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A SOUTHERN REFUGIUM FOR TEMPERATE TREE SPECIES IN THE MEDITERRANEAN MOUNTAINS OF EL PORT MASSIF (NE IBERIA): CHARCOAL ANALYSIS AT COVA DEL VIDRE

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Abstract

This study focuses on the analysis of wood charcoal from Cova del Vidre (Roquetes, Tarragona, Spain). This cave, located at an altitude of 1,000 m a.s.l., is a key site for understanding the transition from hunting and gathering to farming in a mountainous region of north-eastern Iberia so far unexplored by archaeobotany. The anthracological study is based on four archaeological levels from the Epipalaeolithic to the Early Neolithic dated between 12.9 and 6.8 kyr cal BP, i.e. from the Late Glacial period to the Middle Holocene. During the Younger Dryas, the record is dominated by a little varied spectrum of cryophilous pines (*Pinus* tp. *sylvestris*) and thorny shrubs revealing an open landscape where *Prunus* may prefigure the spread of temperate taxa. In the Early Holocene, a significant change in temperature and precipitation is evidenced, which promoted successional changes in plant communities, with a decline of pine and the sudden rise of temperate/Mediterranean taxa, such as *Prunus* and *Quercus coccifera/ilex*. During the Middle Holocene, other temperate taxa appear, such as *Quercus* deciduous, *Buxus sempervirens* and *Taxus baccata*, with yew finally dominating the anthracological record. The appearance and early development of temperate or Mediterranean species as early as the Younger Dryas and the Early Holocene periods, in a mountain context that had long been favourable for Scots pine, allows us to argue the local existence of a glacial refugium. Differences with the nearby sites in the lowlands demonstrate that altitudinal differences in vegetation were already established in the Holocene. Furthermore, the site helps to define the palaeodistribution of *Taxus baccata* and *Fagus sylvatica* in southern Europe.

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1. INTRODUCTION

A gradual succession of plant communities occurred in the western Mediterranean during the Late Glacial period and Early to Middle Holocene. The global warming trend had a significant impact on vegetation cover, increasing biodiversity and affecting the geographical distribution of existing species. Pollen records from lakes and peat bogs generally provide a regional view of plant landscape transformations (Miras et al., 2007; Vegas et al., 2009; Ejarque et al., 2010; Pérez-Obiol et al., 2012; Cunill et al., 2013; Pérez-Sanz et al., 2013; Aranbarri et al., 2014; Revelles et al., 2015). Wood charcoal analyses at archaeological sites supply good local indicators, as wood was collected in the vicinity of the settlements, providing evidence of the woody species and plant communities present in their surroundings (Chabal, 1997; Heinz and Thiébault, 1998; Chabal et al., 1999; Piqué, 1999; Allué, 2002; Chabal and Heinz, 2021). Furthermore, the implementation of wood charcoal analysis in archaeological sequences provides diachronic information on forest management by prehistoric groups. The archaeological record at Cova del Vidre, containing successive Epipalaeolithic, Mesolithic and Neolithic occupations, allows us to understand the local evolution of the vegetal landscape and its human exploitation in the southern mountains of north-eastern Iberia. It reveals the importance of this montane environment as a key region for understanding the southern limit of the palaeodistribution of some important European forest species such as yew (*Taxus baccata*) and beech (*Fagus sylvatica*).

2. ARCHAEOLOGICAL AND BIOGEOGRAPHICAL CONTEXT

2.1. Archaeological background

The Ebro valley is a key region for understanding the Epipalaeolithic-Neolithic transition in north-eastern Iberia. South of the Ebro River, human settlements extended from the coast and inland plains of the Ebro Delta and the Bajo Aragón to the Maestrazgo and El Port mountains (Bosch, 1989; 2001; 2015; Mazo and Montes, 1992; Bosch et al., 1996; Utrilla et al., 2009; 2017; Utrilla and Bea Martínez, 2012; Laborda 2019) (Figure 1). This location allowed the management of different biotopes: forests for hunting, gathering, and wood supply, and the plains for agriculture and livestock breeding since the beginning of the Neolithic.

The late hunter-gatherers of the western Mediterranean benefited from abundant, reliable, and seasonal resources derived from climate improvement at the end of the Last Glacial Period (Gramsch, 1981; Thévenin, 1981). Indeed, the beginning of the Neolithic in north-eastern Iberia around 7.8-7.5 cal kyr BP brought about a radical change in the relationship between human groups and the environment, due to new needs related to the stability of settlements linked to crops and livestock management (Antolín et al., 2015; 2018; Revelles, 2017), as well as the beginning of the anthropic disturbance of the Mediterranean ecosystems (Roberts et al., 2011).

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2.2. Biogeographical setting

The Cova del Vidre cave (Roquetes, Tarragona) is a habitat located around 1,000 m a.s.l. in El Port massif (Tortosa-Beceite), a mountain environment in the southern Catalan Pre-Coastal Ranges connected to the Iberian Range (NE Iberia). Rugged Mesozoic limestone lithology results in steep local relief with pronounced slopes and deep ravines. The highest altitude is reached in the Caro Mountain (1,447 m a.s.l.) while the Mediterranean Sea is located less than 50 km from the site. The mouth of the cave, facing east-northeast, offers a wide panoramic view including the Lower Ebro Basin and the Ebro Delta (Bosch, 2015; 2016).

The current vegetation in this massif is unique, as if it were an island of vegetation. The high diversity of ecosystems and biotopes results from the transition between the Mediterranean coastal and continental mountain climates, shaped by the complexity of the orography (Senar Lluch, 2011). Above 1,000 m a.s.l., a sub-humid or even humid climate enables the presence of Supramediterranean forests mainly formed by Scots (*Pinus sylvestris* L.) and Salzmann pines (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco) and Portuguese (*Quercus faginea* Lam.) and Pyrenean oaks (*Quercus pyrenaica* Willd.), occasionally accompanied by yew (*Taxus baccata* L.), holly (*Ilex aquifolium* L.) and even beech (*Fagus sylvatica* L.).

Patches of Mediterranean yew trees grow in isolation in search of shady places in ravines and valleys and inside forests of pine, beech and holm oak (Costa et al., 2001). Locally the yew can dominate dense understorey layers of boxwood (*Buxus sempervirens* L.), as in the case of some calcareous cliffs in the Maestrazgo (Camprodon et al., 2014). Small beech forests grow in the Vallcaneres ravine around 1,200 m a.s.l., interspersed with pine forests, occupying the shady areas at the foot of the cliffs and the stream banks, where the water deficit of the Mediterranean climate is balanced. They grow besides Mesomediterranean or Supramediterranean shrubs such as boxwood and various Rosaceae such as *Amelanchier ovalis* Medik., *Crataegus monogyna* Jacq., *Rosa canina* L. and *Rubus ulmifolius* Schott (Costa et al., 2001). These small populations constitute the southernmost beech forest in Europe, representing the climatic tolerance limit of the European beech.

