ORIGINAL ARTICLE

The Late Holocene extinction of *Pinus sylvestris* in the western Cantabrian Range (Spain)

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ABSTRACT

Aim To reconstruct the historical biogeography of *Pinus sylvestris* in the Cantabrian Range (Iberian Peninsula) during the Holocene, and to consider the interactions between vegetation dynamics, climate change and the role of man in the present-day distribution of the species.

Location The study site is a mire (1300 m a.s.l.) at Vega de Viejos, on a south-facing slope of the western Cantabrian Range, Spain. The region's present-day landscape is almost treeless, with the exception of some patches of *Quercus pyrenaica* and a few copses of *Salix* and *Betula* along stream banks.

Methods Tree macrofossils from Vega de Viejos were studied by transmitted light and dark-field reflection microscopy; strobili were subjected to comparative morphological analyses. Two *Pinus* macrofossils were dated by conventional ^{14}C methods.

Results The taxonomic accuracy achieved in the identification of the macrofossils provided new information regarding the Holocene history of *Pinus sylvestris* in this territory. Ninety-five cones of this species were identified; in fact, more than 80% of the 36 identified wood remains were of *Pinus* gr. *sylvestris*. Radiocarbon dating revealed that the forest to which the fossils belonged was present until at least 2170 ± 50 yr BP – its disappearance was therefore relatively recent.

Main conclusions *Pinus sylvestris* suffered long-term isolation, and after the Würm glacial period tended to migrate towards the east. In western Iberia, a temperate climate and autogenic succession favoured broadleaved taxa at the expense of *Pinus*. Late Holocene human disturbances may have further accelerated the decline of *P. sylvestris*; in the Cantabrian Range, only a few stands on southern slopes have persisted until the present day. The history of the capercaillie (*Tetrao urogallus*), a bird characteristic of pure or mixed Palaearctic coniferous forests, was almost certainly affected by the demise of these forests in this area. Cantabrian capercaillies are the only members of this species that live in purely deciduous forests, perhaps a recent adaptation to the regional extinction of pines. Today's *P. sylvestris* and capercaillie populations are now highly fragmented and their future, given the predictions of global climate change, is uncertain.

Keywords

Cantabrian mountains, extinction, historical biogeography, Holocene, Iberian Peninsula, macrofossils, megafossils, palaeoecology, *Pinus sylvestris*, *Tetrao urogallus*.

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INTRODUCTION

Few mountain ranges in southern Europe lack a well-developed belt of coniferous forest. The Cantabrian Range in the Iberian Peninsula is an exception. In the 19th century, Willkomm & Lange (1861), relying on Planellas-Giralt (1852) and Olazábal (1856), interpreted the small number of natural pine stands that existed in these mountains to be relictual.

Although Willkomm & Lange (1861) and Willkomm (1896) refer to Lugo (in Galicia) as being the westernmost limit of *Pinus sylvestris* L. in the Iberian Peninsula, the nearest natural stands of this species in the Cantabrian Range today lie at least 150 km to the east, at Lillo. The native character of these stands has been demonstrated (García Antón *et al.*, 1997). Sparse stands and individual trees have also survived around the headwaters of the Esla and Porma rivers (in the region of León, Spain), at Velilla del Río Carrión (Palencia), in the Serra do Gerês (in the Minho region of Portugal), and in the easternmost foothills of the Cantabrian Range (Ruiz Urrestarazu, 1989).

The Holocene (post-glacial) vegetation dynamics of the Cantabrian Range have been thoroughly studied using palynological and radiocarbon-dating methods (e.g. Menéndez Amor & Florschütz, 1963; Allen *et al.*, 1996; García Antón *et al.*, 1997; Muñoz Sobrino *et al.*, 1997, 2001, 2005, 2007), but some aspects of the history of the area's forests are not fully understood. Important questions remain regarding taxonomic resolution, altitudinal migrations, and the importance of climatic and anthropogenic factors on Holocene vegetation.

The accuracy of the identification of the macrofossils studied in this work, as well as the precision achieved regarding the origin of the palaeoecological signal help to improve our knowledge of the Late Quaternary history of *P. sylvestris* in the mountains of north-west Iberia. This paper documents the persistence of *P. sylvestris* stands in the western Cantabrian Range until at least 2170 ± 50 yr BP.

