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New macrofossil evidence of *Pinus nigra* Arnold on the Northern Iberian Meseta during the Holocene

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Abstract

This study describes new macroremains of *Pinus nigra* found in a marsh deposit and two travertines. These fossils enhance our understanding of the past distribution of microthermal pines in Spain. Seventeen sub-fossil trunks and 88 pinecone remains and casts discovered at Tubilla del Lago (Province of Burgos, Spain), Tubilla del Agua (Province of Burgos, Spain) and Fuentetoba (Province of Soria, Spain) were identified by comparative morphological studies (with the aid of microtomy for the wood specimens). The ages of these macroremains were obtained by ^{14}C analysis. The results demonstrate the Quaternary presence of *P. nigra* at each of the collection localities. In conjunction with other paleobotanical evidence, these data show that this species was more widely distributed over the Northern Meseta in the past, suggesting that its local disappearance at the end of the Holocene.

Key words

Holocene, macroremains, megafossil, pinecone casts, Quaternary, Spain, travertine, tufa

1 Introduction

The natural forest landscape of the Northern Iberian Meseta has been reduced to small patches, largely due to the intensive agricultural and stock-raising land uses in the region. Of the nearly nine million hectares occupied by the Castilla y León region in central-northwestern Spain – most of which lies within the Duero Basin – only 32.94% are now forested, and only 10% of these forest areas are of natural origin (Gil Sánchez et al., 2007). The composition of these rare natural forests suggests that formations dominated by broadleaved species once occupied a much greater area, with the sclerophyllous *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. extending into the lowest areas and the deciduous/marcescent *Q. faginea* Lam. subsp. *faginea* and *Q. pyrenaica* Willd. dwelling on calcareous and siliceous soils, respectively, at middle elevations. However, apart from stands of *Pinus pinea* L. and *P. pinaster* Aiton on the sandy soils at the centre of the Duero Basin, conifers are represented primarily by *Juniperus thurifera* L. toward the high plains (Ruiz de la Torre, 1990-1998; Costa et al., 1997). Potential vegetation maps suggest that this pattern extends across the Duero and High Ebro Basins (Rivas-Martínez, 1987; García-Cervigón et al., 2009). The presence of microthermal pines (*P. nigra* Arnold and *P. sylvestris* L.), whose natural ranges within the region are now very small, has led to different interpretations of the current vegetation dynamics (Peinado and Rivas-Martínez, 1987; Rivas-Martínez, 1987; Costa et al., 1997).

However, there is now considerable evidence that *Pinus* was locally dominant on the Northern Meseta and surrounding foothills throughout most of the Holocene (Menéndez Amor, 1968; García Antón et al., 1995; García Antón et al., 1997; Ramil-Rego et al., 1998; Franco Múgica et al., 2001; Iriarte et al., 2001; Iriarte et al., 2003; Muñoz Sobrino et al., 2003) (Fig. 1). In the Meseta, a wide distribution of *P. sylvestris* has been suggested for the late glacial period and the early Holocene on the basis of macroremains found at La Piedra (Muñoz-Sobrino et al., 1996), Quintana Redonda (García Antón et al., 1995), Aguilar de Campoo (Alcalde et al., 2001) and Vega Cintoria (Alcalde et al., 2003) (Fig. 1). For the past distribution of *P. nigra* subsp. *salzmannii* (Dunal) Franco, the only subspecies native to the Iberian Peninsula (Ruiz de la Torre, 2006), very little information exists. Natural populations of this subspecies are now mainly concentrated in the eastern portion of the Duero Basin, where they occupy some 6000 ha at altitudes between 800 and 1700 m (Fig. 1) (Martín et al., 1998). There is evidence, however, that *P. nigra* was more widely distributed on the Northern Iberian Meseta during the Holocene (Roig et al., 1997; Alcalde et al., 2001).

In light of this evidence clarifying the natural origin of *P. nigra*, important questions arise regarding the role of this species on the Northern Iberian Meseta during the Holocene and the causes of its decline. Here we describe the species-level information and local signal provided by plant macroremains (Birks and Birks, 2000) and their casts (Ali et al., 2003) from hygrophilous deposits and travertines. These fossils provide new information regarding the past distribution of this species. Comparison of the past distribution of *P. nigra* (as suggested by these and other data) to the species' present range allows inferences be made regarding its decline.

Figure 1

2 Materials and Methods

We investigated log and pinecone remains found between 2007 and 2010 in a marsh deposit and two travertines in the Northern Iberian Meseta. The pinecone and wood specimens were collected, labeled and stored (2ºC) for later study. Two fragments of tufa containing pinecone casts were extracted from the travertines and transported to the laboratory. Additional pinecone casts were georeferenced, described and photographed *in situ* with a scale for later examination of their morphology.

Wood remains were identified via comparative anatomical studies (Greguss, 1955; Jacquiot, 1955; Wheeler et al., 1989; Schweingruber, 1990), making use of thin sections prepared in all three major planes (Schweingruber et al., 2006). Pinecones and travertine casts were identified by examining their shape and size, the external border of the apophysis and the position and the shape of the mucron in the umbo (Castroviejo et al., 1986-2004; Galera Peral, 1993; Roig et al., 1997; Ruiz de la Torre, 2006). All materials were compared with those in the reference collection of the *History and Dynamics of the Vegetal Landscape Research Group* of the *Universidad Politécnica de Madrid*.