2.3. Site description

Cova del Vidre consists of a main cave with a surface area of 43x30 m and 14 m high, and a smaller chamber next to it, to the north, 15x11 m in size and 2 m high. The entrances of both caves face east-northeast (Figure 1). In the main cave, longitudinal joints are frequent, including a zenithal one that allows water to enter the cave without flooding it, thus contributing to its habitability (Bosch, 2001; 2015; 2016).

The presence of prehistoric occupations at Cova del Vidre has been known since the 19th century. Archaeological work undertaken in the 1940s revealed the existence of a stratified archaeological sequence ranging from the late Upper Palaeolithic to the Early Neolithic. More recent archaeological excavations, conducted by J. Bosch's team in 1992, accomplished the absolute radiocarbon dating of the occupations in the cave (Bosch,

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2001). Systematic sampling of archaeozoological, archaeobotanical and sedimentary materials was also performed at the site to obtain palaeoenvironmental and palaeoeconomic information. Two main excavation areas were sampled in the large cave. The inner area (named *int*) in the deepest part of the cave and the central area (named *cent*) in the middle part (very close to the small cave) provided two complementary stratigraphic sequences (Bosch, 2015; 2016).

2.4. Archaeological sequence

At Cova del Vidre, four main human occupations have been documented (Bosh, 2001, 2015; 2016) in accordance with the cultural processes known in the region (Soto et al., 2015; Oms et al., 2018). Three of them are related to late Pleistocene and early Holocene hunter-gatherer occupation (Epipaleolithic-Mesolithic). The oldest occupation (layer *2 int*) belongs to the Microlaminar Epipaleolithic tradition. Radiocarbon dating situates it during the Younger Dryas (Table 1). Above it, layer *1 int*, with some geometric microliths, belongs to the Early Holocene Sauveterroid tradition in the Mediterranean region. The most recent hunter-gatherer occupation (layer *4 cent*) belongs to the Geometric Mesolithic. Radiocarbon dating places it at the onset of the Middle Holocene, around the 8.2 kyr event (Rasmussen et al., 2006; Thomas et al., 2007). The Neolithic occupation (layer *2 cent*) offers the most abundant and varied material, attributed to the Early Neolithic Cardial culture. Radiocarbon dating supports its belonging to the Middle Holocene (Table 1) (Bosh, 2001; 2015; 2016).

3. MATERIALS AND METHODS

3.1. Materials.

All the analysed samples came from the archaeological excavation in 1992. Hand-picking of charcoal fragments was favoured for radiocarbon dating, while a systematic sampling strategy was carried out for anthracology (Bosch, 2001, 2015; 2016). 947 charcoal fragments, covering the whole described archaeological sequence, have been analysed (Table 2). Most of the charcoal belongs to materials scattered in the sediment (n = 649). The synthetic nature of these deposits makes them good records of the vegetation in the surroundings of the site during its successive human occupations (Chabal et al., 1999; Piqué, 1999; Badal et al., 2003; Chabal and Heinz, 2021). The contents of a large combustion structure (n = 298) from the Early Neolithic occupation (in layer *2 cent*) were also studied, providing a snapshot of its last use and enabling a palaeoeconomic interpretation (Théry-Parisot et al., 2010).

3.2. Methods.

Each charcoal fragment was observed in the three anatomical sections (transverse, longitudinal tangential, and longitudinal radial) using a metallographic dark/bright field incident-light microscope, allowing magnification factors from x50 to x1000. Comparisons with current charred wood samples and wood anatomy atlases made it possible to identify taxa (Greguss, 1955; Jacquiot et al., 1973; Schweingruber, 1990; Vernet et al., 2001; García Esteban et al., 2003). The nomenclature used follows the

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guidelines in *Flora iberica* (Castroviejo, 1986-2012). The relative frequencies of the determined taxa are represented in the form of an anthracological diagram with the data from the layers (Figure 2), made with the software Tilia 2.6.1[1].

Photographs of the most interesting taxa (Figure 3) were taken with an Environmental Scanning Electron Microscope (ESEM)[2]. Maps showing site locations and taxa distribution have been developed in Quantum GIS software v.3.4.13 Madeira. Chorological maps for the main European woody species are developed by Caudullo et al., 2017. Digital Elevation Models are available from the Spanish National Geographic Institute (IGN MDT200). Modern distribution maps and regions of provenance of European species have been provided by the CIFOR-INIA Department of Forest Ecology and Genetics of the Spanish Government (Alía et al., 2009).

4. RESULTS

4.1. Quantifications

Out of the 947 charcoal fragments studied, 13 taxa were determined, of which four belong to conifers and nine to hardwoods, both trees and shrubs (Table 2). The anthracological diagram shows the diachronic evolution of the landscape exploited by the inhabitants of Cova del Vidre (Figure 2). Taxon richness increases significantly from the Late Glacial period (Microlaminar Epipalaeolithic) to the early Atlantic (Early Neolithic), in correlation with climate warming. Conifers adapted to cold or temperate climates constantly predominate, with a decreasing participation of *Pinus* tp. *sylvestris* in favour of *Taxus baccata*, which co-dominates at the end of the sequence. The appearance and progressive diversification of hardwoods mainly involves species of the deciduous oak forest. Weak representations of *Abies alba* at the beginning, and of *Fagus sylvatica* at the end of the sequence are observed, in accordance with the altitudinal conditions.

The differences between the contents of the large combustion structure and the scattered charcoal from the contemporary level (layer *2 int*) are mainly quantitative, due to a more random or short-lived deposition in the hearths. An over-representation of yew and under-representation of Scots pine type and boxwood are observed in the combustion structure, as well as the presence of the only fragment of *Vitis vinifera* at the site. These differences, which do not allow the use of the fire structure to interpret the environment, are consistent with the 'snapshot' character usually observed in such deposits and may signify either a random use of wood or an unknown intentionality (Kabukcu and Chabal, 2021).

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[2] Electron Microscopy Service of Biological Systems of the Research Support Service of the University of Zaragoza.