STUDY AREA

The study site is at Vega de Viejos, in the Laciana area of the western Cantabrian Range (Fig. 1). This range marks the Mediterranean–Atlantic frontier in the northern Iberian Peninsula (Ozenda & Borel, 2000). Vega de Viejos lies on the southern slope of these mountains, 50 km to the east of border of the province of Lugo, at the headwaters of the River Sil.

This part of north-western Iberia is an area of transition between the oceanic climate of the coastal, northern slopes of the Cantabrian area, and the Mediterranean subcontinental climate of the southern slopes and Spain's Northern Plateau. As a result of this barrier effect, great asymmetry is seen in terms of precipitation and temperature gradients (as well as in seasonal temperature fluctuations). Precipitation is greater on the northern slopes than on the southern slopes, which have a rain shadow effect. Furthermore, the westerly oceanic winds render the western mountains more humid (greater rainfall, and less evapotranspiration).

The western mountains generally consist of Early Palaeozoic (Cambrian, Ordovician and Silurian) siliceous bedrock including slate, sandstone, schist, and quartzite. The site (altitude 1300 m, Lat: 42.8697, Long: −6.2326) is a fen located in a landform of fluvioglacial origin, where till sediments have been identified. Macrofossils were collected from an area of some 60,000 m^2, in a continuous peat–sand layer located 120–150 cm below the soil surface. The sampled horizon had been exposed by drainage channels made in the peat.

Three shallow streams currently flow through this fen (those of Campo de la Vega, Gozapeiro and Troiquin). The dominant woody species at this site are *Erica tetralix* L., *Genista anglica* L., *Salix cantabrica* Rech. fil., and *S. atrocinerea* Brot. The surface of the fen is mostly dry and supports a grass-sedge vegetation with *Molinia caerulea* (L.) Moench, *Eriophorum latifolium* Hoppe, species of *Carex*, *Menyanthes trifoliata* L., and *Dactylorhyza* gr. *maculata* (L.) Soó. The vegetation
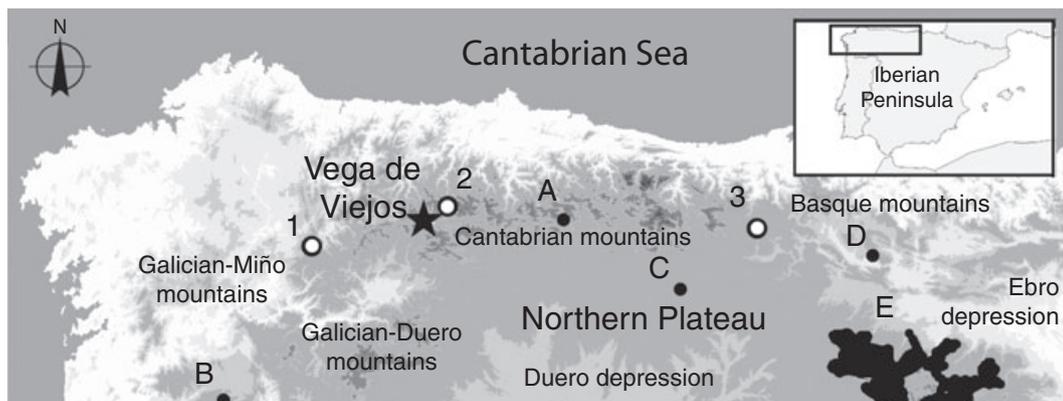

Figure 1 Location of Vega de Viejos (star) and other places mentioned in the text. Living stands of *Pinus sylvestris* are represented with capital letters (A, Pinar de Lillo and headwaters of Esla and Porma rivers; B, Serra do Gerês; C, Velilla del Río Carrión; D, Sierras de Arcena and Gorbea; E, marks the distribution of *P. sylvestris* in the Iberian Range), and the locations of three selected Holocene pollen sites are represented with numbers [1, Pozo do Carballal, 1330 m (Muñoz Sobrino *et al.*, 1997); 2, Lago de Ajo, 1570 m (Allen *et al.*, 1996); 3, Puertos de Riofrío, 1700 m (Menéndez Amor & Florschütz, 1963)]. See Fig. 4.

surrounding the site consists of scrub communities of *Genista hispanica* L., *G. obtusiramea* J. Gay ex Spach, *Cytisus scoparius* (L.) Link, *Pterospartum tridentatum* (L.) Willk. in Willk. & Lange, *Calluna vulgaris* (L.) Hull, *Daboecia cantabrica* (Huds.) K. Koch, and *Halimium lasianthum* (Lam.) Spach. The present-day landscape of the area is almost treeless, with the exception of a few patches of *Quercus pyrenaica* Wild. and a number of *Salix* L. and *Betula* L. copses along the banks of the streams.

