Holocene history of Aleppo pine (*Pinus halepensis* Mill.) woodlands in the Ebro Basin (NE Spain): Climate-biased or human-induced?

Josu Aranbarri a,*, Marta Alcolea b,c, Ernestina Badal d, Silvia Vila e, Ethel Allué f,g, María José Iriarte-Chiapusso a,h, María Sebastián i, Donatella Magri j, Penélope González-Sampériz k

a Departamento de Geografía, Prehistoria y Arqueología, Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU), Francisco Tomás y Valiente s/n., 01006 Vitoria-Gasteiz, Spain

b Departamento de Historia, Universidade de Santiago de Compostela, Praza da Universidade 1, 15782 Santiago de Compostela, Spain

c ISEM, Université de Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, CC 065 34095 Cedex 5 Montpellier, France

d Departament de Prehistòria, Arqueologia i Història Antiga, Universitat de València, Blasco Ibáñez 28, 46010, Valencia, Spain

e Departament d'Història, Universitat de Lleida, Plaça de Víctor Siurana 1, 25003 Lleida, Spain

f IPHES (Institut Català de Paleoecologia Humana i Evolució Social), Zona Educacional 4 Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

g Departamento de Historia e Historia del Arte, Universitat Rovira i Virgili (URV), Avda. Catalunya 35, 43002 Tarragona, Spain

h Ikerbasque - Basque Foundation for Science, Bilbao, Spain

i Departamento de Didáctica de las Ciencias Sociales, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain

j Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Piazzale Aldo Moro 5, 00185 Rome, Italy

k Instituto Pirenaico de Ecología-CSIC, Avda. Montañana 1005, 50059 Zaragoza, Spain

Abstract

This paper reviews the past distribution of Aleppo pine woodlands in the Ebro Basin, Northeastern Iberia, from the Mesolithic to Modern times based on wood charcoal data. The aim is to detail the chronological timing and the drivers explaining the long-term presence of Aleppo pine woodlands and associated thermophilous flora. The available charcoal data support the early spread of *Pinus halepensis* during the Mesolithic (ca. 9000 cal BP) accompanied by Mediterranean trees and shrubs like *Quercus* sp. evergreen, *Juniperus* sp., *Arbutus unedo, Pistacia lentiscus, Rhamnus/Phillyrea*, Cistaceae, and *Rosmarinus officinalis*, as a local response to global climate change in the Early Holocene. During the arrival and the propagation of the Neolithic culture (ca. 7500–5500 cal BP), anthracological records, as well as regional palynological sequences, demonstrate the progressive replacement of a conifer-dominated open parkland by both Quercus sp. deciduous and evergreen woodlands in response to the Middle Holocene rise in temperature and humidity. This evidence, however, converges with the general idea that the presence and the spread of *Pinus halepensis* and associated scrubland have usually been attributed to the onset of landscape anthropization. The frequency of xero-thermophilous open scrubland and the use of Aleppo pine for fuel and wood crafting progressively increased during the Bronze and Iron Ages, and especially in Ibero-Roman and Medieval/Islamic times, when the vegetation landscape in the Middle Ebro Basin was largely deforested as a consequence of increasing demographic pressure, grazing and the establishment of proto-urban centers.

1. Introduction

Studies regarding the past distribution of key tree and shrub taxa at a European scale have increased noticeably during the last decades as a consequence of the effort of collecting and storing data in online databases by many paleobotanical research groups. The considerable number of available pollen and charcoal data that are chronologically well-constrained has allowed not only defining the location of both deciduous and evergreen taxa during the Last Glacial Maximum, but also characterizing the pattern of post-glacial recolonization of central and northern European regions (Brewer et al., 2002; Magri, 2008; Douda et al., 2014). Traditional biogeographical literature locates plant population refuge areas in the Mediterranean coastal areas (Bennett et al., 1991; Carrión et al., 2008), where warmer climate conditions prevailed during glacial environmental stages (Fletcher and Sánchez Goñi, 2008; Combourieu-Nebout et al., 2009). Only few studies have highlighted the role of inner continental enclaves as potential biodiversity reservoirs, despite the presence of mesic and thermophilous taxa has been widely recognized (González-Sampériz et al., 2004, 2010; Manzano et al., 2017).

One of the mostly widespread tree in semiarid Mediterranean Iberia is the Aleppo pine (*Pinus halepensis* Mill.), whose current distribution is confined to the thermo- and meso-Mediterranean biogeographic belts (Rivas Martínez, 1987). It is a post-fire obligate seeder, which does no survive fire but regenerates from seeds in post-fire environment (Ne'eman et al., 2004; Ne'eman and Izhaki, 2006; Pausas et al., 2004). For this reason, it is a common pioneer and invasive species within its natural distribution area (Pausas et al., 2002). Thus, the presence and the concomitant spread of *Pinus halepensis* and associated thermophilous scrubland have usually been attributed to the onset of landscape anthropization in the Mediterranean paleoecological literature (Thiébault, 1997), without considering the role of this species as part of the natural vegetation. Besides, Costa (1987) and Braun-Blanquet and Bolós (1987), among others, define the stands of Aleppo pine as a secondary and marginal forests in Iberia, including the northeastern region belonging to the Ebro Basin. Indeed, the phytosociological literature discards the idea of self-established pine woodlands, in most cases associated with particularly unstable and/or immature topographic and soil conditions, cataloging them as “paraclimax” communities (Quézel and Barbero, 1990). Carrión and Fernández (2009) demonstrate that phytosociological theories do not always match with paleobotanical evidence, especially regarding Mediterranean pines and their presence and role since millennia in Iberia (Rodríguez-Ariza, 1992; Badal et al., 1994; Carrión et al., 2000; Rubiales et al., 2009; Olmedo-Cobo et al., 2019) and across the Mediterranean Basin (Vernet and Thiébault, 1987; Wengler and Vernet, 1992). Therefore, the naturalness of Mediterranean pine populations in Iberia is still a matter of debate.

Similar to the presence of Aleppo pine, the progressive rise or even the long-term presence of xero-thermophilous scrubland has been widely taken as a clear sign of anthropogenic deforestation and landscape opening (Thiébault, 1997). These communities, however, constitute an essential component of the Mediterranean *machia*, whose presence is linked to particular bioclimatic and ecological constrains (Blanco-Castro et al., 1997). Early-Middle Holocene pollen and charcoal data have shown the progressive replacement of open Juniperus parklands by *Olea–Pistacia–Quercus* sp. evergreen assemblages in the circum-Mediterranean region, interpreted as a direct consequence of changes in precipitation and temperature regimes instead of human shaping (Wengler and Vernet, 1992; Tinner et al., 2009; Linstädter and Zielhofer, 2010; Di Rita and Melis, 2013; Djamali et al., 2013; Revelles et al., 2019). Thus, the distinction between human-made landscapes and climate-biased vegetation dynamics, the timing of appearance of the tree/shrub component and the forest disturbance/succession models, should be carefully interpreted, since they can produce similar pollen and charcoal assemblages (Figueiral and Mosbrugger, 2000).

The main goal of this paper is to outline the history of Aleppo pine woodlands and associated thermophilous flora in the Ebro Basin during the Holocene by reviewing published and unpublished charcoal assemblages. Therefore, we aim to discuss the possible drivers explaining the long-term dynamic of Aleppo pine communities in the Ebro Basin.

2. Regional setting

The Ebro River constitutes a huge basin, which runs from the Cantabrian Range to the Mediterranean across the northeastern Iberian Peninsula. It is bordered by the Pyrenees to the north, by the Iberian Range to the south and by the Catalonian Range to the east (Fig. 1A). It was formed by Alpine tectonic shifts that pushed up the outlying mountain chains and formed the sedimentary foreland depression. During the Tertiary, it was gradually filled with sediments as an endorheic continental basin. After the Late Miocene–Pliocene, as it became exoreic, it gained an outflow to the Mediterranean and the sediment moved to its bottom (200–300 m a.s.l.). This was the onset of the Ebro River system and of sediments draining from the basin to the sea, which still continues today.

A remarkable NW-SE climate gradient is shown across the Ebro Basin, determined by the strong Atlantic influence in the north and northwest during most of the year and the Mediterranean influence to the east, leaving a strong water-deficit during summer months. Three main sectors can be distinguished according to biophysical features: Upper Ebro Basin, Middle Ebro Basin and the Lower Ebro Basin (Fig. 1A).

The Upper Ebro Basin is climatically placed in the boundary between the Atlantic and the Mediterranean realm, which explains the fact that different regions have a deficit in summer rainfall. Overall, the vegetation is well-adapted to a mesic environment, mostly composed of *Quercus robur* and *Q. faginea* with A*cer campestre*, *A. monspessulanum*, *Fraxinus excelsior*, *Viburnum lantana*, and *Ligustrum vulgare* in the valley bottoms while higher elevations are dominated by *Quercus pyrenaica*, *Q. petraea*, *Betula pendula*, and *Fagus sylvatica*, depending on altitude, exposure and soil properties (Blanco-Castro et al., 1997). *Quercus ilex* develops on dry south-facing exposures along with *Phillyrea latifolia*, *Arbutus unedo*, *Viburnum tinus*, *Juniperus communis*, *Rhamnus alaternus*, *Hedera helix*, *Rubia peregrina*, and *Ruscus aculeatus*. The mountain ranges located in the Middle Ebro Basin reveal a marked altitudinal zonation. The basal belt is dominated by aMediterranean woodland mainly composed by *Quercus ilex* and *Quercus faginea* communities, along with many xero-thermophilous shrubs such *as Quercus coccifera*, *Rosmarinus officinalis*, *Thymus vulgari*s, and *Genista scorpius*. *Pinus halepensis* is also present (Fig. 2) (Blanco-Castro et al., 1997). Higher altitudes support broadleaved elements like acidophilous *Quercus pyrenaica* and *Q. robur*, as well as *Sorbus aria, S.*

aucuparia, Sambucus racemosa, Ilex aquifolium, and *Fagus sylvatica*, among others (Longares, 2004).

The lowlands of the Middle Ebro Basin form a steppe landscape, mostly dedicated to irrigated agriculture. Annual rainfall values barely reach 350 mm (Fig. 1B). Evapotranspiration rates are high (N800 mm) and temperature values are mostly related to exposure and orientation (Fig. 1C). The vegetation cover is less than 50% and is dominated by cereal crops with only small patches of open parkland of *Pinus halepensis* (Fig. 2), *Quercus coccifera* and *Juniperus phoenicea*, and/or a dense scrubland with *Rhamnus lycioides, Rosmarinus officinalis, Globularia alypum, Ephedra nebrodensis, E. fragilis, Thymelaea tinctoria, Pistacia lentiscus, Phillyrea angustifolia*, and *Brachypodium ramosum*, depending on topography and soil type. Mesophytes are restricted to particularly humid mid-mountain enclaves (Blanco-Castro et al., 1997). Nitrophilous and gypsophilous plants are abundant and include *Salsola vermiculata, Atriplex halimus, Artemisia herba-alba, Peganum harmala, Ferula communis, Malcomia africana, Marrubium alysoon, Ononis tridentata, Gypsophila hispanica, Helianthemum squamatum*, and *Cistus clusii*.

