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

Marta Alcolea[a], Lucie Chabal[b], Josep Bosch-Arguilagós[c], Raquel Piqué[a]

[a] Departament de Prehistòria. Universitat Autònoma de Barcelona. Plaza Cívica. 08193 Bellaterra, Cerdanyola del Vallès, Barcelona, Spain. Email: Marta.Alcolea@uab.cat; Raquel.Pique@uab.cat

[b] ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France. Email: lucie.chabal@umontpellier.fr

[c] Museu de Gavà. Plaza de Dolors Clua, 13-14, 08850, Gavà, Barcelona, Spain. Email: jbosch@gava.cat

Corresponding author: Marta Alcolea (martaalcoleagracia@gmail.com)

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*, *Abies alba* and *Fagus sylvatica* in southern Europe.

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 prehistorical 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. The aims of this work are to characterise the environmental conditions in which late hunter-gatherers and first farmers developed, and to reconstruct the impact of their economic practices on the landscape. The main questions addressed are vegetation history, climate change and human impact from the Late Glacial to the Middle Holocene in the Mediterranean mountains of El Port massif (NE Iberia).

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).

91   2.2. Biogeographical setting
92
93   The Cova del Vidre cave (Roquetes, Tarragona) (31T 273434 4517052) is a habitat
94   located around 1,000 m a.s.l. in El Port massif (Tortosa-Beceite), a mountain environment
95   in the southern Catalan Pre-Coastal Ranges connected to the Iberian Range (NE Iberia)
96   (Figure 1). Rugged Mesozoic limestone lithology results in steep local relief with
97   pronounced slopes and deep ravines. The highest altitude is reached in the Caro Mountain
98   (1,447 m a.s.l.) while the Mediterranean Sea is located less than 50 km from the site. The
99   mouth of the cave, facing east-northeast, offers a wide panoramic view including the
100   Lower Ebro Basin and the Ebro Delta (Bosch, 2015; 2016).
101
102   The current vegetation in this massif is unique, as if it were an island of vegetation. The
103   high diversity of ecosystems and biotopes results from the transition between the
104   Mediterranean coastal and continental mountain climates, shaped by the complexity of
105   the orography (Senar Lluch, 2011). Above 1,000 m a.s.l., a sub-humid or even humid
106   climate enables the presence of Supramediterranean forests mainly formed by Scots
107   (*Pinus sylvestris* L.) and Salzmann pines (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco)
108   and Portuguese (*Quercus faginea* Lam.) and Pyrenean oaks (*Quercus pyrenaica* Willd.),
109   occasionally accompanied by yew (*Taxus baccata* L.), holly (*Ilex aquifolium* L.) and even
110   beech (*Fagus sylvatica* L.).
111
112   Patches of Mediterranean yew trees grow in isolation in search of shady places in ravines
113   and valleys and inside forests of pine, beech and holm oak (Costa et al., 2001). Locally
114   the yew can dominate dense understorey layers of boxwood (*Buxus sempervirens* L.), as
115   in the case of some calcareous cliffs in the Maestrazgo (Camprodon et al., 2014). Small
116   beech forests grow in the Vallcaneres ravine around 1,200 m a.s.l., interspersed with pine
117   forests, occupying the shady areas at the foot of the cliffs and the stream banks, where the
118   water deficit of the Mediterranean climate is balanced. They grow besides
119   Mesomediterranean or Supramediterranean shrubs such as boxwood and various
120   Rosaceae such as *Amelanchier ovalis* Medik.*, Crataegus monogyna* Jacq.*, Rosa canina*
121   L. and *Rubus ulmifolius* Schott (Costa et al., 2001). These small populations constitute
122   one of the southernmost beech forests in Europe, representing the climatic tolerance limit
123   of the European beech together with those of Italian peninsula, Sicily and Balkans.
124
125   2.3. Site description
126
127   Cova del Vidre consists of a main cave with a surface area of 43x30 m and 14 m high,
128   and a smaller chamber next to it, to the north, 15x11 m in size and 2 m high. The entrances
129   of both caves face east-northeast. In the main cave, longitudinal joints are frequent,
130   including a zenithal one that allows water to enter the cave without flooding it, thus
131   contributing to its habitability (Bosch, 2001; 2015; 2016).
132
133   The presence of prehistoric occupations at Cova del Vidre has been known since the 19th
134   century. Archaeological work undertaken in the 1940s revealed the existence of a
135   stratified archaeological sequence ranging from the late Upper Palaeolithic to the Early
136   Neolithic. More recent archaeological excavations, conducted by J. Bosch's team in 1992,
137   accomplished the absolute radiocarbon dating of the occupations in the cave (Bosch,

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

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

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

198 4. RESULTS

200 4.1. Quantifications

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

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

223
224
225
226
227

---

[1] License belonging to the Archeobotanical Laboratory of the Autonomous University of Barcelona.
[2] Electron Microscopy Service of Biological Systems of the Research Support Service of the University of Zaragoza.

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 Beceite (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

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:* increased moisture and leaf-foddering

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

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).

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. *Taxus baccata* might have had a wide distribution in Europe in the past. Although the first archaeobotanical occurrences of yew have been recorded at 12-8 kyr cal BP, its spread throughout the Iberian Peninsula coincides with the deciduous forest colonization (7-3 kyr cal BP) (Martin and Thiébault, 2010; Pérez-Díaz et al., 2013; Uzquiano et al., 2014; Vidal-Matutano, 2015). 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 in charcoal.

At Cova del Vidre, yew appears for the first time (layer *4 cent*) around 8.3-8 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.

368

369 5.3. The unexpected presence of *Abies* in the eastern Iberian Range

370

371 The find of *Abies* during the Epipaleolithic occupation of Cova del Vidre (10,740 BP) is
372 very interesting, as fir is currently absent from the area. The silver fir (*Abies alba*) is
373 native to the mountains of Europe. Its current southern limit coincides with the Parc
374 Natural del Montseny (Barcelona) in the Spanish Pyrenees. The former distribution of
375 *Abies* in Europe has been addressed by several authors in recent years (Terhürne-Berson
376 et al., 2004; Muller et al., 2007; Liepelt et al., 2009; Pèlachs et al., 2009; Alba-Sánchez
377 et al., 2010; Cunill et al., 2015).

378

379 According to Terhürne-Berson et al. (2004) to date there is a lack of *Abies* macroremains
380 between 11500 and 10500 BP, whereas the records from Italy and Greece indicate more
381 than 10% of *Abies* at this time. Based on pollen records (Pérez-Obiol and Julià, 1992)
382 these authors proposed a potential long-lasting refugia for *Abies* in the eastern Pyrenees,
383 joining those proposed by Huntley and Birks (1983) and Bennett et al. (1991). The
384 hypothesis of an isolated refugium area that has not played any role in the spread of *Abies*
385 is supported by the results of isozyme studies on genetic markers (Konnert and Bergmann,
386 1995) indicating that they are clearly separate from those in other European regions.

387

388 Alba-Sánchez et al. (2010) proposed the use of SDMs in conjunction with palaeoclimatic
389 models and fossil-pollen records to locate Quaternary Iberian refugia for *Abies* from the
390 Last Glacial Maximum (LGM) to the present day. The results suggest a wider Quaternary
391 distribution of *Abies* across the Pyrenees Range and also identify habitable areas in the
392 Cantabrian Range and even reaching the eastern Iberian Range towards inland Iberia.

