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

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11          Keywords: charcoal analysis, late hunter-gatherers, first farmers, Younger Dryas, Early  
12          Holocene, *Taxus baccata*, *Fagus sylvatica*.

13  
14          Abstract

15  
16          This study focuses on the analysis of wood charcoal from Cova del Vidre (Roquetes,  
17          Tarragona, Spain). This cave, located at an altitude of 1,000 m a.s.l., is a key site for  
18          understanding the transition from hunting and gathering to farming in a mountainous  
19          region of north-eastern Iberia so far unexplored by archaeobotany. The anthracological  
20          study is based on four archaeological levels from the Epipalaeolithic to the Early  
21          Neolithic dated between 12.9 and 6.8 kyr cal BP, i.e. from the Late Glacial period to the  
22          Middle Holocene. During the Younger Dryas, the record is dominated by a little varied  
23          spectrum of cryophilous pines (*Pinus* sp. *sylvestris*) and thorny shrubs revealing an open  
24          landscape where *Prunus* may prefigure the spread of temperate taxa. In the Early  
25          Holocene, a significant change in temperature and precipitation is evidenced, which  
26          promoted successional changes in plant communities, with a decline of pine and the  
27          sudden rise of temperate/Mediterranean taxa, such as *Prunus* and *Quercus coccifera/ilex*.  
28          During the Middle Holocene, other temperate taxa appear, such as *Quercus* deciduous,  
29          *Buxus sempervirens* and *Taxus baccata*, with yew finally dominating the anthracological  
30          record. The appearance and early development of temperate or Mediterranean species as  
31          early as the Younger Dryas and the Early Holocene periods, in a mountain context that  
32          had long been favourable for Scots pine, allows us to argue the local existence of a glacial  
33          refugium. Differences with the nearby sites in the lowlands demonstrate that altitudinal  
34          differences in vegetation were already established in the Holocene. Furthermore, the site  
35          helps to define the palaeodistribution of *Taxus baccata* and *Fagus sylvatica* in southern  
36          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 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).

## 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 Lluç, 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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3 138 2001). Systematic sampling of archaeozoological, archaeobotanical and sedimentary  
4 139 materials was also performed at the site to obtain palaeoenvironmental and  
5 140 palaeoeconomic information. Two main excavation areas were sampled in the large cave.  
6 141 The inner area (named *int*) in the deepest part of the cave and the central area (named  
7 142 *cent*) in the middle part (very close to the small cave) provided two complementary  
8 143 stratigraphic sequences (Bosch, 2015; 2016).  
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#### 12 145 2.4. Archaeological sequence

13 146  
14 147 At Cova del Vidre, four main human occupations have been documented (Bosh, 2001,  
15 148 2015; 2016) in accordance with the cultural processes known in the region (Soto et al.,  
16 149 2015; Oms et al., 2018). Three of them are related to late Pleistocene and early Holocene  
17 150 hunter-gatherer occupation (Epipaleolithic-Mesolithic). The oldest occupation (layer  
18 151 2 *int*) belongs to the Microlaminar Epipaleolithic tradition. Radiocarbon dating situates it  
19 152 during the Younger Dryas (Table 1). Above it, layer 1 *int*, with some geometric  
20 153 microliths, belongs to the Early Holocene Sauveterroid tradition in the Mediterranean  
21 154 region. The most recent hunter-gatherer occupation (layer 4 *cent*) belongs to the  
22 155 Geometric Mesolithic. Radiocarbon dating places it at the onset of the Middle Holocene,  
23 156 around the 8.2 kyr event (Rasmussen et al., 2006; Thomas et al., 2007). The Neolithic  
24 157 occupation (layer 2 *cent*) offers the most abundant and varied material, attributed to the  
25 158 Early Neolithic Cardial culture. Radiocarbon dating supports its belonging to the Middle  
26 159 Holocene (Table 1) (Bosh, 2001; 2015; 2016).  
27 160

### 31 161 3. MATERIALS AND METHODS

#### 34 163 3.1. Materials.

35 164  
36 165 All the analysed samples came from the archaeological excavation in 1992. Hand-picking  
37 166 of charcoal fragments was favoured for radiocarbon dating, while a systematic sampling  
38 167 strategy was carried out for anthracology (Bosch, 2001, 2015; 2016). 947 charcoal  
39 168 fragments, covering the whole described archaeological sequence, have been analysed  
40 169 (Table 2). Most of the charcoal belongs to materials scattered in the sediment (n = 649).  
41 170 The synthetic nature of these deposits makes them good records of the vegetation in the  
42 171 surroundings of the site during its successive human occupations (Chabal et al., 1999;  
43 172 Piqué, 1999; Badal et al., 2003; Chabal and Heinz, 2021). The contents of a large  
44 173 combustion structure (n = 298) from the Early Neolithic occupation (in layer 2 *cent*) were  
45 174 also studied, providing a snapshot of its last use and enabling a palaeoeconomic  
46 175 interpretation (Théry-Parisot et al., 2010).  
47 176

#### 51 177 3.2. Methods.

52 178  
53 179 Each charcoal fragment was observed in the three anatomical sections (transverse,  
54 180 longitudinal tangential, and longitudinal radial) using a metallographic dark/bright field  
55 181 incident-light microscope, allowing magnification factors from x50 to x1000.  
56 182 Comparisons with current charred wood samples and wood anatomy atlases made it  
57 183 possible to identify taxa (Greguss, 1955; Jacquot et al., 1973; Schweingruber, 1990;  
58 184 Vernet et al., 2001; García Esteban et al., 2003). The nomenclature used follows the

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3 185 guidelines in *Flora iberica* (Castroviejo, 1986-2012). The relative frequencies of the  
4 186 determined taxa are represented in the form of an anthracological diagram with the data  
5 187 from the layers (Figure 2), made with the software Tilia 2.6.1<sup>1</sup>.