Close to the Mediterranean, namely in the Lower Ebro Basin, the precipitation shows a marked seasonality and is more abundant than in the inner sector (Fig. 1B). The mean annual temperature reaches ca. 17 °C (Fig. 1C). The vegetation is well-adapted to meso- and thermo-Mediterranean environments and is composed of evergreen oak forests with small communities of deciduous oak occupying northern slopes and shaded areas. Towards the coast, a thermophilous community is found in where *Quercus coccifera, Olea europaea, Pistacia lentiscus, Pinus halepensis*, and *Chamaerops humilis*, among others, acquires special relevance (Folch, 1986).

The Ebro Basin has been intensely populated by prehistoric human groups since the Paleolithic. The character of the Ebro Basin as crossroad for people and fauna makes it an area with frequent evidence of long term human occupation that makes it a territory with a particular cultural character (Aura et al., 2011; Utrilla et al., 2012; Domingo et al., 2018). The first human impact on the environment is documented in Neolithic times (Montes et al., 2016; Alcolea et al., 2017a) and progressively increased in recent times, paralleling the rise of human peopling and social complexity.

3. Material and methods

The anthracological data reviewed for the Ebro Basin come from different sedimentary archives, including archeological sites and burial paleosols (Fig. 1A and Table 1). A number of 27 sites reporting *Pinus halepensis* wood charcoal have been considered for the present work, which comprises chronologies ranging from the Mesolithic until the Modern Ages.

The taxonomic distinction between Mediterranean and cryophilous montane *Pinus* species, based on anatomical diagnostic traits, is usually feasible when allowed by a good state of preservation ofwood remains. The wood of cryophilous montane European pines (*Pinus nigra* ssp. *salzmanni* (Dunal) Franco, *Pinus sylvestris* L. and *Pinus mug*o Turra) is commonly grouped under the taxon *Pinus sylvestris* type, *Pinus nigra/sylvestris* type, *Pinus nigra/sylvestris* or *Pinus sylvestris/uncinate* (Figueiral and Carcaillet, 2005; Roiron et al., 2013; Allué et al., 2018). Mediterranean pines (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus pinea* L.) can frequently be determined at the species level.

Pinus halepensis is a softwood characterized in transverse section by gradual early-latewood transition and the presence of resin canals throughout the growth ring. They are generally smaller than in other species of the genus (Fig. 3). In the longitudinal sections, the average height of rays is 10 cells, the upper limit being 22 cells. The most characteristic anatomic features are ray parenchyma cells with 1–3 or 4 pinoid pits in cross-fields and the presence of slightly dentate walls in ray tracheids (Jacquiot, 1955; Schweingruber, 1990) (Fig. 3).

In order to facilitate readability and infer landscape changes across different cultural periods, some charcoal data have been grouped according to ecological affinities (Fig. 4).

• Xero-thermophytes comprises taxa related to open scrubland and the Mediterraneanmachia, namely, *Arbutus unedo, Buxus sempervirens,* cf. *Berberis* sp., *Chamaerops humilis*, Chenopodiaceae, Chenopodiaceae cf. salsola, Cistaceae, *Cistus* sp., *Erica* sp., Ericaceae, *Ephedra* sp., Fabaceae, Labiatae, Labiatae cf. *Lavandula*, Monocotyledoneae, *Olea europaea*, cf. *Olea europaea*, *Rhamnus/Phillyrea*, *Pistacia* sp., cf. *Pistacia* sp., *Pistacia lentiscus*, *Pistacia* cf. *terebinthus*, *Rosmarinus officinalis*, and *Retama monosperma*.

• Mesophytes and riparian taxa include *Abies alba, Acer* sp., *Alnus* sp., *Betula* sp., *Celtis australis*, cf. *Celtis*, *Corylus avellana, Corylus-Alnus, Fagus sylvatica, Fraxinus* sp., *Populus* sp., *Populus/Salix*, Rosaceae Maloideae, cf. Rosaceae Maloideae, Rosaceae Pomoideae, Rosaceae Prunoideae, Rosoideae, *Prunus avium/spinosa* type, *Salix* sp., Salicaceae, *Sorbus* sp., *Tamarix* sp., *Taxus baccata, Ulmus* sp., *Viscum* sp., and *Vitis vinifera.*

• *Pinus* sp. cryophilous comprises *Pinus nigra/sylvestris* type and *Pinus sylvestris* type.

• *Pinus* sp. other is composed of *Pinus* sp., *Pinus* bract, *Pinus* cortex, *Pinus halepensis/pinaster* type, *Pinus pinea/halepensis* type, and *Pinus pinea/pinaster* type.

• The group of other taxa includes species with generic ecological affinities and poor adscriptions, namely, Angiosperm indeterminate, Conifer indeterminate, *Prunus* sp., and *Quercus* sp.

• Cultivated taxa group is represented by *Ficus carica, Juglans regia, Prunus amygdalus* type, *Prunus dulcis*, cf. *Punica granatum*, and *Pyrus malus*.

These reviewed wood charcoal assemblages were chronologically constrained by multiple 14C AMS dates submitted to different laboratories. Charcoal-based radiocarbon dates were calibrated using CALIB 7.1 software (Stuiver and Reimer, 1993) based on the latest IntCal 13 curve (Reimer et al., 2013). The majority of radiocarbon dates are derived from sedimentary deposits although direct dating of charred woody elements from P*inus halepensis* were also obtained (Table 3).

4. Results

The collection of wood charcoal data in the Ebro Basin has been strongly linked to archeological contexts. Anthracological analysis has largely increased since the beginning of the 21th century with the progressive intensification of paleobotanical studies and the publication of many reviews centered in the Upper (Ruíz-Alonso, 2014; Ruíz-Alonso and Zapata, 2015; Zapata, 2000; Zapata and Peña Chocarro, 2005) and Middle-Lower Basin (Carrión, 2007; Piqué et al., 2012; Vila and Piqué, 2012; Alcolea 2017, 2018; Vila, 2018). Nevertheless, a gap of knowledge persists, depending on regions and periods.

Upper Pleistocene wood charcoal records (e.g., Cova Gran, Cueva del Gato) show the predominance of montane pinewoods and junipers revealing an open landscape with scattered conifers, all of them well adapted to cold (Piqué, 1995; Allué et al., 2018; Mazo and Alcolea, 2019) and especially dry climate conditions in the valleys during the Last Glacial Maximum (Badal et al., 2012). The Late Glacial (ca. 13,500 cal BP) charcoal spectra reveal a progressive spread of mesic taxa (mainly *Quercus* sp., *Acer* sp., *Prunus* sp., and *Corylus avellana*) although conifers continue being the main landscape components (Allué et al., 2013; Montes et al., 2016). To our knowledge, no Pleistocene Aleppo pine charcoal remains have been reported for the Ebro Basin.

During the onset of the Holocene, local variations in vegetation landscapes are inferred from anthracological assemblages placed between the high and middle mountain regions and the Central Depression. The Pre-Pyrenean Mesolithic records (Allué et al., 2012; García-Martínez de Lagrán et al., 2016; Montes et al., 2016; Ruíz-Alonso and Zapata, 2015) are dominated by montane pine communities with scattered presence of broadleaved elements like *Quercus* sp. deciduous, *Acer* sp., *Fraxinus* sp., *Ulmus* sp., Rosaceae Maloideae at ca. 11,350–8000 cal BP, fitting the typical post-glacial forest succession of the Eurosiberian realm (Carrión et al., 2010; Iriarte-Chiapusso et al., 2016). By contrast, *Pinus halepensis* is especially relevant in the lowlands accompanied by Mediterranean trees and shrubs like *Quercus* sp. evergreen, *Juniperus* sp., *Arbutus unedo, Pistacia lentiscus, Rhamnus/Phillyrea, Prunus* sp., Cistaceae, and *Rosmarinus officinalis* at ca. 9000 cal BP, as revealed by Mesolithic sites, such as Cabezo de la Cruz (Badal, 2013), Espantalobos (Alcolea et al., 2017b), El Pontet (Alcolea, 2017b) and Los Baños de Ariño (Badal, 2004), as well as the nearby alluvial sequence of La Poza (Pérez-Lambán et al., 2018) (Fig. 1A and Table 2). Direct radiocarbon dates on wood charcoal and cone bracts support the local presence of pine communities around 8995–8625 cal BP (Table 3), revealing widespread Aleppo pine populations and associated flora in the Middle Ebro Basin during the Early Holocene.

During the Neolithic (7500–5500 cal BP), the previous open thermophilous landscape persisted, although mesophytes, and especially *Quercus* sp. evergreen, were more in the anthracological assemblages (Fig. 4 and Table 4). *Pinus halepensis* is documented in sites of the Bajo Aragón (Fig. 1A), namely Plano del Pulido (Alcolea, 2017b) and in the Lower Ebro Basin, such as the Ebro Delta (e.g., Barranc d'en Fabra, Ros, 1996). It is found in mid mountain areas in the eastern Pre-Pyrenees (e.g., Cueva de Chaves, Auvelles, Martín-Seijo and Piqué, 2008; Alcolea et al., 2017a) and nearby coastal enclaves like La Cativera, Cova Bonica or El Cavet (Fontanals et al., 2008; Allué et al., 2017). However, in the

Upper Ebro Basin it is not found together with juniper and evergreen oaks, as revealed by the study in the open-air site of Los Cascajos (Peña-Chocarro et al., 2005).

Bronze and Iron Age are well-known periods from the archeobotanical point of view, both for the good conservation of the remains compared to older times and for the large number of studies concentrated in La Plana de Lleida at the eastern Middle Ebro Basin (Fig. 1A). The vegetation landscape is dominated by Aleppo pine communities accompanied by *Juniperus* sp. and *Quercus* sp. evergreen. This is particularly evident in Minferri (Piqué et al., 2012; Vila and Piqué, 2012) and Pla de Tabac I (Esteve et al., 2015) during the Bronze Age but also in the so-called Segre-Cinca I (Punta Farisa, El Vilot 0, Roques del Sarró) and Segre-Cinca II (Genó, Masada de Ratón, Tossal de Solibernat, Vincamet I) archeological groups (Piqué et al., 2012; Vila and Piqué, 2012; Vila, 2018), as well as in Cabezo de la Cruz (Badal, 2009; Carrión, 2009), where the highest representation of *Pinus halepensis* is attained (Fig. 4 and Table 5). However, the frequency of Mediterranean open scrubland progressively acquired more visibility during the following cultural periods (Fig. 4). The Segre-Cinca III group (Vilot I, II and Vincamet II), Cabezo de la Cruz during the Iron Age aswell as Iron Age settlements of Els Vilars (phases 0, I), La Codera, Tozal de los Regallos or Segeda (Fig. 4 and Table 5) reported a remarkable rise in xero-thermophilous scrubland with *Pistacia lentiscus*, *Rosmarinus officinalis*, *Rhamnus/Phillyrea*, and Cistaceae, denoting a progressive landscape opening (Carrión, 2007; Badal, 2009; Piqué et al., 2012; Vila and Piqué, 2012; Vila, 2018). Thewood charcoal assemblages of the Iberian period reveal a trend towards an open heliophyte scrubland (e.g., Estinclells, Missatges, Roques del Sarró; Piqué et al., 2012; Vila and Piqué, 2012) (Table 6). The increase of both *Quercus* sp. Deciduous and *Quercus* sp. evergreen during this phase (Fig. 4) could be related to the depletion of resources close to the archeological site and their search in remote territories. In this case these taxa would not correspond to the local vegetation.