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5. DISCUSSION

5.1. Stages in the vegetation dynamics at Cova del Vidre

5.1.1. The Pleistocene hunter-gatherer environment

At Cova del Vidre, the layer *2 int* reveals that during the Younger Dryas (Microlaminar Epipalaeolithic occupation) *Pinus* tp. *sylvestris* was the most abundant species in the surroundings of the site. Scots pine (*Pinus sylvestris* L.) cannot be differentiated on the basis of wood anatomy from Black pine (*Pinus nigra* Arnold.). In any case, one or two of these cold-climate pines abounded in the surroundings of the site during this period. Since the Younger Dryas is a period of severe climate cooling, Scots pine, better adapted to a cold climate, is the most likely pine species in this area. Nevertheless, Black pine subspecies are drought resistant and competitive in the absence of dense hardwood forest vegetation. Salzmann pine, *Pinus nigra* subsp. *salzmannii* (Dunal) Franco, is the only subspecies, among Black pines, attested in the macro-remains from the Eemian travertines of Beicete (Teruel) (Martínez-Tuleda et al., 1986) and also the only one currently present in mixed stands with Scots pine in north-eastern Spain; for this reason it should be considered in the present study.

Other trees and shrubs are very scarcely represented by one charcoal fragment per taxon, including *Abies alba* and *Juniperus* sp. and a single hardwood, *Prunus* sp. This last genus includes a large number of trees and shrubs (whose fruits may be edible) that grow in open forest under cool and dry conditions. It may signal the early presence of temperate taxa at the site, in a refugium situation. Conifers, especially cryophilous pines and junipers, are the dominant taxa in anthracological records from north-eastern Iberia during the 13th millennium cal BP, often associated with *Prunus* (Allué, 2002; Alcolea, 2017). Some sites, such as the Molí del Salt, the Font Voltada, and the Filador (Allué, 2002), also reveal an open landscape, where pines formed the tree cover accompanied by shrubs well-adapted to the dry and cold climate that prevailed in Iberia during the Late Glacial period.

5.1.2. The Holocene hunter-gatherer environment

At the start of the Early Holocene (Preboreal), *Pinus* tp. *sylvestris* continues to be predominant in layer *1 int*, testifying to a vegetal environment quite similar to during the previous occupation. However, pines are decreasing significantly and *Prunus* acquires a remarkable frequency of nearly 20% in the record. The most noticeable feature about this period, especially given the altitude of the site, is the appearance of evergreen *Quercus* as early as in the plains and middle altitudes (Badal et al., 2017). Together with the fairly high frequency of *Prunus*, this is an indicator of the milder climatic conditions during the onset of the Holocene (Preboreal). The early and rapid rise of these species probably reflects their previous presence in the area. Kermes/holm oak is scarce in anthracological records at this time. It can occasionally be found at coastal, such as La Cativera (Allué et al., 2007), and Pre-Pyrenean sites, such as El Parco (Allué et al., 2013) and El Esplugón (Alcolea et al., 2021), until becoming widespread from the 9th millennium cal BP, in

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association with other Mediterranean taxa in the lowlands of the Ebro valley and in coastal Catalonia.

In layer *4 cent* during the middle Holocene (at least 2000 years after layer *1 int*), Scots pine type remains the dominant taxon associated with a significant proportion of yew (*Taxus baccata*) and a small percentage of such Supramediterranean taxa as boxwood (*Buxus sempervirens*) and deciduous oak (*Quercus* deciduous). The appearance of new temperate taxa indicates climate amelioration, certainly associated with the beginning of the Atlantic period. The frequency of yew of almost 20% (*Taxus baccata*) in layer *4 cent* (further increasing in layer *2 cent*) testifies an increase in humidity at least from the end of the 9th millennium to the end of the 8th millennium cal BP. In this mountain area, around the 8.2 kyr cold event, there was thus no lack of moisture; this situation contrasts with the Central Ebro Basin where at the same time populations deserted the sites during a crisis of aridity (González-Sampériz et al., 2009). This difference highlights a spatial shift in climate. Besides, at the end of the 10th millennium *Pinus* tp. *sylvestris* forest was already rare in the anthracological records at coastal sites in Catalonia (e.g. at La Cativera, 65 m a.s.l.) and absent from the 12th millennium further south at medium altitudes, (e.g. at Santa Maira, 650 m a.s.l.) being replaced by thermophilous or mesothermophilous taxa, such as *Pinus halepensis* or deciduous and evergreen *Quercus* (Allué 2002; Allué et al. 2012; Buxó and Piqué 2008; Badal et al. 2017) reflecting altitudinal and latitudinal dependence of climate.

5.1.3. The first farmers' environment

In layer *2 cent*, i.e. the Early Neolithic occupation, new changes occur in the anthracological record. The surroundings of the cave were still dominated by conifer forests. *Taxus baccata* reached its highest values, in the scattered charcoal as well as in the large combustion structure, sharing prominence with *Pinus* tp. *sylvestris*, which remains suitable due to the altitude, while *Juniperus* maintains a discrete presence in the record. However, the taxonomic diversity of hardwoods, such as *Acer*, *Quercus* deciduous, *Buxus sempervirens* and the Rosaceae Maloideae, must be highlighted. The abundance of yew indicates a significant increase in rainfall and soil moisture, but the temperate and Supramediterranean trees and shrubs reflect the improvement in the climate during the Middle Holocene. *Vitis vinifera*, the wild grapevine, may have grown in oak groves or in riparian areas. The discrete presence of Mesomediterranean taxa, such as *Quercus coccifera/ilex* and Ericaceae, suggest the persistence, since the Early Holocene, of favourable areas for their growth near the site. These thermophilous species also exist at lower altitudes, as documented in the Bajo Aragón (Alcolea, 2017; 2018), and the Ebro Delta (Bosch, 1989; Ros, 1996). The large combustion structure reflects the same pattern of fuel procurement, with quantitative differences of no environmental significance (which may be due to one-off or intentional collection of yew wood in the last fire events before the structure was abandoned) (see 5.3).