6 188  
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8 189 Photographs of the most interesting taxa (Figure 3) were taken with an Environmental  
9 190 Scanning Electron Microscope (ESEM)<sup>2</sup>. Maps showing site locations and taxa  
10 191 distribution have been developed in Quantum GIS software v.3.4.13 Madeira.  
11 192 Chorological maps for the main European woody species are developed by Caudullo et  
12 193 al., 2017. Digital Elevation Models are available from the Spanish National Geographic  
13 194 Institute (IGN MDT200). Modern distribution maps and regions of provenance of  
14 195 European species have been provided by the CIFOR-INIA Department of Forest Ecology  
15 196 and Genetics of the Spanish Government (Alía et al., 2009).

## 17 197 18 198 4. RESULTS

### 19 199 20 200 4.1. Quantifications

21 201  
22 202 Out of the 947 charcoal fragments studied, 13 taxa were determined, of which four belong  
23 203 to conifers and nine to hardwoods, both trees and shrubs (Table 2). The anthracological  
24 204 diagram shows the diachronic evolution of the landscape exploited by the inhabitants of  
25 205 Cova del Vidre (Figure 2). Taxon richness increases significantly from the Late Glacial  
26 206 period (Microlaminar Epipalaeolithic) to the early Atlantic (Early Neolithic), in  
27 207 correlation with climate warming. Conifers adapted to cold or temperate climates  
28 208 constantly predominate, with a decreasing participation of *Pinus* sp. *sylvestris* in favour  
29 209 of *Taxus baccata*, which co-dominates at the end of the sequence. The appearance and  
30 210 progressive diversification of hardwoods mainly involves species of the deciduous oak  
31 211 forest. Weak representations of *Abies alba* at the beginning, and of *Fagus sylvatica* at the  
32 212 end of the sequence are observed, in accordance with the altitudinal conditions.

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34 214 The differences between the contents of the large combustion structure and the scattered  
35 215 charcoal from the contemporary level (layer 2 *int*) are mainly quantitative, due to a more  
36 216 random or short-lived deposition in the hearths. An over-representation of yew and under-  
37 217 representation of Scots pine type and boxwood are observed in the combustion structure,  
38 218 as well as the presence of the only fragment of *Vitis vinifera* at the site. These differences,  
39 219 which do not allow the use of the fire structure to interpret the environment, are consistent  
40 220 with the 'snapshot' character usually observed in such deposits and may signify either a  
41 221 random use of wood or an unknown intentionality (Kabukcu and Chabal, 2021).

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<sup>1</sup> License belonging to the Archeobotanical Laboratory of the Autonomous University of Barcelona.

<sup>2</sup> Electron Microscopy Service of Biological Systems of the Research Support Service of the University of Zaragoza.

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## 229 5. DISCUSSION

230

## 231 5.1. Stages in the vegetation dynamics at Cova del Vidre

232

233 5.1.1. *The Pleistocene hunter-gatherer environment*

234

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

248

249 Other trees and shrubs are very scarcely represented by one charcoal fragment per taxon,  
250 including *Abies alba* and *Juniperus* sp. and a single hardwood, *Prunus* sp. This last  
251 genus includes a large number of trees and shrubs (whose fruits may be edible) that grow  
252 in open forest under cool and dry conditions. It may signal the early presence of temperate  
253 taxa at the site, in a refugium situation. Conifers, especially cryophilous pines and  
254 junipers, are the dominant taxa in anthracological records from north-eastern Iberia  
255 during the 13th millennium cal BP, often associated with *Prunus* (Allué, 2002; Alcolea,  
256 2017). Some sites, such as the Molí del Salt, the Font Voltada, and the Filador (Allué,  
257 2002), also reveal an open landscape, where pines formed the tree cover accompanied by  
258 shrubs well-adapted to the dry and cold climate that prevailed in Iberia during the Late  
259 Glacial period.

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261 5.1.2. *The Holocene hunter-gatherer environment*

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

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

277

278 In layer 4 cent during the middle Holocene (at least 2000 years after layer 1 int), Scots  
279 pine type remains the dominant taxon associated with a significant proportion of yew  
280 (*Taxus baccata*) and a small percentage of such Supramediterranean taxa as boxwood  
281 (*Buxus sempervirens*) and deciduous oak (*Quercus* deciduous). The appearance of new  
282 temperate taxa indicates climate amelioration, certainly associated with the beginning of  
283 the Atlantic period. The frequency of yew of almost 20% (*Taxus baccata*) in layer 4 cent  
284 (further increasing in layer 2 cent) testifies an increase in humidity at least from the end  
285 of the 9th millennium to the end of the 8th millennium cal BP. In this mountain area,  
286 around the 8.2 kyr cold event, there was thus no lack of moisture; this situation contrasts  
287 with the Central Ebro Basin where at the same time populations deserted the sites during  
288 a crisis of aridity (González-Sampériz et al., 2009). This difference highlights a spatial  
289 shift in climate. Besides, at the end of the 10th millennium *Pinus* tp. *sylvestris* forest was  
290 already rare in the anthracological records at coastal sites in Catalonia (e.g. at La Catiuera,  
291 65 m a.s.l.) and absent from the 12th millennium further south at medium altitudes, (e.g.  
292 at Santa Maira, 650 m a.s.l.) being replaced by thermophilous or mesothermophilous taxa,  
293 such as *Pinus halepensis* or deciduous and evergreen *Quercus* (Allué 2002; Allué et al.  
294 2012; Buxó and Piqué 2008; Badal et al. 2017) reflecting altitudinal and latitudinal  
295 dependence of climate.