393

394 The study of *Abies* dynamics in Europe has been strongly associated with other species,
395 mainly *Fagus sylvatica* (Pèlachs et al., 2009). The two trees coincide in their climatic and
396 edaphic requirements. They give rise to mixed forests in equilibrium or competition, that
397 usually resolves itself in favour of, the more aggressive and pioneering beech which has
398 spread widely across Europe since the Subatlantic period (Costa et al., 1997). The finding
399 of an *Abies* macroremain (probably *Abies alba*) during the Late Glacial in El Port massif
400 (NE Iberia) supports the hypothesis of an Iberian Quaternary refugium in the Iberian
401 Range. The disappearance of the fir and the appearance of beech are consistent with the
402 Holocene vegetation dynamics in Europe.

403

404 5.4. New data about the early appearance of *Fagus sylvatica* in the eastern Iberian Range

405

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

413

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 41° N latitude (Figure 5 and 6).

The archaeobotanical record at Cova del Vidre shifts the southern limit of the European beech at the Middle Holocene 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.

5.5. 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 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 and the Ebro Delta sites (Figure 1). 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) as revealed by archaeobotanical records of Barranc d'en Fabra (Bosch, 1989) and Molló de la Torre (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*) as revealed by archaeobotanical records of Plano del Pulido and El Pontet (Alcolea, 2017; 2018; Aranbarri et al., 2020). In the nearby mountainous sites of the Maestrazgo in the Iberian Range, cold-climate pines dominate mid mountain areas during the whole period as revealed by archaeobotanical records of Los Baños (Badal, 2004) and Arenal de Fonseca (Alcolea, 2017). Supramediterranean elements are important above 1,000 m. a.s.l. since the beginning of the Middle Holocene (7.2-6.7 cal kyr BP) in El Port massif as well as in the Maestrazgo as revealed by archaeobotanical records of Cova del Vidre (this paper) and Mas Cremat (1,270 m.a.s.l.) (Vicente et al., 2009; 2010).

Therefore, a comparison of Cova del Vidre (this paper) with nearby sites (Ros, 1996; Bosch, 1989; Badal, 2004; Vicente et al., 2009; 2010; Alcolea, 2017; 2018; Aranbarri et al., 2020) shows the existence of rather different plant communities in the surroundings of the sites. The local differences in forest composition emphasize the importance of altitudinal factors and the Mediterranean influence in the composition of bioclimatic belts. These differences only become noticeable at the Early-Middle Holocene transition being 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 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.

(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 fir, yew and beech is relevant for the reconstruction of the ancient distribution of these species and sheds light on the influence of human impact on their current distribution. It supports the existence of a potential long-lasting refugia in the El Port massif (NE Iberia) where relict populations of *Taxus baccata* and *Fagus sylvatica* still exist today.

REFERENCES

Alba Sánchez F, López Sáez JA, Pando BBD, Linares JC, Nieto Lugilde D, López Merino L (2010) Past and present potential distribution of the Iberian *Abies* species: a phytogeographic approach using fossil pollen data and species distribution models. Diversity and Distributions 16(2): 214-228.

Alcolea M (2017) El paisaje vegetal y la explotación del combustible: estudio antracológico del Arenal de la Fonseca (Ladruñán, Teruel). In: Utrilla P, Domingo R and Bea M (eds) El Arenal de la Fonseca (Ladruñán-Castellote, Teruel). Ocupaciones prehistóricas del Graveatiense al Neolítico. Monografías Arqueológicas 52. Zaragoza: Prensas Universitarias de la Universidad de Zaragoza, pp. 167-176.

Alcolea M (2018) Donde hubo fuego: estudio de la gestión humana de la madera como recurso en el valle del Ebro entre el Tardiglaciar y el Holoceno Medio. Monografías Arqueológicas 53. Zaragoza: Prensas de la Universidad de Zaragoza.

Alcolea M, Domingo R, Piqué R and Montes L (2017) Landscape and firewood at Espantalobos Mesolithic site (Huesca, Spain). First results. Quaternary International 457: 198-210.

599 Alcolea M, Dufraisse A, Royo M, Mazo C, de Luis M, Longares LA, Utrilla P and
600 Fábregas R (2021) Dendro-anthracological tools applied to Scots type pine forests
601 exploitation as fuel during the Mesolithic-Neolithic transition in the southern central pre-
602 Pyrenees (Spain). Quaternary International 593-594: 332-345.

604 Alía R, Mancha JA, Sánchez de Ron D, Barba D, Climent J, García del Barrio JM, Notivol
605 N and Iglesias S (2009) Regiones de procedencia de especies forestales en España.
606 Madrid: Organismo Autónomo Parques Nacionales, pp 107-112.

608 Allué E (2002) Dinámica de la vegetación y explotación del combustible leñoso durante
609 el Pleiistoceno Superior y el Holoceno del Noreste de la Península Ibérica a partir del
610 análisis antracológico. PhD Thesis, Universitat Rovira i Virgili, Spain.

612 Allué E, Caceres I, Fontanals M, García M, Ollé A, Saladié P and Huguet R (2007) La
613 Cativera (el Catllar, Tarragonès). In: Jornades d'Arqueologia Comarques de Tarragona
614 (Tortosa 1999), Tarragona, Spain, pp. 29-45. Barcelona: Generalitat de Catalunya,
615 Departament de Cultura.

617 Allué E, Vernet JL and Cebrià A (2009) Holocene vegetational landscapes of NE Iberia:
618 charcoal analysis from Cova de la Guineu, Barcelona, Spain. The Holocene 19(5): 765-
619 773.

621 Allué E, Fullola JM, Mangado X, Petit MÀ, Bartrolí R and Tejero JM (2013) La séquence
622 anthracologique de la grotte du Parco (Alòs de Balaguer, Espagne): paysages et gestion
623 du combustible chez les derniers chasseurs-cueilleurs. L'Anthropologie 117(4): 420-435.

625 Antolín F, Jacomet S and Buxó R (2015) The hard knock life. Archaeobotanical data on
626 farming practices during the Neolithic (5400–2300 cal BC) in the NE of the Iberian
627 Peninsula. Journal of Archaeological Science 61: 90-104.

629 Antolín F, Navarrete V, Saña M, Viñerta A and Gassiot E (2018) Herders in the
630 mountains and farmers in the plains? A comparative evaluation of the archaeobiological
631 record from Neolithic sites in the eastern Iberian Pyrenees and the southern lower lands.
632 Quaternary International 484: 75-93.

634 Aranbarri J, González-Sampériz P, Valero-Garcés B, Moreno A, Gil-Romera G, Sevilla-
635 Callejo M, García-Prieto E, Di Rita F, Mata MP, Morellón M, Magri D, Rodríguez-
636 Lázaro J and Carrión JS (2014) Rapid climatic changes and resilient vegetation during
637 the Lateglacial and Holocene in a continental region of south-western Europe. Global and
638 Planetary Change 114: 50-65.

640 Aranbarri J, Bartolomé M, Alcolea M, Sancho C, Celant A, González-Sampériz P, Arenas
641 C, Magri D and Rodríguez-Lázaro J (2016) Palaeobotanical insights from early-mid
642 Holocene fluvial tufas in the Moncayo natural park (Iberian range, NE Spain): regional
643 correlations and biogeographic implications. Review of Palaeobotany and Palynology
644 234: 31-43.

Aranbarri J, Alcolea M, Badal E, Vila S, Allué E, Iriarte-Chiapusso MJ, Sebastián M, Magri D and González-Sampériz P (2020) Holocene history of Aleppo pine (Pinus halepensis Mill.) woodlands in the Ebro Basin (NE Spain): Climate-biased or human-induced? Review of Palaeobotany and Palynology 104240.

Auñón-García FJ, Alía R, Sánchez de Ron D, de Miguel J, García del Barrio JM (2011) SIG-FOREST. Visor SIG de especies forestales. Foresta 51: 38-42.

Aura JE, Carrión Y, Estrelles E and Jorda GP (2005) Plant economy of hunter-gatherer groups at the end of the last Ice Age: plant macroremains from the cave of Santa Maira (Alacant, Spain) ca. 12000-9000 BP. Vegetation History and Archaeobotany 14(4): 542-550.