MATERIALS AND METHODS

Preparation and identification of wood samples

Thirty-six woody macrofossils were collected from the fen (Table 1, Fig. 2). The majority of the wood samples were studied in thin section. These were prepared using a sliding microtome, and stained with safranin as described by Schweingrüber (1990). The resin content of the xylem in some samples hindered sectioning. To overcome this, they were immersed in different mixtures of water and alcohol until the desired quality was achieved. When poor preservation prevented analysis by standard procedures, the remains were studied using dark-field reflection microscopy. Identifications were made using keys of wood anatomy identification (Greguss, 1955; Jacquiot, 1955; Peraza, 1964; García & Guindeo, 1988; Schweingrüber, 1990, Vernet *et al.*, 2001), with particular attention being paid to the *Pinus* gr. *sylvestris* remains.

Identification of *Pinus* gr. *sylvestris*

This group includes the species *P. nigra* Arnold, *P. sylvestris* L. and *P. uncinata* Mill. ex Mirb, all of which occur in the north of the Iberian Peninsula today. Different authors have used different wood anatomical features to identify *P. sylvestris*, including:

(**1**) the nature of the early wood–late wood transition (Greguss, 1955; Jacquiot, 1955; García & Guindeo, 1988; Vernet *et al.*, 2001);

(**2**) the size and location of the resin canals in the annual rings (Greguss, 1955; Vernet *et al.*, 2001);

(**3**) the wall thickness of the epithelial cells lining the axial resin ducts (García & Guindeo, 1988);

(**4**) tooth distribution and shape in the radial tracheids (Greguss, 1955; García & Guindeo, 1988);

(**5**) the presence of intercalated radial tracheids (Jacquiot, 1955; Peraza, 1964); and

(**6**) the number and shape of the fenestriform pinoid pits in the cross-fields (Castellarnau, 1883; Greguss, 1955; Jacquiot, 1955; Peraza, 1964; García & Guindeo, 1988; Vernet *et al.*, 2001).

A detailed review of all the anatomical keys available was undertaken. Unfortunately, no consensus exists on which features are the most useful for the identification of *P. sylvestris*. One of the main reasons for this may lie in the origin (geographical and physiological) of the material described in each work. Therefore, the samples were compared with both modern *P.* gr. *sylvestris* wood from Iberia and other fossil samples, taking into account all the variables listed above. Many of the samples could not be identified to the species level since the above features did not match sufficiently well. Trunk samples from mature trees consistently showed the same characteristics. In well-preserved samples, two stable features reliably identified *P. sylvestris* (Fig. 3): (1) resin canals with thin-walled epithelial cells distinguish the species from *P. uncinata* (as suggested by García & Guindeo, 1988); and (2) transversal ray tracheids with concrescent tooth-shaped walls in early wood, occurring occasionally as reticulate thickenings, distinguish the species from *P. nigra* (as suggested by Greguss, 1955).

Identification of strobili

The identification of the cones was based on their morphological features and comparison with descriptions by Farjon (1984) and Franco (1986), and by comparison with modern and fossil specimens (Roig *et al.*, 1997; Alcalde *et al.*, 2000; Rubiales *et al.*, 2007).

