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Late Quaternary dynamics of pinewoods in the Iberian Mountains

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ABSTRACT

The role of pinewoods as native forests in the Iberian Mountains, and their long-term dynamics during the last interglacial, has been intensely debated among geobotanists. This debate has resulted in several different hypotheses regarding the interpretation of the present day landscape.

Recent research on Late Quaternary palaeoecological records has enabled long-term patterns of forest dynamics in the main ranges of the Iberian Peninsula to be tested, and the parallel analysis of micro- (mainly pollen) and macroremains (woods, charcoals, fruits, seeds and leaves) has enhanced the resolution of these palaeobiological records. Additional historical information has allowed a complete overview of the past vegetal landscapes to be obtained.

This work summarises the available data for Iberian mountain pines during the Lateglacial and the Holocene, focussing on the mountain regions in scenarios of absence or dominance. Based on this overview, life history traits and patterns of plant dynamics during the Holocene are discussed and compared with present landscapes.

In the long term, *Pinus* does not always respond as a serial element in succession dynamics, not even in very favourable environments for hardwoods. Processes such as incumbency or resilience, and features such as frugality and their ability to disperse, affect the persistence of pines to the present day. This is exemplified for continental mountain areas, in which the absence of anthropogenic activities could have determined the wider coverage of pinewoods seen today.

1. Introduction

Pinus L. is one of the most important tree genera in the forests of the Iberian Peninsula. The role of pinewoods in current vegetation has, however, traditionally been a matter of some debate (see Ceballos and Ximénez de Embún, 1938; Rivas-Martínez, 1987; Morla, 1993; Costa et al., 1997; Gil, 2008), with different botanical schools of thought defending widely different interpretations. The main areas of disagreement concern both the naturalness of the species and the stability of their formations, as well as the behaviour of the latter towards different climatic or perturbation scenarios. Palaeoecology can provide important information to help unravel these issues as it provides a wide perspective of changes to the landscape over time as well as detailed historical information regarding the climate and anthropogenic activity.

The results of palaeoecological research are increasingly being applied to restoration policies, particularly those concerning the Iberian pinewoods: information regarding the autochthonous nature of the species (e.g. Alcalde et al., 2006; Rubiales et al., 2007), the biogeographical importance of populations (e.g. Rubiales et al., 2008) or the identification of appropriate methods for acting on ecosystems (e.g. Aguiar and Capelo, 2004) are all clear examples of where this information is useful in conservation strategies.

The largest volume of sequential data for Iberia comes from the palynological analysis of sediments, which usually provides information up to the generic range. The study of fossil woods and other macroremains (leaves, strobili, fruits and seeds) provides information which, despite being strictly time-limited, significantly enriches the information obtained from pollen as it allows the fossils to be placed within a specific range (Birks and Birks, 2000; Birks, 2003). This, together with the accurate information they provide regarding the origin of the plant remains, helps us to interpret the possible super/infra-representation of pollen percentages. Finally, the presence of carbonised remains allows the existence of wildfires to be noted.

The fossil record available in Iberia is not always either homogeneous or abundant; therefore the models developed for those regions where palaeoecological information is scarce must necessarily have a hypothetical and temporal nature. In these instances, the geobotanical analysis of existing natural masses, historical records and genetic studies can provide complementary data that can be used to validate the different hypotheses concerning the long-term composition and dynamics of pinewoods.

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This work summarises the Holocene dynamics of pinewoods in the main Iberian mountain ranges based on palaeoecological data and the current composition of the natural masses. Dates are reported as non-calibrated radiocarbon years before present.

2. Geographical setting

The Iberian Peninsula is one of the most mountainous regions in Europe, with a relatively high mean altitude of around 650 m. The Central Plateau is the main geographical unit around which the Peninsula's relief is based. Mountain ranges occupy almost half of the territory: the Pyrenees (in the extreme NE) and the Betic cordillera (SE), both of which are located outside of the Central Plateau, are the highest cordilleras. The Central Plateau itself is surrounded by the Cantabrian cordillera to the North and the Iberian Mountains to the East. The Central range divides the Plateau latitudinally into two smaller units (Fig. 1).

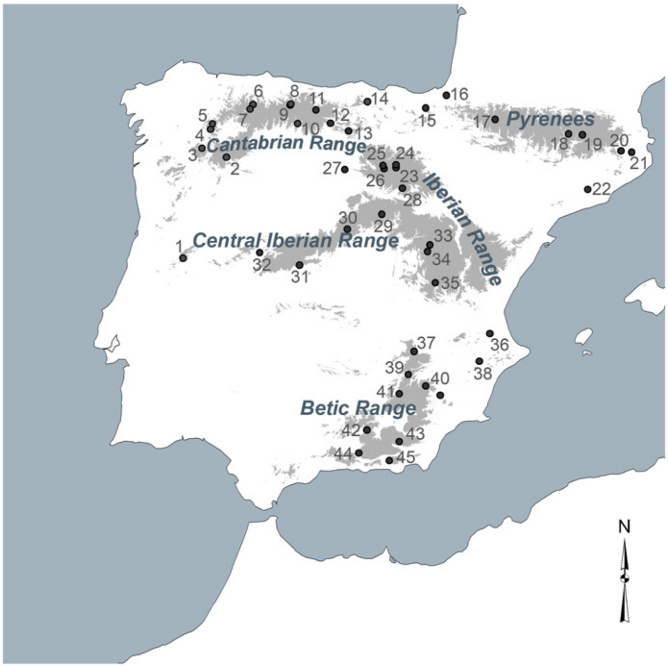

Fig. 1. Map showing the Quaternary cores in the Iberian Peninsula referred to in the text. 1) Charco do Candieira (van der Knaap and van Leeuwen, 1997). 2) Sanabria area (Allen et al., 1996, Muñoz Sobrino et al., 2004). 3) Las Lamas (Maldonado, 1994). 4) Lagoa de Lucenza (Muñoz Sobrino et al., 1997, Santos et al., 2000). 5) Pozo do Carballal (Muñoz Sobrino et al., 1997). 6) Vega de Viejos (Rubiales et al., 2008). 7) Lago de Ajo (McKeever, 1984). 8) Lillo (García Antón et al., 1997, Muñoz Sobrino et al., 2001). 9) Porma (Sánchez Hernando et al., 1999). 10) Cevico Navero (Roig et al., 1997). 11) Puertos de Riofrío (Menéndez Amor and Florschütz, 1963). 12) Lomilla (Alcalde et al., 2000). 13) Turbera de la Piedra (Muñoz Sobrino et al., 1996). 14) Los Tornos (Peñalba, 1994, Muñoz Sobrino et al., 2005). 15) Belate (Peñalba, 1994). 16) Atxuri (Peñalba, 1994). 17) Portalet (González-Sampériz et al., 2005), Tramacastilla (Montserrat Martí, 1992). 18) L'Estany del Burg (Pèlachs et al., 2007). 19) Bosc del Estanyons (Miras et al., 2007). 20) Olot (Burjachs and Allué, 2002). 21) Banyoles Lake (Pérez-Obiol and Julià, 1994). 22) Abric Romaní (Burjachs and Julià, 1994). 23) Hoyos de Iregua (Gil García et al., 2002). 24) Laguna del Hornillo (Gómez Lobo, 1993). 25) Laguna Larga (Ruiz Zapata et al., 2002). 26) Quintanar de la Sierra (Peñalba, 1994, Peñalba et al., 1997). 27) Espinosa del Cerrato (Franco et al., 2001). 28) Quintana Redonda (García Antón et al., 1995). 29) Pelagallinas (Franco et al., 2001). 30) Rascafría (Franco et al., 1998). 31) Gredos (several diagrams, compiled in Franco, 2009); Lanzahíta (López Sáez et al., in press). 32) Garganta del Trampal (Atienza et al., 1990). 33) Taravilla Lake (Moreno et al., 2008). 34) Ojos del Tremedal (Menéndez Amor and Esteras Martín, 1965, Stevenson 2000). 35) Laguna de la Cruz (Burjachs, 1996). 36) Navarrés (Carrión et al., 1999). 37) Villaverde (Carrión et al., 2001b). 38) Villena Lake (Yll et al., 2003). 39) Siles (Carrión, 2002). 40) El Sabinar (Carrión et al., 2004). 41) Cañada de la Cruz (Carrión et al., 2001a). 42) Carihuela Cave (Carrión et al., 1998, Fernández et al., 2007). 43) Baza (Carrión et al., 2007). 44) Padul (Pons and Reille, 1988). 45) Gádor (Carrión et al., 2003).

Most of the mountains in Iberia tend to be aligned mainly in an east–west direction, thereby forming transversal barriers to the expected migratory routes during the tree withdrawal/expansion periods characteristic of glacial and interglacial periods. However, the climatic conditions linked to mountain ranges in a peninsula commonly affected by periods of drought provide various ecological niches. The wide diversity of environments arising from the varying orography, orientation and lithology means that this land mass is comparatively rich in terms of plant biodiversity compared with the rest of Europe and helps to explain the existence of refugia in various different peninsular enclaves (e.g. Leroy and Arpe, 2007; Carrión et al., 2008).

