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Late Holocene ecological history of *Pinus pinaster* forests in the Sierra de Gredos of central Spain

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Abstract This article describes the patterns and processes of vegetation change and fire history in the Late Holocene (c. 2400 calendar year BP) palaeoecological sequence of Lanzahíta, Sierra de Gredos in central Spain, and provides the first Iberian pollen sequence undertaken within a monospecific *Pinus pinaster* woodland. These new data reassess not only the autochthonous nature of this pine species in the region and the Iberian Peninsula, but also the naturalness of well-developed cluster pine forests. Conflicts of palaeoecological evidence with phytosociological models of vegetation dynamics in the study region, and the relationships of *P. pinaster* with fire occurrence in Mediterranean-type ecosystems, are discussed.

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Introduction

The cluster or maritime pine (*Pinus pinaster* Aiton) is a western Mediterranean species occurring in Spain, Portugal, continental France and Corsica, Italy (including Pantelleria and Sardinia islands), and the High Atlas and Tunisia in north Africa. In the Iberian Peninsula, *P. pinaster* covers 1.6 million ha, from which 0.6 million are supposedly resulting from direct planting (Gil et al. 1990; Gil 1991; Alía et al. 1995, 1996; DGCN 2002). Its peninsular distribution is patchy and comprises a broad spectrum of substrates (limestone, granite, schist, marly limestone, peridotite), topographies and climates, including from montane sub-humid to Mediterranean semi-arid with summer drought (Nicolás and Gandullo 1967; Alía et al. 1995, 1996, Carrión et al. 2000). Although it is usually forming open forests with dense scrub and mixed forests with oaks and other pine species, *P. pinaster* can occasionally shape monospecific forests (Costa-Tenorio et al. 1990; Blanco et al. 1997).

In this article, we provide palynological data for the c. 2400-year vegetation and fire history of a *P. pinaster*-dominated area of the Sierra de Gredos in central Spain. There are several reasons why this investigation has been considered pertinent. First, because although the available palaeobotanical data are sufficient to assess the natural character of the cluster pine in the Iberian Peninsula (Carrión et al. 2000, and references therein, 2003b; Franco-Múgica et al. 2001, 2005; Carrión 2002; Alcalde et al. 2004; García-Amorena et al. 2007; Rubiales et al. 2009), palaeoenvironmental information associated with monospecific woodlands has so far not been reported.

Second, because it spans the last millennia, for which gaps in the palaeoecological knowledge of the region are particularly significant. For several reasons, including climatic change and human activities, many peat bog basins of the Iberian Peninsula with potential for palaeoecological research are interrupted before that time (Carrión et al. 2009).

Third, the lack of eco-historical information about monospecific stands has given opportunities to unsupported assumptions on cluster pine biogeography; if not about the naturalness of the species (something indisputable), at least definitely over the spatial pattern, magnitude and influence of recent afforestations in current distribution and dynamics. Only seldom, and in particular soil-conditioned situations such as on peridotites, *P. pinaster* communities have been postulated to represent mature forests (Nieto et al. 1989, 1991; Rivas-Martínez et al. 2001, 2002; Valle 2003), being most frequent in the literature the contention that is an invasive species of sclerophyllous scrub or deciduous forest (Izco 1984; Costa 1987; Peinado and Martínez-Parras 1985; Rivas-Martínez, 1987). The situation with *P. pinaster* in the Sierra de Gredos does illustrate this dispute, and while some argue that its local presence results from historical planting (Rivas-Martínez 1963, 1975, 1987; Sánchez-Egea 1975; Rivas-Martínez et al. 1986, 1987; Sánchez-Mata 1989), others stress the lack of evidence for such an activity (Gil 1991; Manuel and Gil 2001). This is not a trivial issue, for many regard that planting cluster pine is inappropriate from a biological perspective and will invariably conduct to failure in forest development (e.g. Rivas-Martínez 1987, 2007; Rivas-Martínez et al. 2002).

Inextricably merged with the former is the assumption that, in absence of human activities, forests on sufficiently developed soils in the Iberian Peninsula will be dominated by *Quercus* species (Rivas-Martínez 1987). This notion of natural potential vegetation permeates well beyond scholarly articles to deeply penetrate the philosophies that underlie policies on landscape and environmental management. A notorious example is the Habitats Directive and its Natura 2000's interpretation manual of EU habitats (Council of the European Communities 2003). Here lies the fourth reason why this study has been undertaken. Floristically-based, phytosociological models (Rivas-Martínez 1987; Sánchez-Mata 1989), consider that the potential vegetation of the study area, within the mesomediterranean belt, corresponds to an evergreen oak forest (*Pyro bourgaeanae–Quercetum rotundifoliae*), with deciduous oak forest patches (*Luzulo forsteri–Quercetum pyrenaicae*) being allegedly pristine in the uppermost, supramediterranean belt between 800 and 1,600 m. The current situation, however, is not of an oak-dominated forest, evergreen or deciduous.

A final implication of this study concerns fire ecology. Charcoal records combined with pollen analysis have been shown to provide contending models of vegetation dynamics in Mediterranean-climate scenarios (e.g. Carcaillet et al. 1997; Turner et al. 2008; Vannière et al. 2008; Conedera et al. 2009). This approach may be outstanding for dealing with *P. pinaster*, a species often associated to pyrophilous communities and, indeed, very flammable (Barbero et al. 1998; Calvo et al. 2003, 2008). The palaeo-record presented here provides an opportunity to study these complex interactions in a unique ecosystem, characterised by the prevalence of the cluster pine in the arboreal stratum. Most antecedents relate with regions displaying higher species diversity of forest trees, and therefore it has been difficult to isolate the relationships between fire frequency and *P. pinaster* cover changes (e.g. Carrión and van Geel 1999; Carrión 2002; López-Sáez et al. 2009a).