Dating of samples

Conventional radiocarbon dates were obtained for two *P. sylvestris* macrofossils, namely a fossil pine cone and a fossil log (Table 2). Dates were calibrated using the CALIB 5.0 software (Stuiver & Reimer, 1993; version 5.0) with the IntCal04 data set (Reimer *et al.*, 2004), and rounded to the nearest 10 years for the sample with a standard deviation greater than 50 years. The intercept with 2 sigma (probability range at $P = 0.95$) is reported.
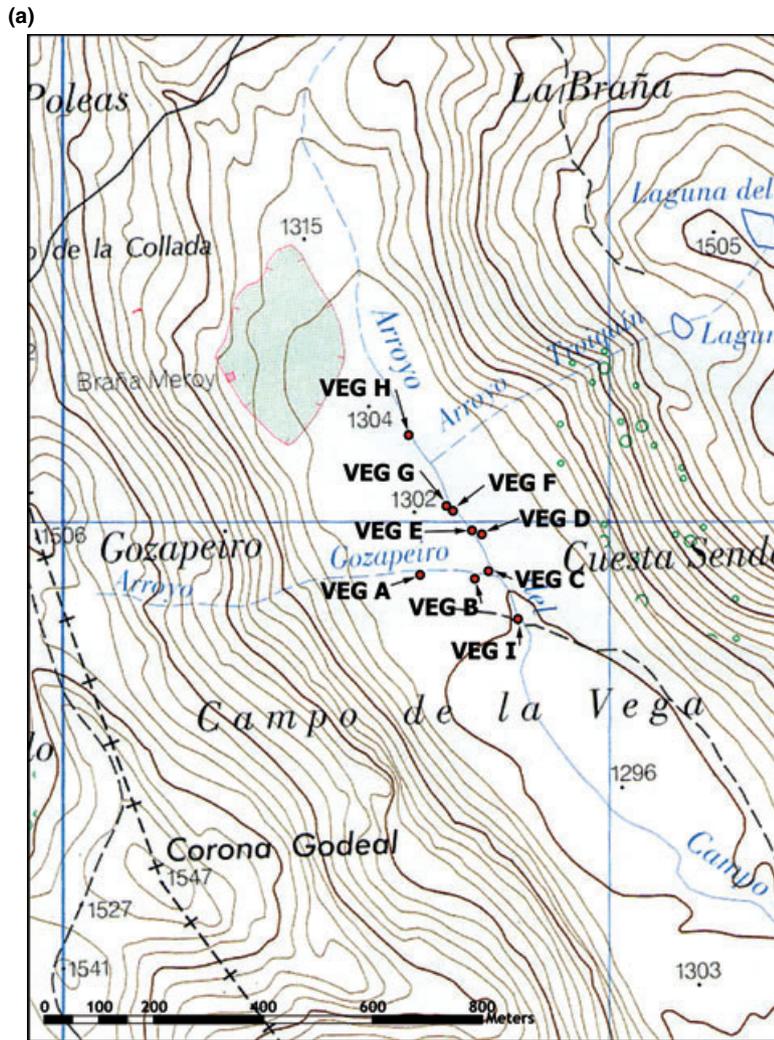
Table 1 Identification and type of wood remains.

Sample no.	Macroremain type	Taxonomic identification
A01, C01, G01, H01, I01	T	*Pinus sylvestris*
B08, B09, B10, C03, C04, C05, D01	B	*Pinus* gr. *sylvestris*
B12, B13, B14, B15, B16, B17, B18, B19, B20, B21, B22, B23, C06, C07, C09, C10, C12, C13	t	*Pinus* gr. *sylvestris*
C02	B	*Betula* gr. *pendula/pubescens*
C08	T, B	*Betula* gr. *pendula/pubescens*
E01, F01	B	*Salix* tp. *atrocinerea*
C11, H02	T	*Salix* tp. *atrocinerea*

Capital letters in the reference number of the sample indicate the place in the site (see Fig. 2) where macrofossils were found.

T, stump or trunk growing in a vertical position (concentric growth, section with pith);

B, branch that grew in a non-vertical position, or trunk from a tilted tree (reaction wood identified, eccentric ring growth); t, twigs, roots or small branches < 5 cm in diameter.

(a)

(b)

Figure 2 (a) Location of the sampling sites at Vega de Viejos. (b) View of Campo de la Vega (Vega de Viejos; 1300 m). The surrounding vegetation is dominated by shrub of broom (*Cytisus scoparius* (L.) Link) and other Leguminosae and Ericaceae species.