Why are we restricting ourselves to Iberian mountain ranges? First of all, the majority of Holocene information available comes from these geographical environments (Alcalde et al., 2006). A large number of the sequences studied (particularly in the north of the peninsula) come from peat bogs located at altitudes of more than 1000 m. Generally speaking, changes to mountain vegetation occurred subsequently to, and less intensely than, those in lowland areas, most probably due to the lower productivity of the mountains. The forest patches found therein are therefore better conserved and these areas have been managed from a forestry perspective. Secondly, the mountains have fascinated biogeographers for a long time as they form barriers, which have compartmentalised the Iberian Peninsula (right next to the Mediterranean Sea) for millions of years. At the same time mountains have provided environments, which have enabled the persistence and migration of taxa in both glacial and interglacial periods. In one way or another they have therefore played an extremely important role in the historical biogeography and genetic flows of tree species.

Six species of pine can currently be found in the Iberian Peninsula: *Pinus uncinata* Ramon ex DC, *P. sylvestris* L, *P. nigra* Arnold, *P. pinaster* Aiton, *P. pinea* L and *P. halepensis* Mill. Whereas the former three species are typical of both Euro-Siberian and Mediterranean montane ecosystems, the latter three can be found in a wide range of environments, not just mountains. The present work aims to explore the dynamics of this important genus in the major Iberian cordillera during the Quaternary period.

3. Palaeoecological data

3.1. The Cantabrian cordillera

The mountainous regions in the NW sector of the peninsula are some of the areas with the best-understood Holocene plant history due, above all, to the large number of peat bog and lake cores studied. The chronological controls are normally accurate and of good temporal resolution (e.g. Ramil-Rego et al., 1998; Muñoz Sobrino et al., 2007). However, pre-Würmian palaeobotanical data for these regions are scarce. In this region, as in other regions of the peninsula, Pleistocene data are only available from deep-sea cores (e.g. Roucoux et al., 2005), which show a significant role for the genus *Pinus* in both glacial and interglacial periods in the Duero basin. Although these records contribute to improving our understanding of Quaternary climate change, they do not provide sufficiently accurate information to be able to interpret mountain landscapes at a regional level.

3.1.1. A well-documented general model of plant dynamics

During the Lateglacial and early Holocene (roughly 14,000–8000 BP), the genus *Pinus* is chiefly responsible for tree recovery in the cordillera as a whole, as well as in other mountain ranges in the NE peninsula and the northern sub-plateau. The fossil macroremains found suggest that *P. sylvestris* was the dominant species in woodlands with different structures, along with xerophytic taxa (*Ephedra*, *Artemisia*, Chenopodiaceae, and Poaceae) and other forest species

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such as *Betula* and *Juniperus* or even both evergreen and deciduous *Quercus* (e.g. Franco et al., 2001; Muñoz Sobrino et al., 2007).

The westernmost regions of the Cantabrian cordillera were the first to be affected by the warm climate of the early Holocene, giving way to other deciduous tree taxa, chiefly *Betula* and *Quercus* (Maldonado, 1994; Allen et al., 1996; Muñoz Sobrino et al., 1997). Thus, the coniferous formations present in the Lateglacial slowly became restricted to southern and eastern parts of the cordillera during the Holocene.

Pinus sylvestris (and, to a lesser extent, *P. nigra* and possibly *P. uncinata*) remained present during the Holocene on southern interior slopes, which are more continental, drier and better lit and therefore less likely to become populated by broadleaved trees. The regional persistence of this species could also be linked to certain adaptive advantages such as its longevity and its stability on histosols and other acidic soils, with surface raw humus, which could favour their resistance against other broadleaved species. The persistence of these populations until the late Holocene can clearly be seen in the cores from Cevico Navero (Roig et al., 1997), Lillo (García Antón et al., 1997; Muñoz Sobrino et al., 2005), Porma, Curueño and Esla (Sánchez Hernando et al., 1999; Rubiales et al., 2007) or Vega de Viejos (Rubiales et al., 2008).

3.1.2. Retreat of the pinewoods during the Holocene

The decline over the last few millennia, and the almost total disappearance of pine trees from the Cantabrian cordillera over the past 3000 years, have been linked to anthropogenic changes, as well as to the existence, over large areas, of a climate not particularly suitable for their persistence in the face of advancing broadleaved species (Rubiales et al., 2008). Both these factors can obviously occur simultaneously in wide areas. There is a clear relationship between historical data and the decrease in tree cover in certain regions. The significant Roman occupation that began in the first century BC (ca. 2000 years BP), the historic changes that occurred throughout the mediaeval period and the implementation of the Mesta (Honrado Concejo de la Mesta in Spanish) in the 13th century AD all appear to have resulted in a significant destruction of woodlands. The use of fire as a tool for clearing large areas of vegetation was probably a determinant factor in the wholesale decline of Cantabrian montane pinewoods on the southern slopes of the cordillera (García Antón et al. 1997; Ezquerra and Gil, 2004). However, some stands containing *Pinus sylvestris* specimens more than 450 years old, which are among the longest-lived examples of this species in the Iberian Peninsula (Génova, 1998), can still be found.

3.2. Central Iberian Cordillera

The amount of data available for the Central cordillera as a whole is quite significant, although these data cover a more limited time span towards the centre of the peninsula (Martínez García and Costa, 2001; Martínez García, 2002). The oldest montane deposits in the entire Central cordillera go back as far as the Lateglacial (ca. 13 ka BP) but are only found in the Portuguese ranges of the Sierra de Estrela (van der Knaap and van Leeuwen, 1997), the most western lying mountain range in the cordillera. According to the records, *Pinus* is the most represented tree genus in the Estrela countryside, thus indicating the presence of pinewoods (most likely microtherms, in structures which could be either open or dense copses) at medium to low altitudes in the Sierra. However, the pollen deposits soon show an abrupt change at the start of the Holocene (ca. 10350 BP) in which *Pinus* makes way for other deciduous taxa with a mesophilous or even Mediterranean character, such as *Quercus*, or a hygrophilous-microthermic character, such as *Betula*, *Sorbus aucuparia* or *Frangula alnus*.

In the more interior ranges (Sierra de Béjar), the temporal records of Garganta del Trampal and Dehesa de Candelario, although much shorter than in Estrela (Atienza et al., 1990; Atienza et al., 1991), show a broadly similar pattern during the second half of the Holocene in which pinewoods do not appear to prosper, probably due to the climatic oceanity. Both the pollen sequences (Atienza et al., 1990; Atienza et al., 1991) and the limited number of macroremains found (unpublished results) suggest that *Betula* was the dominant and stable genus.

3.2.1. Centre of the cordillera

The Sierra de Gredos, which is located slightly further west, shows significantly greater complexity than the other ranges in the Central Range. This mountain range is the widest (ca. 50 km) and highest (2592 m) in the Central Range. The elevation difference can be as much as 2000 m on the southern slopes and there are significant climatic differences between the two sides of the cordillera. The pollen and macrofossil cores are mainly found in higher regions and on the northern slopes. The 6000 years covered by these cores show the predominance and stability of cryophilous pinewoods (*Pinus sylvestris*) (Rubiales et al., 2007; Franco, 2009). In the past two millennia, these pinewoods went into decline, probably due to an increase in the frequency and intensity of man-made or spontaneous fires, which has intensified in the past millennium. In the ecotone regions, other more resistant communities (leguminous shrub lands in higher regions and *Quercus pyrenaica* lower down) have taken over from the pinewoods. These results shed light on an important biogeographical debate as they reveal the nature, which was in doubt until recently, of the *P. sylvestris* and *Pinus nigra* pinewoods found there (i.e. La Rubía, el Arenal, Hoyocasero or Hoyos del Espino), which are the most western lying in continental Europe. Long-lived specimens of both species of around 300 years of age can still be found in the highest regions (ca. 1600–1700 m; Génova et al., 1993).

The pollen sites on the southern slopes of Gredos are less abundant and show no accurate chronological control. Indeed, some cores suggest a dominant or co-dominant role for Mediterranean pinewoods in this region (i.e. Lanzaíta, López Sáez et al., in press). Large woods of *Pinus pinaster* and, to a lesser extent, *Pinus pinea* are found in dispersed stands and small- to medium-sized woodlands, which have been interpreted as being naturally occurring by some authors (Costa et al., 1997).

3.2.2. Eastern sectors

As regards the Sierras de Guadarrama and Ayllón (eastern Central Range, Fig. 2), which are much more interior, the behaviour of their vegetation during the Holocene follows a pattern similar to that of the more continental regions of Gredos (inter-mountain watersheds and northern ranges), as also found in the interior regions of the Iberian Mountain Range. The mountain pinewoods also dominate, according to the oldest pollen records of both ranges. Indeed, their dominance in the Sierra de Guadarrama has continued to the present day (Franco et al., 1998), leading to magnificent pinewoods of *Pinus sylvestris* whose oldest specimens exceed 500 years (probably the most aged of this species in Spain, Génova, 2000); there are also localised remnant groups of *Pinus nigra*.

This dominance of cryophilous pinewoods in mid-mountain regions at the end of the Holocene is also evident in the Sierra de Ayllón (easternmost mountains, Fig. 2). However, this range is characterised by some unique floristic attributes (different from those in the previously mentioned ranges) that begin to appear together linked to the higher humidity of the range. For example, as the pinewoods become less important than in Guadarrama, *Betula*, *Fagus*, and especially Ericaceae take on greater importance in the landscape (Franco et al., 2001). This is probably due to several factors, including the climate (again more humid than in the western part of the range), history of human land use, and the changes in the frequency and intensity of fires (Pardo and Gil, 2005).