Badal E (2004) Análisis antracológico de los restos del fuego doméstico del abrigo de Los Baños (Ariño, Teruel). In: Utrilla P and Rodanés JM (eds.) Un asentamiento mesolítico en el valle del río Martín. El abrigo de los Baños (Ariño, Teruel). Monografías arqueológicas, 39. Universidad de Zaragoza, pp. 63-73

Badal E, Carrión Y, Rivera D and Uzquiano P (2003) La arqueobotánica en cuevas y abrigo: objetivos y métodos de muestreo. In: Buxó R and Piqué R (dirs) La recogida de muestras en arqueobotánica: objetivos y propuestas metodológicas. La gestión de los recursos vegetales y la transformación del paleopaisaje en el Mediterráneo occidental. Barcelona: Museu d'Arqueologia de Catalunya, pp. 17-27.

Badal E, Carrión Y, Chabal L, Figueiral I and Thiébault S (2017) Neolithic human societies and woodlands in the North-Western Mediterranean region: wood and charcoal analysis. In: García-Puchol O and Salazar-García DC (eds) Times of Neolithic Transition along the Western Mediterranean. Springer International Publishing, pp. 135-169.

Bennett KD, Tzedakis PC and Willis KJ (1991) Quaternary refugia of north European trees. Journal of biogeography 18(1): 103-115.

Bosch J (1989) Memòria de les excavacions 1989: el Molló de la Torre (Amposta, Montsià). Report, Servei d'Arqueologia i Paleontologia, Generalitat de Catalunya.

Bosch J (2001) Les ocupacions prehistòriques de caçadors recol·lectors a la Cova del Vidre (Roquetes). Assentament i clima. Recerca 5: 9-20.

Bosch J (2015) La Cueva del Vidre (Roquetes, Bajo Ebro). Asentamiento del Mesolítico y del Neolítico Antiguo en la Cordillera Costera Catalana meridional. In: Gonçalves V, Diniz M and Sousa AC (eds) Actas del 5º Congreso do Neolítico peninsular, Faculdade de Letras da Universidade de Lisboa, 7-9 abril 2011, pp. 182-189. Lisboa: UNIARQ.

Bosch J (2016) La cerámica de la Cova del Vidre (Roquetes) y el Neolítico Cardial Franco-Ibérico. In: Bonet H (ed) Del neolític a l'edat del bronze en el Mediterrani occidental. Estudis en Homenatge a Bernat Martí Oliver. Valencia: Diputació de València, Museu de Prehistòria de València, pp. 109-116.

693 Bosch J, Forcadell T, and Villalbí MM (1996) El "Barranc de Fabra": un asentamiento de
694 inicios del IV milenio a.C. en el curso inferior del Ebro. Rubricatum 1(1): 391-396.
695
696 Bradshaw RHW, Kito N and Giesecke T (2010) Factors influencing the Holocene history
697 of Fagus. Forest Ecology and Management 259(11): 2204-2212.
698
699 Bronk Ramsey C and Lee S (2013) Recent and planned developments of the program
700 OxCal. Radiocarbon 55(2/3): 720-730.
701
702 Burjachs F, Jones SE, Giralt S and Fernández-López de Pablo J (2016) Lateglacial to
703 Early Holocene recursive aridity events in the SE Mediterranean Iberian Peninsula: The
704 Salines playa lake case study. Quaternary International 403: 187-200.
705
706 Buxó R and Piqué R (2008) Arqueobotánica. Los usos de las plantas en la península
707 Ibérica. Barcelona: Ariel Prehistoria.
708
709 Camprodon J, Casals P, Cariati A, Guixé D, Rios AI, Buquera X, Reverte J, Sánchez S,
710 Argerichi G and García-Martí X (2014) Life TAXUS, proyecto para la conservación del
711 habitat del tejo en Catalunya. Objetivos, metodologias y primeros resultados. In:
712 Proceedings IV International Yew Workshop. Management, conservation and culture of
713 the yew forests in the Mediterrenean forest ecosystems, pp. 13-148. Lleida: Centre
714 Tecnològic Forestal de Catalunya.
715
716 Carrión JS, Yll EI, Walker MJ, Legaz AJ, Chaín C and López A (2003) Glacial refugia
717 of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new
718 evidence from cave pollen at two Neanderthal man sites. Global Ecology and
719 Biogeography 12(2): 119-129.
720
721 Carrión Y (1999) Datos preliminares del antracoanálisis de l'Abric de la Falguera (Alcoi,
722 Alacant). Sagvntvm Extra 2: 37-43.
723
724 Caruso L and Piqué R (2014) Landscape and forest exploitation at the ancient Neolithic
725 site of La Draga (Banyoles, Spain). The Holocene 24(3): 266-273.
726
727 Castroviejo S (coord gen) (1986-2012) Flora iberica 1-8, 10-15, 17-18, 21. Madrid: Real
728 Jardín Botánico, CSIC.
729
730 Caudullo G, Welk E, and San Miguel-Ayanz J (2017) Chorological maps for the main
731 European woody species. Data in Brief 12: 662-666. doi: 10.1016/j.dib.2017.05.007.
732
733 Chabal L (1997) Forêts et sociétés en Languedoc (Néolithique final, Antiquité tardive) :
734 l'anthracologie, méthode et paléoécologie. Documents d'Archéologie Française 63. Paris:
735 Éditions de la Maison des sciences de l'homme.
736
737 Chabal L, Fabre L, Terral JF and Théry-Parisot I (1999). L'anthracologie. In: Fédière A
738 (ed) La botanique. Paris: Errance, pp. 43-104.
739

Chabal L and Heinz C (2021) Reconstructing the heterogeneity of past woodlands in anthracology using the spatial distribution of charcoals in archaeological layers: applied to the postglacial occupation of the Abeurador cave (Hérault) in the south of France. Quaternary International 593-594: 19-35.

Costa M, Morla C and Sainz H (2001) Los bosques ibéricos. Una interpretación geobotánica. Madrid: Planeta.

Cunill R, Soriano JM, Bal MC, Pèlachs A, Rodríguez JM and Pérez-Obiol R (2013) Holocene high-altitude vegetation dynamics in the Pyrenees: a pedoanthracology contribution to an interdisciplinary approach. Quaternary International 289: 60-70.

Cunill R, Métailié JP, Galop D, Poublanc S, De Munnik N (2015) Palaeoecological study of Pyrenean lowland fir forests: Exploring mid–late Holocene history of *Abies alba* in Montbrun (Ariège, France). Quaternary International 366: 37-50.

Delhon C, Martin L, Argant J and Thiebault S (2008) Shepherds and plants in the Alps: multi-proxy archaeobotanical analysis of Neolithic dung from "La Grande Rivoire" (Isère, France). Journal of Archaeological Science 35(11): 2937-2952.

Dubreuil M, Riba M, González-Martínez SC, Vendramin GG, Sebastiani F and Mayol M (2010) Genetic effects of chronic habitat fragmentation revisited: strong genetic structure in a temperate tree, Taxus baccata (Taxaceae), with great dispersal capability. American Journal of Botany 97(2): 303-310.

Ejarque A, Miras Y, Riera S, Palet JM, Orengo HA (2010) Testing micro-regional variability in the Holocene shaping of high mountain cultural landscapes: a palaeoenvironmental case-study in the eastern Pyrenees. Journal of Archaeologiical Science 37: 1468-1479.

Ferré M and Piqué R (2002) Explotació del paisatge forestal al Neolític Final: Resultats preliminars de l'estudi antracològic de la Prunera (Olot). In: Pirineus i veïns al 3er mil.lenni AC. De la fi del Neolític a l'edat del Bronze entre l'Ebre i la Garona, pp. 235-243. Moià-Puigcerdà: Institut d'Estudis Ceretans.