296

### 297 5.1.3. The first farmers' environment

298

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

317

### 318 5.2. The abundance of *Taxus baccata*

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



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3 322 in Europe and the Iberian Peninsula is limited due to the impact of human action and  
4 323 climate change that has led to its replacement by more competitive plants. Yew is  
5 324 common in northern Iberia under an Atlantic climate (Figure 4) although the species has  
6 325 been exploited for its wood throughout history. For instance, in the Montseny Mountains  
7 326 in the northeast of the Iberian Peninsula, the genetics of current yew populations can be  
8 327 explained by the long-term exploitation of forest species for firewood and charcoal  
9 328 production, during the 15th-19th centuries (Dubreuil et al., 2010). It is also present in  
10 329 more southern mountain ranges such as in the El Port massif, and is not rare around the  
11 330 site. Mediterranean yew trees, probably isolated during the last Glacial period (Carrión et  
12 331 al., 2003) and currently in decline, grow in small, isolated populations. In Mediterranean  
13 332 environments yew finds adequate moisture above 1,000 m a.s.l. In lower areas, it prefers  
14 333 the protection of shaded valleys, ravines and cliffs. As long as it finds moisture, it can  
15 334 withstand high temperatures (Costa et al., 2001).

16 335  
17 336 *Taxus baccata* must have had a wide distribution in Europe in the past. The spread of yew  
18 337 throughout the Iberian Peninsula since the beginning of the Holocene, in parallel with the  
19 338 deciduous forest colonization, has been highlighted by several authors (Martin and  
20 339 Thiébault, 2010; Pérez-Díaz et al., 2013; Uzquiano et al., 2014; Vidal-Matutano, 2015).  
21 340 Due to the low preservation of yew in Holocene pollen records, contrasting with its  
22 341 abundance in charcoal, anthracology is key to understanding its past distribution. During  
23 342 the Early-Middle Holocene, yew appears sporadically in the anthracological records of  
24 343 north-eastern Iberia, rarely exceeding 5% of the remains, such as at Plansallosa, Cova  
25 344 120, Cova de l'Avellaner (Ros, 1995, 1996), La Prunera (Ferré and Piqué, 2000), La  
26 345 Draga (Caruso and Piqué, 2014), Cova del Frare (Ros, 1996), Balma Margineda (Heinz  
27 346 and Vernet, 1995) and the Moncayo natural park (Aranbarri et al., 2018). Only three sites,  
28 347 Cova de la Guineu (Allué et al., 2009), Camp del Colomer (Piqué, 2016), and Cova del  
29 348 Vidre (this article), record high yew frequencies.

30 349  
31 350 At Cova del Vidre, yew appears for the first time (layer 4 cent) around 8.2-7.9 kyr cal BP.  
32 351 During the Early Neolithic occupation (layer 2 cent), it reaches almost 40% of the studied  
33 352 remains, becoming the plant most used as fuel in the site and certainly a very widespread  
34 353 taxon in the surroundings. As mentioned in section 2.2, this conifer still grows in the El  
35 354 Port massif (Tortosa-Beceite) today (Figure 4) (Costa et al., 2001; Senar Lluch, 2011;  
36 355 Camprodon et al., 2014). Its importance in the territory was probably much greater during  
37 356 the Neolithic.

38 357  
39 358 If we consider the large combustion structure contemporary with the 2 cent layer,  
40 359 showing its last use or uses, the percentage rises to 86%. Random use cannot be ruled out,  
41 360 but it is also possible that yew was voluntarily sourced for specific uses. Among these,  
42 361 uses as fuel and fodder or for sanitary purposes in sheepfolds have been mentioned. The  
43 362 leaves, despite their known toxicity due to the presence of an alkaloid (particularly  
44 363 harmful to horses) are still occasionally used as fodder for livestock (Costa et al., 2001).  
45 364 These practices have been considered in archaeological sites in Mediterranean  
46 365 mountainous areas, in cases when the taxon is abundant among the charcoal (Delhon et  
47 366 al., 2008; Allué et al., 2009; Martin and Thiébault, 2010; Martin et al., 2012, Piqué et al  
48 367 2018). At Cova del Vidre, Neolithic leaf-foddering of livestock may have taken advantage  
49 368 of the natural abundance of this species. Its wood was then reused as fuel for fire.

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4 370 5.3. New data about the early presence of *Fagus sylvatica* in the eastern Iberian Range  
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7 372 The presence of beech (*Fagus sylvatica*) is also noteworthy, although it is a minority  
8 373 taxon in the record. The European beech (*Fagus sylvatica*) is currently one of the most  
9 374 important forest trees in Europe. However, its presence in this territory is relatively recent  
10 375 according to palaeobotanical data (Magri et al., 2006). Charcoal fragments, seeds, fruits,  
11 376 and leaves are parts of plants with a limited dispersion which were probably collected in  
12 377 the immediate vicinity. Hence, when investigating the location of glacial refugia and  
13 378 species migration, macrofossils are the most useful records reflecting local vegetation.

