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Late Holocene pinewoods persistence in the Gredos Mountains (central Spain) inferred from extensive megafossil evidence

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ABSTRACT

Macro- and megafossil studies are of great value in palaeoecology because such evidence is spatially precise, directly radiocarbon dated, and usually taxon-specific. Here, we present new macro- and megafossil data from ten sites from the Gredos Mountains, central Iberian Peninsula, that suggest persistent forest cover through the late Holocene, with a widespread belt of pinewoods in the highlands of the Central Iberian Mountains. Well-preserved pine cones found at several sites revealed that both *Pinus sylvestris* and *Pinus nigra* were present in the area during the middle and late Holocene at locations of important biogeographical interest. The *P. sylvestris* forests represent one of the southernmost locations of its entire range. *P. nigra* was not known to have occurred in central Spain during the Holocene; it was found at the westernmost edge of its range in siliceous soils, a rare environment compared with the rest of its distribution. Finally, we explored the potential for obtaining a long pine chronology from central Iberia using tree-ring measurements and radiocarbon dating of pine subfossil logs.

Introduction

The Gredos Mountains, located in central Spain, have long attracted the interest of ecologists, and dozens of sites have been studied from a palaeoecological perspective since the 1980s (Franco-Múgica, 2009; Carrión et al., 2012; López-Sáez et al., 2014). There, as in the rest of the Iberian Peninsula, palynology has been the main technique employed to reconstruct past vegetation (Carrión et al., 2010, 2012). However, our understanding of the Holocene vegetation history of this region is based on a limited number of well-dated pollen records. Pollen data have suggested a major role of *Pinus* from ca. 6800–1500 cal yr BP (Franco-Múgica, 1995, 2009; Ruiz-Zapata et al., 1997; López-Sáez et al., 2014) and an apparent reduction in forest cover during the last two millennia (Franco-Múgica et al., 1997; López-Merino et al., 2009; Ruiz-Zapata et al., 2011). This regional demise of forests has been attributed to diverse factors such as anthropogenic activity (e.g., Franco-Múgica et al., 1997), climate change (e.g., López-Saez et al., 2009) or shifting fire regimes (e.g., López-Merino et al., 2009).

The spatial distribution of forests through time cannot be addressed successfully through pollen studies. Records of modern pollen deposition in the Gredos Mountains show that arboreal pollen is well represented in areas without tree cover, with percentages of occurrence varying between 10% and 40% of the spectra (Andrade et al., 1994). Contrastingly, local tree presence could be detected even when its pollen is recorded at relatively low percentages (~15% to 20%) in the assemblage (Sánchez Goñi and Hannon, 1999).

A second issue concerns the uncertainties derived from the dating of pollen sequences. Pollen records from central Spain are often discontinuous (e.g., López-Saez et al., 2009; Ruiz-Zapata et al., 2011) and most previous studies have had problems with chronologies (see Franco, 2009; López-Saez et al., 2009).

Finally, there is a lack of information regarding the species involved in the Holocene vegetation history of central Spain. Pollen studies show that *Pinus* was the dominant tree taxon in Gredos during the Holocene, but of the six species of *Pinus* that occur naturally in Iberia only *Pinus pinaster* Ait can be identified to the species level (e.g., López-Sáez et al., 2010).

Currently, most of the Gredos Mountains is included in the largest protected area of the central Iberian highlands (Sierra de Gredos Regional Park, and Site of Community Importance), where the vegetation is dominated by pastures and shrublands with scattered stands and individual trees. During the last few decades, extensive reforestation with pines has occurred, resulting in a complex landscape in which natural and human-induced vegetation are often undistinguishable and leading to a debate about the naturalness and suitability of pine species in the territory (see Gómez Manzaneque, 2009). Even if palaeoecological, dendroecological and historical data support the natural origin of pinewoods in central Iberia (Andrade and Hermín, 2007; Génova et al., 2009; Rubiales et al., 2010; Génova and Moya, 2012), there is still a

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need to understand the past vegetation history at a higher temporal and spatial level of detail to direct conservation efforts and landscape planning.

Here, we provide new megafossil (large woody material) and macrofossil (cones or fruits) data from sedimentary deposits of the Gredos Range. Given the local origin and species-level taxonomic resolution of the remains, along with the direct radiocarbon dating of the materials, we were able to reconstruct the spatio-temporal pattern of forest cover in the Gredos Mountains, as well as to determine which tree species were present in this region during the Holocene.

Study area

The Central Range, which is located in the central part of the Iberian Peninsula, divides the Duero and Tajo basins from west to east. The Gredos Mountains are the most important system in this range. They extend for approximately 150 km and include the highest point of central Iberia (Almanzor, 2592 m asl). The bedrock is composed of siliceous rocks, primarily granites and gneisses that were geomorphologically moulded by horst-graben tectonics. The climate is montane Mediterranean, with an intense summer drought and great seasonal temperature oscillation. The mean annual temperature is approximately 10°C, and the annual rainfall varies between 1000 and 2000 mm (Morla and García, 2009).

The vegetation includes both evergreen and deciduous species. Evergreen oaks (*Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Quercus suber* L. on the southern slopes), pines (*P. pinaster* and *P. pinea* L.) and mixed forest grow up to approximately 1200 m asl. The pinewoods predominate on sandy and xeric sites. *Quercus pyrenaica* L. and *P. pinaster* are found up to 1500 m asl. The tree line reaches approximately 1800 m asl on the southern slopes, with isolated and dispersed stands of *Pinus sylvestris* L and *Pinus nigra* subsp. *salzmannii* (Dunal) Franco (Génova et al., 1988; Génova and Moya, 2012). The upper zone is frequently treeless, although some pine stands occur in the highlands (Hoyos del Espino and Navarredonda). A shrub community composed of broom (*Cytisus oromediterraneus* Rivas Mart.) and prostrate juniper (*Juniperus communis* subsp. *alpina* (Suter) Celak) is dominant at the highest altitudes, along with alpine pastures (Ruiz de la Torre, 2002; Gómez Manzaneque, 2009).

Materials and methods

Sampling strategy

Woody samples were found opportunistically by screening small mires and stream banks at medium to high altitudes (1300–1900 m) in currently forested and treeless areas. Data were obtained from nine different sites (Figs. 1 and 2, Table 1). Additionally, four trunk sections were recovered from a collapsed dwelling in Navarredonda. A total of 236 macrofossils (mainly pine cones, stumps and logs) were identified, and 29 trunk sections were analysed for dendrochronological purposes. The woody remains could occasionally be identified to the species level, but most of the pine remains could only be identified to the group level based on the anatomical features of the wood (Rubiales et al., 2007, 2008).