Follieri M, Roure JM, Giardini M, Magri D, Narcisi B, Pantaleón-Cano J, Pérez-Olbiol R, Sadori L and Yll EI (2000) Desertification trends in Spain and Italy based on pollen analysis. In: Balabanis P, Peter D, Ghazi A. and Tsogas M (eds) Mediterranean desertification. Research results and policy implications, Proceedings of the International Conference 29 October to 1 November 1996, pp. 33-44. Crete: Greece European Commission.

García Esteban L, Guindeo Casasus A, Peraza Oramas C and De Palacios P (2003) La madera y su anatomía. Anomalías y defectos, estructura microscópica de coníferas y frondosas, identificación de maderas, descripción de especies y pared celular. Madrid: Mundi-Prensa.

786   Giesecke T and Brewer S (2018) Notes on the postglacial spread of abundant European
787   tree taxa. Vegetation History and Archaeobotany 27(2): 337-349.
788

789   González-Sampériz P, Utrilla P, Mazo C, Valero B, Sopena MC, Morellón M, Sebastián
790   M, Moreno A and Martínez-Bea M (2009) Patterns of human occupation during the early
791   Holocene in the Central Ebro Basin (NE Spain) in response to the 8.2 ka climatic event.
792   Quaternary Research 71(2): 121-132.
793

794   Gramsch B (ed) (1981) Mesolithikum in Europe. Veröffentlichungen des Museum für
795   Urund Frühgeschichte, Postdam. Berlin: Deutscher.
796

797   Greguss P (1955) Identification of Living Gymnosperms on the Basis of Xylotomy.
798   Budapest: Akadémiai Kiado.
799

800   Heinz C and Thiébault S (1998) Characterization and palaeoecological significance of
801   archaeological charcoal assemblages during late and post-glacial phases in southern
802   France. Quaternary Research 50(1): 56-68.
803

804   Huntley B and Birks HJB (1983) An atlas of past and present pollen maps for Europe, 0-
805   13,000 years ago. Cambridge: Cambridge University Press.
806

807   Jacquiot C, Trenard Y and Dirol D (1973) Atlas d'anatomie des bois des angiospermes
808   (Essences feuillues). Paris: Centre de Technologie du Bois.
809

810   Kabukcu C and Chabal L (2021) Sampling and quantitative analysis methods in
811   anthracology from archaeological contexts: Achievements and prospects. Quaternary
812   International 593-594: 6-10.
813

814   Laborda R (2019) El Neolítico antiguo en el Valle Medio del Ebro. Una visión desde la
815   cerámica y las dataciones radiocarbónicas. Monografías Arqueológicas 55. Zaragoza:
816   Prensas de la Universidad de Zaragoza.
817

818   Liepelt S, Cheddadi R, de Beaulieu JL, Fady B, Gömöry D, Hussendörfer E, Konnertg
819   M, Litth T, Longaueri R, Terhürne-Bersonh R, Ziegenhagen B (2009) Postglacial range
820   expansion and its genetic imprints in *Abies alba* (Mill.): a synthesis from palaeobotanic
821   and genetic data. Review of Palaeobotany and palynology 153(1-2): 139-149.

822   López-Merino L, López-Sáez JA, Ruíz-Zapata MB and Gil-García MJ (2008)
823   Reconstructing the history of beech (Fagus sylvatica L.) in the north-western Iberian
824   Range (Spain): from Late-Glacial refugia to the Holocene anthropic-induced forests.
825   Review of Palaeobotany and Palynology 152(1-2): 58-65.
826

827   Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latałowa M,
828   Litt T, Paule L, Roure JM, Tantau I, Van Der Knaap WO, Petit RJ and De Beaulieu JL
829   (2006) A new scenario for the Quaternary history of European beech populations:
830   palaeobotanical evidence and genetic consequences. New phytologist 171(1): 199-221.
831

832 Martin L and Thiébault S (2010) L'if (Taxus baccata L.) : histoire et usage d'un arbre
833 durant la Préhistoire récente. L'exemple du domaine alpin et circum-alpin. Des hommes
834 et des plantes : exploitation du milieu et gestion des ressources végétales de la Préhistoire
835 à nos jours, Actes des XXXèmes rencontres internationales d'archéologie et d'histoire
836 d'Antibes, pp. 1-20. Antibes: APDCA.
837
838 Martin L, Delhon C, Thiébault S and Pelletier D (2012) Plant exploitation and diet in
839 altitude during Mesolithic and Neolithic: Archaeobotanical analysis from a hunting camp
840 in the Chartreuse massif (l'Aulp-du-Seuil, Isère, France). Review of Palaeobotany and
841 Palynology 185: 26-34.
842
843 Martínez-Tuleda A, Robles-Cuenca F, Santisteban-Bové C, Grün R and Hentzsch B
844 (1986) Los travertinos del rio Matarraña, Beceite (Teruel), como indicadores
845 paleoclimaticos del Cuaternario. In: López-Vera F (ed) Quaternary climate in Western
846 Mediterranean, pp. 307-324. Madrid: Universidad Autonoma de Madrid.
847
848 Mazo C and Montes L (1992) La transición Epipaleolítico-Neolítico antiguo en el abrigo
849 de El Pontet (Maella, Zaragoza). In: Utrilla P (coord) Aragón/Litoral mediterráneo:
850 intercambios culturales durante la Prehistoria, pp. 243-254. Zaragoza: Institución
851 Fernando el Católico.
852
853 Miras Y, Ejarque A, Orengo HA, Riera S and Palet JM (2007) Dynamique holocène de
854 la végétation et occupation des Pyrénées andorranes depuis le Néolithique ancien, d'après
855 l'analyse pollinique de la tourbière de Bosc dels Estanyons (2180 m, Vall del Madriu,
856 Andorre). Comptes Rendus Palevol 6(4): 291-300.
857
858 Muller SD, Nakagawa T, de Beaulieu JL, Court-Picon M, Carcaillet C, Miramont C,
859 Roiron P, Boutterin C, Ali AA, Bruneton E (2007) Post-glacial migration of silver fir
860 (*Abies alba* Mill.) in the south-western Alps. Journal of Biogeography 37: 876-899.
861 Obea L, Celma M, Piqué R, Gassiot E, Martín-Seijo M, Salvador G, Rodríguez-Antón D,
862 Quesada M, Mazzuco N, García-Casas D, Díaz-Bonilla S, Clemente I (2021) Firewood-
863 gathering strategies in high mountain areas of the Parc Nacional d'Aigüestortes i Estany
864 de Sant Maurici (Central Pyrenees) during Prehistory. Quaternary International 593-594:
865 129-143.
866
867 Oms FX, Terradas X, Morell B and Gibaja JF (2018) Mesolithic-Neolithic transition in
868 the northeast of Iberia: Chronology and socioeconomic dynamics. Quaternary
869 International 470: 383-397.
870
871 Pèlachs A, Pérez-Obiol R, Ninyerola M, Nadal J (2009) Landscape dynamics of *Abies*
872 and *Fagus* in the southern Pyrenees during the last 2200 years as a result of anthropogenic
873 impacts. Review of palaeobotany and palynology 156(3-4): 337-349.
874 Pérez Díaz S, López Sáez JA, Ruiz Alonso M, Zapata L and Abel Schaad D (2013)
875 Holocene history of Taxus baccata in the Basque Mountains (Northern Iberian Peninsula).
876 LAZAROA 34: 29-41.
877

Pérez-Obiol R, Julià R (1992) Climatic Change on the Iberian Peninsula Recorded in a 30.000-yr Pollen Record from Lake Banyoles. Quaternary Research 41: 91-98

Pérez-Obiol R (2007) Palynological evidence for climatic change along the eastern Iberian Peninsula and Balearic Islands. Contributions to science 3(3): 415-419.