Radiocarbon dating was performed by Beta Analytic Inc. (Miami, USA) and the *Centro Nacional de Aceleradores* (CNA) (Seville, Spain). Standard radiometric and AMS analyses were used. Dates were calibrated to 2σ cal BP using the online Calib 6.0html software and the INTCAL09 dataset (Stuiver et al., 2005; Reimer et al., 2009).

3 Study sites

The study area lies in the northeastern portion of the Northern Iberian Meseta, within the Duero and High Ebro Basins. The climate is Mediterranean with marked continental characteristics: hot and dry summers (three to five months of summer drought) and very cold winters (Ruiz de la Torre, 1990-1998). All collection sites are located on calcareous lithofacies dominated by gypsum, marls and Cretaceous limestone; in contact with impermeable strata, these minerals lead to the formation of springs of carbonated water. The anoxic conditions of hygrophilous deposits render them ideal for the conservation of plant remains. Travertines are formed by flows of bicarbonate-saturated water and can trap plant remains. These trapped remains eventually decompose, but they leave casts in the matrix of precipitated calcium carbonate (Ali et al., 2003). Macroremains were found by surface sampling at three study sites: Tubilla del Lago, Tubilla del Agua and Fuentetoba (Table I, Fig. 1).

3.1 Tubilla del Lago, Province of Burgos (41º48'33''N, 3º34'14''W, 900 m)

This bed is a fossil marsh deposit with an extent of about 3.8 ha and a thickness of more than 7.5 m. The deposit has been excavated to restore a former lake similar to others nearby, with *Phragmites australis* (Cav.) Trin. ex Steud., *Typha domingensis* Pers. and *Scirpus lacustris* L. The surrounding vegetation is composed of open spaces (crops and formations dominated by *Thymus* Tourn. ex L.) with a few individuals of *Q. ilex* subsp. *ballota*, *Q. faginea* and *J. thurifera*. The nearest natural population of *P. nigra* is about 60 km to the northeast (Fig. 1), although several nearby sites have been reforested with this taxon (Ceballos et al., 1966; Ruiz de la Torre, 1990-1998). Excavation work to create the artificial lake has brought to light large trunks, branches and pine cones from the fossil marsh.

3.2 Tubilla del Agua, Province of Burgos (42º42’33’’N 3º48’14’’W, 765 m)

This site represents an ancient travertine barrier that has been dissected and disconnected from other, smaller travertines that formed later in the drained valley (Fig. 2). The dominant vegetation consists of small shrubs of the family Labiatae Juss. and broadleaved low-forest stands of *Q. faginea* and *Fagus sylvatica* L. on the foothills. The closest natural populations of *P. nigra* are some 40 km away (Fig. 1) (Ceballos et al., 1966; Ruiz de la Torre, 1990-1998). In the surrounding area, however, reforested populations of *P. nigra* and *P. sylvestris* grow quite well on limestone-marl slopes and plains. A pinecone travertine cast was discovered during the construction of the foundations of a house and collected for later study, leading to the exhaustive sampling of other travertine structures at the site in search of further remains.

Figure 2

3.3 Fuentetoba, Province of Soria (41º47’3’’N 2º34’8’’W, 1120 m.)

At this site, water draining from Upper Cretaceous limestone-marl strata emerges to form a large travertine edifice. The vegetation of the area is dominated by *Q. pyrenaica* and *Q. ilex*, with a few dispersed specimens of *P. sylvestris* and *P. pinaster* in lower-lying areas and calcic Labiatae formations in higher areas. The closest natural pine populations are 30 km away at the base of the Iberian Range (Fig. 1) (Ceballos et al., 1966; Ruiz de la Torre, 1990-1998). Among abundant unidentified plant casts, a pinecone cast was found in the rubble at the foot of the travertine edifice and collected for analysis.

4 Results

4.1 Identification

The macroremains extracted during the excavation of the Tubilla del Lago site were piled up before sampling began, impeding their assignment to a particular horizon. A total of 17 trunk sections and 71 pinecones were collected. The absence of thick epithelial cells in the resiniferous channels, the window-like crossfield pits, and the sharp dentitions on the walls of the radial tracheids allowed the wood specimens to be assigned to the *P. sylvestris* / *P. nigra* group (Fig. 3). The features described by some authors to distinguish between these species (Greguss, 1955; Jacquiot, 1955; Peraza, 1964) could not be discerned in the samples. However, the rounded end of the external margin of the apophysis in all of the pinecones and the hook-like mucron eccentrically located in the umbo (Fig. 4) indicated that all of the strobili from the Tubilla del Lago site belonged to *P. nigra* (Table 1).

Figure 3 – Figure 4

Among numerous unidentified broadleaf fossils, up to fifteen pinecone casts and a pinecone fragment were found in four different locations at Tubilla del Agua (Fig. 2). Sample TUAG.BU.01, extracted during the excavation of a house basement and situated within a travertine barrier in the valley bottom, and the pinecone fragment (sample TUAG.P) were collected for morphological description and dating. At Fuentetoba, further surface sampling recovered no pinecone casts in addition to the one collected from the rubble. The pinecone casts from these sites showed rounded apophyses and eccentric, hook-like umbos (Fig. 4) and were of a size that allowed their assignment to *P. nigra* (Roig et al., 1997; Ruiz de la Torre, 2006) (Table 1).