Methods

Site description

The study area is located in the municipality of Lanzahíta (province of Ávila, Central Spain) on the southern slopes of the eastern massif of the Sierra de

Gredos. A 100-cm sediment core was extracted from a small (150 m^2) peat bog (588 m altitude) in the Tiétar Valley (40°13′20″N, 4°56′09″W) (Fig. 1). A granitic bedrock stopped coring at 100 cm depth. The climatic parameters, such as average annual temperatures (15.1°C) and annual rainfall (1,007 mm) were taken from the nearest meteorological station (La Adrada, 1,000 m, 40°18′N and 4°38′W). The soils are from granitic origin and can be classified as humid brown soils (humic cambisols according to the FAO nomenclature) associated with lithosols (Gallardo et al. 1980). The area is situated within the mesomediterranean belt, with a subhumid/humid ombroclimate (Sánchez-Mata 1989).

The vegetation of the peat bog is formed by small oligotrophic bog communities (*Caricetum carpetanae*) dominated by *Carex nigra* (L.) Reichard subsp. *carpetana* (C. Vicioso) Rivas-Martínez, *C. echinata* Murray, *Parnassia palustris* L., *Drosera rotundifolia* L., and towards the drier margins by *Erica tetralix* L. and *Calluna vulgaris* (L.) Hull. Most of the Tiétar Valley is characterised by a dense *P. pinaster* forest with understorey of *Cistus ladanifer* L., *Lavandula stoechas* L., *Rosmarinus officinalis* L., *Thymus mastichina* (L.) L. and *Cytisus scoparius* (L.) Link. Towards the southern slopes of eastern Sierra de Gredos, maritime pine forests still cover an area of approximately 39,200 ha occupying a wide altitudinal gradient (500 to 1,000 m) (Alía et al. 1996; Sierra de Grado 1996) (Fig. 1). *Pinus sylvestris* L. and *Pinus nigra* Arnold are more frequent in altitude, shaping the timberline. Riparian forests of black alder (*Alnus glutinosa* (L.) Gaertn.) inhabit the banks of the Eliza river. Today, the valley is cultivated with tobacco, olive trees, watermelon, peppers and asparagus (López-Sáez 2004). The Tiétar Valley is one of the peninsular areas showing a higher incidence of forest fires (Abad et al. 2007), for which exists abundant documentation of the last few decades (Vázquez and Moreno 1998, 2001). Some recent fires have affected areas of above 6,500 ha, including upto 3,500 ha of *P. pinaster* (Pérez et al. 2003).

Pollen analysis

The core was extracted with a Russian corer and the peat sections placed in PVC tubes and protected in plastic guttering, sealed in polythene tubing, and

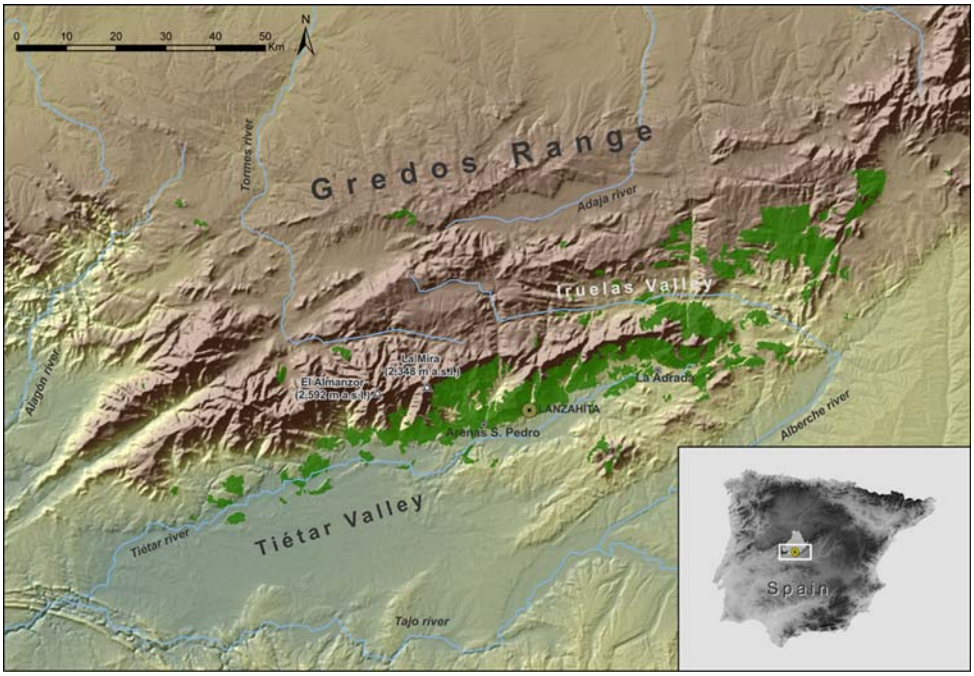

Fig. 1 The study area of southern slopes of Sierra de Gredos (Tiétar Valley, Ávila, Central Spain) and situation of the fossil sequence (Lanzahíta peat bog). Light green represents the modern distribution of the forest formations dominated by *P. pinaster* in the Tiétar Valley