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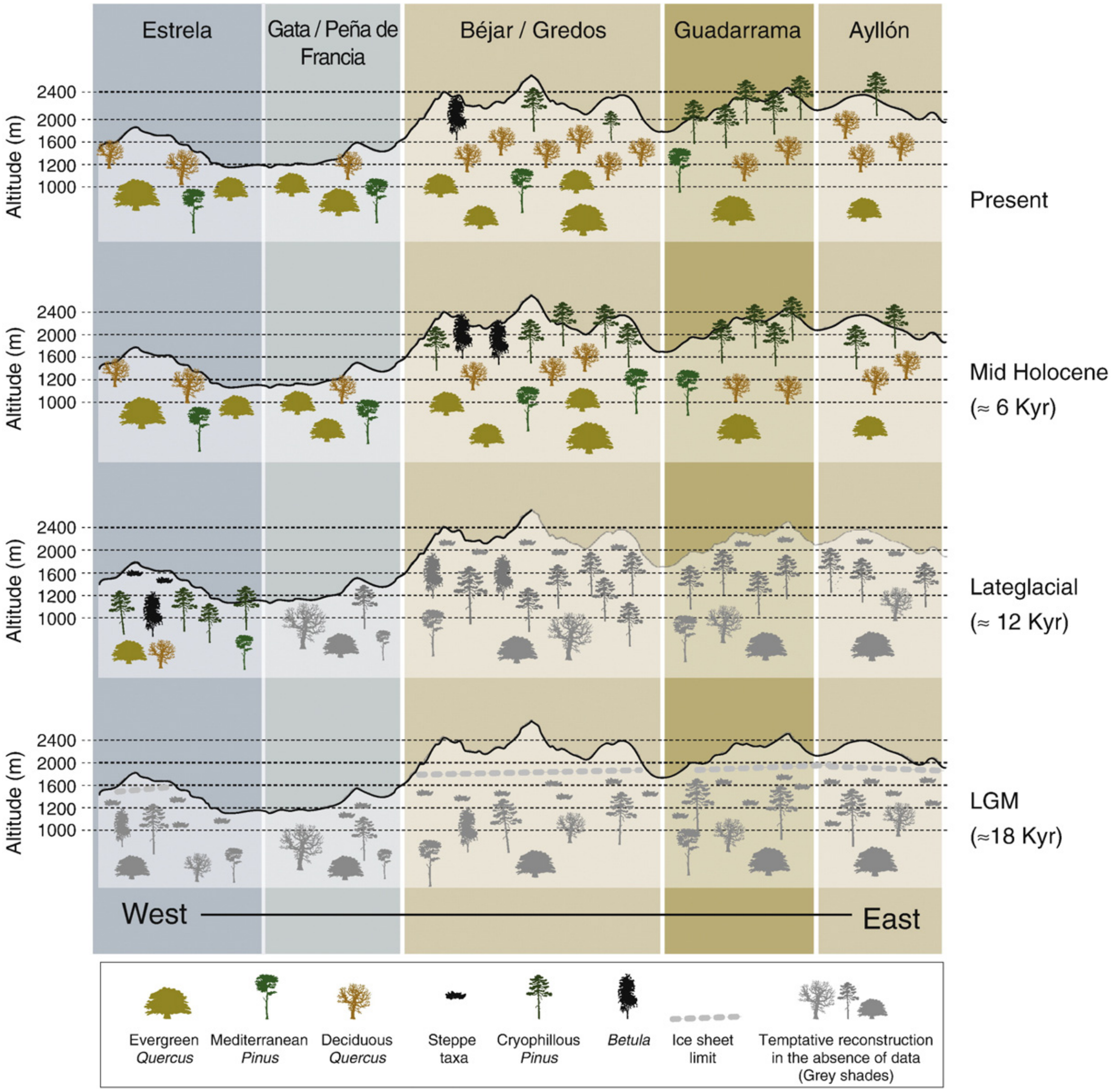

Fig. 2. Proposed evolution of pinewoods and other woody formations since the LGM in the different ranges of the Central Cordillera. Data are taken from Atienza et al., 1990, 1991; Franco, 2009; Franco et al. 1998, 2001; Rubiales et al., 2007; van der Knaap and van Leeuwen, 1997.

3.3. The Pyrenees

The Pyrenees cordillera is a complex mountain system that covers a very wide area and altitude (it extends for around 400 km west to east and is around 100 km from north to south at its widest part). Its complex geological system, with rocks of a very diverse nature and age, has generated a very varied relief composed of parallel mountain chains, internal depressions, north-to-south oriented river valleys, valleys shaped by glaciers, gorges, cliffs, outcrops and moraines. The overall west-to-east orientation also affects the climate, with notable differences between both slopes and the ends, one of which influenced by the Atlantic and the other by the Mediterranean, and the interior. As regards the level of palaeobotanical knowledge, there is a lack of studies in the Iberian slopes of the Pyrenees to comprehensively depict their vegetation history.

3.3.1. Pinewoods in the periods prior to the Last Glacial Maximum (LGM)

As is the case for other cordillera, the pre-LGM montane records are scarce and are limited essentially to the central-western region: the Valle de Tena and nearby areas (e.g. Linás de Broto, Montserrat Martí, 1992; González-Sampériz et al., 2005). The scenario resulting from these records is a landscape consisting of wide-open spaces and woods. The sustained dominance of *Pinus* in this landscape, along with *Juniperus* and occasionally *Ephedra*, is clear. The herbaceous species are dominated by Poaceae, along with smaller numbers of *Artemisia*, Chenopodiaceae and Asteraceae. There are no records at altitude in the east, therefore it is necessary to sample lower regions to find deposits of this age (Burjachs and Julià, 1994; Pérez-Obiol and Julià, 1994; Leroy, 1997, 2008). The information obtained highlights the importance of pinewoods in the vegetation of these foothill regions. Thus, *Pinus* is the predominant tree species from 75,000 BP until the height of the Glacial period, together with *Juniperus*, Poaceae and *Artemisia*. This closely resembles the situation found for the central-western montane region in terms of both floristic composition and the ratio between woods and unforested areas.

3.3.2. Variations during the Lateglacial

The climatic recovery subsequent to the LGM results in an overall increase in the amount of tree pollen. The information from this time period remains fragmented and limited to certain regions but clearly highlights some significant trends. For example, in the Valle de Tena, the dominance in the expansion of woods is shared by *Pinus*

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and *Betula* but with some differences: at mid-altitudes–Tramacastilla (1682 m), Paúl de Bubal (1150 m) (Montserrat Martí, 1992; González-Sampériz et al., 2005)–birch predominates in the initial stages, giving way later to *Pinus*. However, *Pinus* dominates at higher altitudes in the same valley (El Portalet, 1800 m; Ibón de las Ranas, 2092 m) from the base of the diagram, with *Betula* always being present in lower numbers. The Lateglacial recovery began relatively early in the eastern Pyrenees (Burjachs and Allue, 2003; Miras et al., 2007; Pèlachs et al., 2007), and on the southern slopes before the northern slopes, although in all cases it involved an increase in *Pinus* and *Betula*.

3.3.3. Trends in the Holocene

The pollen curves obtained from studies of cores from the Holocene located closest to the westernmost Pyrenees (Peñalba, 1994) show low values for *Pinus*, which clearly diminish until their disappearance. The presence of *Pinus* can again be detected in the final part of the sequence, probably due to the planting which has taken place over the past few decades. In contrast, the deciduous *Quercus* and *Corylus* sequences have very high values, and *Alnus* can also be found in significant quantities in Atxuri. Finally, the strong arrival of *Fagus*, which coincides with significant drops in deciduous *Quercus* and *Corylus*, can be seen in the second half of the Holocene. The overall drop in tree taxa, together with a significant increase in Poaceae and *Calluna*, observed in the more recent ages indicates increased anthropogenic activity. These data therefore indicate that in those regions where the climate is determined by frequent fogs and masses of moist air from the Atlantic (i.e. the westernmost Pyrenees), the montane pinewoods decreased. That was due to milder climatic conditions, which allowed the strong growth of deciduous broadleaved forests.

The limited Holocene data available for the southern slopes of the central-western Pyrenees (Montserrat Martí, 1992; González-Sampériz et al., 2005) suggest that the variations in plant coverage occurred in a different manner. The main difference is that the pinewoods did not disappear, although different trends are found at different altitudes. At higher altitudes (El Portalet, Ibón de las Ranas), for example, the scenario described above for the Lateglacial, where *Pinus* is the most representative tree taxon, is maintained. Other taxa, such as *Betula*, *Corylus* or *Quercus*, can be found throughout the sequence but in lower numbers. At lower altitudes, however, a transition can be seen, with a drop in the proportion of *Pinus* associated with an increase in the importance of broadleaved species such as *Quercus*, *Corylus*, *Ulmus* or *Fraxinus*. This variation appears to occur first at lower altitudes in this region (Paúl de Bubal), and some time later at intermediate levels such as Tramacastilla. This latter record shows a recovery of *Pinus* at around 1400 BP which occurs earlier than the general increase found, in all diagrams for this region, for those pollens indicative of anthropogenic activity (Gramineae, *Olea*/*Phillyrea* and *Plantago*). Finally, it should be noted that *Abies* and *Fagus* appear in the records in the final third of the Holocene and that these species remain present until the end of the diagrams, although always at low but variable levels.