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16 380 Palaeobotanical data suggest a late and rapid migration of beech forests in central, eastern,  
17 381 and northern Europe from the Carpathians Mountains only after 4.5 kyr cal BP (Huntley  
18 382 and Birks, 1983). Nevertheless, the history of beech begins long before the establishment  
19 383 of the beech forests in Europe. Some beech trees, which require wet summers and mild  
20 384 winters, survived during the last glacial period and the Early-Mid Holocene in glacial  
21 385 refugia (Carrión et al., 2003). Most of the glacial refugia were in mountainous territories  
22 386 of the southern peninsulas (Iberian, Italian and Balkan), where the residual populations  
23 387 could find sheltered and humid places to survive (Magri et al., 2006), avoiding continental  
24 388 areas, plains, and valleys.

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27 390 Macrofossil evidence suggests that relict beech populations existed in the Iberian  
28 391 Peninsula since the last glacial period, in the western Pyrenees-Cantabrian Mountains  
29 392 (Ruíz-Alonso et al., 2018) and the north-western Iberian Range (López-Merino et al.,  
30 393 2008). In the eastern Pyrenees the evidence is very scarce (Vernet, 1980; Ros, 1992;  
31 394 Allué, 2002). Its presence had not been documented until now in the Iberian Peninsula  
32 395 below 41° N latitude (Figure 5 and 6).

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35 397 The archaeobotanical record at Cova del Vidre shifts the southern limit of the European  
36 398 beech to the east of the Iberian Range, confirming the existence of a vegetation refugium  
37 399 in El Port massif (Tortosa-Beceite), at least from 7.3 kyr cal BP. The site is currently very  
38 400 close to small relict beech forests (Figure 6). The topography generates a particular  
39 401 environmental situation that may have been favourable for the maintenance of beech  
40 402 patches accompanied by boxwood (*Buxus sempervirens*) (Costa et al., 2001; Alía et al.,  
41 403 2009), like the Pyrenean beech forests. According to genetic data and accepted migration  
42 404 routes, Mediterranean refugia are thought to have contributed to the colonization of  
43 405 central and northern Europe (Magri et al., 2006; Bradshaw et al., 2010; Giesecke and  
44 406 Brewer, 2018). This attestation of the presence of the beech so far south is thus an  
45 407 interesting new element.

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48 409 5.4. The mountain palaeobotanical record at Cova del Vidre: a Late Glacial refugium?  
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52 411 The anthracological sequence at Cova del Vidre between the 13th and 6th millennia  
53 412 cal BP shows a vegetation dynamic that fits into the regional framework proposed on the  
54 413 basis of pollen records in the NE Iberian Peninsula, with fairly large spatial differences  
55 414 due to elevation and latitude (Riera and Esteban, 1994; Follieri et al., 2000; Pérez Obiol,  
56 415 2007; Burjachs et al., 2016). These data reflect the regional response of vegetation during

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3 416 the transition from the Late Glacial period to the Early Holocene, global warming, and  
4 417 the effects of human activity. At the more local geographic scale of the El Port massif and  
5 418 its surroundings, anthracology shows the existence of conifers adapted to the cold within  
6 419 the predominance of Supramediterranean vegetation, characteristic of montane  
7 420 environments in Mediterranean Iberia.  
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10 422 The anthracological record from Cova del Vidre has many distinctive features compared  
11 423 to other sites in different environmental contexts in north-eastern Iberia, despite their  
12 424 geographical proximity, i.e. the Bajo Aragón, the Ebro Delta, and the Maestrazgo sites  
13 425 (Figure 1). In the nearby mountainous sites of the Maestrazgo in the Iberian Range, cold-  
14 426 climate pines dominate during the whole period and Supramediterranean elements are  
15 427 almost absent (Alcolea, 2017). In the lowlands, thermo-Mediterranean vegetation  
16 428 dominates the anthracological records. In the Ebro Delta, a typically Mediterranean  
17 429 maquis shrubland is highlighted by the predominance of olive tree (*Olea europaea*),  
18 430 holm/kermes oak (*Quercus coccifera/ilex*) and heather (Ericaceae) (Bosch, 1989; Ros,  
19 431 1996). In the Bajo Aragón, continental conditions are evidenced by the presence of  
20 432 drought-resistant conifers such as Aleppo pine (*Pinus halepensis*) and junipers, also  
21 433 accompanied by *Quercus coccifera/ilex* (Alcolea, 2018; Aranbarri et al., 2020).  
22 434

23 435 Therefore, a comparison of Cova del Vidre (this paper) with nearby sites (Ros, 1996;  
24 436 Bosch, 1989; Alcolea, 2017; 2018) shows the existence of rather different plant  
25 437 communities. The local differences in forest composition emphasize the importance of  
26 438 altitudinal factors and the Mediterranean influence. These differences only become  
27 439 noticeable at the beginning of the Holocene and are already well-established by the Early  
28 440 Neolithic.  
29 441