placed in cold storage (4°C) prior to laboratory subsampling at 2 cm intervals. Fifty samples of 1 cm^3 were analysed. All samples were treated according to the Faegri and Iversen (1989) method although acetolysis was not carried out to allow the identification of any contamination by modern pollen (Franco-Múgica et al. 1997). One *Lycopodium* tablet per sample was added in order to calculate pollen concentration (grains cm^{-3}) (Stockmarr 1971), and these values were divided by deposition time (year cm^{-1}) to calculate pollen accumulation rate (PAR; grains cm^{-2} $year^{-1}$). Small aliquots of the residues were mounted in glycerine, sealed with Histolaque and all recognisable pollen and spores were counted under a light microscope using a 400× magnification, until a pollen amount of at least 500 units was reached. *P. pinaster* was palynologically discriminated from the rest of the pines based on its relatively larger pollen body, short alveoli and thick proximal exine (Carrión et al. 2000). The remaining pine pollen, including doubtful pollen grains, were included in a general *P. sylvestris* type, which, given the flora of this particular region, may also include *P. nigra*. Non-pollen palynomorphs (NPPs) were identified using the nomenclature proposed by van Geel (2001). Palynological identification and counting was aided by the reference collection available at the Laboratory of Archaeobiology at the CSIC, Madrid.

Charcoal analysis

In order to reconstruct local fire history at Lanzahíta, macroscopic charcoal was identified and counted from subsamples of 1 cm^3 at every 2 cm depth by sediment sieving. The samples were soaked in a 3% sodium metaphosphate solution (72 h) to deflocculate any particles, then washed through a 125 μm mesh sieve. Macrocharcoal was identified a 40× magnification according Rhodes (1998). Particles >125 μm diameter are not transported far from their source and thus provide information on local fire history (e.g. Whitlock and Larsen 2001). Microscopic charcoal were identified and counted at a magnification of 400× on the same slides used for pollen analysis (Tinner and Hu 2003; Finsinger and Tinner 2005). Charcoal accumulation rates (CHARs) were calculated by sedimentation rate (cm $year^{-1}$) and are expressed in particles cm^{-2} $year^{-1}$.

Chronology

Seven peat samples were ^{14}C dated using AMS technique. The dates were calibrated using CALIB 5.0.2 (Stuiver et al. 1998) with the INTCAL04 curve (Reimer et al. 2004) (Table 1). These dates were used to build an age model by linear interpolation (Fig. 2) taking into account the maximum probability intervals at 2 sigma ranges, which is considered to be a robust statistical value (Telford et al. 2004).

Results and interpretation

The results of identification and counting of pollen grains, spores and NPPs are presented as a percentage diagram (Fig. 3). As it is common with pollen analysis, ferns, aquatics and NPPs were excluded from the total pollen sum in order to avoid biases with local pollen representation. Pollen assemblage zones (PAZ) represent pollen-stratigraphical changes, and were constructed on the basis of agglomerative cluster analysis of incremental sum of squares

Table 1 AMS radiocarbon data from the Lanzahíta peat bog record. Each calibrated radiocarbon date (in parentheses) is presented as a median probability with its 2 sigma interval

Depth (cm)	Radiocarbon date (year BP)	Calibrated age (2σ) (calendar year BP)	Calibrated age (2σ) (calendar year BC/AD)	Laboratory reference
7–8	Modern	–	–	CNA-095
24–25	780 ± 35	667 (706) 762	AD 1188 (1244) 1283	Ua-24879
35	1020 ± 35	799 (940) 1051	AD 899 (1010) 1151	Ua-24878
44–45	1315 ± 29	1179 (1259) 1296	AD 654 (691) 771	CNA-105
64–65	1907 ± 35	1820 (1853) 1928	AD 59 (97) 214	CSIC-1877
75–76	2280 ± 55	2132 (2255) 2430	481 BC (306) 183 BC	Ua-19515
100	2387 ± 32	2342 (2417) 2676	727 BC (468) 393 BC	CSIC-1876

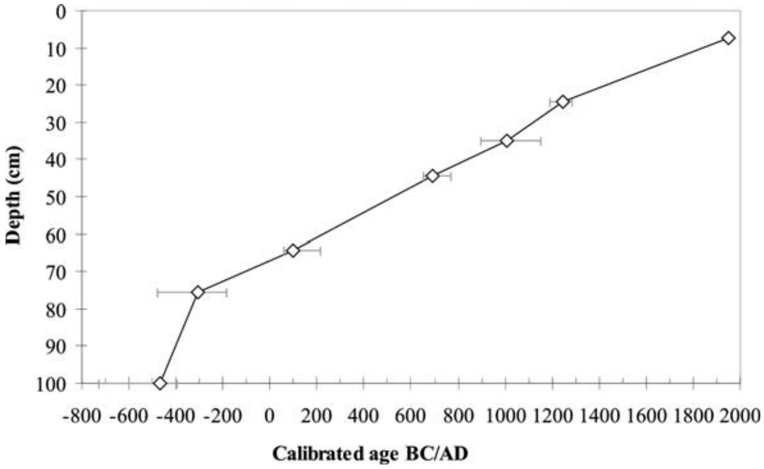

Fig. 2 Age-depth model for Lanzahíta peat bog. Lines connecting each plotted point are linear interpolated sediment-accumulation rates. The horizontal bars show the minimum and maximum ranges at 2σ

(CONISS) with square root transformed percentage data (Grimm 1987). The diagrams were plotted using TILIA and TILIA-GRAPH v. 2.0.b.5 softwares (Grimm 1991). The sequence was divided into five zones (Figs. 3, 4). Figure 4 shows CHARs, PAR, pollen concentration and deposition times related to selected pollen and NPP percentages curves. Sedimentation rates were not constant, but no evidence of an erosive event has been found.