RESULTS

Wood remains

The majority of the wood samples collected were identified as branches, trunks or stumps of *Pinus* gr. *sylvestris*, some of which were still standing in the living position. Other fragments, belonging to small branches or roots of < 5 cm in diameter, were also studied. Table 1 shows the species identified. The anatomical and morphological features of the macrofossil specimens enhance the identification that can be attained by pollen analysis. The specimens of *Betula* could not be identified to species level. Distinguishing between *B. pendula* and *B. pubescens* wood on the basis of anatomical features does not appear to be possible (Hellberg & Carcaillet, 2003).

Strobili

Cones showing sufficiently clear features to allow their identification shared similar characteristics: dimensions

Figure 3 (a) Transverse section of I01 (*Pinus sylvestris* L.): vascular longitudinal tissue made up of tracheids (homoxylous) with resin ducts lined by thin-walled secretory cells. (b) Radial section of I01 (*P. sylvestris* L.): cross-fields between parenchyma cells to tracheids with large, ovoid fenestriform pits. The ray tracheids show dentate walls. (c) Tangential section showing uniseriate/biseriate rays and resin canals in rays with thin-walled epithelial cells. (d) Cross-section of C02. *Betula* sp. scalariform perforation plates with up to 15 bars. (e) Cross-section of *Salix* sp. (sample F01). Detail of the large vessel-parenchyma pits (Pv-p). Heterogeneous rays with two types of parenchyma cells, erect (e) and procumbent (p). (f) Fossil cone identified as *P. sylvestris* L.
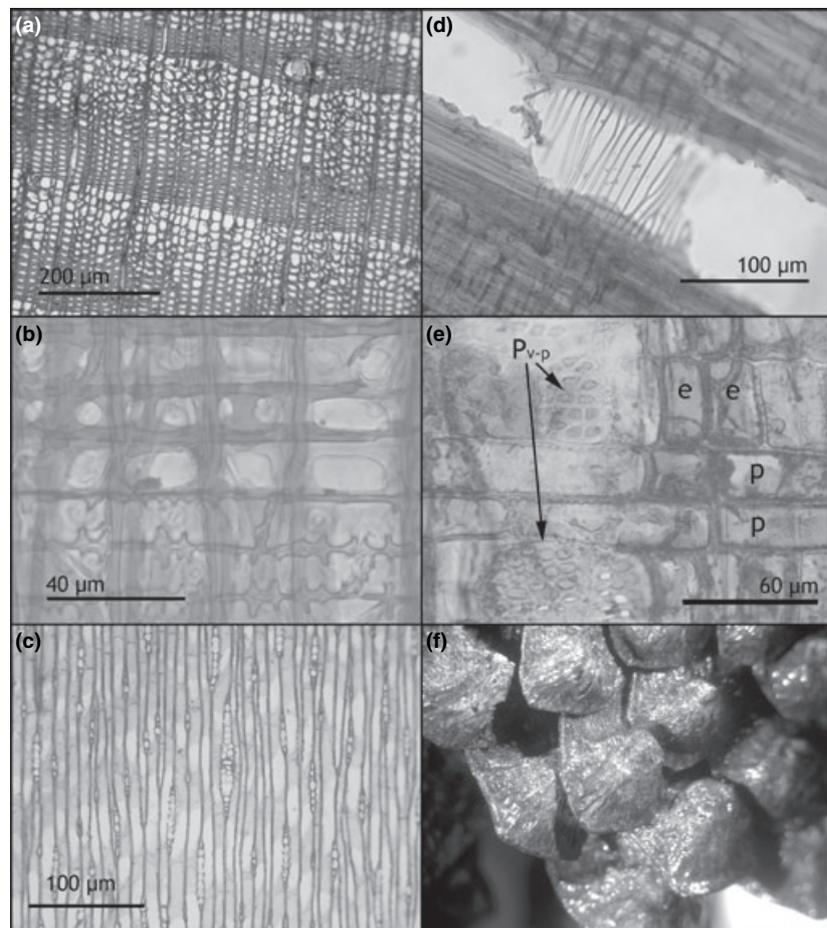
Table 2 Radiocarbon datings of two selected macroremains.

Reference	Laboratory identification number	Taxonomic identification	Type of remains	^{14}C age (yr BP)	Calibrated age (cal. yr BP) (2 sigma, $P = 0.95$)
C14	Beta-203119	*Pinus sylvestris*	Cone	2170 ± 50	2330 – 2010
I01	Beta-203120	*Pinus sylvestris*	Wood	2860 ± 60	3160 – 2840

Calibrated dates were obtained using CALIB version 5.0 software (Stuiver & Reimer, 1993) and the IntCal04 data set (Reimer *et al.*, 2004).