The eastern Pyrenees also show an altitude-related pattern in the Holocene, with an early reduction in the proportion of *Pinus* and a significant increase in *Quercus* and, to a lesser extent, *Corylus* and *Abies* being found at lower altitudes (Burjachs and Allue, 2003). In contrast, the pollen diagrams for higher altitudes–Estany del Burg (1821 m) and Bosc dels Estanyons (2810 m) (Miras et al., 2007; Pèlachs et al., 2007)–are clearly different, with *Pinus* being the taxon with the highest tree pollen levels, with continuous sequences, although varying levels, throughout both diagrams. An important finding in this survey is the presence of stomas, which the authors of this pollen diagram identify as belonging to *Pinus*, thereby demonstrating the presence of this species *in situ*. There is no transition to a predominance of other taxa, although both *Quercus* and *Betula* are continually present in low numbers.

3.3.4. The Pyrenees, a diversity of habitats

The significant geological, geomorphological and climatic diversities of the Pyrenees and surrounding areas generate numerous combinations of ecological and microclimatic factors. This diversity of biotopes and habitats is not a recent phenomenon but has been constant during the Last Glacial period, the Lateglacial and the Holocene in the Pyrenees and the Ebro basin (González-Sampériz et al., 2005). This has allowed the development and survival of a wide range of plant communities from such ancient times, including those constituted, to a greater or lesser extent, by *Pinus*, as shown by the pollen diagrams. The continuity of these diverse habitats over time allows us to suppose that different species of this genus, with different ecological needs, have been able to rely on favourable survival sites throughout these periods. The main species present in the pollen diagrams from the Pyrenees include *Pinus uncinata* (which today is only found at higher altitudes, and some examples of which are more than 700 years old; Creus, 1991), *Pinus sylvestris* (currently abundant at mid-altitudes), *Pinus nigra* (also currently found at mid-altitudes but less abundant) and *Pinus halepensis* (commonly found on the warmer southern and eastern slopes of the Pyrenean foothills).

3.4. Iberian Mountains

The Iberian Mountains, with medium altitudes, stretch for more than 500 km in a NW-SE direction and connect the eastern Cantabrian ridges with the Central and Betic ranges. Their palaeoecological record is, however, very heterogeneous. Thus, whereas the pollen record of the northern region has been widely studied allowing the Late Quaternary forest dynamics to be understood in some details, although only a few of these studies cover the Lateglacial (i.e. Gómez Lobo, 1993; Peñalba, 1994; Gil García et al., 2002; Ruiz Zapata et al., 2002), the Holocene information for the southern region is partial and discontinuous.

3.4.1. Main variations in the northern Iberian Mountains

The high-altitude cores (between 1500 and 1800 masl) from the northern Iberian Mountains indicate a Lateglacial landscape dominated by pines and steppe taxa (*Artemisia*, Poaceae, Chenopodiaceae) in which *Betula* is important in the warmer periods of the Bølling–Allerød. These pinewoods went on to colonise the steppe spaces of the last Würmian maximum, as reflected by the pollen diagram for Hornillo (Picos de Urbión, 1820 m) (Gómez Lobo, 1993). The predominance of pinewoods during the Holocene is clear for the whole northern Iberian Mountains, together with birches (*Betula*) and a greater presence of deciduous *Quercus*, *Acer*, *Tilia* and *Corylus*, the latter of which are characteristic taxa of the temperate Euro-Siberian element. The increase in the numbers of marcescent/evergreen *Quercus* more often found in more Mediterranean climates in Quintanar de la Sierra (1470 masl) appears to be a result of higher summer temperatures midway through the Holocene (Peñalba et al., 1997).

The importance of pinewoods in northern Iberian lessens from the mid-Holocene onwards (Fig. 3). This decrease follows no clear geographical pattern but always coincides with the appearance of indicators of human activity (e.g. an increase in Cerealia, *Vitis*, and *Olea*). On the northern slope, which corresponds to the Ebro valley, this occurs around 5000 BP (Gil García et al., 2002), whereas on the Duero slope it occurs after 3000 BP (Peñalba, 1994; García Antón et al., 1995; Franco et al., 2005). From that point onwards the pinewoods undergo a series of advances and retreats, without losing their dominance of the landscape completely. The latest advance occurred in more recent times due to the replanting undertaken last century.

3.4.2. Central-southern sectors

A similar dynamic to that in the northern Iberian Mountains is found in the central region of the Iberian Mountains at an altitude of 1650 masl in Ojos de Tremedal (Menéndez Amor and Esteras Marín,

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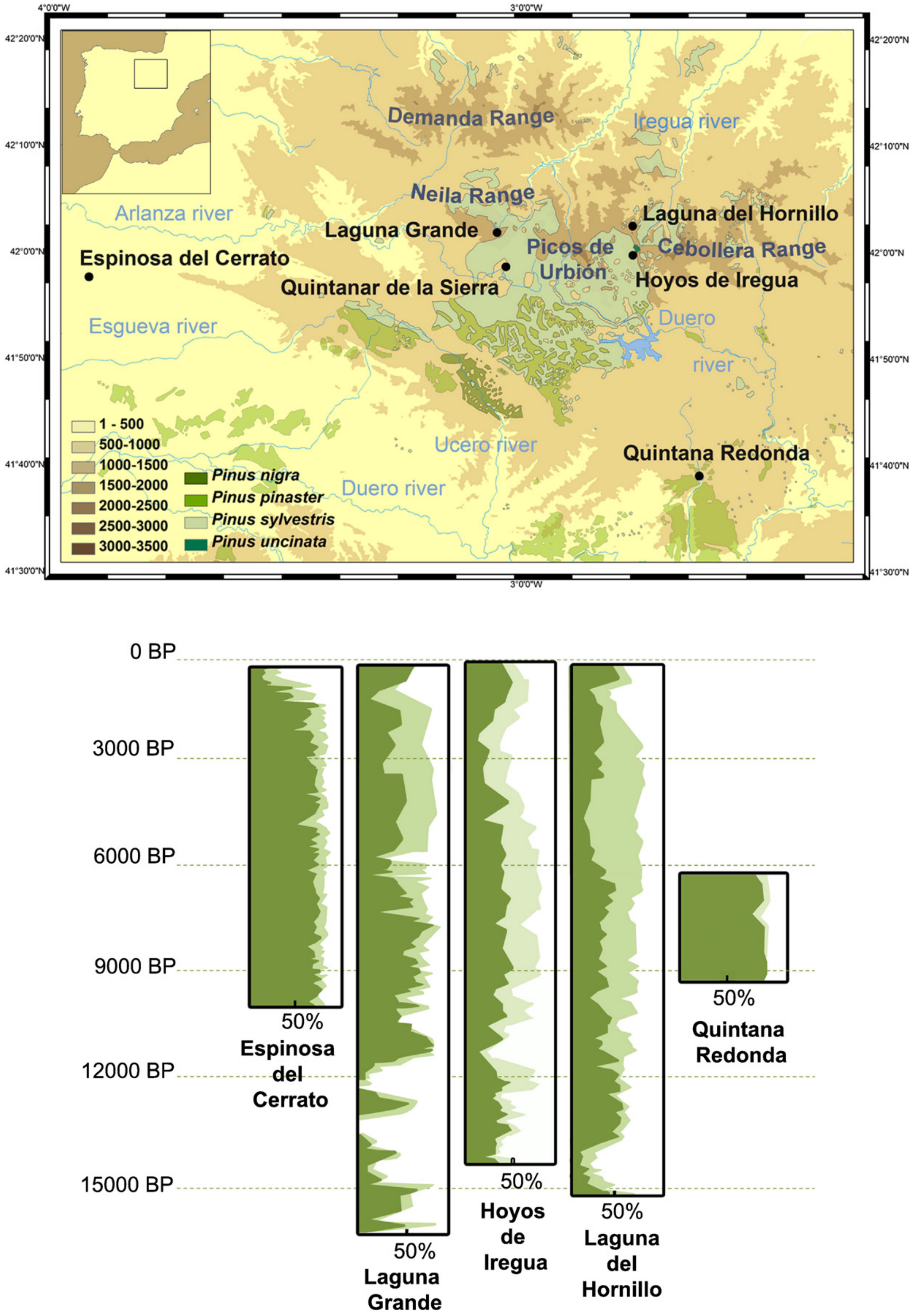

Fig. 3. Map showing the current distribution of pinewoods in the Northern Iberian Mountains and pollen diagrams for the indicated records (a light green colour represents the total tree pollen and dark green the proportion of *Pinus*). Pollen data are taken from the pollen records of Espinosa de Cerrato (Franco et al., 2005), Laguna Grande (Ruiz Zapata et al., 2002), Hoyos de Iregua (Gil García et al., 2002), Laguna del Hornillo (Gómez Lobo, 1993) and Quintana Redonda (García Antón et al., 1995).

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1965; Stevenson, 2000). Here, *Pinus* has dominated continually since at least 7000 BP (Stevenson, 2000), in combination with *Corylus* and *Betula*. The low percentage of pollen from deciduous *Quercus*, which was attributed by the author to marcescent *Quercus pyrenaica*, should be highlighted.