Roman, Medieval/Islamic and Modern times are poorly known due to the almost complete absence of wood charcoal studies from archeological sites. Regional paleoenvironmental studies reveal a sharp landscape transformation in the Middle Ebro Basin (Pérez-Lambán et al., 2018), progressively shaping the current vegetation distribution. Aleppo pine is one of the most exploited taxa for fuel in Roman Ilerda and, to a lesser extent, in Iesso (Fig. 4A), being accompanied by *Pinus* type *nigra/sylvestris*, *Quercus* sp. deciduous, *Quercus* sp. Evergreen and Fabaceae, among others (Piqué et al., 2012) (Table 7). The charcoal spectra evidenced the spread of arboricultural practices across the basin during the Medieval/Islamic period, incorporating tree elements of great economic value, such as *Juglans regia, Prunus spinosa/avium* type, *Prunus amygdalus* type, *Pyrus malus*, and Rosaceae Maloideae to local economies (Alonso et al., 2014; Alcolea et al., 2016) (Table 7). *Pinus halepensis* continued being exploited as an important economic resource in Madîna Lârida, Pla d'Almatà and Juslibol Castle (Piqué et al., 2012; Vila and Piqué, 2012; Alcolea et al., 2016, respectively), while it was the dominant taxon in the pedoanthracological record of Val de Zaragoza (Fig. 1A), chronologically framed within the Little Ice Age (Peña-Monné et al., 2018) (Fig. 4 and Table 7). Agricultural terraces and buried horizons date around the 18th century. They reveal an open scrubland where many thermophytes (e.g., *Rosmarinus officinalis, Pistacia lentiscus*) were present (Boixadera et al., 2016).

5. Discussion

The results of our survey reveal that the modern distribution of *Pinus halepensis* in the Ebro Basin is not only human-induced, but also the consequence of a combination of factors, including long-termecological responses to climate changes, soil character, and micro-topographic features. Overall, the reviewed paleobotanical data reveal woodlands of Aleppo pine in the Ebro Basin during the Mesolithic and demonstrate that its distribution is natural before the Neolithic landscape transformation.

The scarcity of wood charcoal data chronologically framed in the Ebro Basin and comprising Upper Pleistocene chronologies makes it difficult to evaluate the spatial extent of Aleppo pine communities since most of the known archeological sites are from mountainous areas. Up to now, anthracological data suggest the dominance of cryophilous pines (*Pinus sylvestris* type) from the NE-E Iberian Mediterranean coast to the Pyrenees (López-García et al., 2012; Allué et al., 2018). Some charcoal assemblages have shown the local presence of Mediterranean pines in SE Iberian sites in coastal areas during the Middle and Upper Paleolithic. The Mousterian and Solutrean charcoal assemblages from Cueva de Nerja (Badal, 1998), Cueva Antón (Zilhão et al., 2016), and Cueva de Ambrosio (Rodríguez-Ariza, 2006) document the presence of a thermophilous flora in which *Pinus halepensis* acquires special relevance. In any case, the Pleistocene presence of a thermophilous *machia* is restricted to the warmer areas of southern Iberia (Carrión et al., 2008; Badal et al., 2012).

This arises the question if these continental regions may have acted as refuge zones for the thermophilous flora, despite the lack of direct paleobotanical evidence comprising Last Glacial Maximum/Lateglacial chronologies. Long-term pollen records from the Middle Ebro Basin, such as Lake Estanya, support the expansion of conifer forests during the Lateglacial interstadial GI-1, when pine and juniper communities account N60% of total terrestrial pollen (González-Sampériz et al., 2017). Although the distinction among pines based exclusively on pollen morphology is not an easy task (Desprat et al., 2015), the coeval presence of pines and a meso-thermophilous flora suggests that inner continental enclaves may have constituted reservoirs of biodiversity that could expand regionally once warmer temperatures and moister conditions took place (González-Sampériz et al., 2004, 2010). In fact, the Aleppo pine communities placed in NE Iberia reveal a high genetic diversity in comparison to southerly placed populations (Gómez et al., 2005). This would imply a rapid migration from coastal enclaves to inner continental environments.

The onset of the Holocene brought amajor change in terms of forest dynamics in the Iberian Peninsula, showing a lagged response of Mediterranean ecosystems to the increase in humidity and temperatures in the Pre-Pyrenean region and the Central Depression (Morellón et al., 2018). In the Early Holocene, climate model simulations highlight an enhanced seasonality in air temperatures and occurrence of dry summer conditions in the Mediterranean region (Brayshaw et al., 2011), which may explain reduced lake-levels (Morellón et al., 2009; Aranbarri et al., 2014) and limited fluvial activity in the Ebro Basin and the Iberian Range (González-Amuchastegui and Serrano, 2015; Sancho et al., 2015; Aranbarri et al., 2016).

These continental climate constraints may have supported a conifer dominated landscape in the Ebro Basin until ca. 9500 cal BP (Morellón et al., 2018). Long-term pollen records reveal open woodlands, almost exclusively dominated by pines and junipers, whichwere progressively replaced by evergreen oaks and thermophilous scrubland towards the Middle Holocene (Aranbarri et al., 2014; González-Sampériz et al., 2017). Anthracological data show that continental *machia* was already present in the lowlands as revealed by all reviewed Mesolithic settlements (Fig. 4), with Aleppo pine woodlands as important landscape components (Fig. 5), amply used as firewood in Cabezo de la Cruz and Espantalobos sites (Badal, 2013; Alcolea et al., 2017b) (Fig. 1A and Table 2). At that time (8340–8100 cal BP), Aleppo pine was also attested in the Levantine coastal areas, such as in La Falguera (Carrión et al., 2006) or Ebro Basin borderlands as La Cativera (Allué et al., 2000). Its presence was also reported from other regions of inland Iberia, such as Cueva Blanca, where charcoal spectra define an open Mediterranean landscape with Aleppo pine communities, junipers and thorny scrubland between 8400 and 7500 cal BP (Uzquiano et al., 2016). The accompanying flora in the Mediterranean coast, however, clearly differs from the continental realm, where humidity-demanding species are less represented (Fig. 4 and Table 2). In any case, the presence of Aleppo pine prior to the Neolithic is documented in many Iberian archeological sites (Badal and Roiron, 1995; Allué, 2002; Aura et al., 2005; Alcolea, 2017a, among others).

The review of wood charcoal assemblages and the palynological evidence of lacustrine paleoenvironmental records suggest that the regional presence of Mesolithic woodlands in the Ebro Basin was driven by a particular continental climate, as it occurs nowadays, rather than being direct consequence of human activities. Hunter-gatherer societies may have modified forests composition at a local-scale by obtaining resources for fuel and timber wood, but this cannot explain the long-term persistence of Aleppo pine woodland in continental Iberia during the first millennia of the Holocene (Table 2). Thus, the climacic character of this community in the Ebro Basin should be addressed.

The scarcity of continuous archeological pollen records comprising the Mesolithic/Neolithic transition make it difficult to detect the early impact of farming practices in the Ebro Basin. Thus, there has been much discussion about the timing and modes of landscape colonization (Oms et al., 2016; Alday et al., 2018; Rojo-Guerra et al., 2018; Laborda, 2019). The available pollen records reveal minor shifts in the arboreal pollen values, with punctual peaks in the herbaceous components and/or scattered presence of cereal pollen (e.g., Cueva de Chaves: López García and López Sáez, 2000). These assemblages clearly differ from emblematic Neolithic settlements with high demographic pressure and intense landscape transformations, such as La Draga (Revelles et al., 2015), Conquezuela-Ambrona Valley (Aranbarri et al., 2015), and El Mirador (Expósito et al., 2017). Thereby, the common idea that *Pinus halepensis* woodlands spread as secondary forests linked to human activities is not supported by archeological pollen profiles, continuous lacustrine pollen records and wood charcoal assemblages obtained in the Middle Ebro Basin (Fig. 4 and Table 4). In fact, arboreal pollen percentages attained their highest values in continental Iberia between 9000 and 6000 cal BP, in response to the establishment of humid conditions and warmer temperatures (Carrión et al., 2010; Morellón et al., 2018).

The hypothesis that human pressure was a major driver, able to completely change the local vegetation dynamic and woodland composition, is not highlighted by the reviewed sites. Moreover, charcoal assemblages (Fig. 4) show that Aleppo pinewoods are less represented in the Ebro Basin during the Neolithic (7500–5500 cal BP) than the Mesolithic times (9000–7500 cal BP). If Neolithic economic activities and landscape transformations were the main factor favoring the spread of Aleppo pine as secondary forest, its frequencies in the paleobotanical results would be expected to increase in all the sites (Fig. 4 and Table 4). This pattern is also confirmed in coastal Mediterranean sequences such as Cova Bonica in where *Pinus halepensis* values are highly represented in the Early Neolithic (7400–7200 cal BP) but decreases until disappearance in the Late Neolithic (4800–3400 cal BP) when an open scrubland composed of *Erica*, *Arbutus unedo* and *Quercus* sp. Evergreen dominates the landscape (Allué et al., 2017). Charcoal assemblages indicate the dominance of both deciduous and evergreen oaks (Fig. 5), which were among the main exploited taxa in Neolithic times, as confirmed by pollen results obtained from lacustrine records and tufa build-ups at a regional scale (Aranbarri et al., 2014, 2016; González-Sampériz et al., 2017; Luzón et al., 2017). This evidence reinforces the hypothesis that the vegetation change was driven more by a climate forcing than by an indiscriminate use of anthropogenic fire for clearing purposes. In the same time period, independent paleohydrological (Morellón et al., 2009; Aranbarri et al., 2014) and geomorphological proxies (Aranbarri et al., 2016; Luzón et al., 2017) document a climate shift towards moister conditions in the Ebro Basin. Thus, a more mesic climate may partially explain the reduction of pinewoods suggested by the paleobotanical assemblages, as Aleppo pine is physiologically better adapted to dry and arid conditions (Borghetti et al., 1998) and is less competitive against both deciduous and evergreen oaks under humid climate constrains (Zavala et al., 2000). These results are not incompatible with a local shaping of the vegetation landscape documented in many archeological sites, but force us to reconsider that human activities were the major factor favoring the spread of pine populations at a regional scale, at least during the Early-Middle Holocene transition.