5.2. The abundance of *Taxus baccata*

One of the most remarkable results of the anthracological study of Cova del Vidre is the high values of yew (*Taxus baccata*) in the middle Holocene layers. Today, its presence

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in Europe and the Iberian Peninsula is limited due to the impact of human action and climate change that has led to its replacement by more competitive plants. Yew is common in northern Iberia under an Atlantic climate (Figure 4) although the species has been exploited for its wood throughout history. For instance, in the Montseny Mountains in the northeast of the Iberian Peninsula, the genetics of current yew populations can be explained by the long-term exploitation of forest species for firewood and charcoal production, during the 15th-19th centuries (Dubreuil et al., 2010). It is also present in more southern mountain ranges such as in the El Port massif, and is not rare around the site. Mediterranean yew trees, probably isolated during the last Glacial period (Carrión et al., 2003) and currently in decline, grow in small, isolated populations. In Mediterranean environments yew finds adequate moisture above 1,000 m a.s.l. In lower areas, it prefers the protection of shaded valleys, ravines and cliffs. As long as it finds moisture, it can withstand high temperatures (Costa et al., 2001).

Taxus baccata must have had a wide distribution in Europe in the past. The spread of yew throughout the Iberian Peninsula since the beginning of the Holocene, in parallel with the deciduous forest colonization, has been highlighted by several authors (Martin and Thiébault, 2010; Pérez-Díaz et al., 2013; Uzquiano et al., 2014; Vidal-Matutano, 2015). Due to the low preservation of yew in Holocene pollen records, contrasting with its abundance in charcoal, anthracology is key to understanding its past distribution. During the Early-Middle Holocene, yew appears sporadically in the anthracological records of north-eastern Iberia, rarely exceeding 5% of the remains, such as at Plansallosa, Cova 120, Cova de l'Avellaner (Ros, 1995, 1996), La Prunera (Ferré and Piqué, 2000), La Draga (Caruso and Piqué, 2014), Cova del Frare (Ros, 1996), Balma Margineda (Heinz and Vernet, 1995) and the Moncayo natural park (Aranbarri et al., 2018). Only three sites, Cova de la Guineu (Allué et al., 2009), Camp del Colomer (Piqué, 2016), and Cova del Vidre (this article), record high yew frequencies.

At Cova del Vidre, yew appears for the first time (layer *4 cent*) around 8.2-7.9 kyr cal BP. During the Early Neolithic occupation (layer *2 cent*), it reaches almost 40% of the studied remains, becoming the plant most used as fuel in the site and certainly a very widespread taxon in the surroundings. As mentioned in section 2.2, this conifer still grows in the El Port massif (Tortosa-Beceite) today (Figure 4) (Costa et al., 2001; Senar Lluch, 2011; Camprodon et al., 2014). Its importance in the territory was probably much greater during the Neolithic.

If we consider the large combustion structure contemporary with the *2 cent* layer, showing its last use or uses, the percentage rises to 86%. Random use cannot be ruled out, but it is also possible that yew was voluntarily sourced for specific uses. Among these, uses as fuel and fodder or for sanitary purposes in sheepfolds have been mentioned. The leaves, despite their known toxicity due to the presence of an alkaloid (particularly harmful to horses) are still occasionally used as fodder for livestock (Costa et al., 2001). These practices have been considered in archaeological sites in Mediterranean mountainous areas, in cases when the taxon is abundant among the charcoal (Delhon et al., 2008; Allué et al., 2009; Martin and Thiébault, 2010; Martin et al., 2012, Piqué et al 2018). At Cova del Vidre, Neolithic leaf-foddering of livestock may have taken advantage of the natural abundance of this species. Its wood was then reused as fuel for fire.

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5.3. New data about the early presence of *Fagus sylvatica* in the eastern Iberian Range

The presence of beech (*Fagus sylvatica*) is also noteworthy, although it is a minority taxon in the record. The European beech (*Fagus sylvatica*) is currently one of the most important forest trees in Europe. However, its presence in this territory is relatively recent according to palaeobotanical data (Magri et al., 2006). Charcoal fragments, seeds, fruits, and leaves are parts of plants with a limited dispersion which were probably collected in the immediate vicinity. Hence, when investigating the location of glacial refugia and species migration, macrofossils are the most useful records reflecting local vegetation.

Palaeobotanical data suggest a late and rapid migration of beech forests in central, eastern, and northern Europe from the Carpathians Mountains only after 4.5 kyr cal BP (Huntley and Birks, 1983). Nevertheless, the history of beech begins long before the establishment of the beech forests in Europe. Some beech trees, which require wet summers and mild winters, survived during the last glacial period and the Early-Mid Holocene in glacial refugia (Carrión et al., 2003). Most of the glacial refugia were in mountainous territories of the southern peninsulas (Iberian, Italian and Balkan), where the residual populations could find sheltered and humid places to survive (Magri et al., 2006), avoiding continental areas, plains, and valleys.

Macrofossil evidence suggests that relict beech populations existed in the Iberian Peninsula since the last glacial period, in the western Pyrenees-Cantabrian Mountains (Ruíz-Alonso et al., 2018) and the north-western Iberian Range (López-Merino et al., 2008). In the eastern Pyrenees the evidence is very scarce (Vernet, 1980; Ros, 1992; Allué, 2002). Its presence had not been documented until now in the Iberian Peninsula below 41º N latitude (Figure 5 and 6).

The archaeobotanical record at Cova del Vidre shifts the southern limit of the European beech to the east of the Iberian Range, confirming the existence of a vegetation refugium in El Port massif (Tortosa-Beceite), at least from 7.3 kyr cal BP. The site is currently very close to small relict beech forests (Figure 6). The topography generates a particular environmental situation that may have been favourable for the maintenance of beech patches accompanied by boxwood (*Buxus sempervirens*) (Costa et al., 2001; Alía et al., 2009), like the Pyrenean beech forests. According to genetic data and accepted migration routes, Mediterranean refugia are thought to have contributed to the colonization of central and northern Europe (Magri et al., 2006; Bradshaw et al., 2010; Giesecke and Brewer, 2018). This attestation of the presence of the beech so far south is thus an interesting new element.

5.4. The mountain palaeobotanical record at Cova del Vidre: a Late Glacial refugium?

The anthracological sequence at Cova del Vidre between the 13th and 6th millennia cal BP shows a vegetation dynamic that fits into the regional framework proposed on the basis of pollen records in the NE Iberian Peninsula, with fairly large spatial differences due to elevation and latitude (Riera and Esteban, 1994; Follieri et al., 2000; Pérez Obiol, 2007; Burjachs et al., 2016). These data reflect the regional response of vegetation during

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the transition from the Late Glacial period to the Early Holocene, global warming, and the effects of human activity. At the more local geographic scale of the El Port massif and its surroundings, anthracology shows the existence of conifers adapted to the cold within the predominance of Supramediterranean vegetation, characteristic of montane environments in Mediterranean Iberia.