Table 1

4.2 Age

All of the collected samples were of Holocene age. The cast from Fuentetoba was the oldest, dating to the early Holocene. The C^{13}/C^{12} values of the $CaCO_3$ based samples (i.e., those from Fuentetoba and Tubilla del Agua) were around 10‰, validating the inferred dates (Ali et al., 2003). According to these authors, δ^{13} values between 7‰ and 10‰ indicate that the inferred dates may not be polluted by recent organic matter or dissolved early carbonates, in contrast to higher or lower values, respectively. Radiocarbon dates at depths of 1 m (Beta-245872; 1230±40 BP), 5 m (Beta-245873; 3950±40 BP) and 7.35 m (Beta-245874; 6520±40 BP) showed that the marsh deposit at Tubilla del Lago extended from at least 1000 to 7350 cal BP. Given the relatively steady accumulation rate at this site, the macroremains from Tubilla del Lago show surprising chronological homogeneity, with ages between 4230 and 3210 years cal BP.

The dates from Tubilla del Agua (Table 2) are the youngest of those analyzed. However, some of the specimens collected there could be older. Travertine B1 (Fig. 2) is dissected and disconnected from the remaining barriers, suggesting that it is much older, probably dating to the Pleistocene period. A range of younger overlying travertine deposits are present at the bottom of the drained valley. Therefore, in light of the TUAG.BU.01 radiocarbon age (Table 2), casts found at sites 2 and 4 (downstream of site 1) date to the Holocene (Fig 2). Location 3 is set at the bottom of one of the edges of travertine B1. However, the pinecone (TAUG.P) collected there is not necessarily coeval with the travertine. The specimen shows signs of seed predation and therefore was probably brought to the travertine wall by a tree squirrel (*Sciurus* L.). One of the few animals that prey upon pinecones before seed fall, tree squirrels store them in central larders at relatively short distances (<150 m) from the tree source (Steele et al., 2005).

Table 2

5 Discussion

5.1 *Pinus nigra* in the ecosystems of the Northern Iberian Meseta during the Holocene

The studied macroremains show that *P. nigra* was present during the Holocene at all three of the study sites, where there are currently no natural populations of this taxon (Fig. 1). This evidence, along with the remains of *P. nigra* found at Cevico Navero (4590-4710 BP; Roig et al., 1997) and Aguilar de Campoo (7670-8680 BP; Alcalde et al., 2001), is consistent with the importance of pine forests during the period of tree colonization following the Last Glacial Maximum (LGM) in many parts of the Iberian Peninsula (Costa et al., 1990; Franco Múgica et al., 2000). However, the rather limited paleobotanical information for the Northern Meseta (Alcalde et al., 2006) has led to the underestimation of pine forests in this area (Peinado and Rivas-Martínez, 1987; Rivas-Martínez, 1987), until recently.

Palynological evidence from around the study sites (Fig. 1) shows that pines have had an important role since the beginning of the Holocene. Pine pollen exceeds 80% of all pollen in most of the Espinosa de Cerrato pollen record from 10,000 to ~1360 yr BP (Franco Múgica et al., 2001). The *Pinus* pollen record in San Mamés de Abar, which is accompanied by a deciduous floristic element, shows a fluctuating but continuous presence of this taxon since the onset of the Holocene (Iriarte et al., 2001). Its presence is also strong in Quintana Redonda at the foothills of the Iberian Range, where pine-pollen percentages greater than 80% are recorded throughout the sequence between ~9340 and ~6750 yr BP (García Antón et al., 1995). Further north, a general decline in *Pinus* in favor of deciduous species has been recorded at Valle de la Nava, where pine pollen fluctuates from 60% to 80% at the onset of the Holocene to almost null values at the decline in arboreal pollen in the upper part of the core, with levels of 20-50% in between (Menéndez Amor, 1968). The site of La Piedra, which is close to Tubilla del Agua, shows an open forest of *Pinus* and *Betula* with a low representation of deciduous taxa until an undated forest-clearance event (Muñoz-Sobrino et al., 1996; Ramil-Rego et al., 1998). In the foothills of the Cantabrian Range, *Pinus* percentages exceed 25% in late-Holocene samples from Mampodre and Lillo (García Antón et al., 1997; Muñoz Sobrino et al., 2003). *Pinus sylvestris*-type macroremains are found at the bottom of the Lillo peat bog (Sánchez Hernando et al., 1999). Finally, the late-Holocene site of Huidobro and the undated site of Santa Gadea, both located at the northern edge of the Meseta, exhibit varying concentrations of arboreal pollen with low *Pinus* representation (Iriarte et al., 2003) (see Fig. 1 for locations).

These pollen records are consistent with the general Holocene expansion of deciduous species at middle and low elevations in northwestern Iberia (e.g.: Peñalba, 1994; Ramil-Rego et al., 1998; Muñoz-Sobrino et al., 2005; Garcia-Amorena et al., 2008) and with the migration of the *Pinus sylvestris-nigra* group to more northern and higher-elevation Iberian locations since the LGM (Muñoz-Sobrino et al., 2001; Figueiral and Carcaillet, 2005; García-Amorena et al., 2007). In contrast to oceanic areas of the Iberian

Peninsula, where a decline in *Pinus* occurred throughout the Holocene, leading to its local extinction (van der Knaap and van Leeuwen, 1995; Muñoz-Sobrino et al., 2001; Figueiral and Carcaillet, 2005; Rubiales et al., 2008; Rubiales et al., in press), little or no decline in *Pinus* occurred in more continental areas until recently (Peñalba, 1994; García Antón et al., 1997; Franco Múgica et al., 2001; Iriarte et al., 2001; Muñoz-Sobrino et al., 2003; Rubiales et al., 2007).