Pérez-Obiol R, Bal MC, Pèlachs A, Cunill R and Soriano JM (2012) Vegetation dynamics and anthropogenically forced changes in the Estanilles peat bog (southern Pyrenees) during the last seven millennia. Vegetation History and Archaeobotany 21: 385-396.

Pérez-Sanz A, González-Sampériz P, Moreno A, Valero-Garcés B, Gil-Romera G, Rieradevall M, Tarrts P, Lasheras-Álvarez L, Morellón M, Belmonte A, Sancho C, Sevilla-Callejo M and Navas A (2013) Holocene climate variability, vegetation dynamics and fire regime in the central Pyrenees: the Basa de la Mora sequence (NE Spain). Quaternary Sciences Review 73: 149-169.

Piqué R (1999) Producción y uso del combustible vegetal: una evaluación arqueológica. Barcelona: CSIC Press.

Piqué R (2011) Paisatge i aprofitament de recursos vegetals en l'assentament neolític antic de Camp de Colomer (Juberri, Andorra). Report, Dept. Prehistòria, Universitat Autònoma de Barcelona.

Piqué, R.; Revelles, J.; Burjachs, F.; Caruso Fermé, L., Pérez-Obiol, R. 2018. Interdisciplinary approach to the landscape and firewood exploitation during the Holocene at La Garrotxa (Girona, NE Iberia). Quaternary International 463: 401-413.

Rasmussen SO, Andersen KK, Svensson AM, Steffensen JP, Vinther BM, Clausen HB, Siggaard-Andersen SJ, Johnsen LB, Larsen D, Dahl-Jensen M, Bigler R, Röthlisberger H, Fischer K, Goto-Azuma ME and Hansson RU (2006) A new Greenland ice core chronology for the last glacial termination. Journal of Geophysical Research: Atmospheres 111(D6).

Revelles J (2017) Archaeoecology of Neolithisation. Human-environment interactions in the NE Iberian Peninsula during the Early Neolithic. Journal of Archaeological Science: Reports 15: 437-445.

Revelles J, Cho S, Iriarte E, Burjachs F, Van Geel B, Palomo A, Piqué R, Peña-Chocarro L and Terradas X (2015) Mid-Holocene vegetation history and Neolithic land-use in theLake Banyoles area (Girona, Spain). Palaeogeography Palaeoclimatology Palaeoecology 435: 70-85.

Reimer, P.J.; Austin, W.E.N.; Bard, E.; Bayliss, A.; Blackwell, P.G.; Bronk Ramsey, C.; Butzin, M.; Cheng, H.; Edwards, R.L.; Friedrich, M.; Grootes, P.M.; Guilderson, T.P.; Hajdas, I.; Heaton, T.J.; Hogg, A.G.; Hughen, K.A.; Kromer, B.; Manning, S.W.; Muscheler, R.; Palmer, J.G.; Pearson, C.; van der Plicht, J.; Reimer, R.W.; Richards, D.A.; Scott, E.M.; Southon, J.R.; Turney, C.S.M.; Wacker, L.; Adolphi, F.; Büntgen, U.;

924 Capano, M.; Fahrni, S.M.; Fogtmann-Schulz, A.; Friedrich, R.; Köhler, P.; Kudsk, S.;
925 Miyake, F.; Olsen, J.; Reinig, F.; Sakamoto, M.; Sookdeo, A.; Talamo, S. (2020): The
926 IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP).
927 Radiocarbon 62: 725-757.

929 Riera S and Esteban A (1994) Vegetation history and human activity during the last 6000
930 years on the central Catalan coast (northeastern Iberian Peninsula). Vegetation History
931 and Archaeobotany 3(1): 7-23.

933 Roberts N, Eastwood WJ, Kuzucuoğlu C, Fiorentino G and Caracuta V (2011) Climatic,
934 vegetation and cultural change in the eastern Mediterranean during the mid-Holocene
935 environmental transition. The Holocene 21(1): 147-162.

937 Ros MT (1992) Les apports de l'anthracologie á l'étude du paléoenvironment végétal en
938 Catalogne (Espagne). Bulletin de la Societé Botanique de France, Actualités botaniques
939 139 : 483-493.

941 Ros MT (1995) Estudi antracologic de tres jaciments de la vall de Llierca (Garrotxa,
942 Catalunya). L"activitat humana i el medi vegetal des del Neolitic Antic al Bronze Final.
943 X Col.loqui intermancional d'arquelogia de Puigcerdà. Cultures i Medi de la Prehistoria
944 a l'Edat Mitjana. Homenatje al Professor Guilaine, pp. 87-96. Puigcerdà: Institut
945 d'Estudis Ceretans.

947 Ros MT (1996) Datos antracológicos sobre la diversidad paisajistica de Catalunya en el
948 Neolítico. Rubricatum 1: 43-56.

950 Ruiz-Alonso M, Pérez-Díaz S and López-Sáez JA (2019): From glacial refugia to the
951 current landscape configuration: permanence, expansion and forest management of Fagus
952 sylvatica L. in the Western Pyrenean Region (Northern Iberian Peninsula). Vegetation
953 History and Archaeobotany 28(5): 481-496.

955 Schweingruber FH (1990) Anatomie europäischer Hölzer. Berna and Stuttgart: Haupt.

957 Senar Lluch R (2011) Aportaciones botánicas para la comarca valenciana dels Ports. Flora
958 Montibérica 48: 102-107.

960 Soto A, Alday A, Montes L, Utrilla P, Perales U and Domingo R (2015) Epipalaeolithic
961 assemblages in the Western Ebro Basin (Spain): The difficult identification of cultural
962 entities. Quaternary International 364: 144-152.

964 Terhürne-Berson R, Litt T, Cheddadi R (2004) The spread of *Abies* throughout Europe
965 since the last glacial period: combined macrofossil and pollen data. Vegetation history
966 and Archaeobotany 13(4): 257-268.

967 Théry-Parisot I, Chabal L and Chrzavzez J (2010) Anthracology and taphonomy, from
968 wood gathering to charcoal analysis. A review of the taphonomic processes modifying