2.5–5.5 × 2–4 cm, sessile or slightly stalked, ovoid and symmetrical when opened, conic-ovoid when closed, and a dull dark brown colour. The apophysis of the scales was flat or slightly curved and rhombic in shape; the umbo was muticous or minutely mucronate. The scales from the mid and upper zones of the cones (except those surrounding the stalk) provided the best clues for identification at the species level. Ninety-five cones corresponding to this description were identified as *P. sylvestris*; their features agree with those described by Farjon (1984) and Franco (1986). The poor state of preservation of the other 39 cones collected did not allow specific identification, although they looked similar to those of *P. sylvestris*. Some seeds were also retrieved; these were 3–4 mm long with a wing length of 11–14 mm.

Dating

Two samples (C14 and I01) were dated using conventional radiocarbon methods (Table 2). These datings provide Late Holocene dates for the *Pinus* trees in the area.

DISCUSSION

The new findings in the historical context of the pinewoods in north-west Iberia during the Late Quaternary

Vega de Viejos is the westernmost site in the Cantabrian Range at which Holocene *P. sylvestris* macroremains have been found;

these remains reflect the extinction of a relic population of this species after 2170 ± 50 ^{14}C yr BP. These findings are consistent with other palaeoecological evidence that supports the existence of pinewoods in the area over long periods of the Quaternary.

The palaeobotanic record available for the last glacial cycle suggests that pinewoods were important during both the glacial and interglacial stages in the Iberian Peninsula (Badal *et al.*, 1994; Maldonado, 1994; Carrión, 2002; Gómez-Orellana *et al.*, 2007), thereby confirming the peninsula's role as a glacial refuge area.

In north-western Iberia, *P. sylvestris* appeared during the Würm III period (around 40,000 yr BP). Macrofossils of the species dating to the Late Pleistocene have been collected close to the Cantabrian mountains, but always at low- to mid-altitudes (Alcalde *et al.*, 2003; Figueiral & Carcaillet, 2005; Uzquiano, 2005; García-Amorena *et al.*, 2007).

The Northern Plateau is home to a few sites where *P. sylvestris* might have been the protagonist of subsequent colonization between the late glacial period and the onset of the Holocene (14,000–8000 yr BP). It was probably a major component of forests in the western mountain ranges of the Iberian Peninsula (Menéndez Amor & Ortega, 1958; Menéndez Amor & Florschütz, 1961; Muñoz Sobrino *et al.*, 2001, 2004), on the foothills and mid-altitude plateaux of north-western Iberia (Muñoz Sobrino *et al.*, 1996; Alcalde *et al.*, 2000), in some Cantabrian coastal areas (Uzquiano, 1992), and in the lowlands of the Duero Basin (García Antón *et al.*, 1995; Franco-Múgica *et al.*, 2001; Figueiral & Carcaillet, 2005).

Ecological interactions: climate and soil

The onset of wetter, more temperate conditions at the beginning of the Holocene saw the expansion of mesophilous taxa, and promoted the early decline of pinewoods in north-western Iberia. In essence, this pattern of change is quite similar to that reported for the Iberian Central Range by Rubiales *et al.* (2007). In areas with an Atlantic climate (i.e. the western and northern slopes of the Cantabrian Range) the same kind of change (although more sudden) occurred earlier than in the Central Range mountain range. Deciduous taxa were able to compete successfully with the conifers established in the late-glacial, spreading rapidly westwards (see Fig. 4). The sites of Pozo do Carballal, (Muñoz Sobrino *et al.*, 1997), Las Lamas, (Maldonado, 1994) and Lago de Ajo (Allen *et al.*, 1996) all show this pattern of early succession.