The taxon most often cited as participating in the expansion of Iberian forests during the late Glacial Period is *P. sylvestris* (Watts, 1986; Peñalba, 1994; Rubiales et al., in press), although the fossil record has provided little information in this respect. Only a few authors have identified different *Pinus* groups from pollen (i.e., the *pinaster* and *sylvestris* groups) (e.g., Ramil-Rego et al., 1998; Carrión et al., 2000) or distinguished *P. nigra* from *P. sylvestris* based on their wood (e.g., Postigo, 2003; Rubiales et al., 2007). However, recent studies have identified Iberian pines to the species level based on pine-needle remains (García Álvarez et al., 2009a; García Álvarez et al., 2009b). Pinecone remains can provide unequivocal identification if their apophyses or casts are preserved. Based on these types of remains, we can now highlight the important role of *P. nigra* in the landscape of the calcareous Mesetas of northern Iberia during the Holocene.

The macroremains studied here show that *P. nigra* was more widely distributed during the Holocene than at present. This conclusion has also been suggested by the 6000-yr-BP bioclimatic model of Benito Garzón et al. (2007). The pollen record of Espinosa de Cerrato shows that *Pinus* was locally dominant until anthropogenic forest clearance occurred after 1500 yr BP (Franco Múgica et al., 2001). These data agree with the importance of *P. nigra* in the potential vegetation on carbonated soils of the supra-mediterranean Iberian plains, as proposed by other authors (Costa et al., 1988; García-Cervigón et al., 2009) and supported by the presence of relict populations at various sites in the Duero Basin (e.g., at Río Lobos and Río Cega) (Fig. 1). In fact, the predicted distribution of *P. nigra* under the present climatic conditions (Benito Garzón, 2006) shows a wider coverage of the Iberian Range and scattered populations along the Northern Iberian Meseta.

Generally, pines are pioneer species, are heliophitic and drought resistant and colonize open land disturbed by man earlier than do broadleaved species (Costa et al., 1997; Zavala and Zea, 2004). In particular, *P. nigra* shows extraordinary resistance to low temperatures (Climent et al., 2009) and is one of the longest lived of all Iberian tree species (Génova, 2000). These traits allow it to form monospecific stands in supra- and meso-mediterranean zones, forming the timberline in many parts of the Southern Iberian Range, and in areas of the Iberian plains with dry soils. It can also be found in mixed stands with *Q. faginea*, *Q. ilex*, *J. thurifera* and *P. sylvestris* on supra-mediterranean limestone plains. It can appear with *Q. pyrenaica* in natural populations on acidic substrates, although this occurs only in the Central Range (Gredos and Guadarrama) (Costa et al., 1997) (Fig. 1).

5.2 Factors driving the distribution of *P. nigra*

Given that plant distribution is mainly determined by climate, soil type, human activity and topography (Woodward, 1987), variation in distribution must be a consequence of variation in one or more of these factors. During the time frame of this study, the small changes in topography or soil composition could hardly have been responsible for the major changes in the distribution of *P. nigra* evidenced by its macroremains. However, this hypothesis, together with others involving plagues and diseases, is non-testable (as argued by Carrión et al. (2001). Assuming that the anatomical and physiological features of *P. nigra* have been constant throughout the Holocene, human activity and/or climatic fluctuations are the only remaining mechanisms to account for the decline of its populations.

Several types of evidence show a strong correlation between vegetative cover on the Iberian Peninsula and the regional climatic responses to global changes. The last climatic period in which drastic changes in rainfall and temperature have been documented was the Younger Dryas (Peñalba et al., 1997), between 12,900 and 11,700 years ago (Lowe et al., 2008). In the northern part of the Iberian Range, *Pinus* pollen fell below 50% during this period, and *Betula* and *J. thurifera* practically disappeared. This pattern reflects an estimated drop of at least 8ºC and 300 mm in mean annual temperature and mean annual rainfall, respectively (Peñalba et al., 1997). Under such conditions, García Antón et al. (2002) document no tree species to have formed extensive stands on the plains of Castile, as can be observed in the San Mamés de Abar pollen record (Iriarte et al., 2001). The climatic improvement that took place during the Holocene caused *Pinus* to become important in the landscape (García Antón et al., 1995; Ramil-Rego et al., 1998; Franco Múgica et al., 2001; Iriarte et al., 2001). Macroremains of *P. nigra* from Fuentetoba, La Lomilla and Cevico Navero (Roig et al., 1997; Alcalde et al., 2001) show that this taxon was an important colonizer of treeless spaces through both vertical and horizontal displacements from its refugia on the coasts or on sunny slopes in the interior (Cheddadi et al., 2006). The presence of woody macroremains of *P. nigra / P. sylvestris* on the coast of Iberia around Oporto (Portugal) and Huelva (Spain) during the Würm Period reinforces this interpretation (Postigo, 2003; García-Amorena et al., 2007).