Samples were selected for radiocarbon dating based on the site location and the size of the recovered remains. In every site, at least one megafossil was radiocarbon-dated, and the best sections of wood

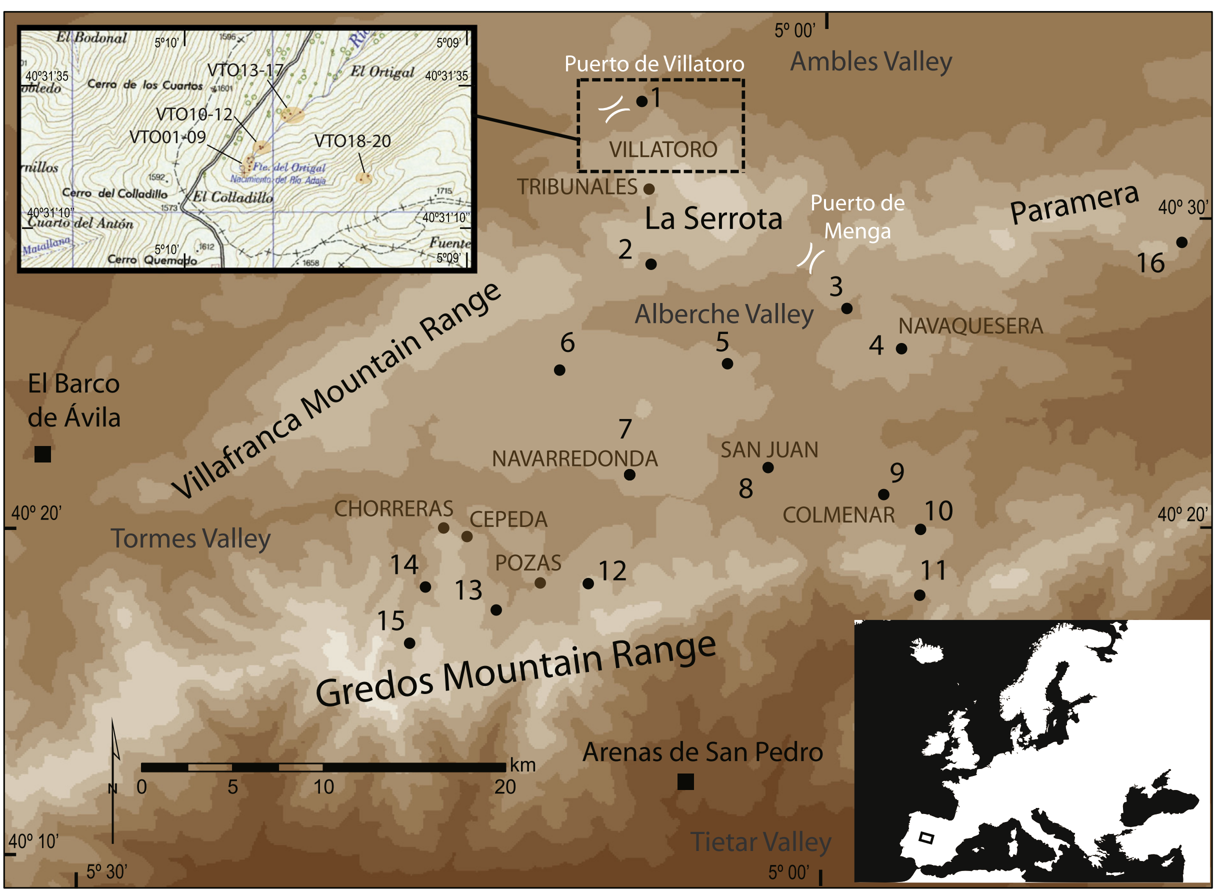

Fig. 1. Locations of the sites with macrofossil (named) and tree-ring data (numbered). 1 Villatoro, 2 Garganta del Villar, 3 Navalacruz, 4 Hoyocasero-La Cañada, 5 Navadijos, 6 San Martín de la Vega del Alberche, 7 Navarredonda de Gredos, 8 San Martín del Pimpollar, 9 Colmenar, 10 San Esteban del Valle, 11 Serranillos, 12 Hoyos del Espino, 13 Navacepeda de Tormes, 14 Navalperal de Tormes, Roncesvalles, 15 Navalperal de Tormes, Garganta de Gredos, and 16 Paramera. The left corner shows the locations of the samples collected at the Villatoro site. Sample labelling corresponds with the samples listed in Table 2.

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Fig. 2. Pictures of some of the locations in where macrofossil data have been retrieved. a) Chorreras, b) Tribunales, and c) Colmenar.

(those having non-decayed wood and numerous tree rings) were radiocarbon-dated and dendrochronologically analysed.

Wood identification

Thin sections (approximately 15 to 20 μm thick) of all of the selected samples were obtained using a sliding microtome. The slices were stained with safranin and dehydrated with alcohol and a solvent and clearing agent (Histoclear). Then, the sections were then mounted on coated slides, coverslipped with a hardening epoxy (Eukitt) and dried at ambient temperature. The other woody remains were examined through reflected-light microscopy at different magnifications (50×, 100× and 200×), which is a method that is commonly used to examine fragments of charcoal. The samples were fractured manually to obtain transversally, radially and tangentially aligned surfaces suitable for microscopic analysis. Wood identification was achieved using wood anatomy keys, including those proposed by García and Guindeo (1988), Schweingruber (1990) and Vernet et al. (2001). In cases in which identification was uncertain, the samples were compared with slides from the wood reference collection of the Universidad Politécnica de Madrid.

Cone identification

The size and shape of the scales and cones were used to identify the recovered fossils to the species level. Cones of 2–5 × 1.5–3.5 cm in size with scales containing flat or slightly curved apophyses, and that are rhombic in shape with muticous or minutely mucronate umbo, were identified as *P. sylvestris*. Rounded apophyses and eccentric, hook-like umboes (Fig. 3) were considered to be diagnostic features corresponding to *P. nigra* Arnold (Farjon, 1984; Franco, 1986).

Radiocarbon dating

Sixteen radiocarbon dates were obtained from samples collected from the outer heartwood rings of the logs (Tables 2 and 3). One additional date was obtained from the scales of a cone that revealed the occurrence of *P. nigra* (Table 3), a species that had not been previously recorded in the Holocene deposits of central Spain. Within each site, subfossil trunks with a higher number of tree rings were selected in order to obtain the best available tree-ring measurements. The subfossil material usually appeared in a clear stratigraphical setting; therefore, radiocarbon dating was applied once per site. However, additional dating within the same site was performed under exceptional circumstances. For example, at the Villatoro site, the specimens were distributed more broadly over the site and clustered in distant locations, and thus several megafossils suitable for tree-ring measurements were found and dated (Fig. 1)

Dates were obtained through both conventional radiocarbon and AMS (Beta Analytic, Inc, Florida, USA; QUADRU—Quaternary Dating Research Unit, Pretoria, South Africa and 14Chrono Centre, Belfast, UK) and were calibrated using CALIB 7.0.4 software (Stuiver and Reimer, 1993) with the last dataset available (INTCAL 13, Reimer et al., 2013). The dated parts of each measured floating series corresponded to the outermost, well preserved tree-rings. The series were crossdated and assigned an approximate location according to the most probable year to which the part corresponded, using the median probability as suggested by Telford et al. (2004).

Table 1
Site location and absolute frequencies of woody macrofossils occurrence.