969   charcoal assemblages, in archaeological contexts. Palaeogeography, Palaeoclimatology,
970   Palaeoecology 291(1) : 142-153.
971
972   Thévenin A (1981) La fin d l''epipaléolithique et les debuts du mésolithique dans le nord
973   du Jura français. In Gramsch B (ed) Mesolithikum in Europe. Veröffentlichungen des
974   Museum für Ur und Frühgeschichte. Postdam, 14/15, pp. 25-32. Berlin: Deutscher.
975
976   Thomas ER, Wolff EW, Mulvaney R, Steffensen JP, Johnsen SJ, Arrowsmith C, White
977   JWC, Vaughn B and Popp T (2007) The 8.2 ka event from Greenland ice cores.
978   Quaternary Science Reviews 26(1-2): 70-81.
979
980   Utrilla P and Bea M (2012) El asentamiento neolítico del Plano del Pulido (Caspe,
981   Zaragoza). Rubricatum 5: 69-78.
982
983   Utrilla P, Domingo R and Bea M (2017) El Arenal de Fonseca (Castellote, Teruel):
984   ocupaciones prehistóricas del Gravetiense al Neolítico. Monografías Arqueológicas 52.
985   Zaragoza: Prensas de la Universidad de Zaragoza.
986
987   Utrilla P, Montes L, Mazo C, Martínez-Bea M and Domingo R (2009) El Mesolítico
988   Geométrico en Aragón. In: Utrilla P and Montes L (eds) El Mesolítico Geométrico en la
989   Península Ibérica. Monografías Arqueológicas 44, pp. 131-190. Zaragoza: Prensas de la
990   Universidad de Zaragoza.
991
992   Uzquiano P, Allué E, Antolín F, Burjachs F, Picornell L, Piqué R and Zapata L (2015)
993   All about yew: on the trail of Taxus baccata in southwest Europe by means of integrated
994   palaeobotanical and archaeobotanical studies. Vegetation History and Archaeobotany
995   24(1): 229-247.
996
997   Vegas J, Ruíz-Zapata B, Ortíz JE, Galán L, Torres T, García Cortés A, Gil-García MJ,
998   Pérez-González A and Galllardo Millán JL (2009). Identification of arid phases during
999   the last 50-cal ka BP from the Fuentillejo mar-lacustrine record (Campo de Calatrava
1000   Volcanic Field, Spain). Journal of Quaternary Science 25: 1051-1062.
1001
1002   Vernet JL (1980) La végétation du bassin de l'Aude, entre Pyrénées et Massif Central, au
1003   tardiglaciaire et au postglaciaire d'après l'analyse anthracologique. Review of
1004   Palaeobotany and Palynology 30: 33-55.
1005
1006   Vernet JL, Ogereau P, Figueiral I, Machado Yanes C and Uzquiano P (2001) Guide
1007   d'identification des charbons de bois préhistoriques et récents. Sud-Ouest de l'Europe:
1008   France, Péninsule ibérique et iles Canaries. Paris: CNRS Éditions.
1009
1010   Vicente M, Martínez R, Guillem P, Iborra MP (2009) El Cingle del Mas Cremat (Portell
1011   de Morella, Castelló). Un asentamiento en altura, con ocupaciones del Mesolítico
1012   reciente. In: Utrilla P and Montes L (eds.) El mesolítico geométrico en la Península
1013   Ibérica. Universidad de Zaragoza. pp. 361-374.
1014

1015 Vicente M Martínez R, Guillem P, de Haro S, Pérez Jordà G, Pérez Millán R, Ruíz Pérez

1016 JM, Iborra MP and Valcárcel A (2010) El Cingle del Mas Cremat (Portell de Morella,

1017 Castellón) Un asentamiento en altura con ocupaciones del Mesolítico Reciente al

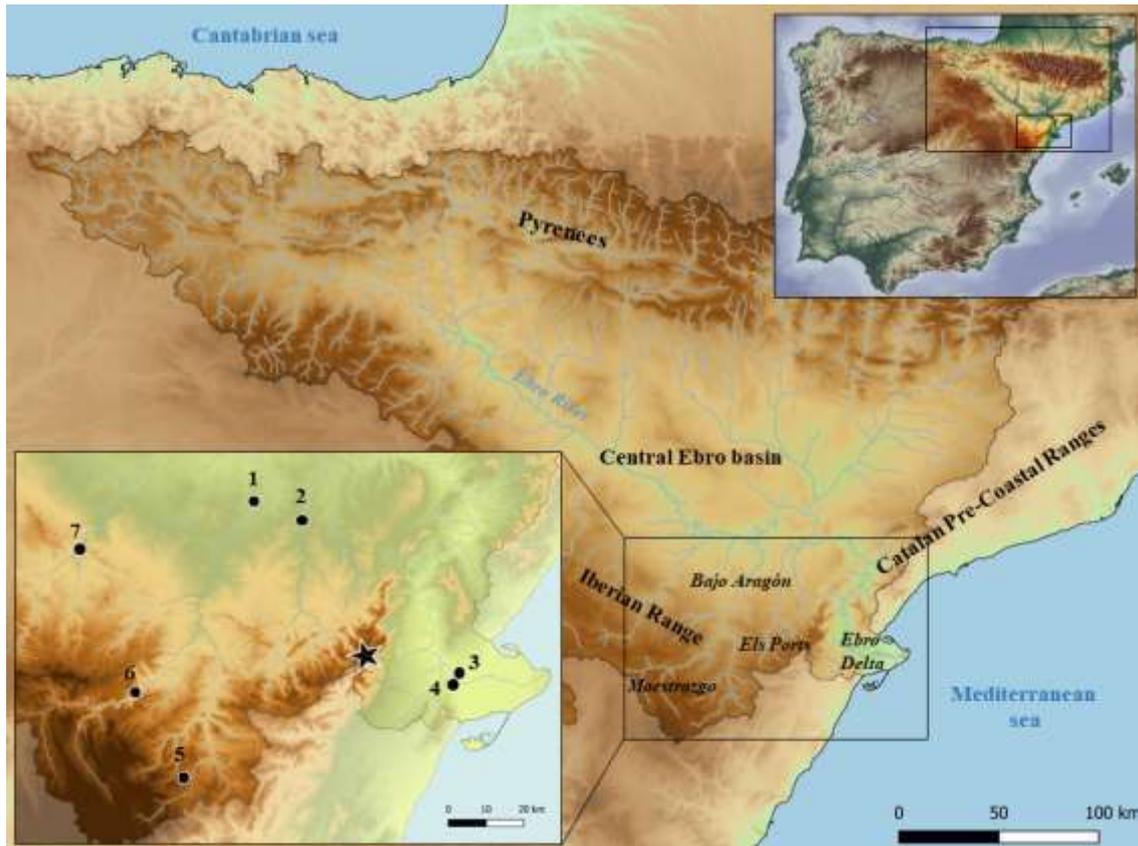1018 Neolítico Final. Renomar S.A. EIN Mediterráneo S.L.

1019

1020 Vidal-Matutano P (2015) Evidència de recol·lecció de teix (*Taxus baccata* L.). Recerques

1021 del Museu d'Alcoi 24: 7-20.

1022

1023 FIGURES

1024

1025

1026

1027 Figure 1. Geographical setting and site location. Black star: Cova del Vidre. Black points
1028 (nearby sites providing archaeobotanical data mentioned in the text): 1. Plano del Pulido
1029 (Caspe, Zaragoza), 2. El Pontet (Maella, Zaragoza), 3. Molló de la Torre (Amposta,
1030 Tarragona), 4. Barranc d'en Fabra (Amposta, Tarragona), 5. Mas Cremat (Portell de
1031 Morella, Castellón), 6. Arenal de Fonseca (Castellote, Teruel), 7. Los Baños (Ariño,
1032 Teruel). Base: MDT50 IGN (Spanish Government). Prepared by the authors.