Across the Holocene, variations of about 2ºC in mean annual and mean summer temperatures and of about 100 mm in annual rainfall have been estimated for the Northern Iberian Range (Peñalba et al., 1997). During this time period, several pulses of aridification have been detected in the Western Mediterranean, co-occurring with an increase in Mediterranean taxa at the expense of the temperate flora (Jalut et al., 2000). Among these pulses, the well-documented 8.2 climatic event has been correlated in Northwestern Iberia with declines in arboreal pollen, increases in Gramineae, *Betula* and *Pinus* and higher fire frequencies (Davis and Stevenson, 2007; Muñoz Sobrino et al., 2007). This phase corresponds to the largest decline in precipitation and temperature during the Holocene (Peñalba et al., 1997; Davis et al., 2003; Andersen et al., 2004). However, the -2.5ºC winter and summer temperature anomaly reconstructed for Southwestern Europe (Davis et al., 2003) and the subsequent aridification pulses (Jalut et al., 2000) could only have benefited *P. nigra* at the expense of its deciduous competitors given its extreme resistance to low temperatures and dry conditions (Ruiz de la Torre, 2006; Climent et al., 2009).

The Holocene Thermal Maximum, which occurred at about 6000 years BP, was characterized by a summer temperature anomaly of +1ºC, high precipitation and high CO_2 atmospheric values (Peñalba et al., 1997; García-Amorena et al., 2008). These conditions may have been more favorable for *P. nigra* deciduous competitors, as evidenced in Southeastern Iberia by the spread of mesophytic forests linked with decreasing fire frequency (Gil-Romera et al., 2010). However, although the deciduous species *Quercetum mixtum* appears to have overcome *Pinus* at the Valle de la Nava site around this date (Menéndez Amor, 1968), *Pinus* maintained its dominance in the arboreal cover of many sites on the Northern Meseta (e.g., Espinosa de Cerrato, San Mamés de Abar, Mampodre, Lillo, Quintanar de la Sierra). This pattern is also reflected in the broad distribution of *P. nigra* at 6000 BP modeled by Benito Garzón et al. (2007). On the other hand, Davis et al. (2003) has identified the last 1000 years as the warmest interval during the Holocene, and Carrión et al. (2001) have documented increasing aridity during the last four millennia in southwestern Iberia. In northeastern Iberia, Morellón et al. (2008) document dominant lower lake levels during the period 4.2-0.8 kyr BP, with phases of higher lake levels ca. 1.7-1 kyr BP and during the last 800 years. If these conditions had favored a contraction of the range of *P. nigra*, confining it to refugial locations as modeled by Benito Garzón (2006), need further research.

In addition to the evidence of climatic-driven Holocene vegetation changes in the western Mediterranean, overwhelming data indicate the anthropization of the landscape in northern Iberia during the second half of the Holocene (e.g., Torras Troncoso et al., 1980; Aira and Vázquez, 1985; Zilhão, 1993; Iriarte, 2003; Peña-Chocarro et al., 2005). Within the study area, the ages of the macroremains examined show them to belong to a period prior to the intense anthropic intervention at Espinosa de Cerrato (after 1500 yr BP), as shown by the increasing percentage of Cerealia and the decline in arboreal pollen (Franco Múgica et al., 2001). At the mountain site of Quintanar de la Sierra, the intensification of human pressure on the landscape is shown by the continuous presence of Cerealia from ~3000 BP to the Modern Epoch (Peñalba, 1994). An earlier presence of Cerealia has been recorded on the Northern Iberian Meseta at Espinosa de Cerrato; Franco et al. (2001) have interpreted this observation as evidence of short episodes of human disturbance at 4500 and 3000 yr BP. Other paleobotanical sites show little evidence of human impact on the landscape (Mampodre, Lillo, Quintana Redonda, Valle de la Nava, San Mamés de Abar) or provide little chronological detail for the earliest record of Cerealia (La Piedra, Huidobro, Santa Gadea) (see Fig. 1 for references and locations).

The palynological evidence for the intensification of human pressure on the landscape at the Espinosa de Cerrato site (Franco Múgica et al., 2001) may be related to the archaeological evidence for the intensification of human occupation in the area during the Neolithic/Chalcolithic transition, around 4500-4000 yr BP (Carretero et al., 2008), and to rural settlements and the development of Roman cities at the end of the first millennium BC (Polo Cutando and Villagordo Ros, 2004). Compared to other areas of the Iberian Peninsula (e.g., the Ebro Valley or the valleys facing the Cantabrian coast), where evidence of Neolithic culture goes back more than 3000 years, this anthropization is relatively late (Zilhão, 1993; Iriarte, 2003). The same pattern has been observed in the mountains of northwestern Iberia (Allen et al., 1996; Ramil-Rego et al., 1998), reflecting the expansion of resource use into climatically harsher (continental and/or mountainous) areas after the Castilian Reconquest (Caballero Zoreda, 1997). The use of fire to clear land for crops and livestock, the high value of *P. nigra* for use in construction and as fuel, and the no resprout capacity of the species are the most likely reasons for its decline and replacement by pastureland, crops and broadleaved plants. The pinecone fragment dated to 1370-1540 cal BP from Tubilla del Agua, the evidence of human population density during the Middle Ages in the northeastern portion of the Iberian Meseta (Cidad, 1988; Campillo, 1997; 2004; Polo Cutando and Villagordo Ros, 2004), and the eighteenth-century name ‘Valdepinedo’ (i.e., pine valley) given to a valley near Tubilla del Agua (García Rámila and Díez de la Lastra, 1969) support the recent extinction of local populations of *P. nigra* in response to increasing anthropic activity.