Other cores taken from lower altitudes in the southern Iberian Mountains also show the continually high presence of pinewoods throughout the Late Quaternary (Menéndez Amor and Florschütz, 1961; López García, 1978, 1983; Dupré Ollivier, 1985; Carrión and Dupré, 1996), with the peculiarity that *Quercus* has greater relevance in these cores. The record of a core taken at Navarrés (900 masl), which is located between the Iberian Mountains and the Betic cordillera, shows an increase in evergreen and, to a lesser extent, deciduous *Quercus*, and a decrease in *Pinus*, at around 5000 BP. A similar situation has been observed at various archaeological sites in this region, where there is a balance between the percentages of tree and non-tree pollen, with *Quercus* appearing in somewhat greater amounts than in Navarrés from the outset (2000 BP; Burjachs, 1996; Valero Garcés et al., 2008). At other sites such as Verdelpino (Cuenca), the increase in *Quercus* that occurs concomitantly with the decrease in *Pinus* is found more recently and parallels the disappearance of *Corylus*. The presence of charcoal and the increase in Mediterranean shrubs linked to the extension of *Quercus* at all these sites would appear to indicate that anthropogenic factors, especially the use of fire, played an important role in this replacement process (Burjachs, 1996; Carrión and van Geel, 1999; Valero Garcés et al., 2008).

3.4.3. Main Pinus woodland species

As regards the specific determination of the main pine species found in Iberian landscapes, the determination of two groups of pines which have been present since 30,000 BP is of great interest: the group *Pinus sylvestris*/*Pinus nigra* and *Pinus pinaster* (Carrión and van Geel, 1999; García Antón et al., 1995). This latter species, which is more commonly found in more Mediterranean regions, must have played an important role in lower altitude woodlands, especially in the southern Iberian Mountains. The natural stands of *P. pinaster* on Buntsandstein and other poorly developed non-carbonate soils (Gil et al., 1990) present in this region, and the enormous genetic variety of this species (González-Martínez et al., 2002), support this hypothesis.

Two pine species currently predominate in the montane regions of the Iberian Mountains: *Pinus sylvestris*, whose greater water needs mean that it is found on peaks and at north-facing high altitudes, and *Pinus nigra*, which forms one of the most widespread Iberian masses in the central and southern Iberian Mountains, with specimens which in some cases can reach 650 years of age (Génova and Fernández, 1998). This predominance is only shared or replaced in certain circumstances by various species of *Quercus* (*Q. faginea*, *Q. pyrenaica*, and *Q. petraea*) or by the above-mentioned *Pinus pinaster*. As in the northern Iberian Mountains, *Pinus uncinata* is present as a relict population in the higher altitude regions of the southern Iberian Mountains (Costa et al., 1997), which suggests that this species was important in these mountains during the Glacial periods, forming more or less open woodlands during this period.

3.5. The Betic Cordillera

The Betic range forms one of the largest orographic complexes in the Iberian Peninsula. With respect to the other peninsular ranges, the degree of palaeobotanical understanding of the Betic Cordillera can be considered to be intermediate. More than 20 cores (mainly reported on Fig. 1), more or less regularly distributed throughout the whole territory and at altitudes of between sea level and around 1600 m, have been studied. Their chronologies are varied, with some dating back as far as the Upper Pleistocene, although the Holocene is without a doubt the best-known period.

3.5.1. Predominance of Pinus in the wooded landscapes close to the LGM

The information provided by cores with pre-LGM chronologies is valuable, although taphonomically and territorially somewhat limited, due to the low number of such cores and, in some cases, their resolution and discontinuities in the record. Two of the most important cores that cover the Würmian maximum can be found at the SW extreme of the Cordillera at Padul (Menéndez Amor and Florschütz, 1964; Pons and Reille, 1988) and the Carihuela cave (Carrión et al., 1998; Fernández et al., 2007). The cores at Navarrés and Villena, in the extreme NW of the region (at the junction with the Iberian Mountains), also cover chronologies prior to this maximum (Carrión and Dupré, 1996; Carrión and van Geel, 1999; Yll et al., 2003). The panorama offered by the plant cover is similar in all cases: landscapes dominated by herbaceous species (mainly Poaceae and *Artemisia*) alternate spatially and/or temporally with wooded landscapes in which *Pinus* is also the dominant taxon, together with *Juniperus* and evergreen or deciduous *Quercus*.

3.5.2. Two patterns until the Lateglacial

The period between the LGM and the start of the Holocene is of vital importance due to the important climatic and vegetational changes, which occurred during the Lateglacial in the Mediterranean region and in Europe as a whole. The pollen records discussed above, along with the important sequence from Siles (Carrión, 2002), with its key location at an altitude of 1320 masl in the centre of the range, provide more accurate information for this time period. Woodlands become the dominant landscapes during the Lateglacial and their evolution follows two different patterns. The first of these patterns shows that an initial Pleniglacial phase in which *Pinus* is the main species in wooded landscapes undergoes a clear compositional change, with *Quercus* becoming predominant. In general terms, this transition occurs during the Lateglacial, with the predominance of broadleaved species (particularly deciduous and evergreen *Quercus*) extending into the Holocene. This process mainly occurs in the range's western regions (Padul, Carihuela), which are more exposed to possible influences of Atlantic air masses (Valle de Genil), and are always associated with the milder climatic conditions of the Lateglacial interstadial. However, it should be noted that these cores are found at mid-altitudes (800–1000 masl) close to the Sierras de Arana and Sierra Nevada, which reach maximum heights of 1943 and 3481 masl, respectively. It is therefore possible that forest formations containing mainly *Pinus* could have been present at higher altitudes and that the upper limit of these woods could have risen as the climate improved. Other regions of the Betic Cordillera show a second pattern, namely a clear predominance of *Pinus* throughout the whole period (Navarrés, Villena, and Siles). Geographically speaking, this second pattern is found at very different altitudes (between 500 and 1350 masl), becoming very widespread in interior and north-eastern regions of the Betic range.

3.5.3. Variability, the Holocene's most notable trait

A significant number of cores from both the interior and south of the Betic range are available covering the past 10,000 years (Carrión, 2001; Carrión et al., 2001a, 2001b; Carrión et al., 2003; Carrión et al., 2004; Fuentes et al., 2005). It is difficult to establish a general model for this period as the information available shows different behaviours for *Pinus* in the plant cover (Fig. 4). Three main patterns can, however, be proposed: i) maintenance of the moderate presence already shown during previous ages (Lateglacial) in the western mid-altitudes, the landscape is still dominated by *Quercus* throughout the Holocene; ii) continuous predominance of *Pinus* in woodland composition over the whole period or those parts recorded in the different cores; and iii) dominance of pines in the first part of this period with subsequent transition (occurring around 6000/5000 BP) to *Quercus* predominance.

In short, the various scenarios described for previous ages are generally found to extend into the first part of the Holocene. However,

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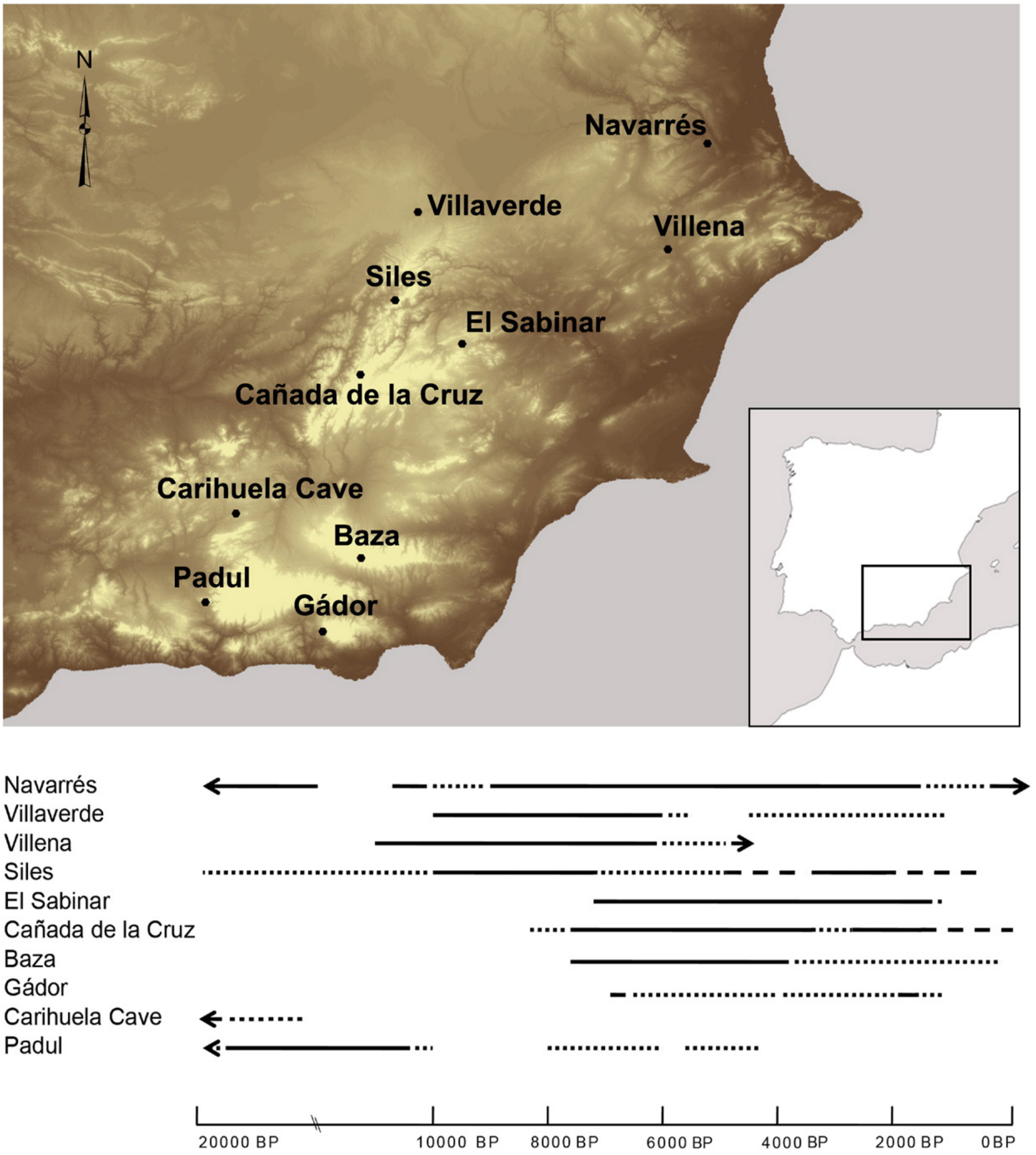