1033
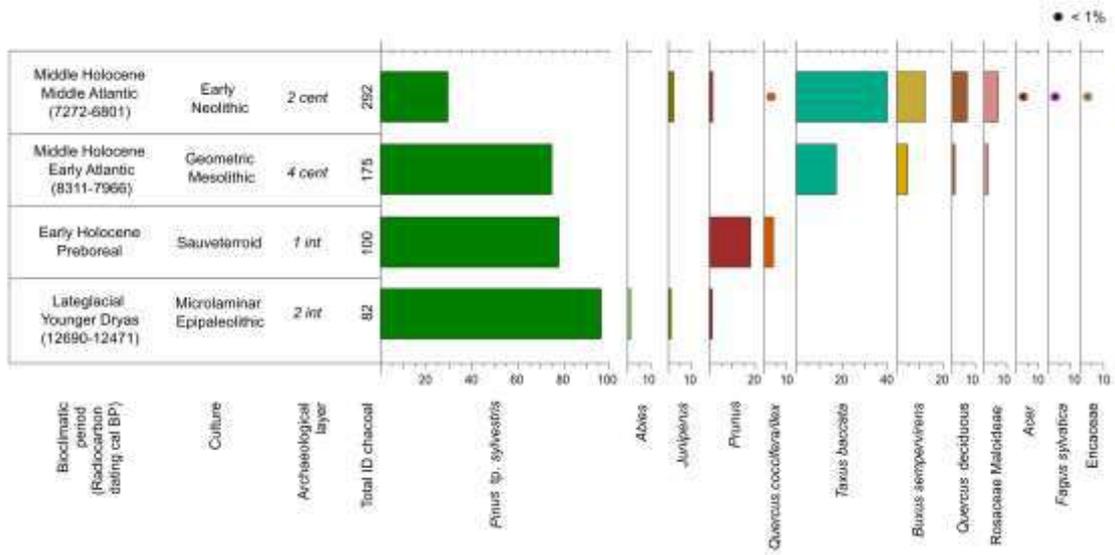
1034
1035
1036   Figure 2. Frequency diagram of anthracological remains from Cova del Vidre.
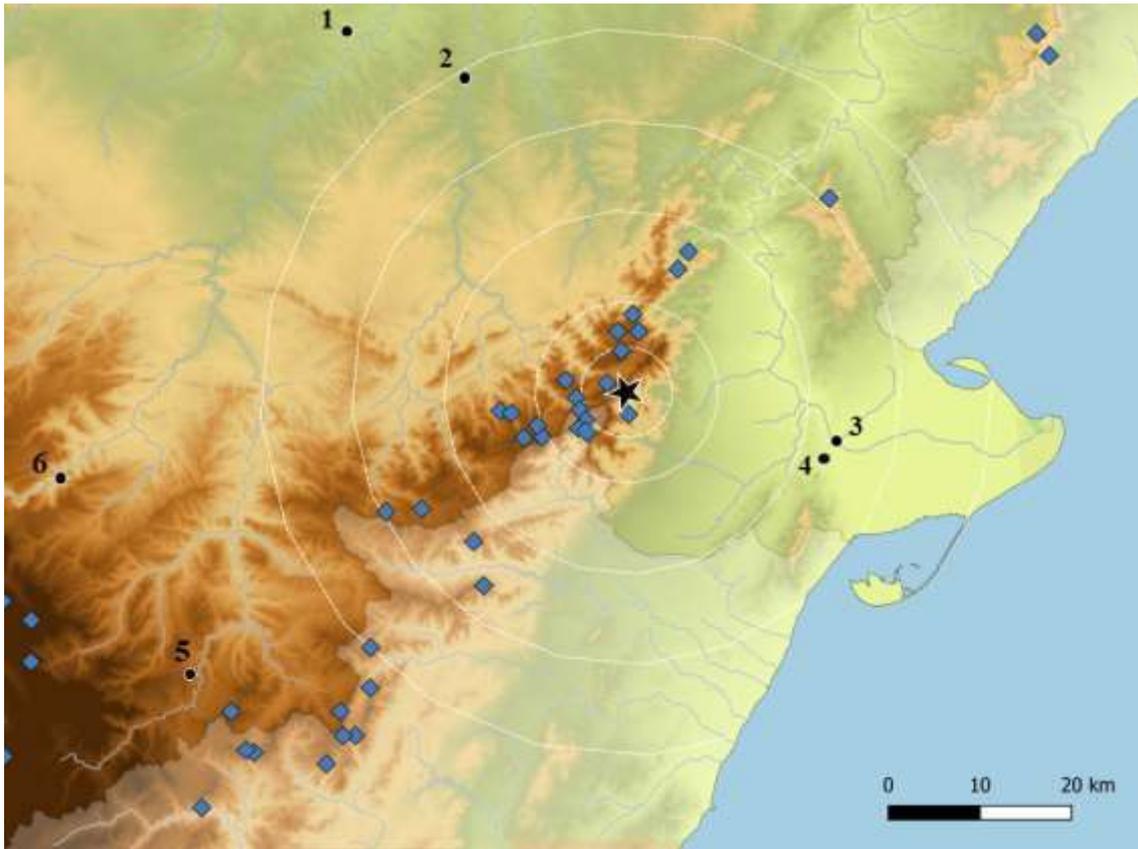1037
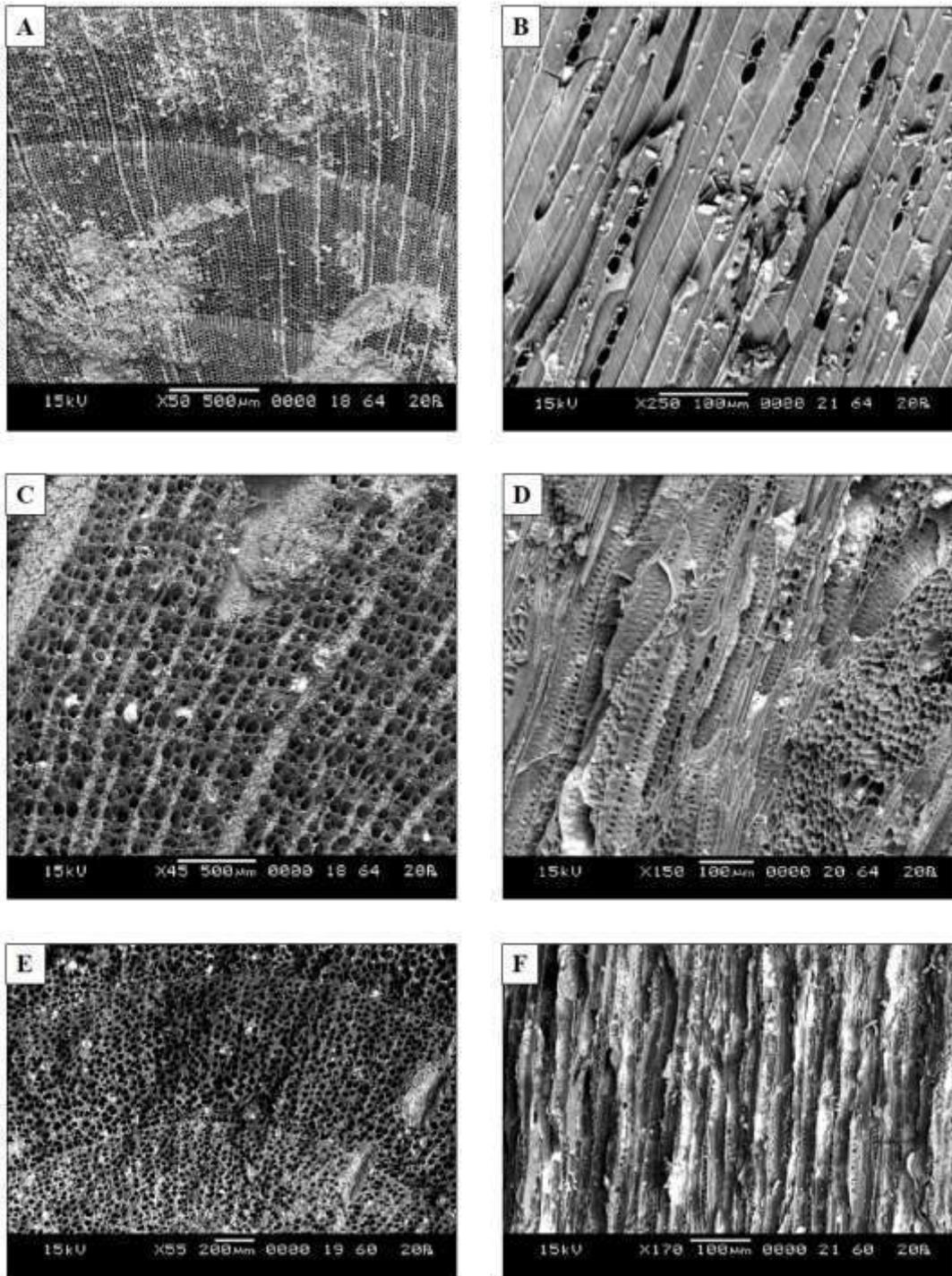
1038
1039
1040 Figure 3. ESEM images of selected taxa: A) *Taxus baccata*. Transverse section, B) *Taxus*
1041 *baccata*. Radial section, C) *Fagus sylvatica*. Transverse section, D) *Fagus sylvatica*.
1042 Radial section, E) Rosaceae Maloideae. Transverse section, F) Rosaceae Maloideae.
1043 Radial section.
1044