6 Conclusions

The discovery of *P. nigra* macroremains at locations where its natural populations are currently absent demonstrates that this species had a wider Holocene distribution at its global western limit. It suggests this species to have joined in the local dominance of pines recorded in some sites of the Northern Iberian Meseta. *P. nigra* may have readily endured multiple climatic fluctuations during the Holocene and increasing competition pressure from broadleaved species due to the wide availability of different biotopes in these areas (high plains, valleys and canyons, slopes oriented in all directions, gypsum, marls and limestones). Given the continental climate that characterizes the calcareous high plains of the Northern Iberian Meseta and the paleobotanical evidence described here, it is reasonable to propose that *P. nigra* underwent recent local extinction probably induced by the increasing human activity.

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Figure 1. Study sites (rombs: A-Tubilla del Agua, B-Tubilla del Lago, C-Fuentetoba) and nearby sites for which published palaeobotanical studies are available (pollen and macroremain studies). The natural distribution of *P. nigra* (Ceballos et al., 1966) is shown in white. 1: Mampodre (Muñoz Sobrino et al., 2003). 2: Lillo (García Antón et al., 1997). 3: Valle de la Nava (Menéndez Amor, 1968). 4: Santa Gadea, 5: Huidobro (Iriarte et al., 2003). 6: San Mamés de Abar (Iriarte et al., 2001). 7: La Piedra (Ramil-Rego et al., 1998). 8: Espinosa de Cerrato (Franco Múgica et al., 2001). 9: Quintanar de la Sierra (Peñalba et al., 1994; 1997). 10: El Hornillo (Gómez-Lobo, 1993). 11: Quintana Redonda (García Antón et al., 1995). 12: Curueño, 13: Porma, 14: Esla (Sánchez Hernando et al., 1999). 15: Aguilar de Campoo (Alcalde et al., 2001). 16: Cevico Navero (Roig et al., 1997). 17: Vega Cintoria (Alcalde et al., 2003)

Figure 2. Travertine barriers at Tubilla del Agua (B1: Pleistocene tufa barrier. B2: Lateglacial-Holocene tufa barrier), and locations of the moulds found (TUAG.BU.0i, for i = 1 to 4). TUAG.P was found at location 3. Distance 1-4=597 m.

Figure 3. Microscopic detail of the A) transverse section (1: resiniferous channel) and B) radial section (2: crossfield pits, and 3: dentition of the radial tracheid walls). Scale bars = 0.1 mm.

Figure 4. Detail of a pine cone scale of a travertine mould (A – TUAG.BU.03.6) and of a pine cone macrorremain (B – TUB-C-17-10-07-032). The edge is rounded and the mucron hook-like and eccentric. Scale bar= 20 mm.

Table 1. Characteristics of the pine cone remains from the different study sites (R: rounded; H: hooked; E: eccentric).

Site	Samples	Type	Cone length (cm)	Cone width (cm)	Apophysis length (cm)	Apophysis width (cm)	Scale shape	Mucron	Taxon
T. del Lago	TUB	71 Cones	4.45 ± 0.61	2.82 ± 0.33	0.83 ± 0.68	0.70 ± 0.42	R	HE	*P. nigra*
T. del Agua	TUAG.BU.01	1 mould	--	3.1	0.85 ± 0.05	0.75 ± 0.05	R	HE	*P. nigra*
	TUAG.BU.02	4 moulds	--	2.43 ± 0.01	0.56 ± 0.13	0.52 ± 0.12	R	HE	*P. nigra*
	TUAG.BU.03	9 moulds	4.38 sample 8	2.63 ± 0.58	0.51 ± 0.08	0.72 ± 0.13	R	HE	*P. nigra*
	TUAG.BU.04	1 mould	--	1.53	0.26 ± 0.043	0.36 ± 0.04	R	HE	*P. nigra*
	TUAG.P	1 cone	3.05	1.25	--	--	--	--	*P.* gr. *sylvestris*
Fuentetoba	TOBA.SO.01	1 mould	4.42	3.04	0.76 ± 0.06	0.091 ± 0.05	R	HE	*P. nigra*

Table 2. Radiocarbon dates.

SITE	SAMPLE CODE	TYPE	^{14}C AGE (BP)	- 13C/12C (‰)	2σ CALIBRATED AGE (cal BP)
T. DEL LAGO	Beta-243503 (TUB G01)	wood	3160±50	- 25.3	3260-3480
	CNA-171 (TUB-A-04)	wood	3680±70	- 26.53‰	3840-4230
	CNA-172 (TUB-D-04)	wood	3150±70	- 24.77‰	3210-3550
FUENTETOBA	Beta-260005 (TOBA.SO.01)	$CaCO_3$	8220±50	- 10.4‰	9020-9400
T. DEL AGUA	Beta-260006 (TUAG.BU.01)	$CaCO_3$	2650±40	- 9.6‰	2730-2850
	Beta-277713 (TUAG.P)	cone	1570±40	- 21.0 ‰	1370-1540