Site	Long	Lat	Altitude (m. asl)	*Pinus* gr. *sylvestris/nigra*	Cones *P. sylvestris*	Cones *P. nigra*	*Betula*	*Quercus* deciduous	*Juniperus*	Leguminosae	Unidentifiable	Total
San Juan	3282	44,683	1350	26	15							41
Villatoro	3169	44,883	1460–1510	29	47	1		3		1		81
Tribunales	3194	44,877	1720–1780	12					2		1	15
Cepeda	3178	44,646	1620	5								5
Chorreras	3085	44,646	1790	15								15
Pozas	3085	44,594	1900				15					15
Navarredonda (fen)	3211	44,725	1530	2								2
Colmenar	3033	44,689	1470	2	10							12
Navaquesera	3338	44,769	1670	2	9							11
Paramera	3575	44,871	1500	5	34							39

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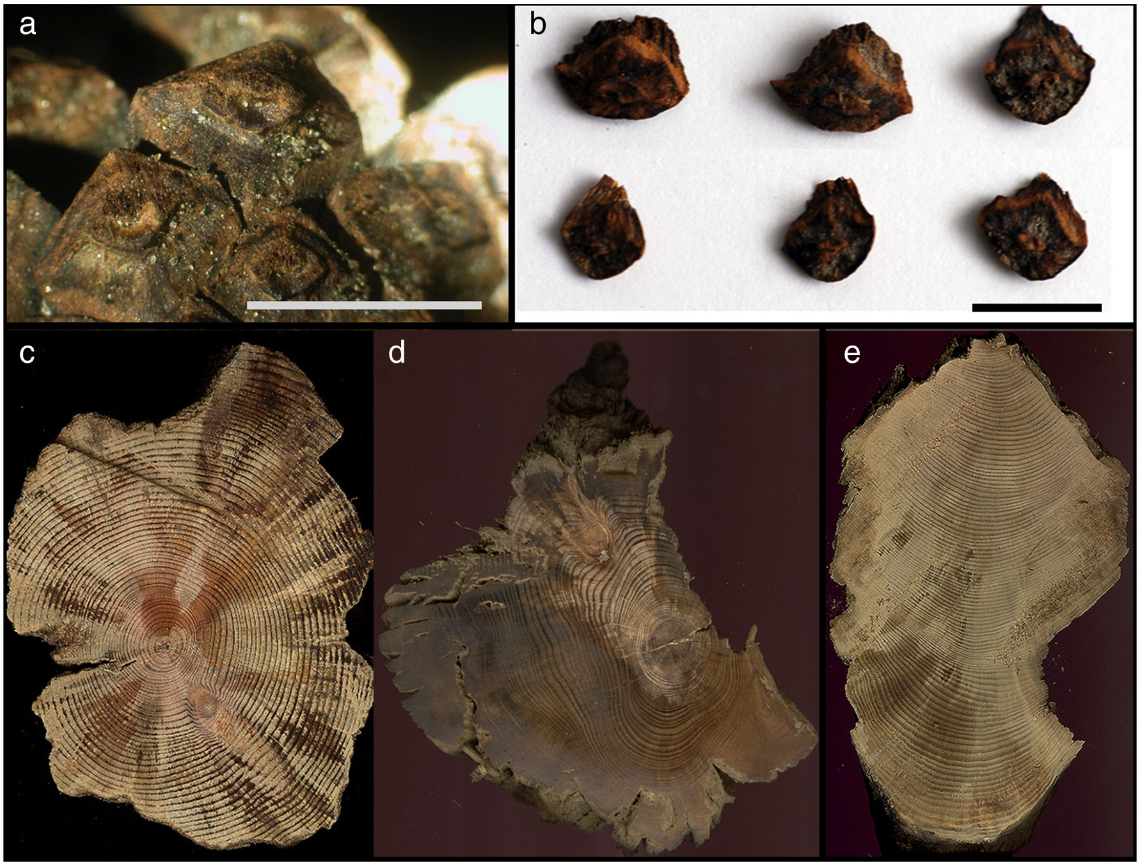

Fig. 3. Cone (a) and scales (b) identified as *Pinus nigra* in Villatoro. Scale bars = 1 cm. The pictures below correspond to polished tree sections from different sites: c) Villatoro, d) and e) Navarredonda b (dated at approximately 1000 and 3500 cal yr BP, respectively).

Tree-ring measurements

Cross sections of the megafossils were obtained, air-dried and progressively sanded down to a 400-grit sanding paper. The tree rings were counted and the widths measured on several radii of the sample (up to 6, depending on the shape and origin). In general, fewer radii were needed for regularly shaped stems. Sections of irregularly shaped stumps required a careful examination because these portions of the trees were likely affected by root growth and root-related mechanical effects. The ring widths were measured to an accuracy of 1/100 mm using a digital LINTAB positioning table connected to a stereomicroscope and TSAPWin software (Rinn, 2005). The COFECHA (Holmes, 1983) and TSAPWin software programs were used to perform the cross-dating and correlation analysis of the series that were used in the floating chronologies.

Results

Mega- and macrofossils

Seven taxa were identified in the assemblages. The highland pines (*Pinus* gr. *sylvestris*/*nigra*) were the most well-represented group (Table 1). The tree macrofossils were recovered from a wide altitudinal interval, from 1470 m asl (Colmenar) to approximately 1900 m asl (Pozas, Table 1). The wood assemblage included other taxa, such as birch (*Betula* L.), which occurred at the highest altitudes, deciduous oaks (*Quercus*), junipers (*Juniperus*), and shrubs (Leguminosae). Scales and seeds provide taxonomic information at the species level in Pozas (*Betula pubescens* Ehrh). Several hazelnuts were recorded in Villatoro, indicating that *Corylus avellana* L co-occurred with pines and oaks.

Cones

Most of the cones had features that enabled us to identify them at the species level. 115 cones identified as *P. sylvestris* were found at four different sites, namely San Juan, Colmenar, Navaquesera and Villatoro. One pine cone recovered in Villatoro corresponded to *P. nigra*. Eight cones were not sufficiently well preserved for identification.

Radiocarbon dating and tree-ring series from selected megafossils

Radiocarbon dating (Tables 2 and 3) indicated that the preserved pine material appears to span the past 6500 yr (Fig. 4). The radiocarbon date obtained for the cone of *P. nigra* revealed that the species was present at 1660 cal yr BP (Table 3).

A total of 100 radii from 29 trees were obtained and cross-dated within each site (Fig. 5). Radiocarbon dates show that the tree-ring samples were clustered around three periods: 800–1200, 1500–2000 and 2400–2600 cal yr BP. Additionally, the four trunk sections recovered from the collapsed dwelling in Navarredonda were dated to approximately 450 cal yr BP. No samples suitable for dendrochronological studies have been dated to the periods 500–700 cal yr BP, 2000–2300 cal yr BP, 2700–3400 cal yr BP and a longer period between ~4000 and ~6000 cal yr BP. The first two gaps in the tree-ring record (500–700 and 2000–2300 cal yr BP) are critical for the development of a long chronology; bridging them would allow most of the floating series from subfossil wood to be linked to tree-ring series from extant specimens.

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Table 2
Radiocarbon dates and internal statistics of the samples dendrochronologically studied. The dates were calibrated and the median probabilities were calculated (2 sigma) using the CALIB 7.0.4 software (Stuiver and Reimer, 1993) with the latest INTCAL13 dataset (Reimer et al., 2013). * indicates that dates were published in Rubiales et al. (2007).