PAZ 1 (100–63 cm): c. 470 BC to AD 140

Pinus pinaster percentages are high (52–62%) indicating a maritime pine forest in the vicinity. Deciduous (4–8%) and evergreen *Quercus* (3–5%) show continuous occurrences, while *Alnus*, *Betula*, *Castanea*, *Fraxinus*, *Juglans*, *Juniperus* and *P. sylvestris* pollen types are low (<3%). The amounts of shrub pollen are between 10 and 19% including *Arbutus unedo*, *C. vulgaris*, *C. ladanifer*, *Erica arborea*, Labiatae undiff., *L. stoechas*, *Phillyrea*, *Pistacia terebinthus* and *Viburnum* types. Herbaceous pollen is between 9 and 21% and PAR very high (42–166, 10^3 grains cm^{-2} year^{-1}). Both micro and macrocharcoal particles are present in low concentrations (<70 and <40 particles cm^{-2} year^{-1}, respectively).

PAZ 2 (63–45 cm): c. AD 140–675

Pinus pinaster is at its minimum in this pollen zone, oscillating from 29 to 45%. Other components increase such as *Olea* (4–11%), *Castanea*, *Asphodelus albus* (1–3%), *Aster* (2–6%), Cardueae (1–3%), Cichorioideae (3–5%) and Poaceae (9–16%). Altogether, these data suggest clearance of the pine woodland, perhaps linked to the local cultivation of olive trees. PAR oscillates between 20 and 80 × 10^3 grains cm^{-2} year^{-1}. This zone is also characterised by rapid accumulation of charcoal, the average influx for macrocharcoal reaching 142 particles cm^{-2} year^{-1}, while microcharcoal influx was 713 (<50 µm) and 211 (50–125 µm) particles cm^{-2} year^{-1}. This suggests that fire events were of local origin (Whitlock and Larsen 2001). Trends in CHARs correspond with shifts in those pollen assemblages that have higher values of anthropogenic taxa (*Aster*, Cardueae, Cichorioideae, *Rumex acetosella*), *A. albus* and *C. ladanifer*. A large amount of *Pteridium aquilinum* spores occurred in PAZ 2 suggesting fernland spread, which could be related to increased burning (Gliessman 1978; van der Knaap and van Leeuwen 1994). Fungal spores include important counts of the carbonicolous *Chaetomium* (maxima 15%).

PAZ 3 (45–25 cm): c. AD 675–1225

In this zone, *P. pinaster* (53–69%) values are the highest of the sequence and parallel increases in *C. ladanifer*, *Phillyrea* and *P. terebinthus*. Pollen of *Alnus*, *Betula*, *Castanea*, *Fraxinus*, *Juglans*, *Juniperus* and *P. sylvestris* is below 3% and *Olea* disappears. Most of shrubs maintain a continuous and significant presence throughout, reflecting the increased importance of the woodland understorey. Anthropogenic taxa, *A. albus*, Poaceae, *P. aquilinum*