The Late Holocene phase in the Ebro Basin is defined as a period of rapid and intense environmental changes (Morellón et al., 2009; Pérez-Lambán et al., 2014). Pollen profiles reveal a long-term substitution of mixed Mediterranean woodland by an open conifer forest dominated by pine woodlands (González-Sampériz et al., 2017). Broadleaved elements almost disappear or are confined to humid enclaves near watercourses. Similarly, independent proxies, such as the geochemical signature of lacustrine sediments and geomorphic evidence related to tufa accumulation, reveal a major climate change towards reduced water availability at a basin scale (Morellón et al., 2009; Aranbarri et al., 2016; Luzón et al., 2017).

Anthracological data reveal a progressive reduction of woodlands and the establishment of a Mediterranean scrubland dominated by *Arbutus unedo*, *Rhamnus/Phillyrea*, *Rosmarinus officinalis*, *Pistacia lentiscus*, and Fabaceae, chronologically framed during the Bronze and Iron Ages (Fig. 4 and Tables 5 and 6). Aleppo pine populations could have been partially favored by the establishment of a warmer and drier climate in the lowlands and mountain foothills similar to present day.

However, the increased demographic pressure documented during this period along the Ebro Valley (Blanco-González et al., 2018; Fyfe et al., 2019) necessarily implies a more frequent use of wood as fuel and timber (Carrión, 2007; Badal et al., 2010). The development of craft activities, namely pottery and metallurgy, demanded the use of fuel beyond the domestic sphere. The characteristics of Aleppo pine trees, a fast-growing species producing long and straight trunks, makes it widely used as timber wood (Ntinou et al., 2013; Picornell-Gelabert and Dufraisse, 2018). Although its use as raw material is difficult to document due to the scarcity of non-charred plant-based materials in archeological records, Aleppo pine woodcraft is attested in the Middle Ebro Basin (Alcolea and Rodanés, 2019) and in other Mediterranean areas (Carrión and Rosser, 2010) during Iberian and Roman times.

Differently from the Mesolithic (Table 3) and Neolithic (Table 4) assemblages, the Mediterranean scrubland component increased since the Metal Ages (Tables 5 and 6), and especially during historical times (Table 7), which may be interpreted as the result of a more intensive land use linked to higher demographic pressure and diversification of economic activities. Indeed, pollen data reveal a progressive a spread of grazing activities, rise of cereal cultivation and introduction of arboricultural practices (Riera et al., 2004; Corella et al., 2013; González-Sampériz et al., 2017), witnessing a profound woodland depletion at basin scale and favoring the expansion of Aleppo pine communities in recent times.

6. Conclusions

The vegetation record of the Ebro Basin reveals a long-term dominance of Aleppo pine forest and Mediterranean scrubland since the Mesolithic, with the exception of the Neolithic, when a more humid demanding flora spread in the region. The degree of anthropogenic pressure across the Holocene, however, did not have always the same intensity, so the interaction between people and trees and the interplay with the regional climate background must be interpreted in its historical context.

Acknowledgments

Present research derives from GAS (HAR2017-85023-P), DINAMO2 (CGL2012-33063), DINAMO 3 (CGL2015-69160-R) and PRASED (HAR2016-78277-R) national research projects funded by the Spanish Government as well as the Consolidated Research Group in Prehistory, University of the Basque Country (IT1223-19). Marta Alcolea work is funded by the Post-Doc Grant Plan Xunta de Galicia modalidade A (ED481B 2018/016). The authors give thanks to Miguel Macías from Universitat Politècnica de València for his software used for generating the diagram.

References

Alcolea, M., 2017a. Mesolithic fuel use and woodland in the Middle Ebro Valley (NE Spain) through wood charcoal analysis. Quat. Int. 431, 39–51.

Alcolea, M., 2017b. El paisaje vegetal y la explotación del combustible: estudio antracológico del Arenal de Fonseca (Ladruñán, Teruel). In: Utrilla, P., Domingo, R., Bea, M. (Eds.), El Arenal de Fonseca (Castellote, Teruel): ocupaciones prehistóricas del Gravetiense al Neolítico. 52, p. 163.

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. Universidad de Zaragozea.

Alcolea, M., Rodanés, J.M., 2019. Ephemeral Archaeology south of the Central Pyrenees (Huesca, NE Iberia): The exceptional preservation of woody objects in Moro de Alins cave-site. Environ. Archaeol. https://doi.org/10.1080/14614103.2019.1654642.

Alcolea, M., Longares, L.A., Cunill, R., Peña-Monné, J.L., Royo, M., 2016. Aportaciones de la antracología al conocimiento del marco paleoecológico y paleoeconómico del Castillo de Juslibol (Zaragoza) en época medieval. Zephyrus 77, 173–189.

Alcolea, M., Utrilla, P., Piqué, R., Laborda, R., Mazo, C., 2017a. Fuel and acorns: Early Neolithic plant use from Cueva de Chaves (NE Spain). Quat. Int. 457, 228–239.

Alcolea, M., Domingo, R., Piqué, R., Montes, L., 2017b. Landscape and firewood at Espantalobos Mesolithic site (Huesca, Spain). First results. Quat. Int. 457, 198–210.

Alday, A., Domingo, R., Sebastián, M., Soto, A., Aranbarri, J., González-Sampériz, P., Sampietro-Vattuone, M.M., Utrilla, P., Montes, L., Peña-Monné, J.L., 2018. The silence of the layers: Archaeological site visibility in the Pleistocene-Holocene transition at the Ebro Basin. Quat. Sci. Rev. 184, 85–106.

Allué, E., 2002. Dinámica de la vegetación y explotación del combustible leñoso durante el Pleistoceno Superior y el Holoceno del Noreste de la Península Ibérica a partir del análisis antracológico. Ph.D. Facultat de Lletres, Universitat Rovira i Virgili, Tarragona, p. 343.

Allué, E., Angelucci, D., Cáceres, I., Fiocchi, C., Fontanals, F., García, M., Huguet, R., Ollé, A., Saladié, P., Vergès, J.M., Zaragoza, J., 2000. El registro paleoecológico y arqueológico de La Cativera (El Catllar, Tarragona): Datos preliminares sobre el límite Pleistoceno-Holoceno en el sur de Cataluña. Actas do 3° Congreso de Arqueología Peninsular IX Contributos das ciências e das tecnologias para a arqueologia da Península Ibérica, pp. 81–96.

Allué, E., Martínez-Moreno, J., Alonso, N., Mora, R., 2012. Changes in the vegetation and human management of forest resources in mountain ecosystems at the beginning of MIS 1 (14.7–8 ka cal BP) in Balma Guilanyà (Southeastern Pre-Pyrenees, Spain). Compt. Rend. Palevol. 11, 507–518.

Allué, E., Fullola, J.M., Mangado, X., Petit, M.A., Bartroli, R., Tejero, J.M., 2013. La séquence anthracologique de la grotte du Parco (Alòs de Balaguer, Espagne): paysages et gestion du combustible chez les derniers chasseurs-cueilleurs. L'anthropologie 117, 420–435.

Allué, E., Picornell-Gelabert, L., Daura, J., Sanz, M., 2017. Reconstruction of the palaeoenvironment and anthropogenic activity fromthe Upper Pleistocene/Holocene anthracological records of the NE Iberian Peninsula (Barcelona, Spain). Quat. Int. 457, 172–189.

Allué, E., Martínez-Moreno, J., Roy, M., Benito-Calvo, A., Mora, R., 2018. Montane pine forests in NE Iberia during MIS 3 and MIS 2. A study based on new anthracological evidence from Cova Gran (Santa Linya, Iberian Pre-Pyrenees). Rev. Palaeobot. Palynol 258, 62–72.

Alonso, N., Bergadà, M., Gené, M., Gómez, X., Juan, J., Junyent, E., Lafuente, A., López, J.B., Mazo, C., Moya, A., Nadal, J., Piqué, R., Riera, S., Tartera, E., 2002. Recuperant el passat a la línia del Tren d'Alta Velocitat. L'assentament protohistoric, Medieval i d'època romana de El Vilot de Montagut (Alcarràs, Lleida). Lleida, Gestora de Infraestructuras Ferroviarias and Generalitat de Catalunya.

Alonso, N., Antolín, F., Kirchner, H., 2014. Novelties and legacies in crops of the Islamic period in the northeast Iberian Peninsula: the archaeobotanical evidence in Madîna Balagî, Madîna Lârida, and Madîna Turṭûša. Quat. Int. 346, 149–161.

Aranbarri, J., González-Sampériz, P., Valero-Garcés, B., Moreno, A., Gil-Romera, G., Sevilla- Callejo, M., García-Prieto Fronce, E., Di Rita, F., Mata, M.P., Morellón, M., Magri, D., Rodríguez-Lázaro, J., Carrión, J.S., 2014. Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of southwestern Europe. Glob. Planet. Chang. 114, 50–65.

Aranbarri, J., González-Sampériz, P., Iriarte, E., Moreno, A., Rojo-Guerra, M., Peña-Chocarro, L., Valero-Garcés, B., Leunda, M., García-Prieto, E., Sevilla-Callejo, M., Gil-Romera, G., Magri, D., Rodríguez-Lázaro, J., 2015. Human–landscape interactions in the Conquezuela–Ambrona Valley (Soria, continental Iberia): fromthe early Neolithic land use to the origin of the current oak woodland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 436, 41–57.

Aranbarri, J., Bartolomé, M., Alcolea, M., Sancho Marcén, C., Celant, A., González-Sampériz, P., Arenas, C., Magri, D., Rodríguez-Lázaro, J., 2016. Palaeobotanical insights from Early-Mid Holocene fluvial tufas in the Moncayo Natural Park (Iberian Range, NE Spain): Regional correlations and biogeographic implications. Rev. Palaeobot. Palynol. 234, 31–43.

Aura, E., Carrión, Y., Estrelles, E., Pérez, G., 2005. Plant economy of hunter–gatherer groups at the end of the last Ice Age: Plant macrorremains from the cave of Sta. Maira (Alacant, Spain), ca 12000–9000 BP. Veg. Hist. Archaeobotany 14, 542–550.

Aura, J.E., Jordá, J.F., Montes, L., Utrilla, P., 2011. Human responses to Younger Dryas in the Ebro valley and Mediterranean watershed (Eastern Spain). Quat. Int. 242, 348–359.

Badal, E., 1998. El interés económico del pino piñonero para los habitantes de la Cueva de Nerja. Las culturas del Pleistoceno superior en Andalucía, pp. 287–300.

Badal, E., 2004. Análisis antracológico de los restos del fuego doméstico del abrigo de Los Baños (Ariño, Teruel). In: Utrilla, P., Rodanés, J.M. (Eds.), Un asentamiento epipaleolítico en el valle del río Martín. El Abrigo de Los Baños (Ariño, Teruel), Monografías Arqueológicas. Prehistoria 39. Prensas Universitarias Universidad de Zaragoza, Zaragoza, pp. 63–74.