Warmer temperatures probably allowed vertical migration of pines. They persisted over time when they reached mountain environments with a drier, more continental climate, for example on the inland (subcontinental) slopes of the Cantabrian Range. In addition, the regional persistence of *P. sylvestris* stands might be related to the longevity of the species and its capacity to persist on histosols and other soils with acidic humus layers. As well as their persistence in Vega de Viejos, pinewoods maintained their dominance during the Late Holocene on the eastern sites of Cevico Navero (Roig

et al., 1997), Lillo (García Antón *et al.*, 1997; Muñoz Sobrino *et al.*, 2005) and the headwaters of the Porma, Curueño and Esla rivers (Sánchez Hernando *et al.*, 1999) (Fig. 4).

Biotic interactions, human impact and pine survival

Abiotic factors such as climate and soil are not the only factors that should be considered when trying to understand Cantabrian post-glacial vegetation dynamics. Deforestation and erosion processes triggered by human activity also seem to have been crucial over historical time. However, resistance through inertia may also have influenced these dynamics. Once *P. sylvestris* became dominant, it would have tended to prevent the establishment of equally suitable or even potentially superior taxa. Established pine forests were 'playing at home' (the 'pre-emptive competition' effect *sensu* Hallam, 1987), and limited turnover by resisting invasion by hardwoods, which were favoured by the climate. Human activity may have destabilized this equilibrium, encouraging (with help from other factors) important changes in the landscape. Although the magnitude of this change probably varied widely depending on the region, the regression of highland forests at the end of the Holocene occurred all over the Iberian Peninsula. Changes in the frequency and severity of fires (of either human or climatic origin), grazing, tree felling and even agriculture may all have led to important disturbances with decisive effects on succession patterns. Fire-resilient communities and re-sprouters would have been favoured over *P. sylvestris*, which is much more sensitive to human disturbance. In the Cantabrian Range, the time of proliferation of Neolithic settlements matches that of forest decline. The first evidence of human activity appears around 5000 yr BP, although the majority of palynological sites record significant impact only after 2000 yr BP (which intensified over the last millennium) (Allen *et al.*, 1996; García Antón *et al.*, 1997; Muñoz Sobrino *et al.*, 1997, 2007).