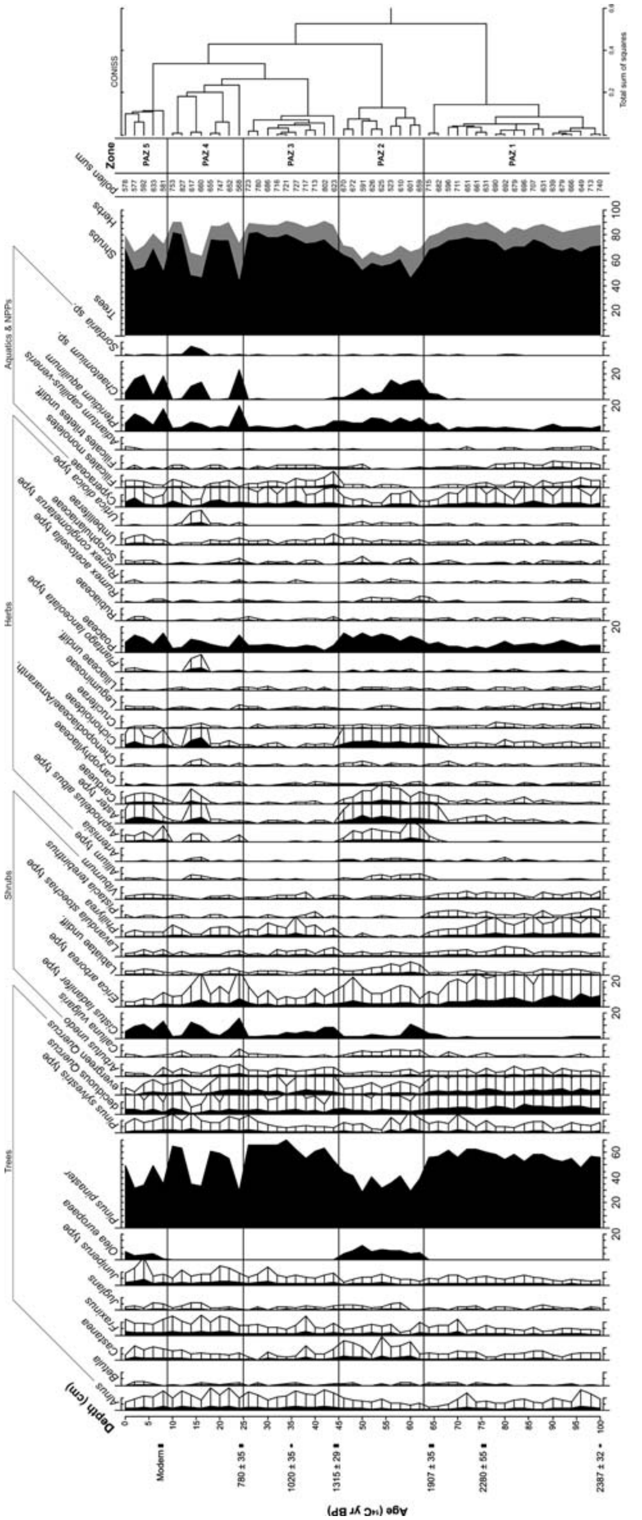

Fig. 3 Pollen and NPP diagram of Lanzahíta peat bog. Exaggerated curves show percentage data with 5× exaggeration

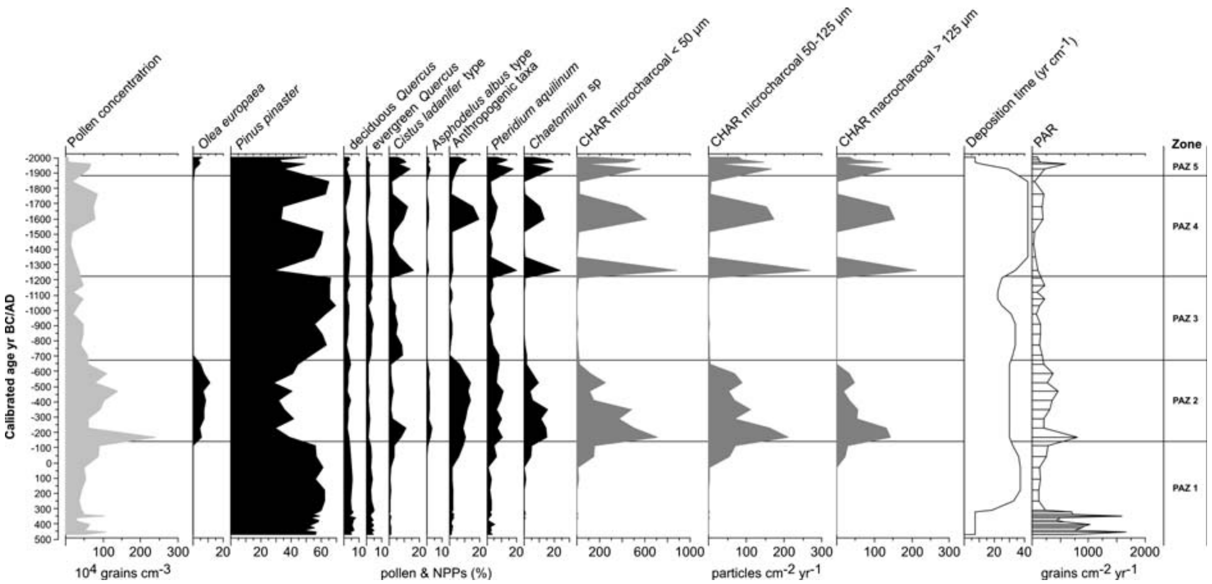

Fig. 4 Charcoal accumulation rates (CHAR), pollen accumulation rate (PAR), deposition time, pollen concentration, and selected pollen and NPP percentage diagram from Lanzahíta peat bog

and *Chaetomium* decrease significantly. Charcoal accumulation rates are in their lowest values (<13 particles cm^{-2} year^{-1}) while PAR diminishes up to 6–21 × 10^3 grains cm^{-2} year^{-1}.

PAZ 4 (25–9 cm): c. AD 1225–1885

In this zone, significant oscillations of *P. pinaster* are noticed (29–65%). *C. ladanifer* (maxima 16%), *E. arborea*, *A. albus*, *Aster*, Cardueae, Cichorioideae (maxima 8%), *Plantago lanceolata*, Poaceae, *Urtica dioica*, *P. aquilinum* (maxima 20%), *Chaetomium* and *Sordaria* show a greater presence in PAZ 4, but *P. pinaster* sharply declines. PAR remains relatively stable (4–20 × 10^3 grains cm^{-2} year^{-1}). The charcoal accumulation rates are higher than those of PAZ 2 zone, suggesting enhanced fire events (c. AD 1265 and c. AD 1600–1680) in relation to the previous fire episode (c. AD 115–170). The strong increase of *Sordaria* (coprophilous fungus, 4–7%) and maxima values of *P. lanceolata* and *U. dioica* indicate woodland clearance and grazing between c. AD 1600–1680.