30 442 These observations show that the global climate that determined vegetation prior to the  
31 443 Holocene shaped the plant communities of these nearby sites roughly equally. From the  
32 444 Holocene onwards, differences in local conditions become decisive, such as (i)  
33 445 differences in precipitation and temperature due to orography, (ii) differences in water  
34 446 and heat retention due to geological features, (iii) Mediterranean influences due to the  
35 447 proximity to the sea and (iv) finally, differential human activities that have completed the  
36 448 shaping of the landscapes.  
37 449

38 450 El Port massif currently has the appearance of an island of vegetation containing forest  
39 451 species that probably originated during the Last Glacial period. Indeed, at Cova del Vidre,  
40 452 the presence of *Prunus* during the Younger Dryas, followed by its abrupt increase in the  
41 453 Early Holocene, accompanied by *Quercus coccifera/ilex*, and later during the Middle  
42 454 Holocene by other temperate species, like *Quercus* deciduous, *Buxus sempervirens* and  
43 455 *Fagus sylvatica*, echoes the presence of the same taxa today, at more than 1,000 m a.s.l.,  
44 456 under limiting conditions for these species. We believe that during the Late Glacial, these  
45 457 taxa found suitable local thermal conditions that allowed them to resist and to restart  
46 458 rapidly in the Early Holocene. Then, during the Middle Holocene, precipitation  
47 459 conditions were favourable for their maintenance until today.  
48 460

49 461 According to Carrión et al (2003), there is a common misapprehension that Iberian glacial  
50 462 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.

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3 511 (iii) A comparison with archaeobotanical data from nearby sites in the lowlands  
4 512 suggests that altitudinal differences in vegetation were already well-  
5 513 established by the late Mesolithic (Early Atlantic). While cold-climate  
6 514 conifers and Supramediterranean vegetation predominated in the mountains,  
7 515 Mediterranean trees and shrubs were already dominant in the plains. Local  
8 516 differences occurred within a small geographical area due to altitudinal factors  
9 517 and Mediterranean influence. Soil aridity appears to be one of the main factors  
10 518 limiting vegetation in the Mediterranean mountains.  
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13 519 (iv) Macrofossil evidence of yew and beech provides new data about the southern  
14 520 limit of their range. A Holocene refugium of temperate and Mediterranean  
15 521 taxa is identified in the 7th millennium cal BP in El Port massif (Tortosa-  
16 522 Beceite), where relict populations of these taxa still exist today. Their presence  
17 523 is relevant for the reconstruction of the palaeodistribution of these species and  
18 524 sheds light on the influence of human impact on their current distribution.  
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23 527  
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947  
 948 TABLE AND FIGURE CAPTIONS

949  
 950 Table 1. Radiocarbon dates available for the archaeological sequence in Cova del Vidre  
 951 (Bosch, 2001; 2015; 2016). Material: B: bone (*Ovis*), C: Charcoal. Culture: ME:  
 952 Microlaminar Epipalaeolithic, GM: Geometric Mesolithic, EN: Early Neolithic.  
 953 Calibrations with OxCal v4.4. Bronk Ramsey (2017); r: 5 IntCal20 atmospheric curve  
 954 (Reimer et al., 2020). Beta-58943 comes from the large structure in layer 2 *cent*.

955  
 956 Table 2. Absolute and relative frequencies of the taxa identified in Cova del Vidre.

957  
 958 Figure 1. Geographical setting and site location. Black star: Cova del Vidre. Black points  
 959 (nearby sites mentioned in the text): 1. Plano del Pulido, 2. El Pontet, 3. Arenal de  
 960 Fonseca, 4. Barranc d'en Fabra, 5. Molló de la Torre. Base: MDT200 IGN (Spanish  
 961 Government).

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

964  
 965 Figure 3. ESEM images of selected taxa: A) *Taxus baccata*. Transverse section, B) *Taxus*  
 966 *baccata*. Radial section, C) *Fagus sylvatica*. Transverse section, D) *Fagus sylvatica*.  
 967 Radial section, E) Rosaceae Maloideae. Transverse section, F) Rosaceae Maloideae.  
 968 Radial section.