The anthracological record from Cova del Vidre has many distinctive features compared to other sites in different environmental contexts in north-eastern Iberia, despite their geographical proximity, i.e. the Bajo Aragón, the Ebro Delta, and the Maestrazgo sites (Figure 1). In the nearby mountainous sites of the Maestrazgo in the Iberian Range, cold-climate pines dominate during the whole period and Supramediterranean elements are almost absent (Alcolea, 2017). In the lowlands, thermo-Mediterranean vegetation dominates the anthracological records. In the Ebro Delta, a typically Mediterranean maquis shrubland is highlighted by the predominance of olive tree (*Olea europaea*), holm/kermes oak (*Quercus coccifera/ilex*) and heather (Ericaceae) (Bosch, 1989; Ros, 1996). In the Bajo Aragón, continental conditions are evidenced by the presence of drought-resistant conifers such as Aleppo pine (*Pinus halepensis*) and junipers, also accompanied by *Quercus coccifera/ilex* (Alcolea, 2018; Aranbarri et al., 2020).

Therefore, a comparison of Cova del Vidre (this paper) with nearby sites (Ros, 1996; Bosch, 1989; Alcolea, 2017; 2018) shows the existence of rather different plant communities. The local differences in forest composition emphasize the importance of altitudinal factors and the Mediterranean influence. These differences only become noticeable at the beginning of the Holocene and are already well-established by the Early Neolithic.

These observations show that the global climate that determined vegetation prior to the Holocene shaped the plant communities of these nearby sites roughly equally. From the Holocene onwards, differences in local conditions become decisive, such as (i) differences in precipitation and temperature due to orography, (ii) differences in water and heat retention due to geological features, (iii) Mediterranean influences due to the proximity to the sea and (iv) finally, differential human activities that have completed the shaping of the landscapes.

El Port massif currently has the appearance of an island of vegetation containing forest species that probably originated during the Last Glacial period. Indeed, at Cova del Vidre, the presence of *Prunus* during the Younger Dryas, followed by its abrupt increase in the Early Holocene, accompanied by *Quercus coccifera/ilex*, and later during the Middle Holocene by other temperate species, like *Quercus* deciduous, *Buxus sempervirens* and *Fagus sylvatica*, echoes the presence of the same taxa today, at more than 1,000 m a.s.l., under limiting conditions for these species. We believe that during the Late Glacial, these taxa found suitable local thermal conditions that allowed them to resist and to restart rapidly in the Early Holocene. Then, during the Middle Holocene, precipitation conditions were favourable for their maintenance until today.

According to Carrión et al (2003), there is a common misapprehension that Iberian glacial refugia were confined to southernmost parts of the peninsula, as palaeobiological and

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genetics information shows that numerous viable Quaternary refugia did exist for woodland species in the mountain ranges, both in continental central Spain and northern Spain. Thus, even if the main refugia for deciduous trees lay further east in the Italian and Balkan Peninsulas, the Iberian Peninsula may have retained sclerophyllous and some broad-leaved species.

According to the suggestions of Bennett et al. (1991), in southern Europe trees that survived in mid-altitude refugia during cold stages probably also persisted during warm Quaternary stages, constituting long-term refugia with a suitable climate. Trees could easily have survived at densities too low to escape detection in the pollen record of any site so far analysed.

Based on the very early Holocene dynamics of deciduous trees and the current maintenance of thermophilic taxa in the El Port massif, the surroundings of Cova del Vidre seem to be a very good candidate as a refuge during the Last Glacial period.

6. CONCLUSIONS

The present study fills an important gap in palaeobotanical information on medium-high altitudes in the eastern Iberian Range. Until now, the available records were limited to the Mediterranean lowlands of the Bajo Aragón and the Ebro Delta. Conclusions have been drawn regarding (i) the vegetation dynamics in Mediterranean mountain environments, (ii) the uses of forest resources by the last hunter-gatherers and the first farmers, (iii) the beginning of local differences in vegetation as a function of altitude-dependent factors, and (iv) the palaeodistribution of some European trees. The most important points of these findings are summarized below:

(i) The Cova del Vidre data cover a period between the 13th and 6th millennia cal BP. During the Late Glacial and Early Holocene, the anthracological record is dominated by a spectrum of cold-climate pines and thorny shrubs, with a diversification of taxa underway. They suggest an open landscape formed by pioneering, opportunistic, fast-growing, and well-dispersed plants. During the Atlantic period, an important shift in temperature and precipitation regime promoted successional changes in plant communities on a long-term scale. The Scots type pine never disappeared given the altitude of the site but acquired a secondary role with the gradual establishment of a mixed deciduous forest, increasing in biodiversity over time, reflecting the consolidation of climatic improvement that began in the Early Holocene.

(ii) Firewood was supplied mainly from the surroundings of the cave. Changes in fuel use reflect the evolution of vegetation cover. During the hunter-gatherer occupations, cold-climate pines persistently dominated the anthracological spectrum, as in the case of Ebro valley records at that time. The extensive use of yew by the last hunter-gatherers and early farmers reflects an increase in humidity that favoured the species. In the context of an environment poor in hardwood species until the end of the sequence, we cannot rule out a preferential use of this species for livestock feed, with the remaining wood then being burnt.

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(iii) A comparison with archaeobotanical data from nearby sites in the lowlands suggests that altitudinal differences in vegetation were already well-established by the late Mesolithic (Early Atlantic). While cold-climate conifers and Supramediterranean vegetation predominated in the mountains, Mediterranean trees and shrubs were already dominant in the plains. Local differences occurred within a small geographical area due to altitudinal factors and Mediterranean influence. Soil aridity appears to be one of the main factors limiting vegetation in the Mediterranean mountains.

(iv) Macrofossil evidence of yew and beech provides new data about the southern limit of their range. A Holocene refugium of temperate and Mediterranean taxa is identified in the 7th millennium cal BP in El Port massif (Tortosa-Beceite), where relict populations of these taxa still exist today. Their presence is relevant for the reconstruction of the palaeodistribution of these species and sheds light on the influence of human impact on their current distribution.

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TABLE AND FIGURE CAPTIONS

Table 1. Radiocarbon dates available for the archaeological sequence in Cova del Vidre (Bosch, 2001; 2015; 2016). Material: B: bone (*Ovis*), C: Charcoal. Culture: ME: Microlaminar Epipalaeolithic, GM: Geometric Mesolithic, EN: Early Neolithic. Calibrations with OxCal v4.4. Bronk Ramsey (2017); r: 5 IntCal20 atmospheric curve (Reimer et al., 2020). Beta-58943 comes from the large structure in layer *2 cent*.

