 2000a) and do so oppositely to pollen of aquatic angiosperms (*Ruppia*, *Potamogeton*, *Myriophyllum*). It can be also significant in terms of climatic dynamics the fact these fluctuations alternate with *Corylus* peaks.

The high pollen percentages of hazelnut may well signify the local existence of a gallery forest with prevailing *Corylus* (Huntley & Birks 1983), accompanied by *Alnus*, *Betula*, *Salix*, *Ulmus*, *Juglans*, and deciduous *Quercus* (Valero-Garcés et al. 2000a), which could have behaved as phreatophytes. Since pollen analysis is not particularly well suited to determine species area, the possibility that these pollen spectra derive partially from extralocal sources cannot be discarded. Either the case, the presented pollen records for *Corylus* are outstanding because the modern distribution of hazelnut is quite restricted in Mediterranean Iberia, being mainly associated to humid gorges.

Broadly geographically, the change from glacial to holocene conditions involves a series of rapid changes in temperature and moisture availability (Walker 1995, Isarin & Renssen 1999), influenced in some regions of southern Europe by water inputs proceeding from deglaciation in mountain areas (González-Sampérez et al. 2002, Valero-Garcés et al. in press). During the Lateglacial, a rapid increase of temperatures of 8°C and 20°C in summer and winter, respectively, is suggested by European fossil proxy data (Walker 1995). These temperatures were semi-equivalent to the modern day, although displaying more seasonal differences (Montserrat 1992) and influenced in some areas next to glaciated mountains by water inputs due to deglaciation effects. Synchronous hydrological and vegetation changes during the Lateglacial in the central Ebro Basin have been observed in several palaeoecological sequences of the Lateglacial

(Valero-Garcés et al. 2000a, in press, González-Sampérez et al. 2002).

After approximately 10 ky B.P., there was a shift in the climate from cold, dry conditions to warmer (Huntley & Prentice 1993) due to a shift northwards of the Polar Front to 65°N (Ruddiman & McIntyre 1981). The result was an increase in summer insolation and moisture availability across Europe in the beginning of the Holocene: an optimal period for the expansion of mesophilous tree species. In the central Pyrenees, *Corylus* shows two maxima starting at 9 and 8 ky B.P., with rapid and substantial increases (Jalut et al. 1992, Montserrat 1992, González-Sampérez et al. 2000, 2001, 2002). The proximity of refugia could certainly permit this rapid development. A regional signal of lateglacial developments of *Quercus* is noticeable in the Delta del Ebro pollen sequence (Yll & Pérez Obiol 1992).

An important issue to be addressed for the Iberian Peninsula relates to 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 south extreme 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 glacial-interglacial period (13-11 ky B.P.) 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). Interestingly, this involved a diversity of habitats, including open, montane and coniferous environments.

Lateglacial pollen records of the Iberian Peninsula offer a picture of great spatial heterogeneity in landscapes and inferred values of moisture availability (Stevenson 1984, 2000, Dupré 1988, Pons & Reille 1988, Jalut et al. 1992, Montserrat 1992, Pérez-Obiol & Julià 1994, Allen et al. 1996, Carrión et al. 1999, 2000, 2001, Sánchez-Goñi & Hannon 1999, Valero-Garcés et al. 2000a, Muñoz et al. 2001, Carrión 2002, González-Sampérez et al. 2002). Lateglacial and/or postglacial colonisation by angiosperms is frequently observed, but cannot be considered a rule, as exceptions are prominent in Levante (Carrión & van Geel 1999) and the Meseta (Franco et al. 2001). But generally they show the recurrence of tree and shrub pollen taxa, thus favouring the notion of a complex network of last glacial refugia, even if these involved small-sized populations eventually clonal.

Conclusions

We conclude that the Ebro Valley, a currently semi-arid, plain, and continental area, seems to have represented a glacial refugium for *Corylus* and *Quercus* during the last ice age, although this will only be categorically demonstrated when there are available full-glacial palaeobotanical records. In the context of the presented results, we can uniquely maintain that, if refugia were not local, they were very close to the study site. The Ginel watercourse and other tributaries of the Ebro basin provide a plausible scenario for tree survival under a regionally cold and dry climate. Plausibly, the expansion of *Corylus* in the Pyrenees and Iberian Range was limited in altitude by low temperatures. This scenario could be well extrapolated to other territories of northern and central Iberia. Local moisture availability and topographic variability along rivers, humid gorges and endorheic areas would have facilitated the survival of mesothermophilous tree species in glacial times if the limiting factor had been moisture availability instead of temperature.

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