PAZ 5 (9–0 cm): c. AD 1885–2000

This zone is characterised by oscillations in the *P. pinaster* pollen curve (between 32 and 50%). Also noteworthy are the continuous presence of *Olea* (1–6%) and the increases of *C. ladanifer*, *A. albus*, *Aster*, Cardueae, Cichorioideae, Poaceae, *P. aquilinum* and *Chaetomium* spores. Increases in micro and macro-charcoal particles suggest local fires at c. AD 1930 and c. AD 1975. A progressive enrichment, between CHARs maxima, in PAR (59 × 10^3 grains cm^{-2} year^{-1}), is observed.

Discussion

Palaeobotanical data demonstrate that the maritime pine is natural of the Iberian Peninsula

Charcoal analysis from several archaeological settlements in Portugal (Figueiral 1995; Figueiral and Terral 2002) demonstrates the presence of *P. pinaster* in coastal and inland areas since c. 33,000 BP and through the Bronze Age (Figueiral and Bettencourt 2004). Recently, 32 stumps were found in situ at Barreiro, at the mouth of the River Tagus, corresponding to stands of *P. pinaster* more than 7,000 years old (García-Amorena et al. 2007). Southwards in western Spain, in the Badajoz province, about 150 km south of the Tiétar Valley, *P. pinaster* charcoal has been found for a c. 2250 calendar year BP, Iron Age settlement in Castillejos II. These recent findings together with others in northern Iberia (Alcalde et al. 2004; Rubiales et al. 2005, 2007) and the surroundings of the Baetic Cordillera (Rodríguez-Ariza 2000), confirm the natural character of *P. pinaster* in Spain.

Given the difficulties with the palynological identification of *P. pinaster* (Carrión et al. 2000), pollen sequences probably fail to reflect the past cover of this species in the Quaternary forests. In fact, if due regard is made of the current distribution, a good part of the pine pollen in sites like El Carrizal (Franco-Múgica et al. 2005) or Montes Universales (Stevenson 2000) could be from the maritime pine. In any case, there are Pleistocene and Holocene pollen records of *P. pinaster* in almost all the regions of the Iberian Peninsula. Examples include the northern territories (Aira and Saá 1989; Reille 1990, 1991; Ramil 1992; López-Sáez et al. 2009b), Portugal (Mateus 1989; Mateus and Queiroz 1993), the southeastern and eastern regions of Mediterranean-sea influence (Carrión and van Geel 1999; Carrión et al. 2003a, 2003b), the Baetic Cordilleras and adjacent highplains (Carrión 2002; Carrión et al. 2001a, 2001b, 2004, 2007) and Gibraltar (Carrión et al. 2008). The pollen record of the Navarrés peatbog (Valencia, eastern Spain; Carrión and van Geel 1999) shows a synchronous Late Quaternary fluctuation of *P. pinaster*, and *Quercus*-dominated assemblages. It is also noticeable that, during glacial times, *P. pinaster*, although retreated, survived in refugia accompanied by deciduous trees (*Corylus*, *Fraxinus*, *Quercus*) and Mediterranean woody species (*Arbutus*, *E. arborea*, *Olea*, *Phillyrea*, *P. terebinthus*, *Myrtus communis*, *Viburnum tinus*). A similar picture, although more complex in terms of species interactions, is seen in the full-glacial of the Siles lake pollen sequence (Carrión 2002). The pollen record of Lanzahíta described here join to these former findings to warrant not only the authochthonous character of *P. pinaster* in the Iberian Peninsula, but also the naturalness of well-developed cluster pine forests.

The genetic structure of modern populations point to a complex multi-refugia peninsular pattern of *P. pinaster*

Parallel research lines of arguments have led to the hypothesis that the Quaternary climatic changes have played a major role in the genetic structuring of maritime pine (Baradat and Marpeau 1988; Salvador et al. 2000). It has been hypothesised that the actual distribution of this species is the result of events that occurred during the last glaciation (Baradat and Marpeau 1988; Bahrman et al. 1994). At temperate latitudes, thermophilous species may have consequently been restricted to small southerly ranges with implications for subsequent migration patterns and population genetic structure (McLachlan and Clark 2004). In fact, different maternal lineages in maritime pine may represent different isolated glacial refugia of the species because the existence of a population genetic structure has a main role in adaptation to local environment variation (Petit et al. 1995; Wahid et al. 2004). The typical scattered distribution may have prevented, or limited, gene flow among the different groups of populations, thereby determining genetic drift and high genetic divergence among populations (Vendramin et al. 1998).

Genetic variation patterns across the native range of the species are quite complex (Baradat and Marpeau 1988; Vendramin et al. 1998; Salvador et al. 2000; Burban and Petit 2003) and large genetic differences among populations have been reported at regional and wide-range spatial scales (Salvador et al. 2000; González-Martínez et al. 2001, 2004, 2005). In the Iberian Peninsula, maritime pine populations show high levels of genetic diversity and an important genotype-by-environment interaction that favours the existence of adaptations to local ecological conditions (Alía et al. 1995, 1997; Salvador et al. 2000; Miguel-Pérez et al. 2002). A recent study by Bucci et al. (2007) has identified one “hotspot” of haplotype diversity in central and southeastern Spain and two areas of low haplotypic diversity located in the western peninsula and Morocco. Postglacial developments, starting earlier in the zones of higher diversity, may have contributed to shape the distribution until relatively recently. The picture that emerges from all these genetic studies combined with fossil evidence is that the current-day distribution of maritime pine in the Iberian Peninsula could be explained by the location of glacial refugia, environmental restrictions, Holocene spreads, human impact and fire-mediated replacement dynamics with other Mediterranean conifers (Salvador et al. 2000; Gómez et al. 2005; Gómez and Lunt 2006).