Sample	Lab code	Site	Length	Mean growth (mm)	Mean sensitivity	Relative mean sensitivity (%)	Tendency changes (%)	Auto correlation (lag = 1)	Radiocarbon date (^{14}C yr BP)	Calibrated date (cal yr BP)	Median (cal yr BP)
NRG01	Beta-278512	Navarredonda 1	65	2.74	14	11	56	0.95	330 ± 50	302–495	393
NVL06	* Pta-9240	Navalacruz	58	2.53	21	24	47	0.76	860 ± 20	726–892	763
NVT12	* Beta-187347	Navalperal-Garganta de Gredos	172	0.46	18	25	65	0.76	970 ± 60	739–976	866
VTO14	Beta-278516	Villatoro	73	1.17	21	34	60	0.66	1070 ± 40	927–1059	980
VTO15	Beta-278517	Villatoro	60	2.10	16	20	61	0.86	1080 ± 50	918–1172	996
HOY09	* Pta-9249	Hoyos del Espino	67	1.62	16	23	55	0.82	1090 ± 30	937–1057	997
SMV03	* Beta-215651	San Martín de la Vega del Alberche	124	1.85	18	13	61	0.93	1170 ± 40	977–1221	1098
COL02	Beta-278509	Colmenar	82	1.73	17	19	57	0.89	1250 ± 40	1072–1278	1201
HOY10	* Pta-9261	Hoyos del Espino	53	1.78	23	21	60	0.82	1300 ± 60	1171–1307	1228
NVT13	* Pta-9243	Navalperal de Tormes (Roncesvalles)	78	3.31	26	34	53	0.62	1560 ± 35	1377–1534	1464
VTO08	Beta-278513	Villatoro	106	1.04	24	12	61	0.92	1650 ± 40	1414–1690	1553
NVD01	* Pta-9231	Navadijos	61	1.66	22	18	53	0.87	1750 ± 45	1557–1809	1661
VTO10	Beta-278514	Villatoro	99	2.43	18	10	48	0.96	1770 ± 40	1571–1733	1682
SEV01	* Pta-9235	San Esteban del Valle	63	1.02	29	28	61	0.71	1815 ± 25	1636–1821	1758
VTO16	Beta-278518	Villatoro	115	1.50	23	23	51	0.78	1920 ± 40	1737–1967	1868
SJG08	* Pta-9247	Navacepeda	87	0.74	22	18	52	0.81	2085 ± 25	1992–2125	2056
SMP05	* Beta-215651	San Martín del Pimpollar	74	1.94	16	44	66	0.42	2350 ± 40	2214–2677	2375
VTO13	Beta-278515	Villatoro	79	2.03	23	28	55	0.71	2380 ± 40	2334–2687	2417
GDV02	* Pta-9253	Garganta del Villar	87	3.05	24	20	49	0.87	2430 ± 15	2360–2678	2445
SER001	* Beta-187348	Puerto de Serranillos	184	1.68	19	25	54	0.79	2440 ± 60	2354–2710	2521
PAR05	UBA-20801	Paramera	197	1.21	12	12	65	0.95	2528 ± 40	2489–2747	2605
NGR04	Beta-278511	Navarredonda 2	118	2.28	16	27	56	0.75	3220 ± 40	3368–3558	3439
NGR02	Beta-278510	Navarredonda 2	153	0.77	32	24	53	0.73	3280 ± 40	3401–3606	3510
NVQ02	* Beta-208822	Hoyocasero-La Cañada	50	3.98	10	26	49	0.78	5630 ± 70	6289–6615	6415

Discussion

Biogeographic considerations

The site-specific megafossil data presented here confirm the long-term persistence of a widespread belt of pinewoods in the highlands of the Central Iberian Mountains. Furthermore, the finding of well-preserved cones in a number of new sites enlarges and improves the available taxonomic information. The cones suggest that, during the mid- to late Holocene, the distribution of *P. sylvestris* was much more extensive than that of *P. nigra*, a taxon for which the first known clear subfossil evidence is reported here.

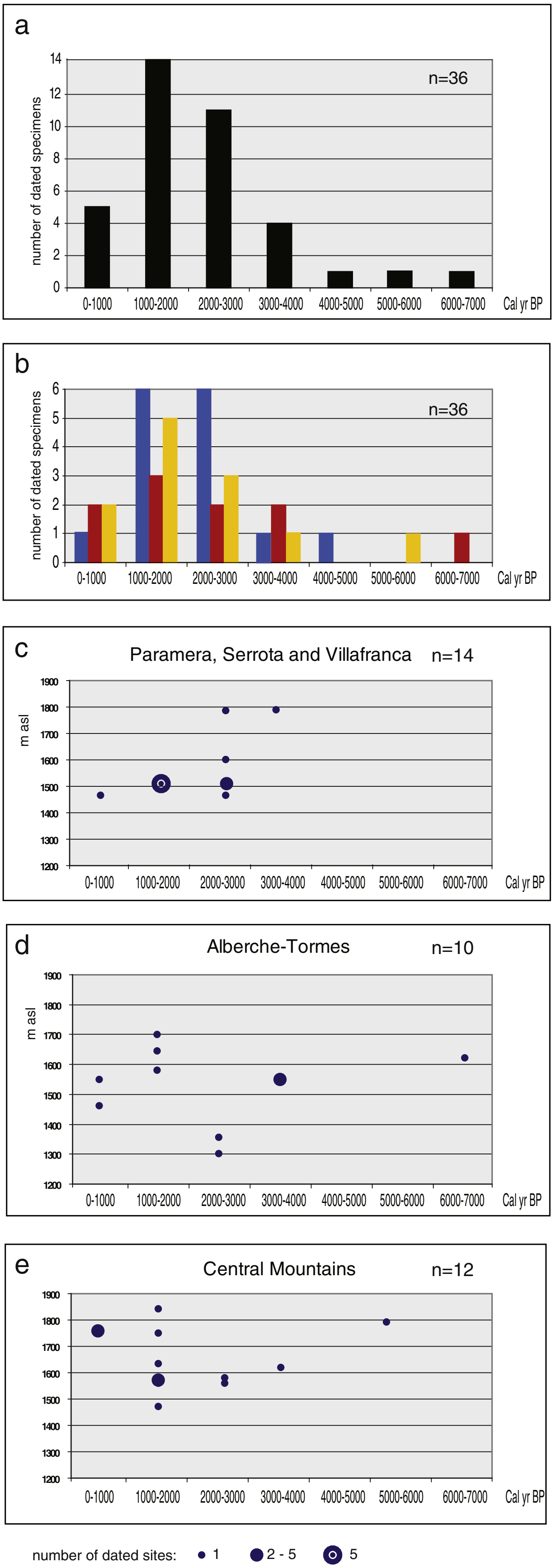
Viewed together, the macrofossil data from the 36 sites in the Gredos Mountains suggest that the spatial and altitudinal distribution of trees has been relatively stable over the last six millennia (Fig. 4). This finding does not support the hypothesis that tree populations expanded and declined in response to late-Holocene climatic variations. Instead, the radiocarbon-date macrofossils indicate that trees were continuously present during the second half of the Holocene at altitudes ranging from 1350 to 1800 m asl, which is in accordance with biogeographic modelling (Benito Garzón et al., 2007, 2008). The dating of multiple wood samples from Villatoro illustrates this continuity at a single site. With the exception of the two youngest samples, which date to ~1000 cal yr BP, the recovered remains did not overlap and appear to represent the long-term, persistent presence of pines, dating to 1550, 1690, 1870, and 2420 cal yr BP and thus spanning several generations.