Table 2. Absolute and relative frequencies of the taxa identified in Cova del Vidre.

Figure 1. Geographical setting and site location. Black star: Cova del Vidre. Black points (nearby sites mentioned in the text): 1. Plano del Pulido, 2. El Pontet, 3. Arenal de Fonseca, 4. Barranc d'en Fabra, 5. Molló de la Torre. Base: MDT200 IGN (Spanish Government).

Figure 2. Frequency diagram of anthracological remains from Cova del Vidre.

Figure 3. ESEM images of selected taxa: A) *Taxus baccata*. Transverse section, B) *Taxus baccata*. Radial section, C) *Fagus sylvatica*. Transverse section, D) *Fagus sylvatica*. Radial section, E) Rosaceae Maloideae. Transverse section, F) Rosaceae Maloideae. Radial section.

Figure 4. Current distribution of *Taxus baccata* L. in El Port massif and Ebro Delta (NE Iberia) (blue diamonds). Data from CIFOR-INIA (Auñón-García et al. 2011). Black star: Cova del Vidre. Black points (nearby sites mentioned in the text): 1. Arenal de Fonseca, 2. Plano del Pulido, 3. El Pontet, 4. Barranc d'en Fabra, 5. Molló de la Torre, 6. Coves del Fem. Black circles: distance from the site of 10, 20, 30, and 40 km. Base: MDT200 IGN (Spanish Government). Prepared by the authors.

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Figure 5. Map of the modern and past distribution of beech (*Fagus sylvatica*) in Europe. Striped area: modern distribution after Alía et al., 2009 CIFOR-INIA. Triangles: geographical distribution of records containing macrofossil evidence (see references in Magri et al., 2006 supplementary material). Black star: Cova del Vidre record. Prepared by the authors.

Figure 6. Current distribution and seed zones of *Fagus sylvatica* L. in NE Iberia. Data from CIFOR-INIA (www.inia.es/genfored.html) (Auñón-García et al. 2011). Black star: Cova del Vidre within the area containing small relict forests of *Fagus sylvatica* L. in El Port massif (*Buxo sempervirentis-Fagetum sylvaticae*) (Costa et al., 2001) Base: MDT200 IGN (Spanish Government). Prepared by the authors.

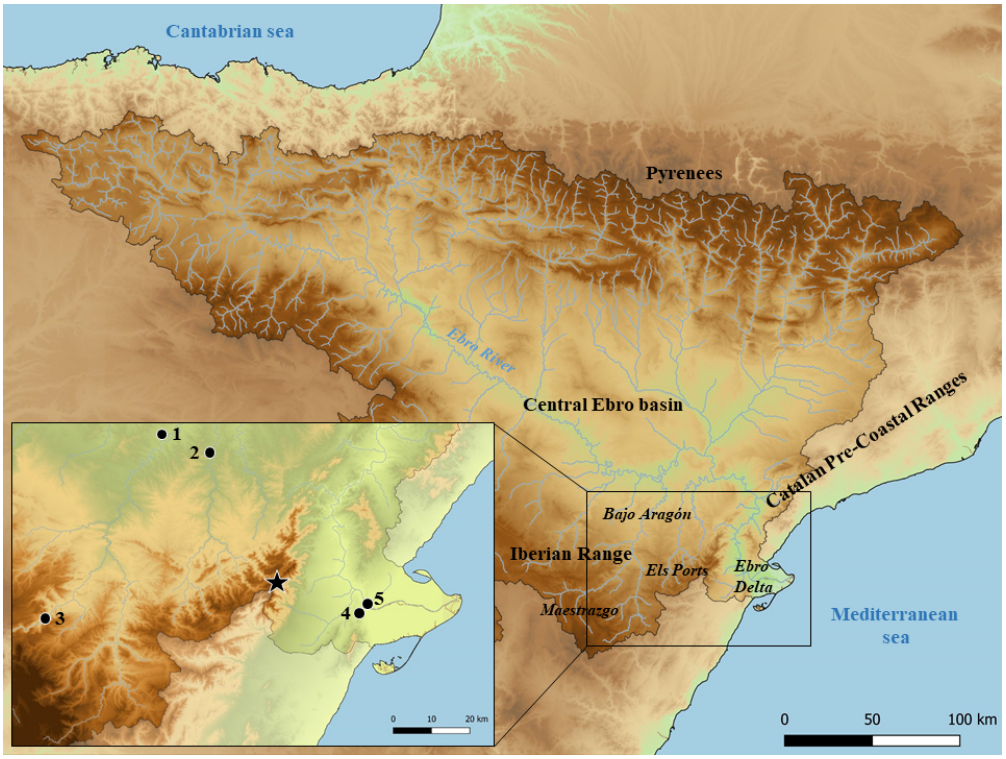
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Layer	Culture	Date BP	+/-	Ref. lab.	Calibrated age BP (2σ)	Material	Reference
2 cent	EN	6,248	33	OxA-26065	7,259-7,021	B	Bosch, 2016
2 cent	EN	6,181	35	OxA-26064	7,167-6,957	B	Bosch, 2016
2 cent	EN	6,180	90	Beta-58934	7,272-6,801	C	Bosch, 2016
4 cent	GM	7,290	70	UBAR-832	8,311-7,966	C	Bosch, 2015
2 int	ME	10,740	130	Beta-58933	12,690-12,471	C	Bosch, 2001

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Culture	Microlaminar Epipaleolithic		Sauveterroid		Geometric Mesolithic		Early Neolithic			
Bioclimatic period	Lateglacial		Early Holocene		Middle Holocene		Middle Holocene			
	Younger Dryas		Preboreal		Early Atlantic		Middle Atlantic			
Layer	*2 int*		*1 int*		*4 cent*		*2 cent*		Large structure	
Taxa	n	%	n	%	n	%	n	%	n	%
Abies alba	1	1.2	-	-	-	-	-	-	-	-
Acer sp.	-	-	-	-	-	-	1	0.3	2	0.7
Buxus sempervirens	-	-	-	-	8	4.8	36	12.3	2	0.7
Ericaceae	-	-	-	-	-	-	1	0.3	-	-
Fagus sylvatica	-	-	-	-	-	-	1	0.3	2	0.7
Juniperus sp.	1	1.2	-	-	-	-	7	2.4	-	-
Pinus tp. *sylvestris*	79	96.3	78	78.0	125	74.9	86	29.5	12	4.0
Prunus sp.	1	1.2	18	18.0	-	-	4	1.4	-	-
Quercus coccifera/ilex	-	-	4	4.0	-	-	2	0.7	3	1.0
Quercus deciduous	-	-	-	-	2	1.2	20	6.8	12	4.0
Rosaceae Maloideae	-	-	-	-	3	1.8	18	6.1	7	2.3
Taxus baccata	-	-	-	-	29	17.4	116	39.7	257	86.2
Vitis vinifera	-	-	-	-	-	-	-	-	1	0.3
Total determined	82		100		167		292		298	
Undeterminables	-		-		8		-		-	
Total fragments	82	100	100	100	175	100	292	100	298	100
Total taxa	4		3		5		11		9	