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

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3 977 Figure 5. Map of the modern and past distribution of beech (*Fagus sylvatica*) in Europe.  
4 978 Striped area: modern distribution after Alía et al., 2009 CIFOR-INIA. Triangles:  
5 979 geographical distribution of records containing macrofossil evidence (see references in  
6 980 Magri et al., 2006 supplementary material). Black star: Cova del Vidre record. Prepared  
7 981 by the authors.  
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10 982  
11 983 Figure 6. Current distribution and seed zones of *Fagus sylvatica* L. in NE Iberia. Data  
12 984 from CIFOR-INIA ([www.inia.es/genfored.html](http://www.inia.es/genfored.html)) (Añón-García et al. 2011). Black star:  
13 985 Cova del Vidre within the area containing small relict forests of *Fagus sylvatica* L. in El  
14 986 Port massif (*Buxo sempervirentis-Fagetum sylvaticae*) (Costa et al., 2001) Base:  
15 987 MDT200 IGN (Spanish Government). Prepared by the authors.  
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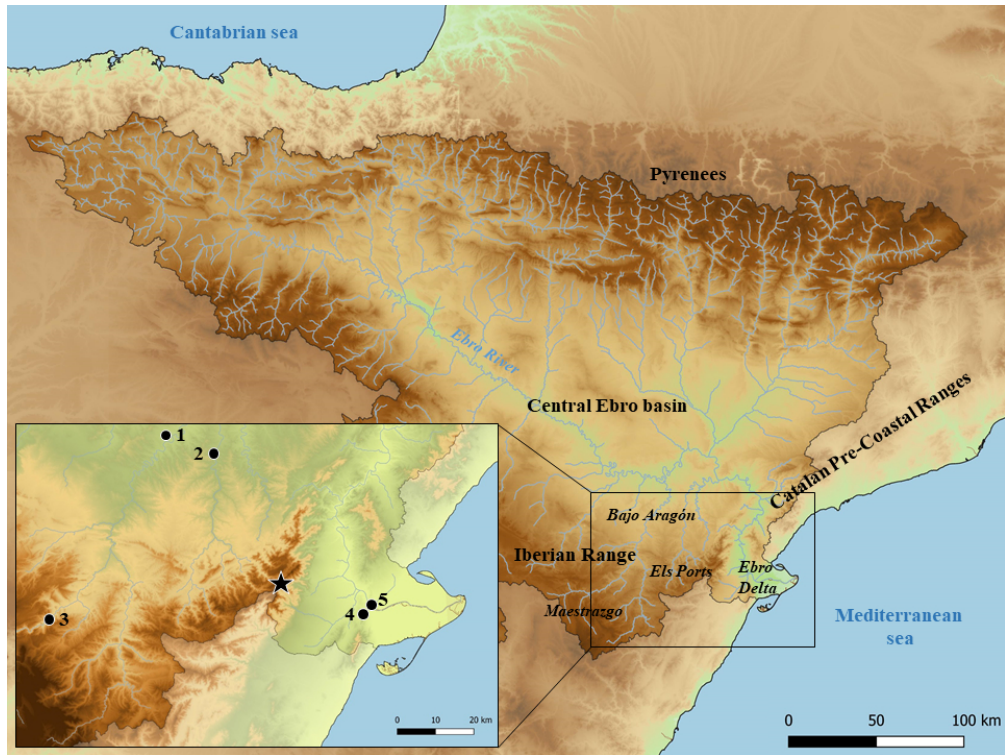
Layer	Culture	Date BP	+/-	Ref. lab.	Calibrated age BP (2 $\sigma$ )	Material	Reference
2 cent	EN	6,248	33	OxA-26065	7,259-7,021	B	Bosch, 2016
2 cent	EN	6,181	35	OxA-26064	7,167-6,957	B	Bosch, 2016
2 cent	EN	6,180	90	Beta-58934	7,272-6,801	C	Bosch, 2016
4 cent	GM	7,290	70	UBAR-832	8,311-7,966	C	Bosch, 2015
2 int	ME	10,740	130	Beta-58933	12,690-12,471	C	Bosch, 2001