Pollen records have reported the dominance of *Pinus* in the highlands of Gredos during the mid and late Holocene (Franco-Múgica et al., 1997, 1998; Andrade and Hermín, 2007; Franco, 2009; López-Merino et al., 2009). However, to the northeast of the study area (northern slopes of La Serrota and Amblés Valley), the past distribution of forests has remained unclear. At approximately 3000 cal yr BP, the palynological signal of *Pinus* is moderate (~60%) in the westernmost zones of the Amblés valley and mid altitudes in the Sierra de Ávila (site of Narrillos del Rebollar; López-Saez et al., 2009). However, the percentage of *Pinus* is low (20%) at the bottom of the valley (Baterna; López-Saez et al., 2009) and almost lacking at any of the other sites situated further East. Macrofossil data from Villatoro and Tribunales indicates the presence of pinewoods at these northern locations, expanding its late Holocene distribution to the northern slopes of La Serrota, and suggesting that the pine dominance was restricted to mountain areas (altitudes higher than 1400 m).

The first subfossil evidence of *P. nigra* in northern Gredos (Villatoro) is of particular interest. This species is found widely in the mountains of Eastern and Northern Spain, but it is currently rarely found in the Central Range and other areas of siliceous bedrock (Costa et al., 1997). Our results are in accordance with the predictive modelling carried out by Benito Garzón et al. (2007), which suggested that these northern areas of Gredos, unlike the Central Massif, were suitable for *P. nigra* at the mid-Holocene and at present. This finding is also consistent with other palaeoecological data showing that in areas bordering the Northern Iberian Plateau (García-Amorena et al., 2011), as well as in other areas of southern and eastern Spain, the distribution of *P. nigra*

Table 3
Radiocarbon dates of wood samples that have not been dendrochronologically analysed. The calibrated dates and median probabilities (2 sigma) were obtained with CALIB 7.0.4 software (Stuiver and Reimer, 1993) using the latest INTCAL13 dataset (Reimer et al., 2013).

Site	Lab code	Type	Dating method	Radiocarbon date (^{14}C yr BP)	Calibrated date (cal yr BP)	Median (cal yr BP)
Chorreras	Beta-263701	Wood	Radiometric	1010 ± 50	794–1050	926
Villatoro	UBA-17597	Cone scales	AMS	1756 ± 25	1571–1727	1661
San Juan	Beta-263697	Wood	Radiometric	2600 ± 50	2494– 2843	2735
Tribunales-a	Beta-263698	Wood	Radiometric	2620 ± 50	2510–2852	2752
Tribunales-b	Beta-263699	Wood	AMS	2920 ± 40	2951–3205	3065
Cepeda	Beta-263700	Wood	Radiometric	3030 ± 50	3076–3360	3230



was wider during the mid and late Holocene than at present (Badal et al., 1994; Alejano and Martínez Montes, 2006). Palynological records also suggest that the abundance of *P. nigra* was higher during the mid Holocene than at present (e.g., Stevenson, 2000; Carrión et al., 2001; Anderson et al., 2011; Aranbarri et al., 2014), although the lack of detailed taxonomic information in pollen records hampers the precise role of this species when other pines may have been present (*P. pinaster* or *P. sylvestris*). This is also the case of the mid altitudes of Cerrato or the Cantabrian Mountains (García-Antón et al., 2011; Rubiales et al., 2012a).

Samples corresponding to the period from 3000 to 800 cal yr BP were widely distributed in Gredos, but more recent pine macrofossil records are lacking and dated series from living specimens begin in the 17th century (Génova, 2009). Fire has been considered to represent an important ecological disturbance affecting Iberian mountain pines (*P. nigra* and *P. sylvestris*) during the last three millennia (Rubiales et al., 2012b). These two pines are classified as "resister strategy" species (sensu Agee, 1998), with some history traits that would allow them to survive low-severity fires (thick bark and self-pruning) but a lack of adaptations to resist to crown fires, such as serotiny or early reproduction (Pausas, 2015). Coupled analyses of pollen and microscopic charcoal in sedimentary sequences usually show that a demise of mountain pines corresponds with increasing trends or maxima in fire-prone shrublands and the micro- and macroscopic charcoal record (e.g. Connor et al., 2012; Rubiales et al., 2012b; Morales-Molino and García-Antón, 2014). The palaeoecological record of López-Merino et al. (2009), the only sedimentary sequence recording fire history in Gredos, suggests that fires were intense and associated with other human activities such as grazing (López-Merino et al., 2009). The coincidence of an intensification of human activities and fire with the pine demise may be responsible of this gap of subfossil material during part of the last millennium (Rubiales et al., 2007; Morla and García, 2009).

Dendroecological considerations concerning subfossil specimens: prospects and limitations

The discovery of large numbers of megafossils suitable for dendrochronological examination and the subsequent development of floating chronologies open new directions for the study of the long-term history of pinewoods and climate in this region. At present, there are few high-resolution paleoenvironmental records from Spain that span the late Holocene, and only limited data exist from central Iberia (Pérez and Boscolo, 2010). In the highlands of central Spain, most information about the climate of the last three millennia come from pollen records, which are likely affected by anthropogenic disturbance of the vegetation (Franco-Múgica et al., 1998; López-Merino et al., 2009; Rubiales et al., 2012b). Thus, the development of late-Holocene climate reconstructions with annual resolution would represent a major advance

The length of the series varied between 197 and 50 yr, with a mean of 91 yr. The series showed mean sensitivity values (i.e., the relative change in ring-width from 1 year to the next) ranging from 0.10 to 0.32 (Table 2). Mean sensitivity (MS) is a good measure of the relative ease of cross-dating, and excluding the youngest specimens (less than 70 yr), all of the series had MS values higher than 0.17. These values were comparable with the present range for *P. sylvestris* and *P. nigra* in central Spain (Richter et al., 1991; Génova et al., 1993; Benso, 2007; Génova and Moya, 2012).

In central Iberia, dendroclimatological studies from *P. sylvestris* and *P. nigra* have provided climatic information for the past four centuries

Fig. 4. Age distribution of subfossil *Pinus* gr. *sylvestris* wood in the Gredos Mountains. Top panel: composite data for all sites. Second panel: composite data by location (blue: Paramera, Serrota and Villafranca mountains, red: Alberche and Tormes headwaters, and yellow: Central Mountains). Third to fifth panels: altitudinal distribution of the sites by age. The samples are grouped by millennium (cal yr BP). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