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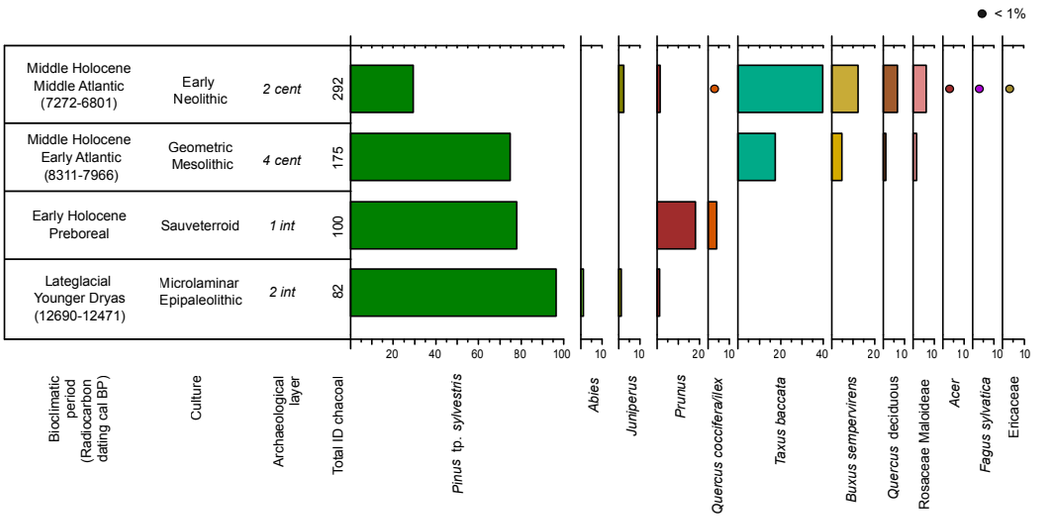
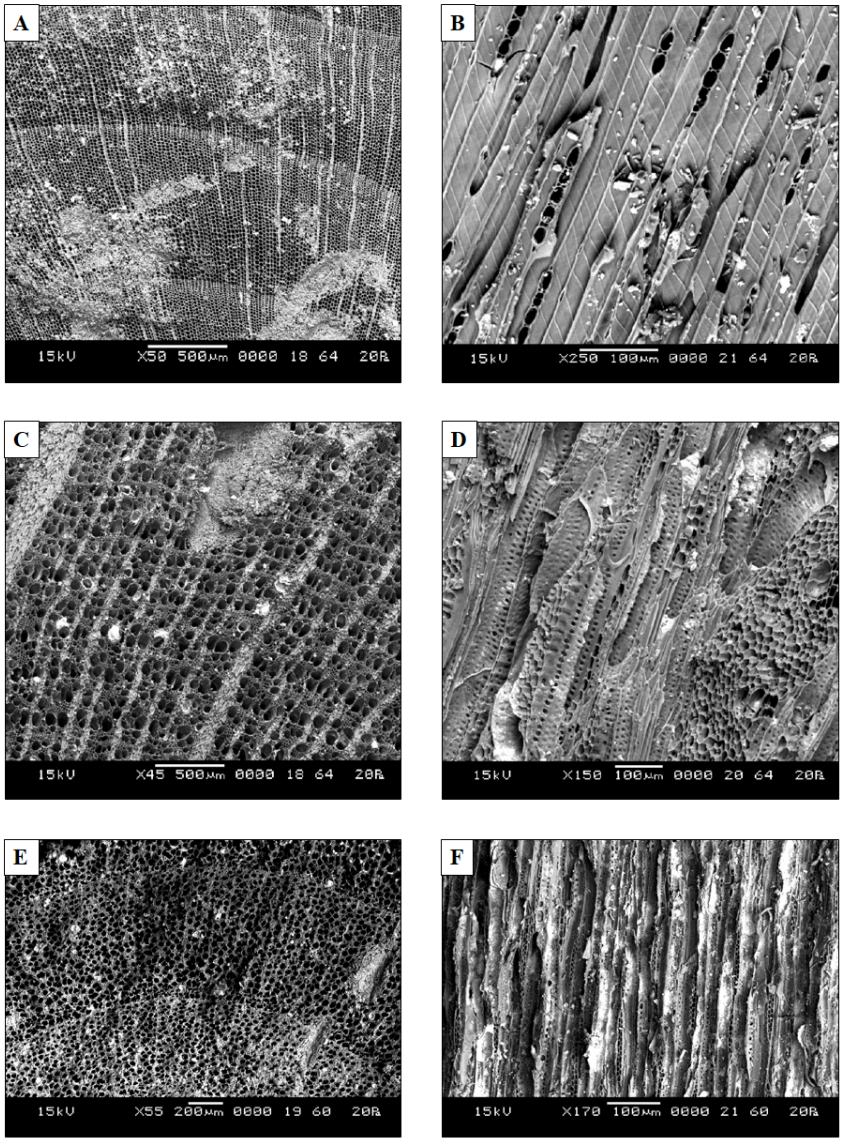
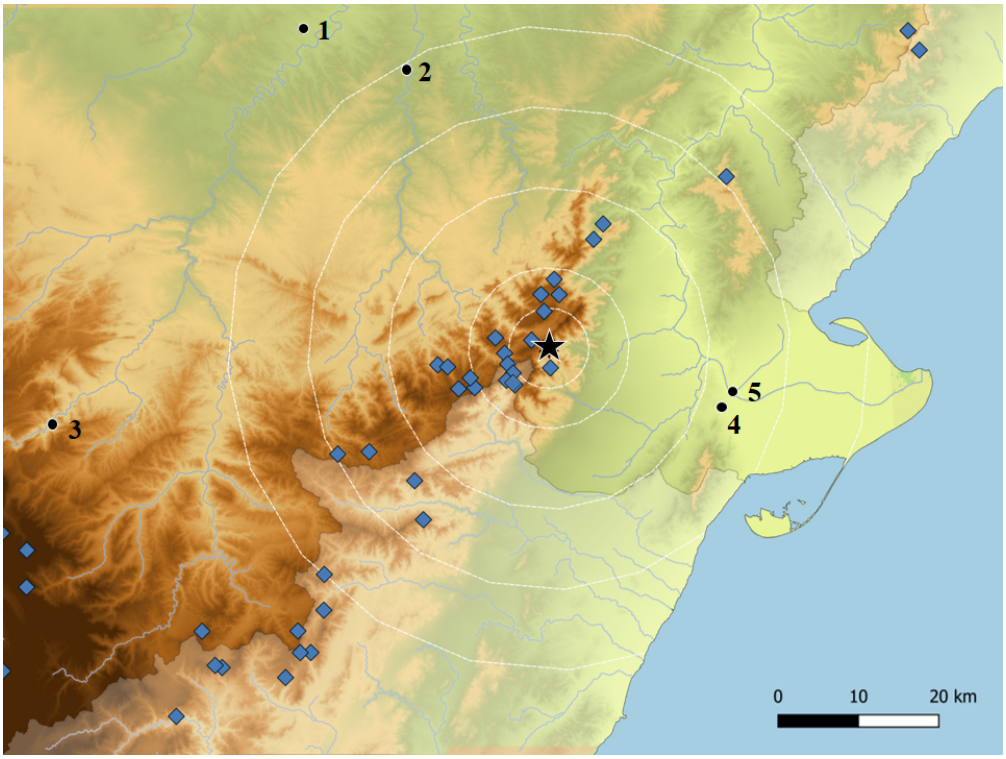