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 providing archaeobotanical data mentioned in the text): 1. Plano del Pulido, 2. El Pontet, 3. Molló de la Torre, 4. Barranc d'en Fabra, 5. Mas Cremat, 6. Arenal de Fonseca. Dashed white circles: distance from the site of 10, 20, 30, and 40 km. Base: MDT50 IGN (Spanish Government). Prepared by the authors.
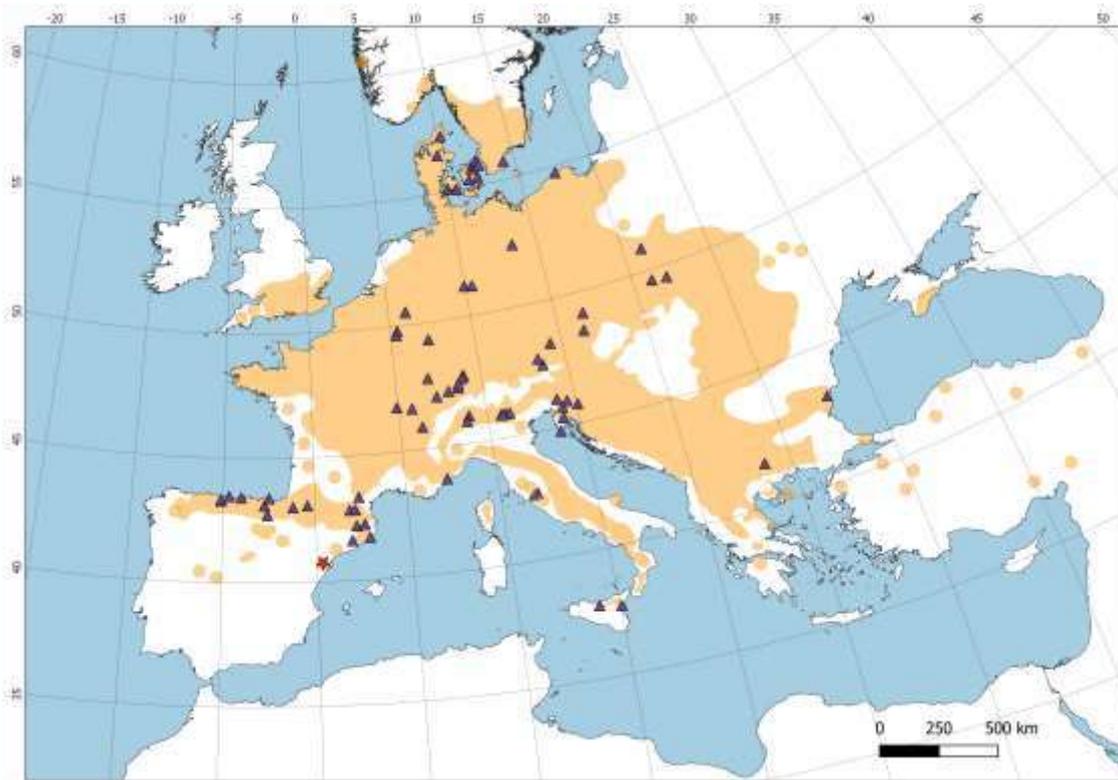
1054
1055
1056 Figure 5. Map of the modern and past distribution of beech (*Fagus sylvatica*) in Europe.
1057 Orange area: modern distribution after Alía et al., 2009 CIFOR-INIA. Purple triangles:
1058 geographical distribution of records containing macrofossil evidence (see references in
1059 Magri et al., 2006 supplementary material). Red star: Cova del Vidre site. Prepared by
1060 the authors.
1061
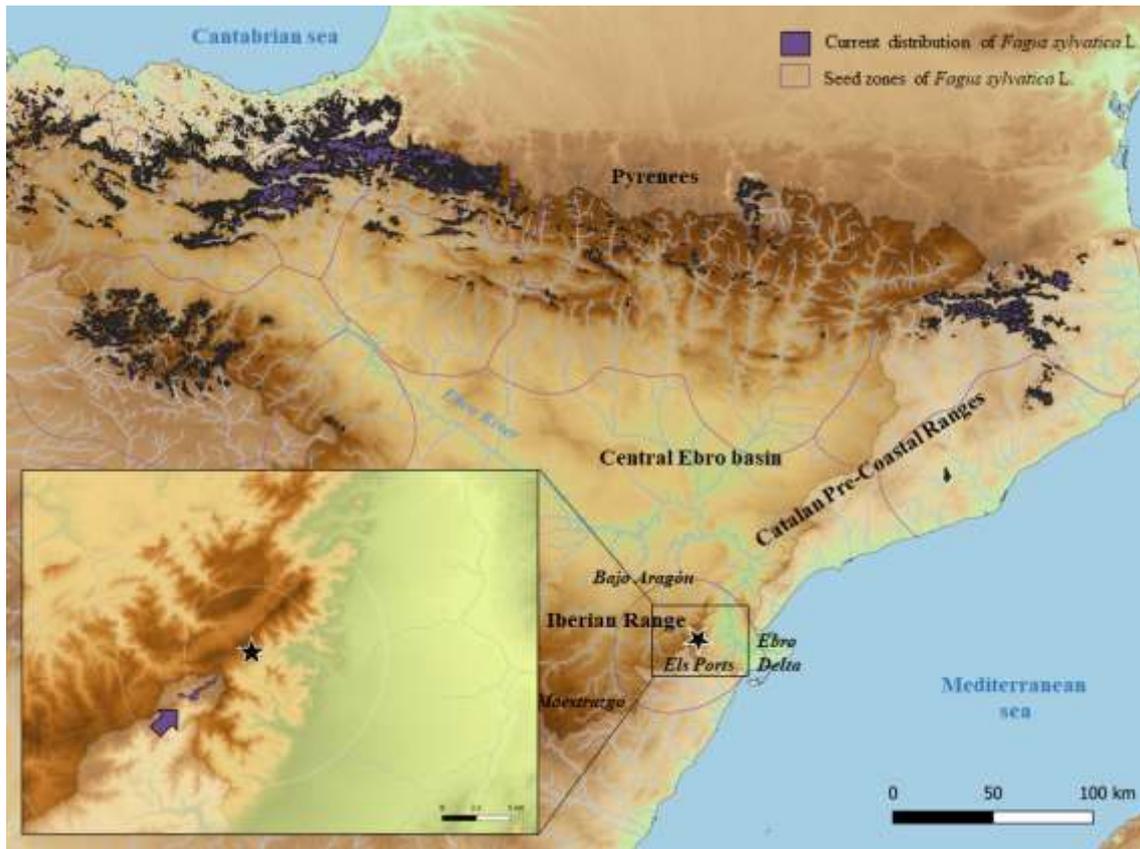
Figure 6. Current distribution and seed zones of *Fagus sylvatica* L. in NE Iberia. Data from CIFOR-INIA (http://www.inia.es/genfored.html) (Auñón-García et al. 2011). Black star: Cova del Vidre within the area containing small relict forests of *Fagus sylvatica* L. in El Port massif (*Buxo sempervirentis-Fagetum sylvaticae*) (Costa et al., 2001) Base: MDT50 IGN (Spanish Government). Prepared by the authors.