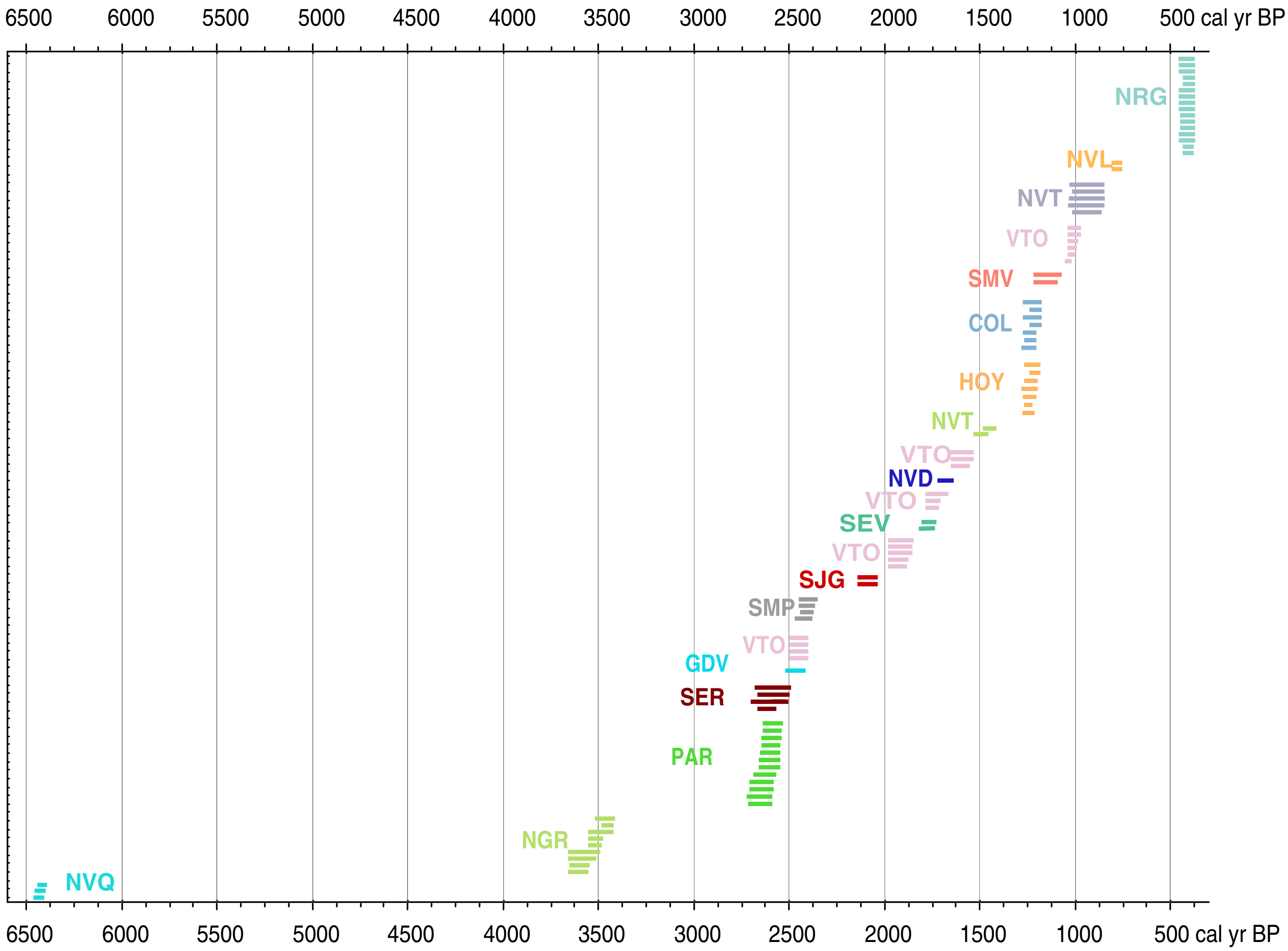


Fig. 5. Floating tree-ring series from subfossil material. The outermost rings of the samples were radiocarbon dated, the dates calibrated and the floating series were assigned an approximate location according to the most probable year to which the part corresponded, using the median probability as suggested by Telford et al. (2004). The best replicated part of the overall dataset is between 2000 and 800 cal yr BP, but some gaps hindered the cross-dating of the split floating chronologies. The codes represent the sites and correspond with those of Table 2.

(Fernández et al., 1996; Génova, 2000, 2009), demonstrating the potential for the reconstruction of long-term regional climatic parameters in the Central Range. These studies have detected that both temperature and precipitation control ring widths at high elevations. Tree-ring studies have been able to provide annually resolved proxy time series of climatic variations for different European locations that cover millennial time scales (Gunnarson and Linderholm, 2002; Büntgen et al., 2005; Grudd, 2008). However, uncertainties regarding possible climatic reconstructions from subfossil material have appeared because the majority of the analysed samples were recovered from peatlands. At least at northern latitudes, the climate–growth response of trees growing in peatlands is different than those from trees growing on dry sites. For example, the climatic information furnished by peatland Scots pines was weaker than for those living in dry soils (Linderholm et al., 2002; Moir and Leroy, 2011). Other ecological features (i.e., periods of climate-related hydrological variations) have been also reconstructed from growth-rings from bog pines. Here, increased tree growth usually reflects lowerings of the groundwater table and, contrastingly, growth depressions are linked with higher groundwater tables, most likely related to colder and wetter climate (e.g., Gunnarson, 2008; Moir et al., 2010; Edvardsson et al., 2012).

In light of our results, cross-dating across sites may be a key step in the development of a usable tree-ring chronology. We identified clear periods of overlap among the sites, but correlations were relatively weak (Fig. 5). This is largely due to the relatively low number of measured tree rings in each series (average ~90). Visual cross-dating can be additionally supported by a multi-step approach (Wilson et al., 2012), using other tree ring parameters that could help into the chronology development, such as wood density or blue intensity (Rydval et al., 2014).

Future tree-ring research in the mountains of central Spain should focus on extending the chronologies from living trees to the first floating series, which are radiocarbon dated to 800–900 cal yr BP. Efforts should be concentrated on obtaining more samples from archaeological sites and from those sites where the youngest radiocarbon-dated samples were found. The addition of samples spanning the current gap would allow the conversion of the floating chronologies from the Gredos Mountains into the first securely dated, annually resolved paleoenvironmental record for the western Mediterranean.

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References

Agee, J.K., 1998. Fire and pine ecosystems. In: Richardson, D.M. (Ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 193–218.

Alejano, R., Martínez Montes, E., 2006. Aportaciones de la paleobotánica a la interpretación del área natural de *Pinus nigra* Arn. subsp. *salzmannii* en las Sierras Béticas (sureste de España). Investigacion Agraria: Sistema Recursos Forestal Fuera de Serie 124–136.

Anderson, R.S., Jiménez-Moreno, G., Carrión, J.S., Pérez-Martínez, C., 2011. Postglacial history of alpine vegetation, fire and climate from Laguna del Río Seco, Sierra Nevada, southern Spain. Quaternary Science Reviews 30, 1615–1629.

Andrade, A., Hermín, R., 2007. El pinar de Hoyocasero (Ávila): ¿antigua repoblación o pinar natural conservado? Anales de Biologia 29, 33–51.

Andrade, A., Valdeolmillos, A., Ruíz-Zapata, B., 1994. Modern pollen spectra and contemporary vegetation in the Paramera Mountain range (Ávila, Spain). Review of Palaeobotany and Palynology 82, 127–139.

Aranbarri, J., González-Sampériz, P., Valero-Garcés, B., Moreno, A., Gil-Romera, G., SevillaCallejo, M., García-Prieto, 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 south-western Europe. Global and Planetary Change 114, 50–65.

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. Vegetation History and Archaeobotany 3, 155–166.

Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2007. Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. Ecography 30, 120–134.

Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. The evolution of the *Pinus sylvestris* L. area in the Iberian peninsula from the last maximum glacial (21000 BP) to 2100 under climate change. The Holocene 18, 1–10.

Benso, M., 2007. Estudio dendrocronológico de *Pinus sylvestris* L. en los Montes de Valsaín (Segovia). Proyecto Fin de Carrera. Escuela Universitaria de Ingeniería Técnica Forestal. Universidad Politécnica de Madrid.