Badal, E., 2009. El combustible y el paisaje vegetal. In: Picazo, J.V., Rodanés, J.M. (Eds.), Los poblados del Bronce Final y Primera Edad del Hierro. Cabezo de la Cruz (La Muela, Zaragoza). Gobierno de Aragón, pp. 132–155.

Badal, E., 2013. Los usos de los vegetales leñosos en el Cabezo de la Cruz (La Muela, Zaragoza) durante la ocupación mesolítica. In: Rodanés, J.M., Picazo, J.V. (Eds.), El Campamento Mesolítico Del Cabezo de La Cruz. La Muela, Zaragoza, Monografías Arqueológicas. Prehistoria 45. Universidad de Zaragoza, Zaragoza, pp. 83–99.

Badal, E., Roiron, P., 1995. La prehistoria de la vegetación en la Península Ibérica. Saguntum 28, 29–48.

Badal, E., Bernabeu, J., Vernet, J.L., 1994. Vegetation changes and human action from the Neolithic to the Bronze Age (7000-4000 B.P.) in Alicante (Spain) based on charcoal analysis. Veg. Hist. Archaeobotany 3, 155–166.

Badal, E., Carrión, Y., Picazo, J., Rodanés, J.M., 2010. Los usos de los vegetales en el Cabezo de la Cruz (La Muela, Zaragoza) durante la Edad del Hierro. VIII Congreso Ibérico de Arqueometría, pp. 5–19.

Badal, E., Carrión, Y., Figueiral, I., Rodríguez-Ariza, M.O., 2012. Pinares y enebrales. El paisaje solutrense en Iberia. Espacio Tiempo y Forma. Ser. I Prehist. Arqueol. 5, 259–271.

Bennett, K.D., Tzedakis, P.C.,Willis, K.J., 1991. Quaternary refugia of north European trees. J. Biogeogr. 18, 103–115.

Blanco-Castro, E., Casado, M., Costa, M., Escribano, R., García-Antón, M., Génova, M., Gómez, A., Moreno, J., Morla, C., Regato, P., Sainz Ollero, H., 1997. Los bosques ibéricos. Una interpretación geobotánica, Barcelona.

Blanco-González, A., Lillios, K.T., López-Sáez, J.A., Drake, B.L., 2018. Cultural, demographic and environmental dynamics of the copper and Early Bronze Age in Iberia (3300–1500 BC): Towards an interregional multiproxy comparison at the time of the 4.2 ky BP event. J. World Prehist. 31, 1–79.

Boixadera, J., Riera, S., Vila, S., Esteban, I., Albert, R.M., Llop, J.M., Poch, R.M., 2016. Buried A horizons in old bench terraces in Les Garrigues (Catalonia). Catena 137, 635–650.

Borghetti, M., Cinnirella, S., Magnani, F., Saracino, A., 1998. Impact of long-term drought on xylem embolism and growth in Pinus halepensis Mill. Trees 12, 187–195.

Braun-Blanquet, J., Bolós, O., 1987. Las Comunidades Vegetales de la Depresión del Ebro y su Dinamismo. Zaragoza, España, Ayuntamiento de Zaragoza.

Brayshaw, D.J., Rambeau, C.M.C., Smith, S.J., 2011. Changes inMediterranean climate during the Holocene: insights from global and régional climate modeling. The Holocene 21, 15–32.

Brewer, S., Cheddadi, R., De Beaulieu, J.L., Reille,M., 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. For. Ecol. Manag. 156, 27–48.

Buxó, R., Canal, D., Guitart, J., Pera, J., Piqué, R., 2004. Excavació de dos pous d'època Romana a Guissona. L'explotació dels recursos vegetals a la ciutat de Iesso als segles I a.C-II d.C. In: Guitart, J., Pera, J., Iesso, I. (Eds.), Patronat d'Arqueologia de Guissona. Guissona-Barcelona, pp. 213–278.

Carrión, J.S., Fernández, S., 2009. The survival of the 'natural potential vegetation' concept (or the power of tradition). J. Biogeogr. 36 (12), 2202–2203.

Carrión, J.S., Navarro, C., Navarro, J., Munuera, M., 2000. The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeocological data: Relationships with phytosociological classification. The Holocene 10, 243–252.

Carrión, J.S., Finlayson, C., Férnández, S., Finlayson, G., Allué, E., López-Sáez, J.A., López-García, P., Gil-Romera, G., Bailey, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E., Burjachs, F., 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Rev. Palaeobot. Palynol. 162, 458–475.

Carrión, Y., 2007. Woodland in the middle Ebro valley (Spain). Dendrological analysis of archaeological timber from Bell Baker and Iron Age periods. ArchéoSciences 31, 151–161.

Carrión, Y., 2009. La construcción en madera. In: Picazo, J.V., Rodanés, J.M. (Eds.), Los poblados del Bronce Final y Primera Edad del Hierro. Cabezo de la Cruz (LaMuela, Zaragoza). Gobierno de Aragón, pp. 156–169.

Carrión, Y., Rosser, P., 2010. Revealing Iberian woodcraft: conserved wooden artefacts from south-east Spain. Antiquity 84, 747–764.

Carrión, Y., Molina, L.L., Pérez, M., García, O., Pérez, G., Verdasco, C., McClure, S.B., 2006. Las evidencias de una orientación ganadera. Los datos. (Coords.) (Eds.). In: García, O., Aura, J.E. (Eds.), El Abric de La Falguera (Alcoi, Alacant). 8000 años de ocupación humana en la cabecera del río Alcoi. Diputación de Alicante, Ayuntamiento de Alcoy, Caja de Ahorros del Mediterráneo, Alcoy, pp. 219–236.

Combourieu-Nebout, N., Peyron, O., Dormoy, I., 2009. Rapid climatic variability in the west Mediterranean during the last 25 000 years from high resolution pollen data. Clim. Past Discuss. 5, 671–707.

Corella, J.P., Stefanova, V., El Anjoumi, A., Rico, E., Giralt, S., Moreno, A., Plata-Montero, A., Valero-Garcés, B.L., 2013. A 2500-year multi-proxy reconstruction of climate change and human activities in northern Spain: the Lake Arreo record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 555–568.

Costa, M., 1987. El País Valenciano. In: Peinado,M., RivasMartínez, S. (Eds.), La Vegetación de España. Servicio de Publicaciones de la Universidad de Alcalá, Madrid, pp. 281–308.

Desprat, S., Díaz-Fernández, P.M., Coulon, T., Ezzat, L., Pessarossi-Langlois, J., Gil, L., Morales-Molino, C., Sánchez-Goni, M.F., 2015. Pinus nigra (European black pine) as the dominant species of the last glacial pinewoods in south-western to central Iberia: A morphological study of modern and fossil pollen. J. Biogeogr. 42, 1998–2009.

Di Rita, F., Melis, R.T., 2013. The cultural landscape near the ancient city of Tharros (central West Sardinia): Vegetation changes and human impact. J. Archaeol. Sci. 40 (12), 4271–4282.

Djamali, M., Gambin, B., Marriner, N., Andrieu-Ponel, V., Gambin, T., Gandouin, E., Lanfranco, S., Medail, F., Pavon, D., Ponel, P.,Morhange, C., 2013. Vegetation dynamics during the early to mid-Holocene transition in NW Malta, human impact versus climatic forcing. Veg. Hist. Archaeobotany 22, 367–380.

Domingo, R., Alcolea,M., Bea,M.,Mazo, C., Montes, L., Picazo, J.V., Rodanés, J.M., Utrilla, P., 2018. Call it home:Mesolithic dwellings in the Ebro Basin (NE Spain). J. Archaeol. Sci. Rep. 18, 1036–1052.

Douda, J., Doudová, J., Drasnarová, A., Kunes, P., Hadincová, V., Krak, K., Zákravský, P., Mandák, B., 2014. Migration patterns of subgenus Alnus in Europe since the Last Glacial Maximum: A systematic review. PLoS One 9 (2), e88709.

Esteve, X., Armentano, N., Espejo, J.M., Gallart, J., Gibaja, J.F., López, D., Mangado, J., Marín, D., Nadal, J., Oms, F.X., Orri, E., Sánchez, M., Vila, S., 2015. El Pla de Tabac I (Montoliu de Lleida), un assentament de l'edat del bronze a la Plana de Lleida. Rev. Arqueol. Ponent 25, 137–168.

Expósito, I., Burjachs, F., Vergès, J.M., 2017. Human trace on the landscape during the Holocene at El Mirador Cave (Sierra de Atapuerca, Spain): The palynological evidence. The Holocene 27 (8), 1201–1213.

Figueiral, I., Carcaillet, C., 2005. A review of Late Pleistocene and Holocene biogeography of highland Mediterranean pines (Pinus type sylvestris) in Portugal, based on wood charcoal. Quat. Sci. Rev. 24, 2466–2476.

Figueiral, I., Mosbrugger, V., 2000. A review of charcoal analysis as a tool for assessing Quaternary and Tertiary environments: Achievements and limits. Palaeogeogr. Palaeoclimatol. Palaeoecol. 164, 397–407.

Fletcher,W.J., Sánchez Goñi, M.F., 2008. Orbital- and sub-orbital-scale climate impacts on vegetation of the western Mediterranean basin over the last 48,000 yr. Quat. Res. 70 (3), 451–464.

Folch, R., 1986. La vegetació dels països catalans. Ketres, Barcelona.

Fontanals, M., Euba, I., Morales, J.I., Oms, F.X., Vergés, J.M., 2008. El asentamiento litoral al aire libre de El Cavet (Cambrils, Tarragona). In: Hernández, M.S., Soler, J.A., López, J.A. (Eds.), Actas del IV Congreso del Neolítico Peninsular. Museo Arqueológico de Alicante, Alicante, pp. 168–175.

Fyfe, R.,Woodbridge, J., Palmisano, A., Bevan, A., Shennan, S., Burjachs, F., Legarra Herrero, B., García Puchol, O., Carrión, J.S., Revelles, J., Roberts, N.C., 2019. Prehistoric palaeodemographics and regional land cover change in eastern Iberia. The Holocene 29 (5), 799–815.

García-Martínez de Lagrán, I., Iriarte, E., García-Gazólaz, J., Tejedor-Rodríguez, C., Gibaja-Bao, J.F., Moreno-García, M., Pérez-Jordà, G., Ruiz-Alonso, M., Sesma-Sesma, J., Garrido-Pena, R., Carrancho-Alonso, á., Peña-Chocarro, L., Rojo-Guerra, M.A., 2016. 8.2 ka BP paleoclimatic event and the Ebro Valley Mesolithic groups: Preliminary data from Artusia rock shelter (Unzué, Navarra, Spain). Quat. Int. 403, 151–173.

Gómez, A., Vendramin, G.G., González-Martínez, S.C., Alía, R., 2005. Genetic diversity and differentiation of two Mediterranean pines (*Pinus halepensis* Mill. and *Pinus pinaster* Ait.) along a latitudinal cline using chloroplast microsatellite markers. Divers. Distrib. 11, 257–263.