For Peer Review



Culture	Microlaminar Epipaleolithic		Sauveterroïd		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	%
<i>Abies alba</i>	1	1.2	-	-	-	-	-	-	-	-
<i>Acer</i> sp.	-	-	-	-	-	-	1	0.3	2	0.7
<i>Buxus sempervirens</i>	-	-	-	-	8	4.8	36	12.3	2	0.7
Ericaceae	-	-	-	-	-	-	1	0.3	-	-
<i>Fagus sylvatica</i>	-	-	-	-	-	-	1	0.3	2	0.7
<i>Juniperus</i> sp.	1	1.2	-	-	-	-	7	2.4	-	-
<i>Pinus</i> tp. <i>sylvestris</i>	79	96.3	78	78.0	125	74.9	86	29.5	12	4.0
<i>Prunus</i> sp.	1	1.2	18	18.0	-	-	4	1.4	-	-
<i>Quercus coccifera/ilex</i>	-	-	4	4.0	-	-	2	0.7	3	1.0
<i>Quercus</i> deciduous	-	-	-	-	2	1.2	20	6.8	12	4.0
Rosaceae Maloideae	-	-	-	-	3	1.8	18	6.1	7	2.3
<i>Taxus baccata</i>	-	-	-	-	29	17.4	116	39.7	257	86.2
<i>Vitis vinifera</i>	-	-	-	-	-	-	-	-	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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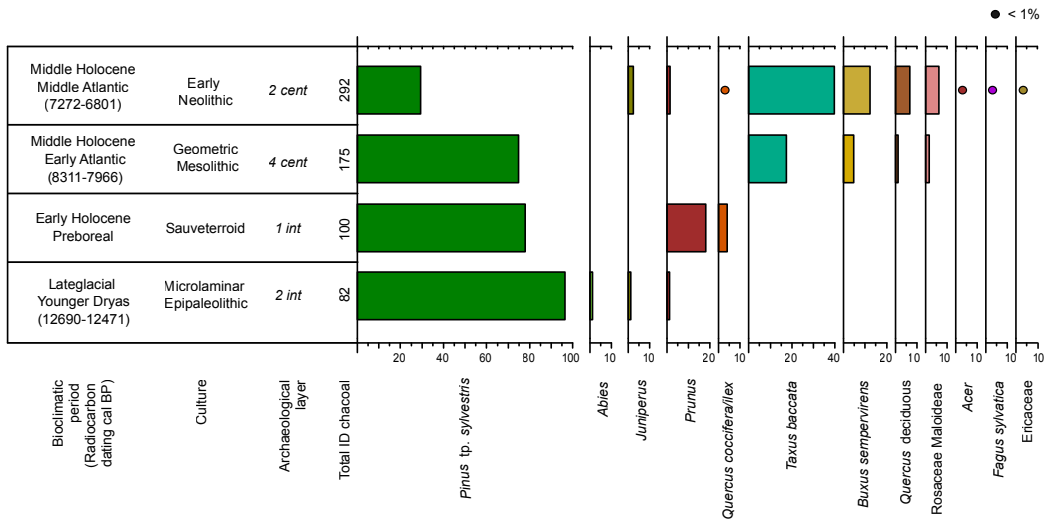
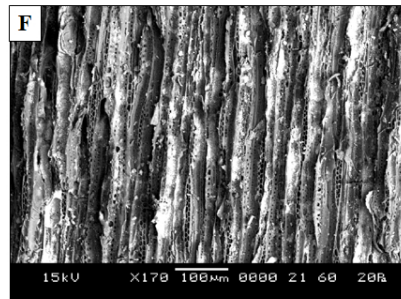
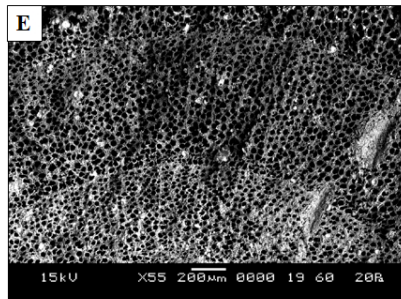
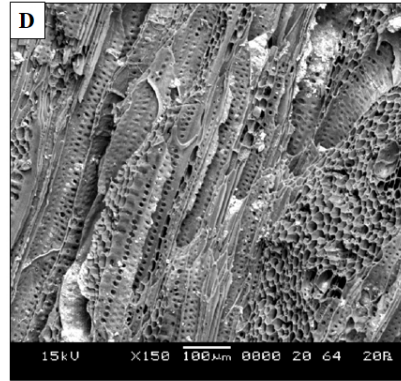
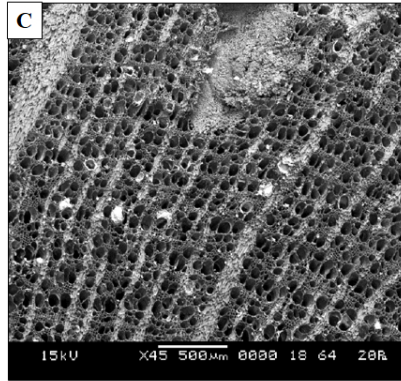
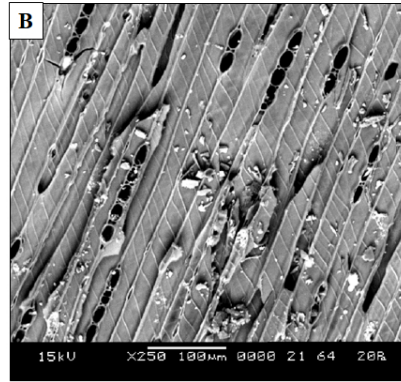
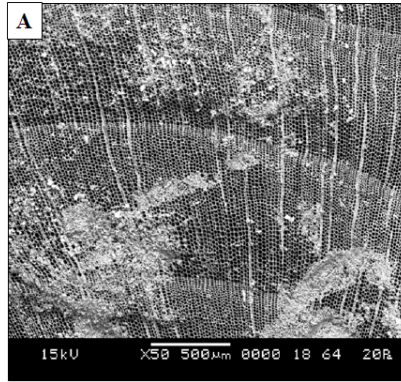


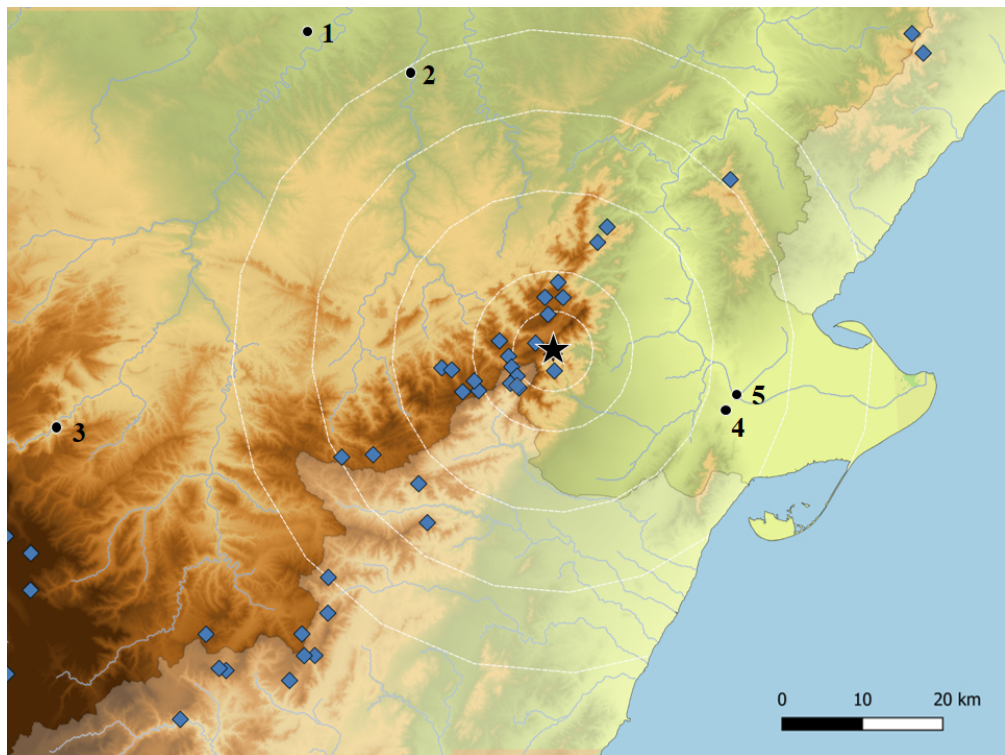
Figure 2. Frequency diagram of anthracological remains from Cova del Vidre.