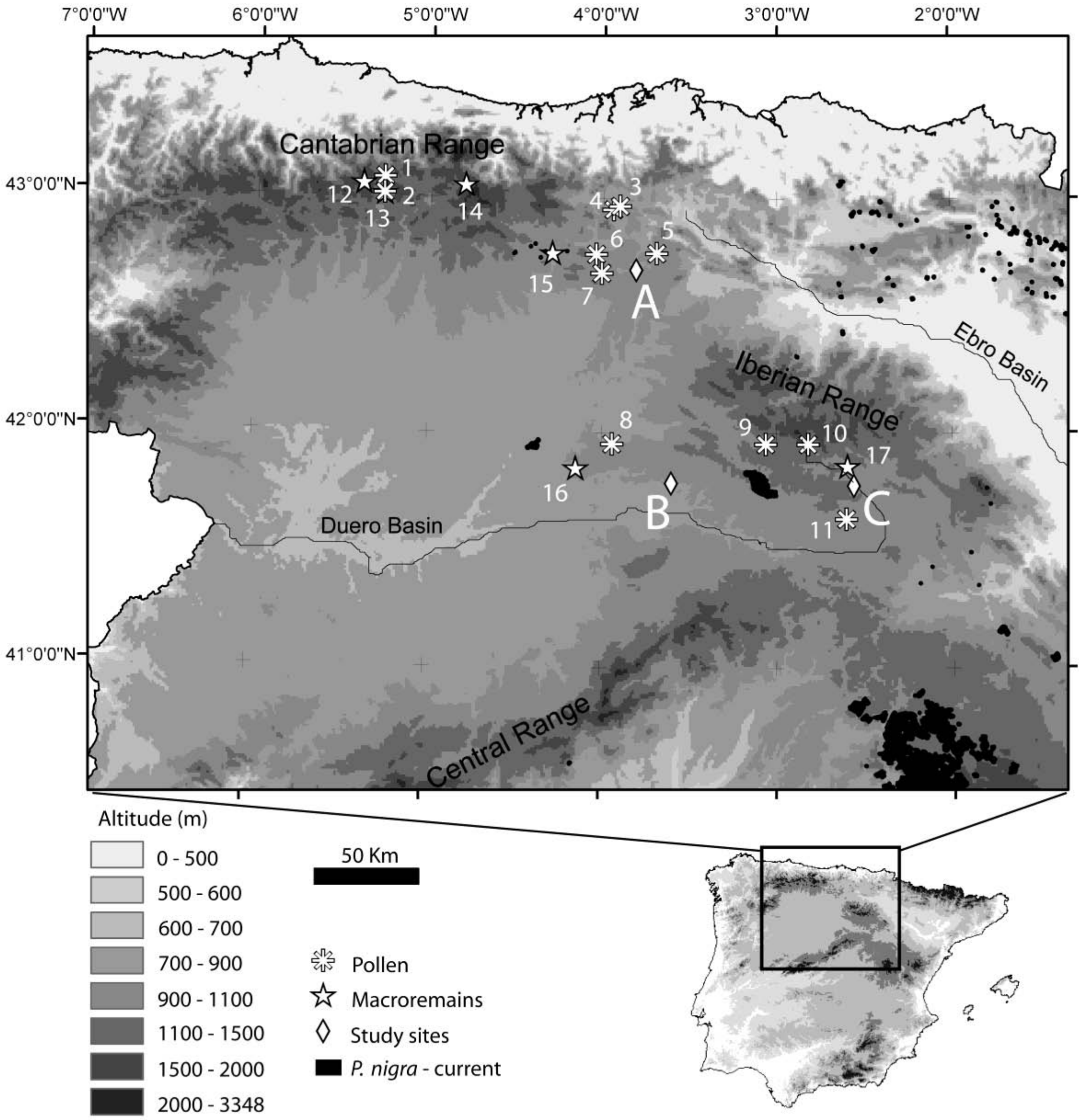
7°0'0"W
6°0'0"W
5°0'0"W
4°0'0"W
3°0'0"W
2°0'0"W
43°0'0"N
42°0'0"N
41°0'0"N
Cantabrian Range
Iberian Range
Ebro Basin
Duero Basin
Central Range
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
A
B
C
Altitude (m)
0 - 500
500 - 600
600 - 700
700 - 900
900 - 1100
1100 - 1500
1500 - 2000
2000 - 3348
50 Km
Pollen
Macroremains
Study sites
P. nigra - current