González-Amuchastegui, M.J., Serrano, E., 2015. Tufa buildup, landscape evolution and human impact during the Holocene in the Upper Ebro Basin. Quat. Int. 364, 54–64.

González-Hidalgo, J.C., Brunetti, M., de Luis, M., 2011. A new tool for monthly precipitation analysis in Spain: MOPREDAS database (monthly precipitation trends December 1945-November 2005). Int. J. Climatol. 31 (5), 715–731.

González-Hidalgo, J.C., Peña-Angulo, D., Brunetti, M., Cortesi, N., 2015. MOTEDAS: A new monthly temperature database for mainland Spain and the trend in temperature (1951-2010). Int. J. Climatol. 35 (15), 4444–4463.

González-Sampériz, P., Valero-Garcés, B., Carrión, J.S., 2004. Was the Ebro valley a glacial refugium for temperate trees? An. Biol. 26, 13–20.

González-Sampériz, P., Leroy, S.A.G., Carrión, J.S., Fernández, S., García-Antón, M., Gil-García, M.J., Uzquiano, P., Valero-Garcés, B., Figueiral, I., 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. Rev. Palaeobot. Palynol. 162, 427–457.

González-Sampériz, P., Aranbarri, J., Pérez-Sanz, A., Gil-Romera, G., Moreno, A., Leunda, M., Sevilla-Callejo, M., Corella, J.P., Morellón, M., Oliva, B., Valero-Garcés, B., 2017. Environmental and climate change in the southern Central Pyrenees since the Last Glacial Maximum: A view from the lake records. Catena 149, 668–688.

Iriarte-Chiapusso, M.J., Muñoz Sobrino, C., Gómez-Orellana, L., Hernández-Beloqui, B., García-Moreiras, I., Fernández Rodríguez, C., Heiri, O., Lotter, A.F., Ramil-Rego, P., 2016. Reviewing the Lateglacial-Holocene transition inNWIberia: A palaeoecological approach based on the comparison between dissimilar regions. Quat. Int. 403, 211–236.

Jacquiot, C, 1955. Atlas d’anatomie des bois des coniferes. Cent. Tech. Bois., Paris.

Laborda, R., 2019. El Neolítico antiguo en el Valle Medio del Ebro. Una visión desde la cerámica y las dataciones radiocarbónicas. Monografías Arqueológicas, 55. Universidad de Zaragoza.

Linstädter, A., Zielhofer, C., 2010. Regional fire history shows abrupt responses o fMediterranean ecosystems to centennial-scale climate change (Olea–Pistacia woodlands, NE Morocco). J. Arid Environ. 74 (1), 101–110.

Longares, L.A., 2004. El paisaje vegetal en el sector aragonés delMoncayo. Geografía Física de Aragón. Aspectos generales y temáticos. Universidad de Zaragoza e Institución Fernando el Católico 187–197.

López-García, J.M., Blain, H.-A., Bennàsar, M., Euba, I., Banuls, S., Bischoff, J., López-Ortega, E., Saladié, P., Uzquiano, P., Vallverdú, P., 2012. A multiproxy reconstruction of the palaeoenvironment and paleoclimate of the late Pleistocene in northeastern Iberia: Cova dels Xaragalls, Vimbodí-Poblet, Paratge Natural de Poblet, Catalonia. Boreas 41, 235–249.

López García, P., López Sáez, J.A., 2000. Le paysage et la phase épipaléolithique mésolithique dans les Pre-Pyrénées aragonaises et le bassin moyen de l’Ebre à partir de l’analyse palynologique, en Les derniers chasseurs-cueilleurs d’Europe occidentale (13.000-5.5000 av J.C.). Actes du colloque international de Besançon. Ann. Littér. 699, 59–69.

Luzón, A., Gauthier, A., Pérez, A., Pueyo-Anchuela, O., Mayayo, M.J., Muñoz, A., 2017. Late Pleistocene-Holocene palaeoenvironmental evolution of the Añamaza River valley (Iberian Range, NE Spain): Multidisciplinary approach on the study of carbonate fluvial systems. Quat. Int. 437, 51–70.

Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). J. Biogeogr. 35, 450–463.

Manzano, S., Carrión, J.S., López-Merino, L., González-Sampériz, P., Munuera, M., Fernández, S., Martín-Lerma, I., Gómez Ferreras, M.d.C., 2017. Mountain strongholds forwoody angiosperms during the Late Pleistocene in SE Iberia. Catena 149, 701–712.

Martín-Seijo, M., Piqué, R., 2008. Consumo especializado de combustibles en el Neolítico: los datos antracológicos del yacimiento de Auvelles (Castelló de Farfanya, Lleida). En. In: Hernández, M.S., Soler, J.A., López, J.A. (Eds.), IV Congreso de Neolítico Peninsular de Alicante, tomo I, pp. 432–437.

Maya, J.L., Cuesta, F., López, J., 1998. Genó: Un poblado del Bronca Final en el Bajo Segre (Lleida). Publicacions Universitat de Barcelona, Barcelona.

Mazo, C, Alcolea, M, 2019. New data concerning Neanderthal occupation in the Iberian System: First results from the late Pleistocene (MIS 3) Aguilón P5 cave site (NE Iberia). Quaternary International https://doi.org/10.1016/j.quaint.2019.07.025.

Montes, L., Domingo, R., González-Sampériz, P., Sebastián, M., Aranbarri, J., Castanos, P., García-Simón, L.M., Alcolea, M., Laborda, R., 2016. Landscape, resources and people during the Mesolithic and Neolithic times in NE Iberia: The Arba de Biel Basin. Quat. Int. 403, 133–150.

Morellón, M., Valero-Garcés, B., Vegas-Vilarrúbia, T., González-Sampériz, P., Romero, O., Delgado-Huertas, A., Mata, P., Moreno, A., Rico, M., Corella, J.P., 2009. Lateglacial and Holocene palaeohydrology in the western mediterranean region: the Lake Estanya record (NE Spain). Quat. Sci. Rev. 28, 2582–2599.

Morellón, M., Aranbarri, J., Moreno, A., González-Sampériz, P., Valero-Garcés, B.L., 2018. Early Holocene humidity patterns in the Iberian Peninsula reconstructed from lake, pollen and speleothem records. Quat. Sci. Rev. 181, 1–18.

Ne'eman, G., Izhaki, I., 2006. Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forest. Ecography 21, 535–542.

Ne'eman, G., Goubitz, S., Nathan, R., 2004. Reproductive traits of Pinus halepensis in the light of fire – a critical review. Plant Ecol. 171, 69–79.

Ntinou, M., Badal, E., Carrión, Y., Fueyo, J.L.M., Carrión, R.F., Mira, J.P., 2013.Wood use in a medieval village: the contribution ofwood charcoal analysis to the history of land use during the 13th and 14th centuries A.D. at Pobla d'Ifach, Calp, Alicante, Spain. Veg. Hist. Archaeobotany 22, 115–128.

Olmedo-Cobo, J.A., Cunill-Artigas, R., Gómez-Zotano, J., 2019. The native status of *Pinus pinaster* on serpentine soils: Charcoal analysis and palaeoenvironmental history in Sierra Bermeja (southern Iberian Peninsula, Spain). Veg. Hist. Archaeobotany 28 (4), 417–432.

Oms, F.X., Martín, A., Esteve, X., Mestre, J., Morell, B., Subirà, M.E., Gibaja, J.F., 2016. The Neolithic in North-East Iberia: Chronocultural phases and C14. Radiocarbon 58, 1–19.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T., Vallejo, R., 2002. Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. Plant Ecol. 169, 205–213.

Pausas, J.G., Ribeiro, E., Vallejo, R., 2004. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. For. Ecol. Manag. 203, 251–259.

Peña-Chocarro, L., Zapata, L., García Gazólaz, J., González Morales, M., Sesma, J., Straus, L.G., 2005. The spread of agriculture in northern Iberia: new archaeobotanical data from El Mirón cave (Cantabria) and the open-air site of Los Cascajos (Navarra). Veg. Hist. Archaeobotany 14, 268–278.

Peña-Monné, J.L., Sampietro-Vattuone, M.M., Longares-Aladrén, L.A., Pérez-Lambán, F., Sánchez-Fabre, M., Alcolea, M., Vallés, L., Echeverria-Arnedo, M.T., Baraza, C., 2018. Holocene alluvial sequence in the Val de Zaragoza (Los Monegros) in the palaeoenvironmental context of the Ebro Basin (NE Spain). Cuadernos Investig. Geogr. 44, 321–348.

Pérez-Lambán, F., Peña-Monné, J.L., Fanlo, J., Picazo, J.V., Badía-Villas, D., Rubio-Fernández, V., García-Giménez, R., Sampietro-Vattuone, M.M., 2014.

Paleoenvironmental and geoarchaeological reconstruction from late Holocene slope records (lower Huerva valley, Ebro Basin, NE Spain). Quat. Res. 81, 1–14.

Pérez-Lambán, F., Peña-Monné, J.L., Badía-Villas, D., Picazo, J.V., Vicente, J., Sampietro- Vattuone, M.M., Alcolea, M., Aranbarri, J., González-Sampériz, P., Fanlo, J., 2018. Holocene environmental variability in the Central Ebro Basin (NE Spain) from geoarchaeological and pedological records. Catena 163, 147–164.

Picornell-Gelabert, L., Dufraisse, A., 2018. Wood for building: Woodland exploitation for timber procurement in the prehistoric and protohistoric Balearic Islands (Mallorca and Menorca; Western Mediterranean). Environ. Archaeol. 1–16.

Piqué, R., 1995. Aproximació a l'entorn vegetal durant el Paleolític i Mesolític al vessant sud dels prepirineus a partir dels carbons vegetals. Cultures i Medi de la prehistoria a l'edat mitjana. X Colloqui Internacional d'Arqueologia de Puigcerdà. Homenatje a Jean Guilaine. 71–78.

Piqué, R., Vila, S., Alonso, N., 2012. Changes in vegetation and fuel use from the Neolithic to the Middle Ages in the Western Catalan plain. Sagvntvm 13, 85–96.

Quézel, P., Barbero, M., 1990. Les forêts méditerranéennes. Problèmes posés par leur signification historique, écologique et leur conservation. Acta Bot. Malacit. 15, 145–178.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatte, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A, Turney, C.S.M., van der Plicht, J., 2013. INTCAL13 AND MARINE13 radiocarbon age calibration curves 0-50,000 years cal BP. Radiocarbon 55, 1869–1887.

Revelles, J., Cho, S., Iriarte, E., Burjachs, F., van Geel, B., Palomo, A., Piqué, R., Peña-Chocarro, L., Terradas, X., 2015. Mid-Holocene vegetation history and Neolithic land-use in the Lake Banyoles area (Girona, Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 435, 70–85.

Revelles, J., Ghilardi, M., Rossi, V., Currás, A., López-Bultó, O., Brkojewitsch, G., Vacchi, M., 2019. Coastal landscape evolution of Corsica island (W. Mediterranean): palaeoenvironments, vegetation history and human impacts since the early Neolithic period. Quat. Sci. Rev. 225, 105993.