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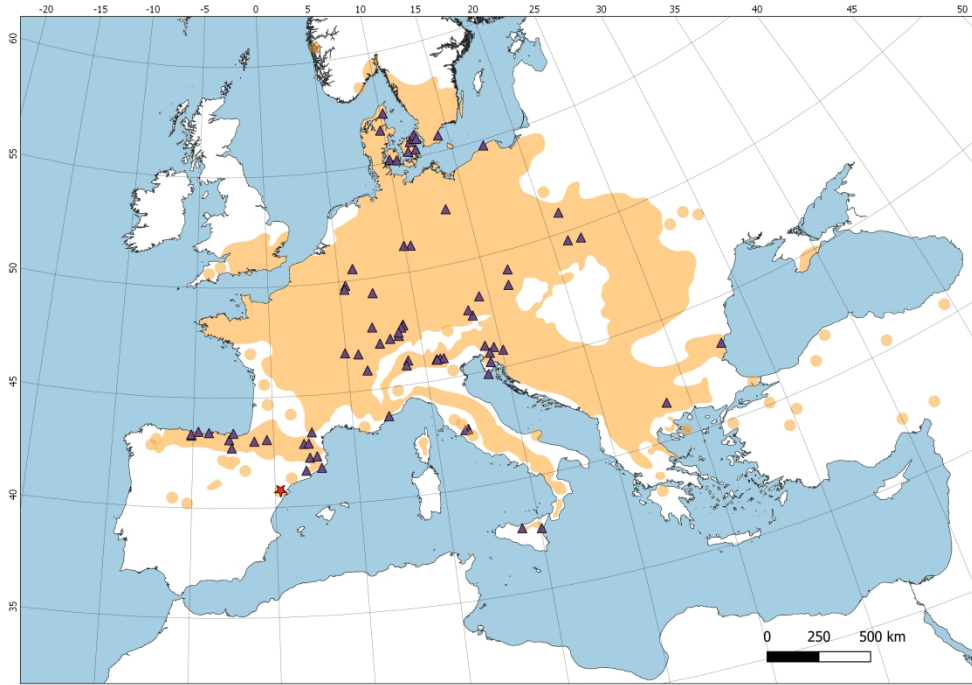


254x338mm (96 x 96 DPI)

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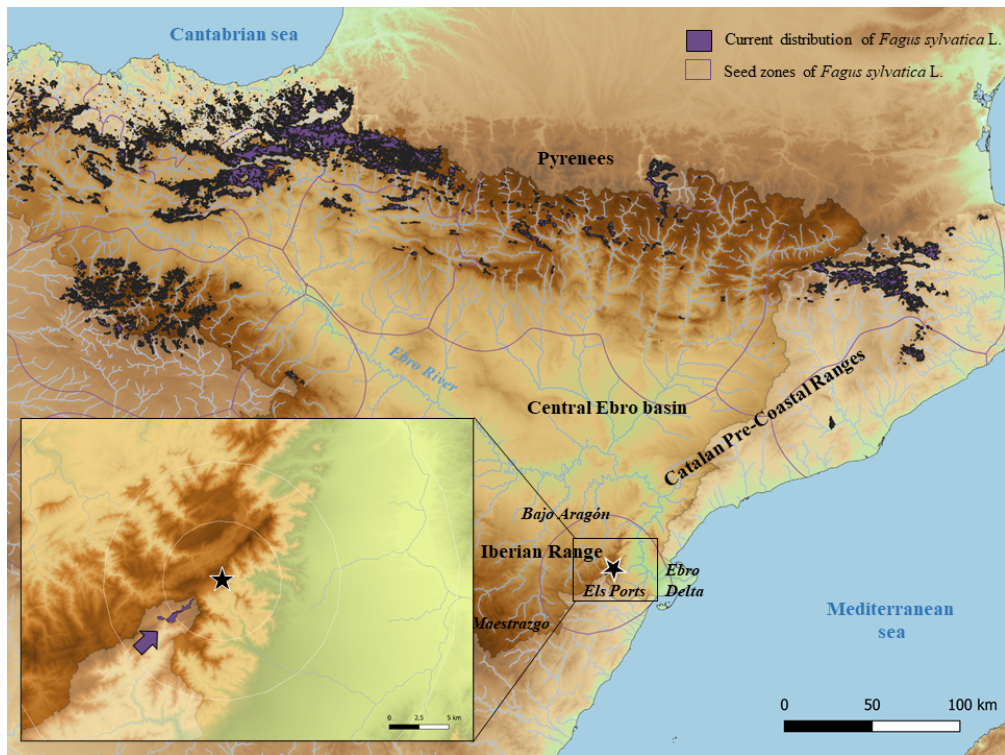


254x190mm (96 x 96 DPI)



754x533mm (118 x 118 DPI)

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