Fig. 4. Representation of the *Pinus* records from major cores in the Betic Cordillera. Pollen data taken from Pons and Reille (1988), Carrión (2002) Carrión and van Geel (1999), Carrión et al. (1998, 2000b, 2003, 2004, 2007), Yll et al. (2003) and Fernández et al. (2007). Pollen ocurrences of *Pinus* are reported as follows: ____Continuous record >40% •••••• Continuous record between 10 and 40% ▪ ▪ ▪ Record with abrupt oscillations between 10 and 40% — — Continuous pollen record >10%.

from around 6000/5000 BP onwards, the landscape diversity increases in terms of both a greater number of patterns and greater internal variability. This can initially be strongly linked to increased anthropogenic activity (Carrión and Díez, 2004), although the greater density of records available as the Holocene progresses could allow us to detect a greater number of responses arising. Environmental differences on a local scale could better reflect the range of random events and factors associated with palaeoecological dynamics (Arroyo et al., 2004; Carrión et al., 2000a; Costa et al., 1997).

3.5.4. The infra-genus *Pinus* record

We now have sufficient data to paint a broad picture of the *Pinus* species that shaped the landscapes discussed in previous sections. First of all, the find of pollen types and/or macroremains corresponding to *P. pinaster*, *P. nigra* and *P. halepensis* (Badal et al., 1994; Badal and Roiron, 1995; Carrión et al., 2000b; Finlayson et al., 2008) at different times or geographical locations should be noted. This firstly confirms that the taxa found today lived spontaneously in the Betic range. Furthermore, their spatial integration most likely depended on the adjustment of their respective needs to the varied environmental spectra (the diversity and climatic variations, the complexity of the competition/incumbency relationships, the response to different types of perturbations, etc.). It should be finally highlighted that the oldest trees in the Iberian Peninsula have been found in the Betic range, specifically in *Pinus nigra* specimens in the Sierra de Cazorla, some of which have been found to be older than 1000 years (Creus, 1998).

It seems appropriate at this point to mention the relatively recent discovery of a stand of *Pinus sylvestris* on the western slopes of

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the Sierra de Banderillas (Cazorla Range, Betic Cordillera), which could be considered the link between the populations in the Iberian Mountains and those in the Trevenque in Sierra Nevada (Soriano, 1993; Alejano and Martínez, 2006). This would confirm the logical and expected spontaneous presence of *P. sylvestris* in the Sierra de Cazorla, which reduces the distance between the bulk of its area and its most southerly representatives, on a worldwide scale, in the Sierra Nevada.

4. The long-term dynamics of Iberian pinewoods

The interpretation of the behaviour of pinewoods in the montane regions of the Iberian Peninsula during the Late Würmian and Holocene can now be outlined in general terms. This, however, has required bringing together and analysing the significant amount of palaeobotanical data already reported while at the same time taking into account the biological and autoecological characteristics of the genus in question with respect to palaeodynamic processes. Below, we will attempt to highlight the most relevant traits of this relationship and then to structure the palaeophytogeographical behaviour of the Iberian montane pinewoods into broad patterns. Finally, we will discuss some examples from the Iberian Peninsula of the importance of palaeodynamic processes for understanding these fascinating forest formations.

4.1. Life history traits with ecological implications

The montane pines in the Iberian Peninsula are often found in habitats characterised by their medium or poor productivity, with the occasional existence of harsh conditions that limit tree growth. Generally speaking, pines (and other conifers) are considered to be more tolerant of abiotic stress than angiosperms. In contrast, in mesic environments, many broadleaved species are able to successfully compete with conifers. Nevertheless, this competition occurs in a scenario that is so heterogeneous on several fronts (such as the Iberian mountain ranges), that the normal dynamic plant-succession processes do not always end up favouring the broadleaved species (Morla, 1993). This uncertainty is supported by several groups of factors, such as differences in environmental requirements (edaphic, climatic, and topographical restrictions), biological interactions (competition, incumbency, and facilitation) or ecophysiological mechanisms (photosynthetic ability, anatomical characteristics of the wood, and water-use efficiency), all of which are implicated to some extent in the plant-succession patterns (Gil et al., 1990). In the following, we will consider the different ecological effects that can be linked to the evolution of vegetation in the medium and long terms.

The behaviour towards light has traditionally been considered one of the main factors affecting species-succession processes in Iberian woodlands. The shade tolerance has been used to explain the succession dynamics in theoretical models in forestry, geobotanical and phytosociological studies. This idea appeared very early on in the ecological literature (e.g. Thoreau, 1860) and was developed with examples from Spain by Ceballos and Ximénez de Embún (1938). The phytosociological school subsequently adopted and developed this principle from a floristic and syntaxonomic perspective. This school assumes a climax dominated mainly by shade-tolerant species (usually broadleaved) as the final stage, which would lead, at a regional level, to the disappearance of pines from all those regions whose climate is suitable for taxa from both groups. The map of natural potential vegetation by Rivas-Martínez (1987) is a classic summary of this viewpoint that also makes recommendations for restoration with tree species from which Mediterranean pines were often excluded from mountains as final vegetation. Sunlight is without a doubt a key element in adaptive history and is of vital importance in pinewood dynamics as well as in a large number of woodland habitats throughout the world (e.g. Gómez-Aparicio et al., 2006; Valladares and Niinemets, 2008). However, in the long term, neither ecological (e.g. Zavala et al., 2000, Zavala and Zea, 2004) nor palaeoecological evidence reflects this direct relationship between pines and open spaces. The coexistence of pines and broadleaved species has been detected in a number of scenarios throughout the Quaternary, often with no link to perturbation events that generate open spaces.

Regeneration stands out as a critical stage that affects woodland dynamics in Mediterranean ecosystems. The availability of water during this stage interacts with the shade tolerance more than ever and, depending on the trade-off between photosynthetic productivity, competition for water and plant–plant interactions, the succession process can easily change: pines can coexist with, dominate or retreat in the face of angiosperms. Over and above these considerations, however, we must also consider the advantage conferred by being the first species to become established, a phenomenon which could influence the overall results of a competition process (incumbency).

Pines are also well known for their colonisation ability. The dispersion of small winged seeds is a characteristic that optimises the sudden long-distance colonisation ability versus other competing taxa. This could be key to the recovery of spaces in the Lateglacial, where a large number and variety of empty ecological niches (free from vegetation) appeared after the post-LGM climatic change. In summary, both the persistence ability of pines in the landscape under dry and cold climates (those of the glacial periods), and their rapid dispersion ability linked to the onset of a milder climate, can explain their enormous success in Lateglacial Iberian landscapes.

Mediterranean environments are also characterised, among others, by a group of environmental factors that maintain the communities in a state of non-equilibrium that periodically recreates, to some degree, this moment of first occupation. The latter are commonly known as perturbation factors, and include fire, which plays a significant role. The majority of Iberian *Pinus* species can act as both pioneers (in initial succession communities) and by forming permanent and stable communities in areas where resources are especially limited for various reasons.

The evolutionary interaction between pines and fires is not simple. Many of our *Pinus* species have developed adaptations to fire (Table 1) and are therefore generally well suited to regions with recurring fires, such as the Mediterranean region. However, the six indigenous Iberian pines are obligate seeders and therefore periodic fires represent a serious disadvantage in comparison to resprouters and other resistant communities (see Pausas, 2001; Tapias et al., 2004). The steady increase in the frequency of fires at the end of the Holocene as a result of human activity could have had serious repercussions for the pine populations in some mountainous environments (Figueiral and Carcaillet, 2005; Rubiales et al., 2007) and, in the event of these pines being only marginally present, could have removed them from that region entirely.

Another factor which should be taken into account when considering the persistence of those pines that make up the timberline (*Pinus uncinata* and *Pinus sylvestris*) is their long life (García and Zamora, 2003). Longevity confers on them an advantage with respect to those broadleaved species that can survive under these high-altitude climatic conditions. Certain large-scale perturbations, such as fires, are less frequent and intense at these altitudes. Natural fires on higher mountain slopes are usually limited in scale due to the low growth rate, open structure and therefore low biomass production of their vegetation; this is particularly true in the Mediterranean region due to the lower water availability. However, the climatic conditions at these altitudes are usually quite harsh, which is likely to mean that the establishment of seedlings is highly variable. In this unfavourable scenario, long-lived species (and some of our high-altitude pines can be found towards the top of this scale, see Creus, 1991; Génova, 2000), have a significant advantage, which means that the threat of their being displaced by competition from shorter-lived taxa is low (Keeley and Zedler, 1998). This persistence model can help to explain the

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success of this group of pines in Iberia during the Lateglacial and their continuity during the Holocene.