Büntgen, U., Esper, J., Frank, D., Nicolussi, K., Schmidhalter, M., 2005. A 1052-year tree-ring proxy for Alpine summer temperatures. Climate Dynamics 25, 141–153.

Carrión, J.S., Andrade, A., Bennett, K.D., Navarro, C., Munuera, M., 2001. Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. Holocene 11 (6), 635–653.

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. Review of Palaeobotany and Palynology 162, 458–476.

Carrión, J.S., Fernández, S., González-Sampériz, P., López-Merino, L., Peña, L., Burjachs, F., López-Sáez, J.A., García-Antón, M., Carrión Marco, Y., Uzquiano, P., Postigo, J.M., Barrón, E., Allué, E., Badal, E., Dupré, M., Fierro, E., Munuera, M., Rubiales, J.M., García Amorena, I., Jiménez Moreno, G., Gil Romera, G., Leroy, S., García-Martínez, M.S., Montoya, E., Fletcher, W., Yll, E., Vieira, M., Rodríguez-Ariza, M.O., Anderson, S., Peñalba, C., Gil García, M.J., Pérez Sanz, A., Albert, R.M., Díez, M.J., Morales-Molino, C., Gómez Manzaneque, F., Parra, I., Ruiz Zapata, B., Riera, S., Zapata, L., Ejarque, A., Vegas, T., Rull, V., Scott, L., Abel Schaad, D., Andrade, A., Manzano, S., Navarro, C., Pérez Díaz, S., Moreno, E., Hernández-Mateo, L., Sánchez Baena, J.J., Riquelme, J.A., Iglesias, R., Franco, F., Chaín, C., Figueiral, I., Grau, E., Matos, M., Jiménez Espejo, F., Valle-Hernández, M., Rivas-Carballo, R., Arribas, A., Garrido, G., Muñiz, F., Finlayson, G., Finlayson, C., Ruiz, M., Pérez Jordá, G., Miras, Y., 2012. Paleoflora y Paleovegetación de la Península Ibérica e Islas Baleares: Plioceno-Cuaternario. Ministerio de Economía y Competitividad, Madrid.

Connor, S.E., Araújo, J., van der Knaap, W.O., van Leeuwen, J.F.N., 2012. A long-term perspective on biomass burning in the Serra da Estrela, Portugal. Quaternary Science Reviews 55, 114–124.

Costa, M., Morla, C., Sainz, H. (Eds.), 1997. Los bosques ibéricos. Una interpretación geobotánica. Planeta, Barcelona.

Edvardsson, J., Leuschner, H.H., Linderson, H., Linderholm, H.W., Hammarlund, D., 2012. South Swedish bog pines as indicators of Mid-Holocene climate variability. Dendrochronologia 30, 93–103.

Farjon, A., 1984. Pines: drawings and descriptions of the genus. In: Brill, E.J., Backhuys, W. (Eds.), Leiden, the Netherlands.

Fernández, A., Génova, M., Creus, J., Gutiérrez, E., 1996. Dendroclimatological investigation covering the last 300 years in Central Spain. In: Dean, J.S., Meko, D.M., Swetnam, T.W. (Eds.), Tree Rings, Environment and Humanity. Radiocarbon. University of Arizona Press, Tucson, pp. 181–190.

Franco, J.A., 1986. *Pinus* L. In: Castroviejo, S., Laínz, M., López, G., Montserrat, P., Muñoz, F., Paíva, J., Villar, L. (Eds.), Flora Iberica. Real Jardín Botánico, C.S.I.C., Madrid, Spain, pp. 168–174.

Franco-Múgica, F., 1995. Estudio palinológico de turberas holocenas en el sistema central: reconsturcción paisajística y acción antrópica. Ph.D. Thesis. Universidad Autónoma, Madrid, Spain.

Franco-Múgica, F., 2009. El análisis polínico en la reconstrucción del paisaje vegetal. In: Génova, M., Gómez Manzaneque, F., Morla, C. (Eds.), Los bosques de Gredos a través del tiempo. Junta de Castilla y León, Valladolid.

Franco-Múgica, F., García-Antón, M., Sainz-Ollero, H., 1997. Impacto antrópico y dinámica de la vegetación durante los últimos 2000 años BP en la vertiente septentrional de la Sierra de Gredos: Navarredonda (Ávila, España). Révue de Paléobiologie de Genève 16 (1), 29–45.

Franco-Múgica, F., García-Antón, M., Sainz-Ollero, H., 1998. Vegetation dynamics and human impact in the Sierra de Guadarrama, Central System, Spain. The Holocene 8 (1), 69–82.

García, L., Guindeo, A., 1988. Anatomía e identificación de las maderas de coníferas españolas. AITIM, Madrid (142 pp.).

García-Amorena, I., Rubiales, J.M., Moreno, E., Iglesias, R., Gómez Manzaneque, F., 2011. New macrofossil evidence of *Pinus nigra* Arnold on the Northern Iberian Meseta during the Holocene. Review of Palaeobotany and Palynology 163, 281–288.

García-Antón, M., Franco-Múgica, F., Morla-Juaristi, C., Maldonado-Ruiz, F.J., 2011. The biogeographical role of *Pinus* forest on the Northern Spanish Meseta: a new Holocene sequence. Quaternary Science Reviews 30, 757–768.

Génova, M., 2000. Anillos de crecimiento y años característicos en el Sistema Central (España) durante los últimos cuatrocientos años. Boletin de la Real Sociedad Historia Natural (Seccion Biologia) 96 (1-2), 33–42.

Génova, M., 2009. Cronologías milenarias de anillos de crecimiento. In: Génova, M., Gómez Manzaneque, F., Morla, C. (Eds.), Los bosques de Gredos a través del tiempo. Junta de Castilla y León, Valladolid.

Génova, M., Moya, P., 2012. Dendroecological analysis of relict pine forests in the centre of the Iberian Peninsula. Biodiversity and Conservation 21, 2949–2965.

Génova, M., Gómez Manzaneque, F., Regato, P., 1988. Sobre los pinares relictos de la sierra de Gredos (Ávila). Actas del Simposio Internacional de Botánica Pius Font i Quer II. pp. 439–442.

Génova, M., Fernández Cancio, A., Creus, J., 1993. Diez series medias de anillos de crecimiento en los sistemas Carpetano e Ibérico. Investigación agraria. Sistemas y Recursos Forestales 2, 151–172.

Génova, M., Gómez Manzaneque, F., Morla, C. (Eds.), 2009. Los bosques de Gredos a través del tiempo. Junta de Castilla y León, Valladolid.

Gómez Manzaneque, F., 2009. La cubierta vegetal y la flora. In: Génova, M., Gómez Manzaneque, F., Morla, C. (Eds.), Los bosques de Gredos a través del tiempo. Junta de Castilla y León, Valladolid.

Grudd, H., 2008. Torneträsk tree-ring width and density AD 500–2004: a test of climatic sensitivity and a new 1500-year reconstruction of north Fennoscandian summers. Climate Dynamics 31, 843–857.

Gunnarson, B.E., 2008. Temporal distribution pattern of subfossil wood in central Sweden: perspective on Holocene humidity fluctuations. The Holocene 18, 569–577.