Pinus pinaster forests are natural in southern Sierra de Gredos

The Lanzahíta pollen diagram covers a c. 2700-year record of vegetation history from the southern slopes of Sierra de Gredos (Tiétar Valley). The landscape of the study area from c. 470 BC to AD 140 (PAZ 1) and c. AD 675–1225 (PAZ 3) is dominated by a dense pinewood of *P. pinaster* with patches of evergreen and deciduous *Quercus*. Plausibly, this represents not only some local patchiness but a regional signal of the mountain vegetation belts (*P. sylvestris* and/or *P. nigra* at highest altitudes), as seen in the modern landscape (Sánchez-Mata 1989). Studies of pollen rain support this view (Andrade et al. 1994). Qualitatively, the PAZ 1 and PAZ 3 pollen assemblages match well with the composition and structure of modern communities (Barkman 1990) such as the *Pinus-Phillyrea* woodland type characterised by *P. pinaster*, *A. unedo* L., *C. ladanifer*, *E. arborea* L., *V. tinus* L., *Pistacia* sp. and *Phillyrea* sp.

The continuous dominance of maritime pine throughout the Late Holocene support the contention that the *P. pinaster* belt in the Tiétar Valley is of natural origin. Taking into account the detailed Spanish *P. pinaster* chorology given by Alía et al. (1996, 1997), Lanzahíta site is located in a recognised natural stand for this taxon (Sierra de Gredos). Our results reveal the natural presence of maritime pine in the study area before the Roman occupation of the southern slopes of Sierra de Gredos.

Mediaeval documentary records make reference the Lanzahíta pine forests. The *Consignación de Rentas* sent by Cardinal Gil Torres to the Bishop of Ávila in 1250, listed, under the heading of ‘pines’, the forests of many localities in southern Gredos such as Arenas de San Pedro, La Parra, Lançaita (Lanzahíta) or La Adrada (González 1974). The *Libro de la Montería de Alfonso XI* (1350) also refers the presence of maritime pine forests in the Tiétar Valley, some of which are reflected in current toponyms, demonstrating unequivocally their existence during the Late Middle Ages in the study area (Martínez-Ruiz 1998; Chavarría 1999). Thus, the recovery in the percentages of *P. pinaster* in the first half of PAZ 4 (c. AD 1265–1515) could be related with mediaeval regulations for the prevention of forest fires in the Sierra de Gredos such as *Fuero del Barco de Ávila* (1211), the ordinances of Rincón (1472) and La Adrada (1502) (Martínez-Ruiz 1998). In fact, it is at a later date to such regulations where maritime pine pollen percentages decreased again coinciding with a new charcoal accumulation rate maximum.

Afforestations with maritime pine were unimportant in the Iberian Peninsula before 1887 (Gil 1991). The oldest management project of the forests in the Sierra de Gredos dates from 1885 (Iruelas Valley) and the second was written in 1918 for the pine forest of Santa Cruz del Valle. The remaining forests of the valley were not managed until the last half of the 20th century (Sierra de Grado 1996). Therefore, no historical document reflects afforestation of the study area with maritime pine before the dates discussed above. Rather, toponymic information indicates the common occurrence of *P. pinaster* woodlands throughout the Sierra de Gredos (Gil 1991; Chavarría 1999). The large-scale coniferous reafforestation in the Sierra de Gredos is reflected in the pollen diagram (PAZ 5) after c. AD 1960.

Floristic-phytosociological models conflict with palaeoecological data about the “natural” potential vegetation

The data provided by the Lanzahíta pollen record (Figs. 3, 4) appear not to fit into the floristically-based phytosociological model of vegetation change for the study area, which, as mentioned earlier, postulates that an oak forest is the “climax” vegetation of the Tiétar Valley (Rivas-Martínez 1963, 1975; Sánchez-Mata 1989). This is to say that the forest patches of *P. pinaster* are incidental and mainly derived from afforestations. The vegetation history at Lanzahíta spans a relatively recent period, which was not free of human impact, probably in the form of prehistoric pastoralism and historical agriculture, as in other regions of the Iberian Peninsula (e.g. van der Brink and Janssen 1985; van der Knaap and van Leeuwen 1995; Carrión et al. 2003a). On the other hand, it is difficult to isolate natural from man-made events since they often overlap in historical records and have similar effects on the present-day landscape. In any case, if contextualised in the Holocene pollen succession of the central mountain systems of Iberia (Ruiz-Zapata et al. 1996; Franco-Múgica et al. 1997, 2001; van der Knaap and van Leeuwen 1997), it seems that Lanzahíta is just another record reflecting the multi-millennial resilience of Holocene pinelands.

In sum, this might be another case of “failure” in the dynamic model by phytosociologists. Many allegedly pristine oak woodlands of the Iberian Peninsula and Balearic Islands are indeed pine and pine-oak mixed forests, as seen in pollen records of the pre-anthropic phases of the Holocene (e.g. Peñalba 1994; Franco-Múgica et al. 2001, 2005; Ruiz-Zapata et al. 2002; Carrión and Díez 2004). The potentiality of *Quercus ilex* forests under dry and sub-humid ombroclimates was early discussed by Reille and Pons (1992), and similar disagreements are found year by year in other regions such as recently in Slovenia (Andric and Willis 2003). The conflict between palynology and phytosociology has extended to the Canary Islands, where pre-anthropic forests have been shown to be dominated by *Quercus–Carpinus* forests (de Nascimento et al. 2009), thus contradicting the conventional “wisdom” about laurel forests (Rivas-Martínez et al. 1993).