Finally, the potential importance of other biotic factors over long time periods should be noted. Processes such as plant–animal interactions, herbivory, parasitism, pests and disease, or mycorrhizal associations are normally considered as being less important in long-term processes. However, these topics have received little treatment in the literature and their actual consequences are therefore largely still unknown.

4.2. Pinewood evolution trends in the Iberian Mountains

The palaeoecological data available for Iberian Mountains during the Quaternary are very heterogeneous and still incomplete for large areas (Fig. 5; Alcalde et al., 2006). The Cantabrian, Central and northern Iberian Range and parts of the Betic chain have been well-studied palaeoecologically for the Holocene, although studies corresponding to the Pleistocene remain relatively scarce. The data for other regions, such as the southern Iberian Range, southern Pyrenees and the rest of the Betics, are scarce for all periods. Generally speaking, however, the evolution trends for pinewoods have been partially determined and some patterns have been established for different regions and ages.

Thus, although the data set for the Glacial period (LGM and start of the Lateglacial) is small, particularly for mountain records, Iberian fossil remains show the huge importance of pines in all areas with wooded landscapes. From the onset of the Lateglacial, however, major changes to the vegetation in some western Mediterranean regions become evident; these changes become more significant during the Holocene. The responses were not always the same throughout the peninsula or immediate or globally synchronous. However, the data available allow us to classify the behaviour of Iberian mountain pinewoods (between the onset of the Lateglacial and the Late Holocene) territorially into a series of major types or patterns (Fig. 5):

(1) Widespread changes in the composition of woodlands where climate change appears to play a leading role, particularly with respect to an oceanity gradient. The influence of an ocean, as manifested by long mild winters during which the biotopes maintain their moisture conditions, could affect mountain pinewoods negatively (Crawford, 2005). This oceanity axis is evident in regions such as the western and northern Cantabrian cordillera, western parts of the Central and Betic cordilleras and the Pyrenees, although with some differences depending on their latitude: the climatic transition is noted first in the southern cordilleras (from the onset of, or even before, the Lateglacial) than in the rest (generally towards the end of the Lateglacial/Early Holocene).

(2) Stable pinewoods, with no major changes, throughout the Lateglacial and Holocene. The pinewoods persist in numerous regions to the present in the interior of the Central cordillera, in the Iberian Mountains, in the central Pyrenees and in some interior parts of the Betic cordillera. Their persistence is presumably related to their adaptation to the thermally different climatic conditions found in the interior of the peninsula, far from any influence of the oceanic effects noted above.

This situation of inertia with respect to the climatic changes which occur during these periods is likely to be related to the ability of pinewoods to “resist” these changes, either due to their autoecological characteristics (frugality, microthermy, and xericity), their phenotypic flexibility, their low likelihood of being displaced by potential competing species, their incumbency, which gives them a competitive advantage, or a synergy between some or all of these factors.

(3) Intraregional variability. Records that clearly show different plant cover behaviours within the same region can be found at various points throughout the peninsula. In the case of mountains, this can be seen, for example, in the northern Iberian, the interior and northern faces of the Betic cordillera and other peninsular ranges. These differences result from the importance of both the woodlands themselves and their composition When these different behaviours occur during the Lateglacial or Early Holocene, they can be attributed above all to (1) the existence of natural perturbations; (2) varying responses to environmentally complex scenarios (markedly Mediterranean) due to regional or local climates, varying topographies and substrates; and (3) stochastic (contingent) phenomena.

In contrast, the huge impact of anthropogenic activity should be taken into account from the mid-Holocene onwards. These can be added to the three causes described in the previous paragraph, although it is more likely that their influence on the origin of the variability increased progressively throughout the Holocene.

(4) Finally, we come to a group of territories for which data are still very scarce, which means that they cannot as yet be reliably incorporated into any of the above models. This is the case for various regions in the southern Pyrenees and some southern areas of the Iberian Range.

4.2.1. Dominant species

Three pine species appear at high altitudes in the south-west Mediterranean, forming part of the tree line. *Pinus uncinata*, which is almost restricted to the Pyrenees, grows under extreme climatic conditions (cold winters followed by a short but relatively hot growing season) on poorly developed or rocky soils. At lower latitudes (e.g. Central System and the northern Iberian Mountains), this role of high-altitude pine is currently taken by *Pinus sylvestris* and also, in the higher woodland regions of the Betic System (such as Sierra Nevada and Sierra de Cazorla), by *Pinus nigra* (Costa et al., 1997; Quézel and Médail, 2003).

Pinus sylvestris has been found to be the main species detected in the pollen curves for *Pinus* sequences. Indeed, the good tolerance of this species to drought and cold environments makes it the best candidate for mountainous regions (together with *Pinus uncinata* in the Pyrenees), which agrees well with the data obtained from macro- and megafossil records. The majority of macrofossils found for the Late Pleistocene and Holocene chronologies in Iberian mountain ranges correspond to this taxon, with *Pinus nigra* being the second most common. However, in general terms, all six species of spontaneous pines should be considered when decoding these records, particularly for the Holocene. Indeed, the majority of these species coexist today in systems such as the Pyrenees and the Betic Cordillera, with the more thermophilous species (*Pinus pinaster*, *Pinus halepensis* and *Pinus pinea*) being found in mid- to low-altitude valleys, although the former two can sometimes ascend the sunnier slopes to much higher altitudes (Costa et al., 1997). It therefore seems highly likely that all Iberian pine species could have persisted naturally in montane regions of the peninsula or on basal slopes throughout the Late Quaternary. Indeed, the genetic data available also support this hypothesis (Salvador et al., 2000; González-Martínez et al., 2002; Tapias et al., 2004; Cheddadi et al., 2006; Vendramin et al., 2008; Dzialuk et al., 2009).

4.3. Interpreting current Iberian pinewood landscapes on the basis of long-term records

Some classic examples of the interpretation of pinewood landscapes within the mosaic of Iberian plant cover can be considered coherent, particularly in the context of a palaeodynamic perspective, in light of the different factors considered above. Below, we will

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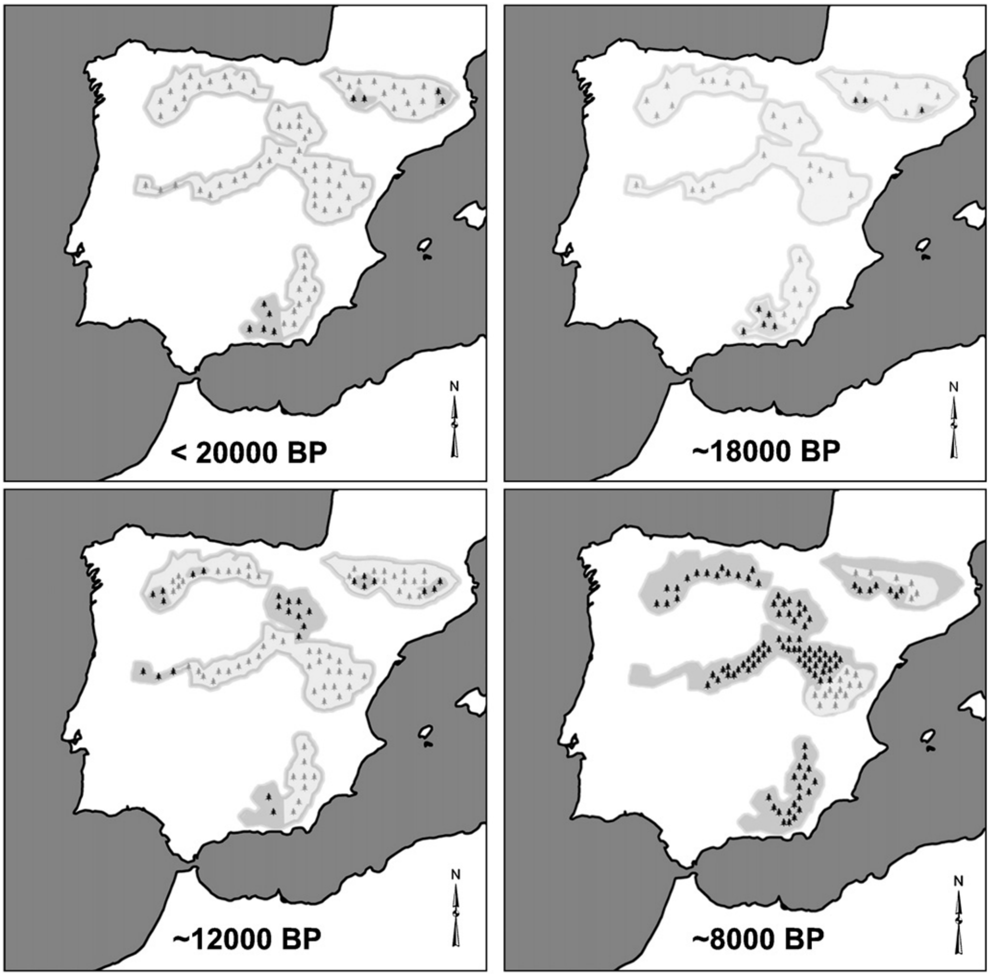

Fig. 5. Reconstruction of the proposed variations in the importance of pinewoods between chronologies prior to the Würmian maximum and the Holocene. The figures show both situations derived from palaeobotanical data and probable hypotheses in regions lacking in these trees. ▲*Pinus* presence supported by palaeobotanical evidence.; △ Hipothetic *Pinus* occurrence;▒ Areas with palaeobotanical data available; ☐Areas without palaeobotanical data available.

attempt to show the relationship or connection between what we know about the past and what we see now, in other words, to link the palaeobotanical results to their geobotanical interpretation.