Gunnarson, B.E., Linderholm, H.W., 2002. Low frequency climate variation in central Scandinavia since the 10th century inferred from tree rings. The Holocene 12, 667–671.

Holmes, R.L., 1983. Computer assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69–78.

Linderholm, H.W., Moberg, A., Grudd, H., 2002. Peatland pine as climate indicators? A regional comparison of the climate influence on Scots pine growth in Sweden. Canadian Journal of Forest Research 32, 1400–1410.

López-Merino, L., López-Sáez, J.A., Alba-Sánchez, F., Pérez-Díaz, S., Carrión, J.S., 2009. 2000 years of pastoralism and fire shaping high-altitude vegetation of Sierra de Gredos in central Spain. Review of Palaeobotany and Palynology 158, 42–51.

López-Saez, J.A., Blanco-Gonzalez, A., López-Merino, L., Ruiz-Zapata, M.B., Dorado-Valiño, M., Perez-Diaz, S., Valdeolmillos, A., Burjachs, F., 2009. Landscape and climatic changes during the end of the Late Prehistory in the Ambles Valley (Avila, central Spain), from 1200 to 400 cal BC. Quaternary International 200, 90–101.

López-Sáez, J.A., López-Merino, L., Alba-Sánchez, F., Pérez-Díaz, S., Abel-Schaad, D., Carrión, J.S., 2010. Late Holocene ecological history of *Pinus pinaster* forests in the Sierra de Gredos of central Spain. Plant Ecology 206, 195–209.

López-Sáez, J.A., Abel-Shaad, D., Pérez-Díaz, S., Blanco González, A., Alba-Sánchez, F., Dorado, M., Ruíz Zapata, B., Gil-García, M.J., Gómez González, C., Franco Múgica, F., 2014. Vegetation history, climate and human impact in the Spanish Central System over the last 9000 years. Quaternary International 353, 98–122.

Moir, A.K., Leroy, S.A.G., 2011. Role of substrate on the dendroclimatic response of Scots pine from varying elevations in northern Scotland. Canadian Journal of Forest Research 41, 822–838.

Moir, A.K., Leroy, S.A.G., Brown, D., Collins, P.E.F., 2010. Dendrochronological evidence for a lower water-table on peatland around 3200–3000 BC from subfossil pine in northern Scotland. The Holocene 20, 931–942.

Morales-Molino, C., García-Antón, M., 2014. Vegetation and fire history since the last glacial maximum in an inland area of the western Mediterranean Basin (Northern Iberian Plateau, NW Spain). Quaternary Research 81, 63–77.

Morla, C., García, R., 2009. Gredos y el interés de su pasado forestal. In: Génova, M., Gómez Manzaneque, F., Morla, C. (Eds.), Los bosques de Gredos a través del tiempo. Junta de Castilla y León, Valladolid.

Pausas, J.G., 2015. Evolutionary fire ecology: lessons learned from pines. Trends in Plant Science 20, 318–324.

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Pérez, F.F., Boscolo, R., 2010. Clima en España: pasado, presente y futuro. Informe de Evaluación del Cambio Climático Regional (Madrid).

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., 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 (4), 1869–1887.

Richter, K., Eckstein, D., Holmes, R.L., 1991. The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. Tree-Ring Bulletin 51, 1–13.

Rinn, F., 2005. TSAPWin: time series analysis and presentation for dendrochronology and related applications, version 0.53: user reference. Heidelberg.

Rubiales, J.M., García-Amorena, I., Génova, M., Gómez Manzaneque, F., Morla, C., 2007. The Holocene history of highland pine forests in a submediterranean mountain: the case of Gredos mountain range (Iberian Central range, Spain). Quaternary Science Reviews 26, 1759–1770.

Rubiales, J.M., García Amorena, I., García Álvarez, S., Gómez Manzaneque, F., 2008. The Late Holocene extinction of *Pinus sylvestris* in the West of the Cantabrian Range. Journal of Biogeography 35, 1840–1850.

Rubiales, J.M., García-Amorena, I., Hernández, L., Génova, M., Martínez, F., Gómez Manzaneque, F., Morla, C., 2010. Late Quaternary dynamics of pinewoods in the Iberian mountains. Review of Palaeobotany and Palynology 162, 476–491.

Rubiales, J.M., Ezquerra, F.J., Muñoz Sobrino, C., Génova, M., Gil, L., Ramil Rego, P., Gómez-Manzaneque, F., 2012a. Holocene distribution of woody taxa at the westernmost limit of the Circumboreal/Mediterranean boundary: evidence from plant macrofossils. Quaternary Science Reviews 33, 74–83.

Rubiales, J.M., Morales-Molino, C., García, Álvarez S., García Antón, M., 2012b. Negative responses of highland pines to anthropogenic activities in inland Spain: a palaeoecological perspective. Vegetation History and Archaeobotany 21, 397–412.

Ruiz de la Torre, J., 2002. Mapa forestal de España: memoria general. Escala 1:1.000.000 Organismo Autónomo Parques Nacionales, D.L., Madrid, 554 pp.

Ruiz-Zapata, M.B., Gil-García, M.J., Dorado, M., Andrade, A., Martín, T., Valdeolmillos, A., 1997. Vegetación y paleoambientes en el Sistema Central español. In: Rodríguez-Vidal, J. (Ed.), Cuaternario Ibérico. AEQUA, Huelva, pp. 248–260.

Ruiz-Zapata, M.B., Carrasco, R.M., Gil-García, M.J., Pedraza, J., Razola, L., Domínguez Villar, D., Gallardo, J.L., 2011. Dinámica de la vegetación durante el Holoceno en la Sierra de Gredos (Sistema Central Español). Boletín de la Real Sociedad Española de Historia Natural (Sección Geología) 105, 109–123.

Rydval, M., Larsson, L.Å., McGlynn, L., Gunnarson, B.E., Loader, N.J., Young, G.H., Wilson, R., 2014. Blue intensity for dendroclimatology: should we have the blues? Experiments from Scotland. Dendrochronologia 32, 191–204.

Sánchez Goñi, M.F., Hannon, G.E., 1999. High-altitude vegetational pattern on the Iberian Mountain Chain (north-central Spain) during the Holocene. The Holocene 9, 39–57.

Schweingruber, F., 1990. Anatomy of European woods. WSL/FNP, Paul Haupt Berne & Stuttgart Publishers, Stuttgart (800 pp.).

Stevenson, A.C., 2000. The Holocene forest history of the Montes Universales, Teruel, Spain. The Holocene 10, 603–610.

Stuiver, M., Reimer, P.J., 1993. Extended 14C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.

Telford, R.J., Heegaard, E., Birks, H.J.B., 2004. The intercept is a poor estimate of a calibrated radiocarbon age. The Holocene 14, 296–298.

Vernet, J.L., Ogererau, P., Figueireal, I., Machado Yanes, C., Uzquiano, P., 2001. Guide d'identification des charbons de bois préhistoriques et récents. Sud-Ouest de l'Europe: France, Péninsule ibérique et Iles Canaries. CNRS Editions, Paris.

Wilson, R., Loader, N.J., Rydval, M., Patton, H., Frith, A., Mills, C.M., Crone, A., Edwards, C., Larsson, L., Gunnarson, B.E., 2012. Reconstructing Holocene climate from tree rings—the potential for a long chronology from the Scottish Highlands. The Holocene 22, 3–11.

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