Riera, S.,Wansard, R., Julià, R., 2004. 2000-Year environmental history of a karstic lake in the Mediterranean Pre-Pyrenees: The Estanya lakes (Spain). Catena 55, 293–324.

Rivas Martínez, S., 1987. Memoria del Mapa de Series de Vegetación de España. ICONA. Ministerio de Agricultura, Pesca y Alimentación, Madrid.

Rodríguez-Ariza, M.O., 1992. Human-plant relationships during the Copper and Bronze Ages in the Baza and Guadix Basins (Granada, Spain). Bull. Soc. Bot. Fr. 139, 451–464.

Rodríguez-Ariza, M.O., 2006. Análisis antracológico del yacimiento solutrense de La Cueva de Ambrosio (Vélez Blanco, Almería). En. In: Sanchidrián, J.L., Márquez, A.M., Fullola, J.M. (Eds.), IV Simposio de Prehistoria Cueva de Nerja. La Cuenca Mediterránea durante el Paleolítico superior (38.000-10.000 años), Málaga, pp. 226–233.

Roiron, P., Chabal, L., Figueiral, I., Terral, J.-F., Ali, A.A., 2013. Palaeobiogeography of *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco in the north-western Mediterranean Basin: A review based on macroremains. Rev. Palaeobot. Palynol. 194, 1–11.

Rojo-Guerra, M.A., García-Martínez de Lagrán, I., Royo-Guillén, I., 2018. The beginning of the Neolithic in the mid-Ebro valley and in Iberia's Inland (Northern and Southern submeseta) Spain. Quat. Int. 470, 398–438.

Ros, M.T., 1993. Análisis antracológico del yacimiento del Bronce Medio de Punta Farisa (Fraga, Huesca). Estud. Antig. 6/7, 45–47.

Ros, M.T., 1994/96. La vegetació de la Catalunya Meridional i territoris propers de la depressió de l'Ebre en la Prehistòria recent i protohistòria a partir dels estudis antracològics. Gala 3–5, 19–339.

Ros, M.T., 1996. Datos antracológicos sobre la diversidad paisajística de Catalunya en el neolítico. Rubricatum: revista del Museu de Gavà 1, 43–56.

Rubiales, J.M., García-Amorena, I., García-Álvarez, S., Morla, C., 2009. Anthracological evidence suggests naturalness of Pinus pinaster in inland southwestern Iberia. Plant Ecol. 200, 155–160.

Ruíz-Alonso, M., 2014. Evolución y explotación de los recursos vegetales desde el Tardiglaciar en la vertiente mediterránea del País Vasco: datos antracológicos. Tesis doctoral inédita. Universidad del País Vasco.

Ruíz-Alonso, M., Zapata, L., 2015. Transformation and human use of forests in the Western Pyrenees during the Holocene based on archaeological wood charcoal. Quat. Int. 364, 86–93.

Sancho, C., Arenas, C., Vázquez-Urbez, M., Pardo, G., Lozano, M.V., Peña-Monné, J.L., Hellstrom, J., Ortiz, J.E., Osácar, M.C., Auqué, L., Torres, T., 2015. Climatic implications of the Quaternary fluvial tufa record in the NE Iberian Peninsula over the last 500 ka. Quat. Res. 84, 398–414.

Schweingruber, F.H., 1990. Anatomie Europaïscher Hölzer. European Wood Anatomy, Bern and Stuttgart. Haupt.

Stuiver, M., Reimer, P.J., 1993. Extended 14C data base and revised CALIB 3.0 14C age calibration program. Radiocarbon 35, 215–230.

Thiébault, S., 1997. Early-Holocene vegetation and the human impact in central Provence (Var, France): Charcoal analysis of the Baume de Fontbrégoua. The Holocene 7, 343–349.

Tinner,W., van Leeuwen, J.F.N., Colombaroli, D., Vescovi, E., van der Knaap, W.O., Henne, P.D., Pasta, S., D'Angelo, S., La Mantia, T., 2009. Holocene environmental and climatic changes at Gorgo Basso, a coastal lake in southern Sicily, Italy. Quat. Sci. Rev. 28, 1498–1510.

Utrilla, P., Domingo, R., Montes, L., Mazo, C., Rodanés, J.M., Blasco, F., Alday, A., 2012. The Ebro Basin in NE Spain: a crossroads during the Magdalenian. Quat. Int. 272–273, 88–104.

Uzquiano, P., Casas-Gallego, M., Mingo, A., Barba, J., Yravedra, J., 2016. Vegetation, climate and human settlement interactions at the lateMesolithic site of Cueva Blanca (Hellín, Albacete, SE Spain). The Holocene 26 (1), 102–112.

Vernet, J.-L., Thiébault, S., 1987. An approach to northwestern Mediterranean recent prehistoric vegetation and ecologic implications. J. Biogeogr. 14, 117–127.

Vila, S., 2018. L'explotació dels recursos vegetals a la plana occidental catalana durant la protohistòria a partir de l'anàlisi antracològica (III-I mil·lenni). Tesis Doctoral. Universidad de Lleida.

Vila, S., Piqué, R., 2012. Paisatge vegetal i gestió del combustible a la plana occidental catalana entre el neolític i l'edat mitjana: estat de la qüestió des de l'anàlisi antracològica. Rev. Arqueol. Ponent 22, 9–36.

Wengler, L., Vernet, J.-L., 1992. Vegetation, sedimentary deposits and climates during the Late Pleistocene and Holocene in eastern Morocco. Palaeogeogr. Palaeoclimatol. Palaeoecol. 94, 141–167.

Zapata, L., 2000. La recolección de plantas silvestres en la subsistencia mesolítica y neolítica. Datos arqueobotánicos del País Vasco. Complutum 11, 157–169.

Zapata, L., Peña Chocarro, L., 2005. Los macrorrestos vegetales del yacimiento de Mendandia. En. In: Alday, A. (Ed.), El campamento prehistórico de Mendandia: ocupaciones mesolíticas y neolíticas entre el 8500 y el 6400 B.P. Colección

Barandiarán 9. Diputación Foral de Álava, Vitoria, pp. 411–425.

Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean plant communities: The case of holm oak-Aleppo pine forests. Bot. Rev. 66, 119–149.

Zilhão, J., Ajas, A., Badal, E., Burow, C., Kehl, M., López-Sáez, J.A., Pimenta, C., Preece, R.C., Sanchis, A., Sanz, M., Weniger, G.-C., White, D., Wood, D., Angelucci, D.E., Villaverde, V., Zapata, J., 2016. Cueva Antón: a multi-proxy MIS 3 to MIS 5a paleoenvironmental record for SE Iberia. Quat. Sci. Rev. 146, 251–273.

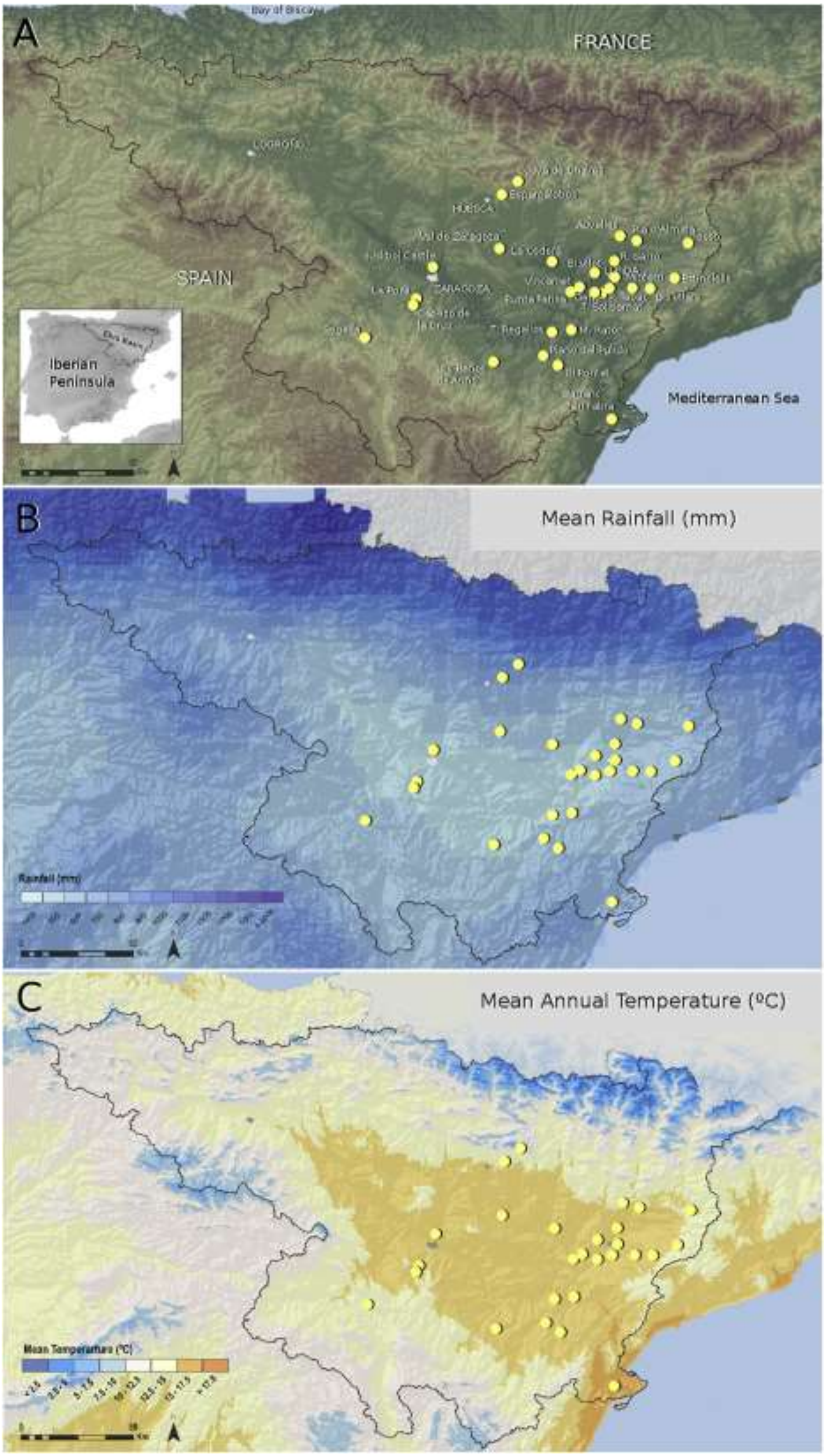

Fig. 1. A) Location map of the Ebro Basin reporting *Pinus halepensis* wood charcoal. Source: Confederación Hidrográfica del Ebro (http://www.chebro.es). B) Main rainfall features of the Ebro Basin and borderlands (González-Hidalgo et al., 2011). C) Mean annual temperature of the Ebro Basin and borderlands (González-Hidalgo et al., 2015).