Figure 1

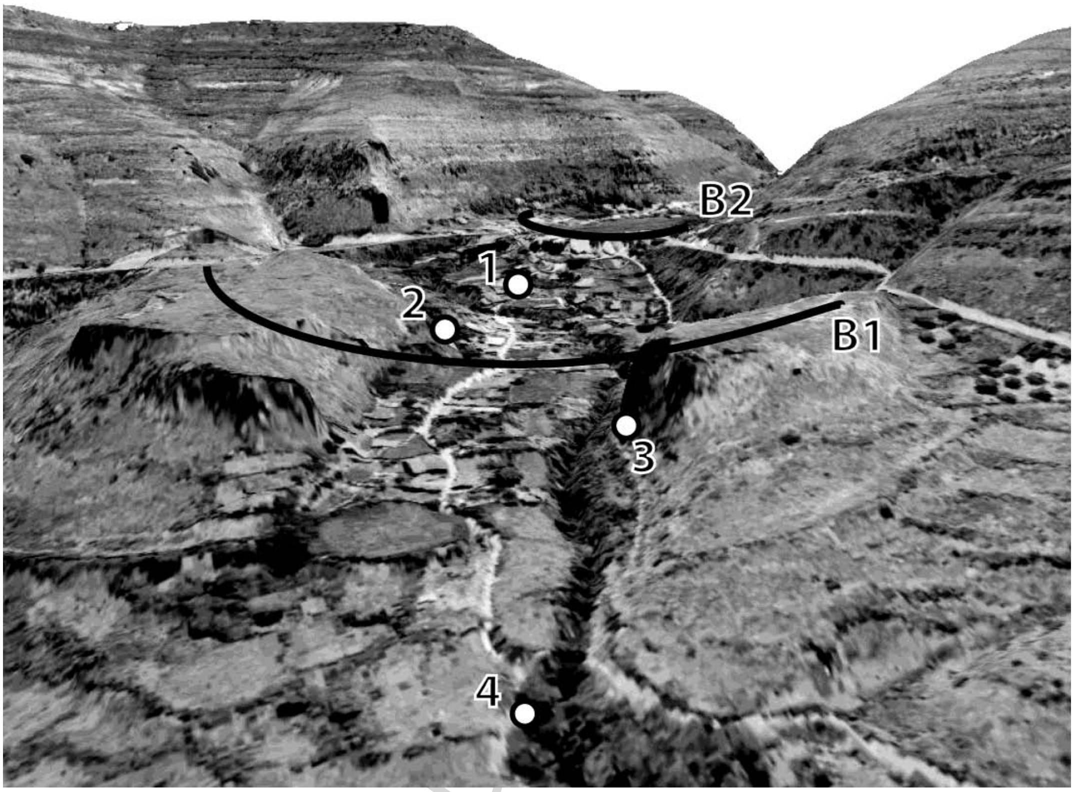

Figure 2

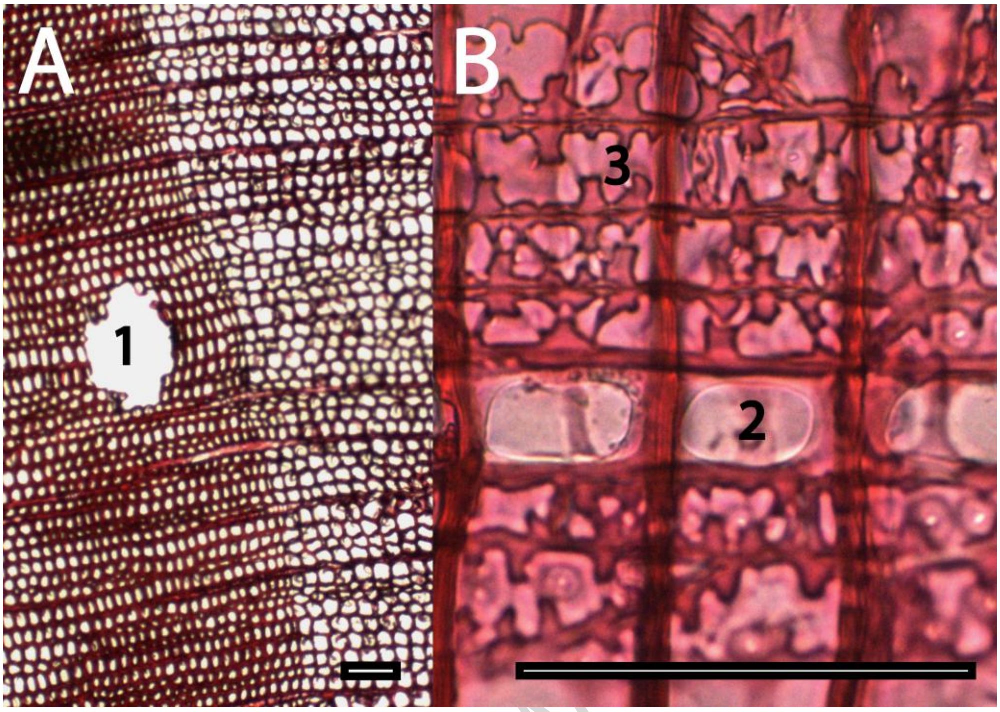

Figure 3

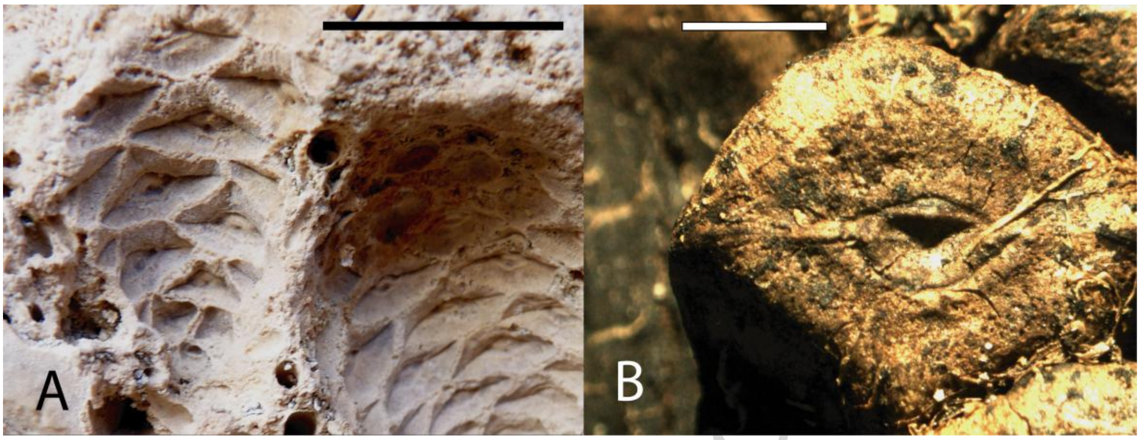

Figure 4