Maritime pine forests linked to fire occurrence

Overall, the Lanzahíta palaeoecological sequence reflects the association of *P. pinaster* with fire occurrence. From the charcoal evidence, it even appears that the vegetation changes recorded in PAZ 2 (c. AD 140–675), PAZ 4 (c. AD 1225–1885) and PAZ 5 (c. AD 1885–2000) may have been a consequence of intensifying fire regimes and olive tree cultivation. The fires could have been anthropogenically induced, since the first important charcoal peak (c. AD 115–170) coincides with the first Roman rural settlements in the area (Martino 2004), the second (c. AD 1265) with the Christian repopulation of the Tiétar Valley (Mariné 1995), the third (c. AD 1600–1680) with the height of the “Concejo de La Mesta” transhumance system (Troitiño 1987) and high values for anthropozoogenous taxa (*P. lanceolata*, *U. dioica*) and coprophilous fungi (*Sordaria* sp.) (López-Sáez and López-Merino 2007), and the last two-ones (c. AD 1930 and c. AD 1975) with intensive fire forests reported in the vicinity of Lanzahíta peat bog (Vázquez and Moreno 2001). Hypothetically, burning by local communities may have provoked woodland clearance, permitting the expansion of heliophytic and pyrophytic communities such as those dominated by *C. ladanifer* or *A. albus* (Franco-Múgica et al. 2005). The abundance of anthropogenic taxa and carbonicolous ascospores in these zones supports this hypothesis (López-Sáez et al. 1998).

Other Holocene pollen records have linked the presence and/or expansions of *P. pinaster* with fire events, continued fire occurrence or intensification of burning. The Navarrés pollen record shows that, around 6000 BP, maritime pine was involved in a post-fire replacement of *Pinus* forests towards oak-dominated vegetation (Carrión and van Geel 1999). *P. pinaster* exhibited here an ecological behaviour closer to evergreen oaks than *P. nigra*, and became favoured by anthropogenic disturbance. A partial, competitively-mediated replacement of *P. nigra* by *P. pinaster* in absence of human activities has been reported in the early Holocene of the Segura Mountains in southern Spain (Carrión 2002). In a pedoanthracological study undertaken in Corsica, Carcaillet et al. (1997) showed a late Holocene expansion of *Quercus ilex, P. pinaster* and *E. arborea* after burning of a *P. nigra* forest.

Fire is a natural factor of many Mediterranean landscapes and has an important influence on the biological productivity and composition of several ecosystems (Calvo et al. 2008). The role of fire as a disturbance that generally favours the *Pinus* genus is well recognised, fire being a major factor in the dynamics of Mediterranean pine forests (Barbero et al. 1998). In Spain, the maritime pine is one of the conifer forest types most frequently subject to fire, which affects 33% of all such forests (Pérez and Moreno 1998). Seed production and the life-history strategy of maritime pine are related to forest fire regimes and their communities of natural origin occur in lightning-prone mountains (González-Martínez et al. 2002; Fernandes and Rigolot 2007) such as the Sierra de Gredos (Vázquez and Moreno 2001). Among the *P. pinaster* populations across Spain, those located on the southern slopes of Sierra de Gredos are particularly subject to frequent arsons (Vázquez and Moreno 1998, 2001; Abad et al. 2007). The study area is very sensitive to the risk of forest fires due to the sharp orography, abundant storms and pronounced summer deficit, as well as high temperatures in the inner valley. Owing to this high frequency, the maritime pine forests in this area have acquired a series of adaptative characteristics that help their perpetuation in fire-prone Gredos environments such as early flowering, presence of serotinous cones, an important canopy seed bank and a thick bark (Gil et al.

1990; Tapias et al. 2001, 2004; Fernandes and Rigolot 2007; Calvo et al. 2008). However, regardless of the high seed germination capacity of *P. pinaster* after a fire (Torres et al. 2006), its forest regeneration is dependent on post-fire environmental conditions which affect seed germination and seedling establishment (Rodrigo et al. 2004; Calvo et al. 2008).

Competitive effects on the establishment of *P. pinaster* seedlings can also be expected in forests where the dominant understorey species consist mostly of woody (such as *Quercus pyrenaica* or *C. ladanifer*) and herbaceous resprouters (Calvo et al. 2003), but understorey vegetation appears to have a positive influence on the height of maritime pine seedlings (Calvo et al. 2008). In fact, in the studied area *C. ladanifer* plays an important role in the pattern of recolonization of *P. pinaster* stands after wildfire (e.g. PAZ 3). This shrub species is a pioneer after a fire, for it germinate rapidly from a persistent soil seed bank which is stimulated by a thermal increase (Calvo et al. 2003). Vázquez and Moreno (2001) have confirmed the tendency for fires to be highly aggregated in space in the southern slopes of Sierra de Gredos and furthermore it was also evidenced that reburning tended to occur preferentially in certain areas such as Lanzahíta. The result of these tendencies is a concentration of the likely impacts of fires in the study area with low elevations, lower slopes and deeper soils. Under such an accelerated fire cycle, maritime pine forest would not regenerate naturally without management, which would lead to lasting vegetation change (Pérez and Moreno 1998).

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