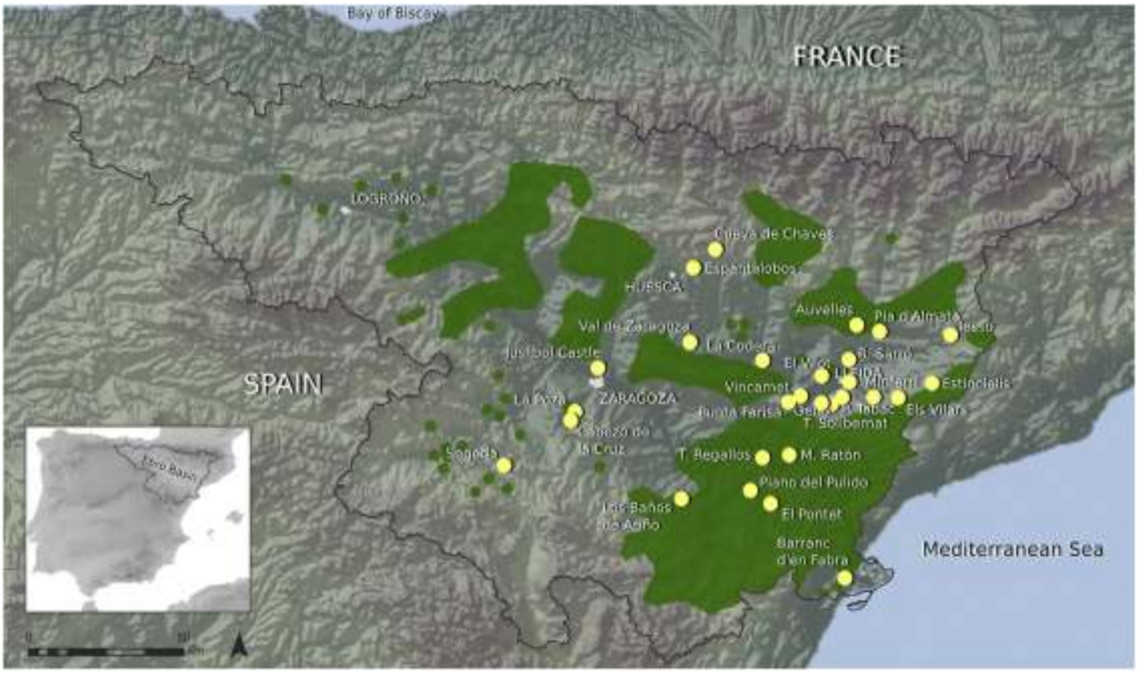

Fig. 2. Modern distribution of Pinus halepensis in the Ebro Basin. The references of the sites are shown in Table 1. Source: EUFORGEN (http://www.euforgen.org/).

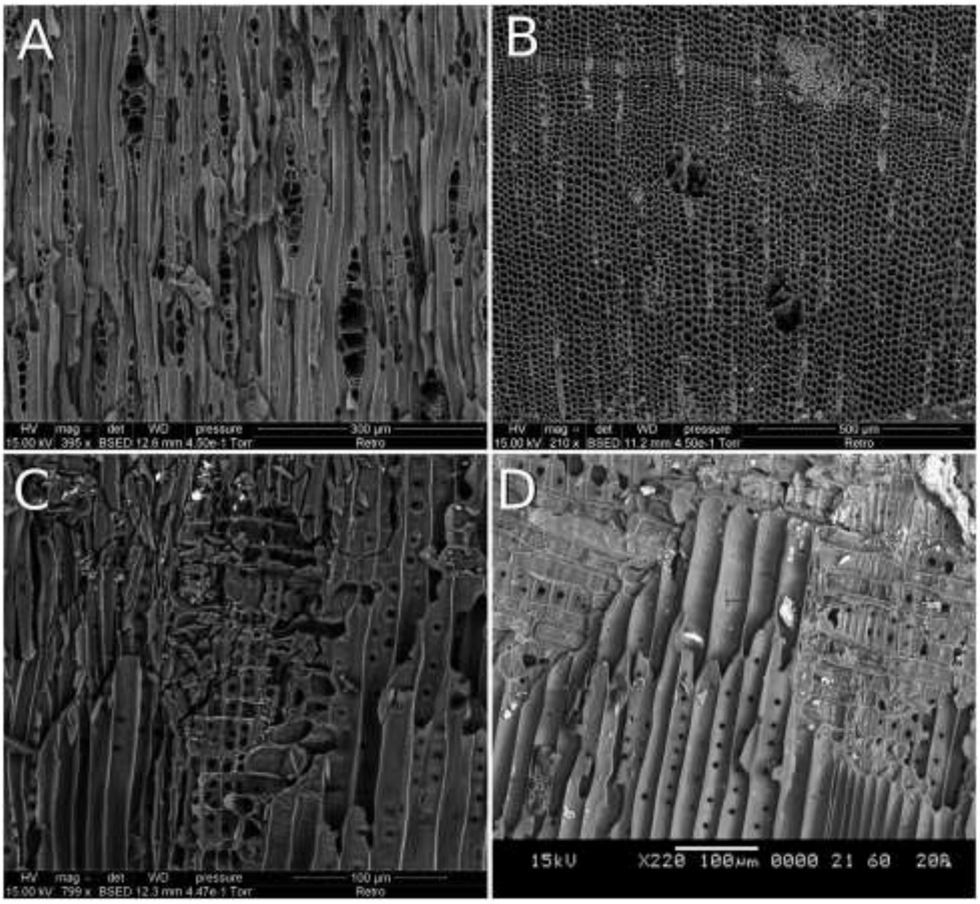

Fig. 3. Scanning Electron Microscope images of selected fragments of Pinus halepensis. Radial, transverse and tangential sections from Espantalobos archeological site (A–C, respectively) (Alcolea, 2018). D) Tangential section from El Pontet archeological site (Alcolea, unpublished).

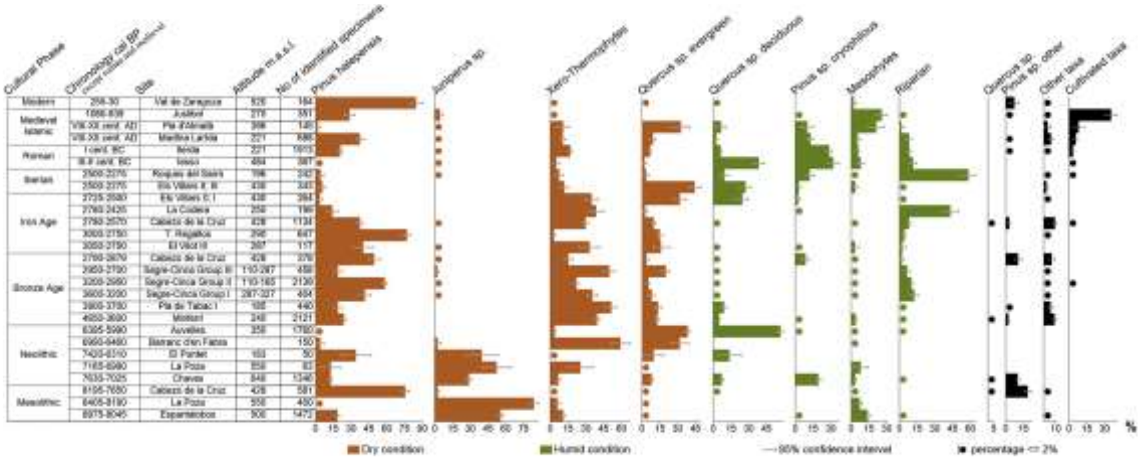

Fig. 4. Synthetic diagram showing main charcoal-based ecological groups throughout Mesolithic to Modern Ages. Raw data is presented in Tables 2, 4, 5, 6 and 7.

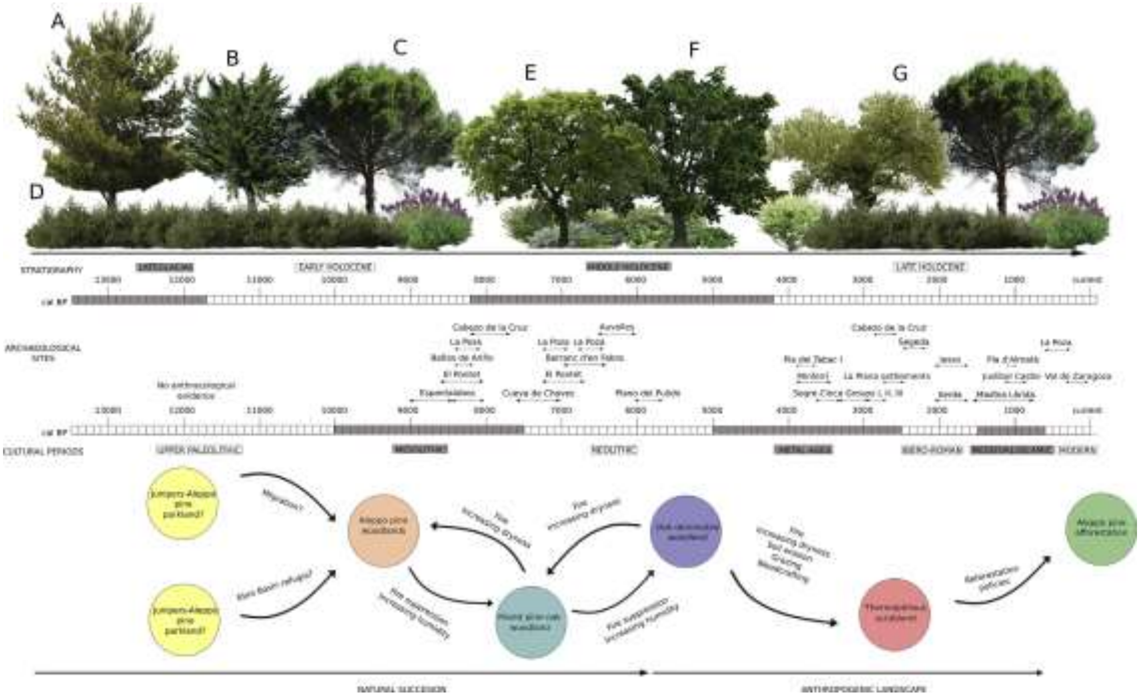

Fig. 5. Aleppo pine (*Pinus halepensis*) disturbance–successionmodel across different cultural/climate periods in the Ebro Basin. Mainwood charcoal-based landscape components have also been drawn: A) *Pinus nigra/sylvestris* type, B) *Juniperus* sp., C) *Pinus halepensis*, D) xero-thermophilous scrubland, E) *Quercus* sp. evergreen, F) *Quercus* sp. deciduous, G) *Olea europaea*. Segre-Cinca Group I includes Punta Farisa, El Vilot 0, Roques del Sarró; Segre-Cinca Group II comprises Genó, Masada de Ratón, Tossal de Solibernat and Vincamet I; Segre-Cinca Group III, Vilot I, II and Vincamet II. La Plana settlements refers to El Vilot III, Els Villars 0, I, La Codera and Tozal de Regalos Iron Age sites.