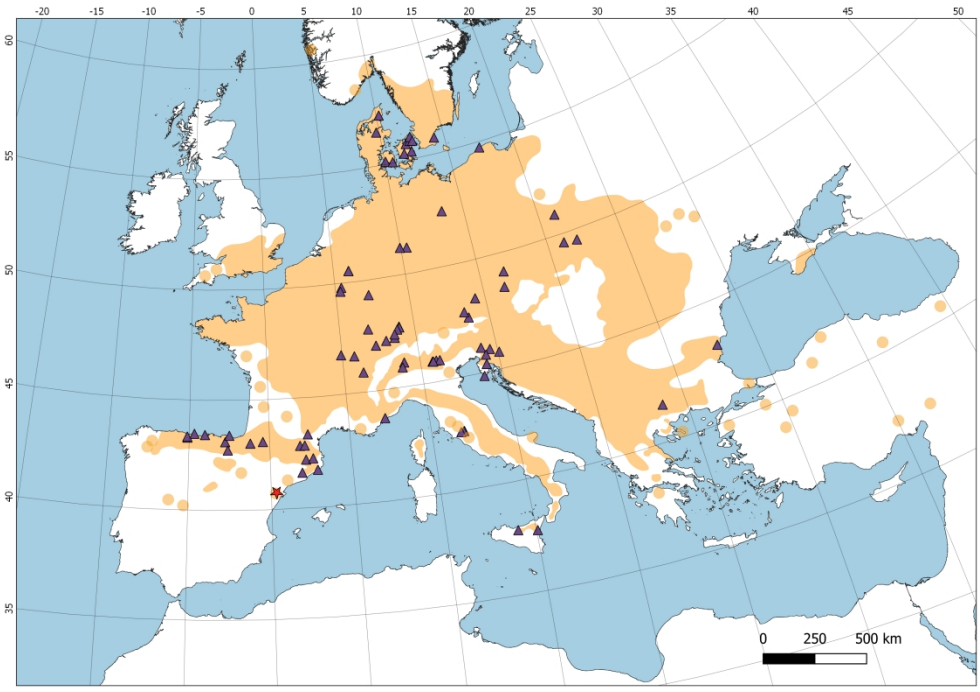
Figure 2. Frequency diagram of anthracological remains from Cova del Vidre.



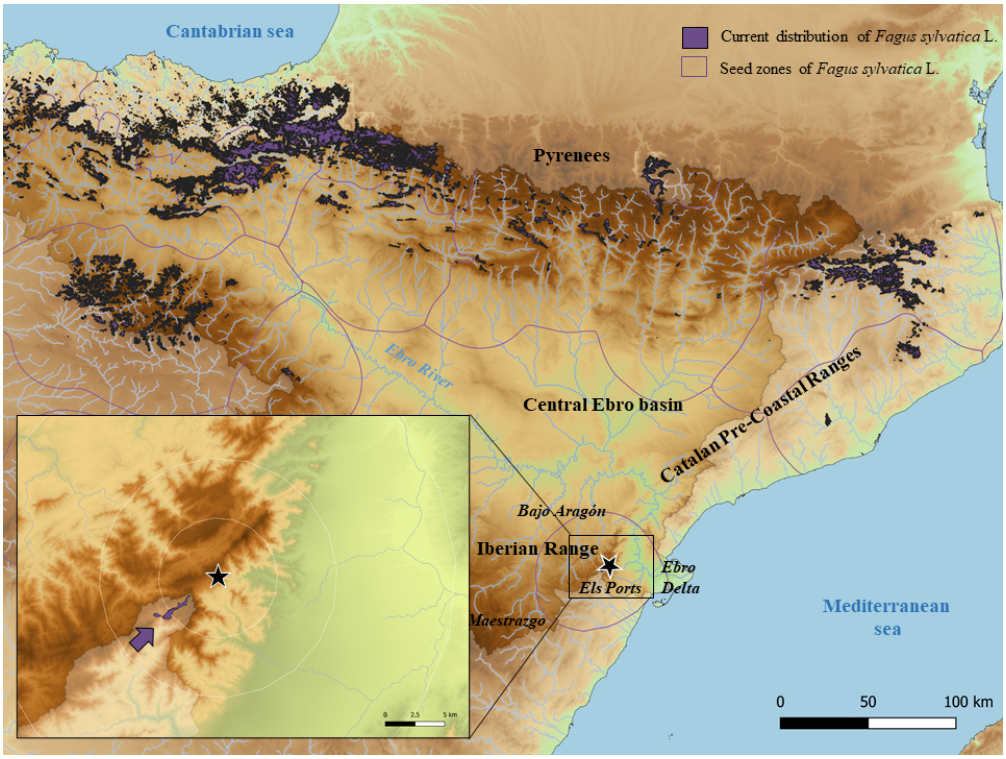
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