4.3.1. Pinewoods in the upper Tajo basin: priority, stability and resistance

The Iberian Mountains are one of the regions in which the pollen diagrams most clearly show the persistence of pinewood landscapes in the Lateglacial and Holocene. This situation has remained unchanged, in most places, until today. Chalky soils predominate in the upper Tajo basin and other tree species form part of the plant mosaic (*Quercus ilex* subsp. *ballota* and *Q. faginea* subsp. *faginea*). However, the hegemony of *Pinus nigra* pinewoods between 900 and 1200 m is clear (*Pinus sylvestris* begins to appear higher up). Historic data exist which show the huge importance of pinewoods in the Iberian Mountains, and at this point it is worth quoting a phrase from Willkomm (1896), who noted that "…with the exception of a few bare crests and peaks, the whole Cuenca range is covered by *Pinus laricio* (=*P. nigra*) woods…". One plausible explanation for the persistence of *P. nigra* pinewoods, especially with respect to their potential competitor *Q. faginea*, is a scenario in which the priority in the Lateglacial would explain a strong position of stability and resistance. The soil and the regional climate are compatible with *Q. faginea*, as can be seen from some locations where, in the absence of pinewoods, this taxon installs itself perfectly well. The argument that *P. nigra* is better suited than *Q. faginea* to such interior Mediterranean

Table 1

Adaptive characteristics of importance for the long-term ecology of masses. Information partially obtained from Ceballos and Ruiz de la Torre (1979), Tapias et al. (2004) and personal observations.

	Shade tolerant	Cone maturation before the fire season	Long-distance seed dispersal	Cone production in young specimens	Longevity	Serotiny	Seedling performance after fire	Bark thickness
Pinus uncinata	+	−	+++	−	++	−	?	−
Pinus sylvestris	−	−	+++	−	++	−	−	+
Pinus nigra	−/++	−	+++	−	+++	−	−	++
Pinus pinaster	−−	+	++	++	+	+++	+++	+++
Pinus pinea	−/+	+	−	−	+	−	+	+++
Pinus halepensis	−−	+	+++	++	+	+++	+++	++

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mountain climates, with their strongly contrasting nature, can also be added (Regato, 1992).

4.3.2. Relict pinewood nuclei and anthropogenic activity in the Cantabrian Cordillera

Very few enclaves of pinewoods considered to be spontaneous persist in the central-western sector of the Cantabrian Cordillera: Velilla de Río Carrión, Alto Porma and Xeres (Costa et al., 1997). As has been seen in previous sections, the palaeobotanical indicators show an early retreat (Lateglacial or Early Holocene) of the pinewoods from those slopes influenced by the ocean, mainly due to climatic factors. However, they also show the great regional importance of these populations in the southern and interior sectors and their persistence until the end of the Holocene. The current poor representation of natural pinewoods on the southern slopes of the Cantabrian Cordillera suggests that the action of humans is responsible for this drastic reduction in natural pinewoods at the end of the Holocene. However, it is not easy to determine the specific nature of this effect: it could be due to direct (pines have always been important in the regional economy) or indirect deforestation (deforestation for pastures and/or crops), which was subsequently taken advantage of by potential competitor species present in the surrounding region (beech and oak). The actual cause is likely to be a mixture of these two.

4.3.3. Stability related to regional soil outcrops: the Betic dolomitic and peridotitic pinewoods (Sierras de Cazorla and Bermeja)

Soil-related autoecological aspects often determine the persistence of pinewoods in regions in which potentially important competitors, well adapted to the regional macroclimate, exist. This could help in explaining the variable responses in the fossil record over a wide regional framework, as it often occurs in the Betic ranges. Indeed, certain soil-related characteristics can provide important benefits, which help to maintain a pinewood's hegemony. This can be attributed directly to the chemical characteristics of the bedrock (which could be incompatible or disadvantageous for the competitor species) or to its edaphic evolution, which could lead to soils whose physical characteristics are advantageous for pines. The former is well illustrated by the Sierra Bermeja in Estepona (an example which can be extended to other peridotitic outcrops in the Betic range). This *Pinus pinaster* pinewood dominates the landscape completely, with broadleaved species (*Quercus ilex* subsp. *ballota* and *Quercus suber*) only occupying small enclaves of gneiss or quartzite outcrops or very localised depressions that accumulate water and whose edaphic evolution weakens or cancels out the harmful effect of the soil. A good example of the second case can be found in the dolomitic soils of the Sierra de Cazorla, where the edaphic conditions (highly porous and dry sands formed from the dolomite rock) generate physical conditions that are favourable for maintaining the pinewood's hegemony (Costa et al., 1997).

4.3.4. Fragility of the isolated relict populations of Pinus uncinata in the Iberian Mountain Range

An aspect of particular interest in difficult-to-diagnose cases (e.g. pollen) is the role played by specific *Pinus* species in the generic signal in the fossil record. A current case, which we can use as an example of a substitution process, which would have been almost impossible to detect previously using only the pollen method, concerns the residual populations of *P. uncinata* in the Iberian Mountain Range. This case can be considered as the shrinkage of these populations, which probably proceed from a more vigorous situation during colder times in the past, at altitude. *P. sylvestris* currently covers the slopes of the mountains, whereas *P. uncinata* remains confined to a narrow region close to their peaks (Ruiz de la Torre, 1990–1998). This is best seen in Gúdar and Urbión, the only locations in the Iberian Peninsula, except for the Pyrenees, where *P. uncinata* can be found. As these two pine species have some degree of genetic compatibility (they are the only spontaneous pines in the peninsula which produce natural hybrids), the intrusion of *P. sylvestris* into these isolated *P. uncinata* populations is very significant. Indeed, hybrid specimens predominate in Urbión and are very common in Gúdar (pure *P. uncinata* specimens are concentrated at higher altitude). This process can be described as the result of the ascent of the plant belts due to the warmer conditions found on a very wide scale since the Lateglacial. At this point in the Holocene, as the conditions most suitable for microtherm pinewoods tend to be confined to higher altitudes, *P. uncinata* can no longer find suitable locations in these mountains to preserve its genetic identity, which means this species is likely to disappear in the short to medium term.

4.3.5. Pinewoods on Buntsandstein in the Iberian Mountain Range (Alto Tajo, Serranía de Cuenca, Albarracín): climate- and soil-based stability

The example considered here concerns *Pinus pinaster* pinewoods that live in soils formed from Buntsandstein sandstone. These woods are typical of the Sierra de Albarracín but can also be found in other parts of the Iberian Mountains. This situation can also be related to the pollen records from the inland, which show a significant persistence of the hegemony of these pinewoods up to the end of the Holocene. In this case, however, different factors that contribute to their interpretation can be identified. For instance, they grow in an interior Mediterranean mountain climate, far from the softening oceanic influences, which have proved so inimical to the persistence of Iberian montane pinewoods. Similarly, the soils in these mountains are very sandy, a situation which is particularly suitable for this species of *Pinus*. Both these factors are in agreement with a high stability for the pinewood. Broadleaved species adapted to this climate (*Quercus pyrenaica*), which form woods on the nearby Palaeozoic outcrops but which do not appear to be able to compete with the pinewoods, can be found away from these soils. Finally, these sandy soils do not appear to be particularly attractive for agricultural use, which completes our understanding of why these pinewoods have remained up to the present day.

5. Conclusions

Accumulating evidence from Quaternary palaeoecological records elucidates the paramount importance of pinewoods in the vegetation of Iberian Mountains across millennia. Besides confirming the autochthonous nature of all the Iberian pine species, the compiled data reflect their occurrence at stable phases of dominance or codominance in both Eurosiberian and Mediterranean environments. *Pinus sylvestris*, *Pinus nigra* and *Pinus pinaster* are the most common species that have been reported on the Iberian Mountains by macrorremain analysis.

Two of the distinct patterns observed are i) the stability of pinewoods on the inner environments through the Late Quaternary and ii) the pinewood demise on mountains influenced by the oceanic climate during the Holocene. However, Iberian environments remain considerably complex due to both its geographical heterogeneity and the extensive occurrence of interacting environmental drivers of change and stability. Consequently, high intraregional variability in some mountain ranges is detected.

Regarding the role of pinewoods in natural systems, the contribution of Palaeoecology is relevant in the Iberian context. Spanish policies on

Fig. 6. Examples of Iberian regions where pinewoods have been present throughout the Holocene. a) *Pinus uncinata* (Aran Valley, Pyrenees). b) *Pinus sylvestris* (Hoyocasero, Central Iberian Range). c) *Pinus sylvestris* (Guadarrama Mountains, Central Iberian Range). d) *Pinus pinaster* (Tejeda Mountains, Betic Range). e) *Pinus pinaster* (Hoz del Gallo, Iberian Range). f) *Pinus pinaster* (Bermeja Mountains, Betic Range). g) *Pinus nigra* (Zaorejas, Iberian Range). h) and i) *Pinus nigra* (Cazorla Mountains, Betic Range) Photo credits: a) and b) Hernández L., c), d), g) and i) Morales, C. e) and f) Rubiales, J.M., h) Morla, C.

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landscape and environmental management have been frequently influenced by a floristic-phytosociological school that is reluctant to consider Mediterranean pinewoods as end-stages of ecological succession. Extensive palaeoecological data supports a contrasting perspective that may help addressing management decisions for conservation and restoration ecology at the local or regional scales.

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