Long-term genetic consequences and relationships with *Tetrao urogallus*

The historical isolation model for *P. sylvestris* strongly agrees with data obtained from genetic studies. Its populations on the Iberian Northern Plateau and its peripheral mountain ranges show high haplotypic diversity and low among-population differentiation, consistent with recent (post-glacial) fragmentation (Robledo-Arnuncio *et al.*, 2005). Both the palaeoecological record and simulations support the existence of glacial refugia for this species in the Iberian Peninsula (Benito *et al.*, 2007; García-Amorena *et al.*, 2007), but also in the Alps, on the Hungarian Plain, in the Danube area, and in the Italian and Balkan peninsulas (Cheddadi *et al.*, 2006). The European distribution of the three haplotypes of *P. sylvestris* shows that their northward post-glacial expansion originated in refugia outside Iberia (Sinclair *et al.*, 1999; Soranzo *et al.*, 2000). In other words, during the last glacial cycle the Iberian populations underwent migration, expansion, retraction and
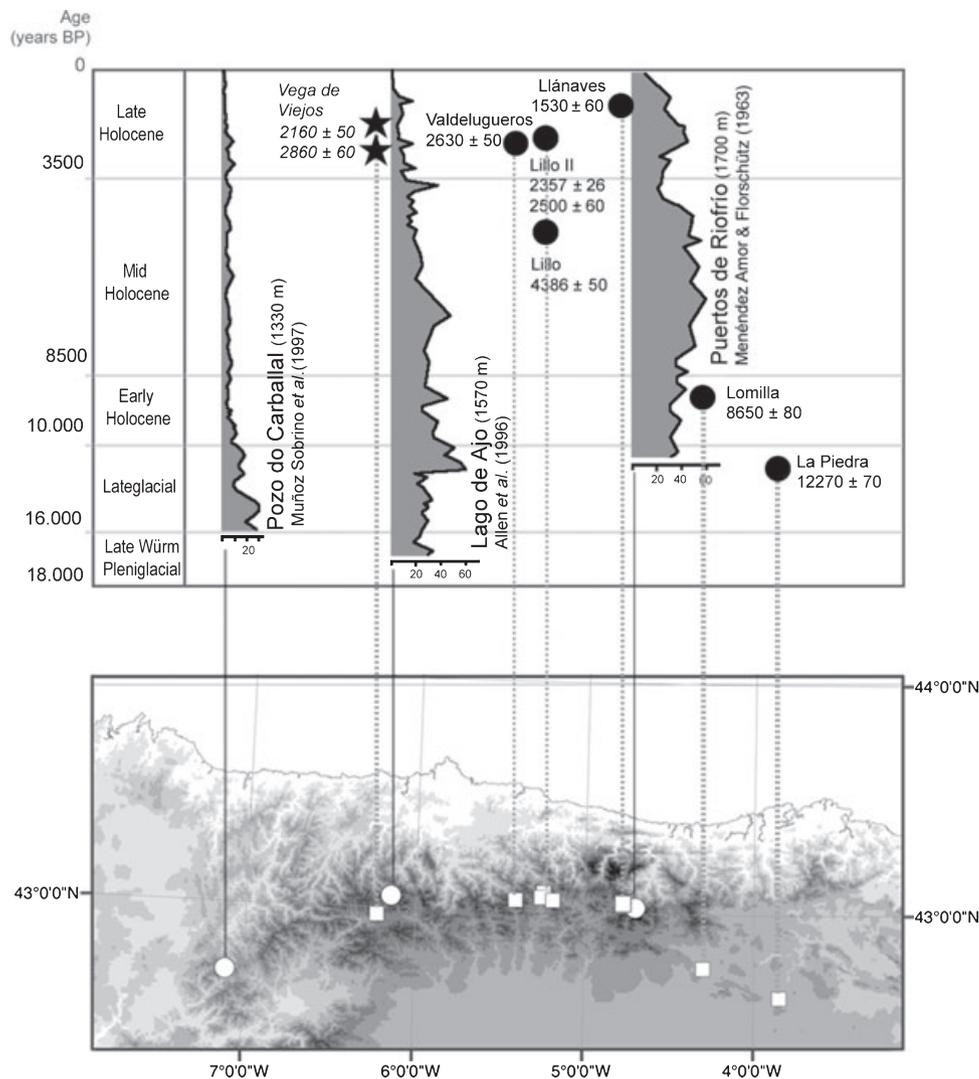
Figure 4 Fossil history of *Pinus* since the Last Glacial Maximum. The pollen percentages of *Pinus* at three selected sites along a west–east transect are shown. The palaeoecological evidence suggests a correspondence between the west–east climatic gradient (oceanicity/continentality) and the persistence of highland pinewoods. Stars represent the locations of the macroremains collected at Vega de Viejos; solid circles represent those at other sites for which references are included in the text.

extinction, but did not contribute to the Holocene recolonization beyond the Pyrenees.

The post-glacial changes in the distribution of *P. sylvestris* appear to be very similar to those experienced by the capercaillie (*Tetrao urogallus*), a bird symbolic of Eurasian coniferous forests. Phylogeographic studies involving mitochondrial DNA from capercaillie feathers and faeces have shown that the Cantabrian populations are the most genetically distinct (and depauperate) in Europe; other populations, in contrast, seem to be very homogeneous (Duriez *et al.*, 2007; Rodríguez Muñoz *et al.*, 2007). Only the capercaillies of the Pyrenees, which may have experienced recent contact with, or isolation from, the Cantabrian populations, show genetic similarities with the latter. The available genetic data for the Iberian populations agree with their ancient fragmentation, revealing a trend in their distribution that parallels that of *P. sylvestris* (the dominant species of the capercaillie's habitat

over most of its current range in the Pyrenees and outside the Iberian Peninsula; Fig. 5). The capercaillie is a typical folivore of Palaearctic coniferous forests, and the majority of its populations feed almost exclusively on conifer needles for most of the year. However, in today's mountain environments of north-western Iberia, which are home mainly to shrub communities and hardwood forests, they have developed unique adaptations, changing their diet to make use of different resources depending on the site. During winter and spring they usually consume beech buds, holly leaves, ferns or heather instead of pine needles (Rodríguez & Obeso, 2000). Given the pattern of Holocene forest history, their diet probably changed only recently, when pine populations declined and were replaced by shrubs, oak stands (*Quercus pyrenaica* and *Quercus petraea*) and beech forests – the rapid expansion of which occurred only after *c.* 4000 yr BP in these mountains (Martínez Atienza & Morla, 1992; Magri *et al.*, 2006).
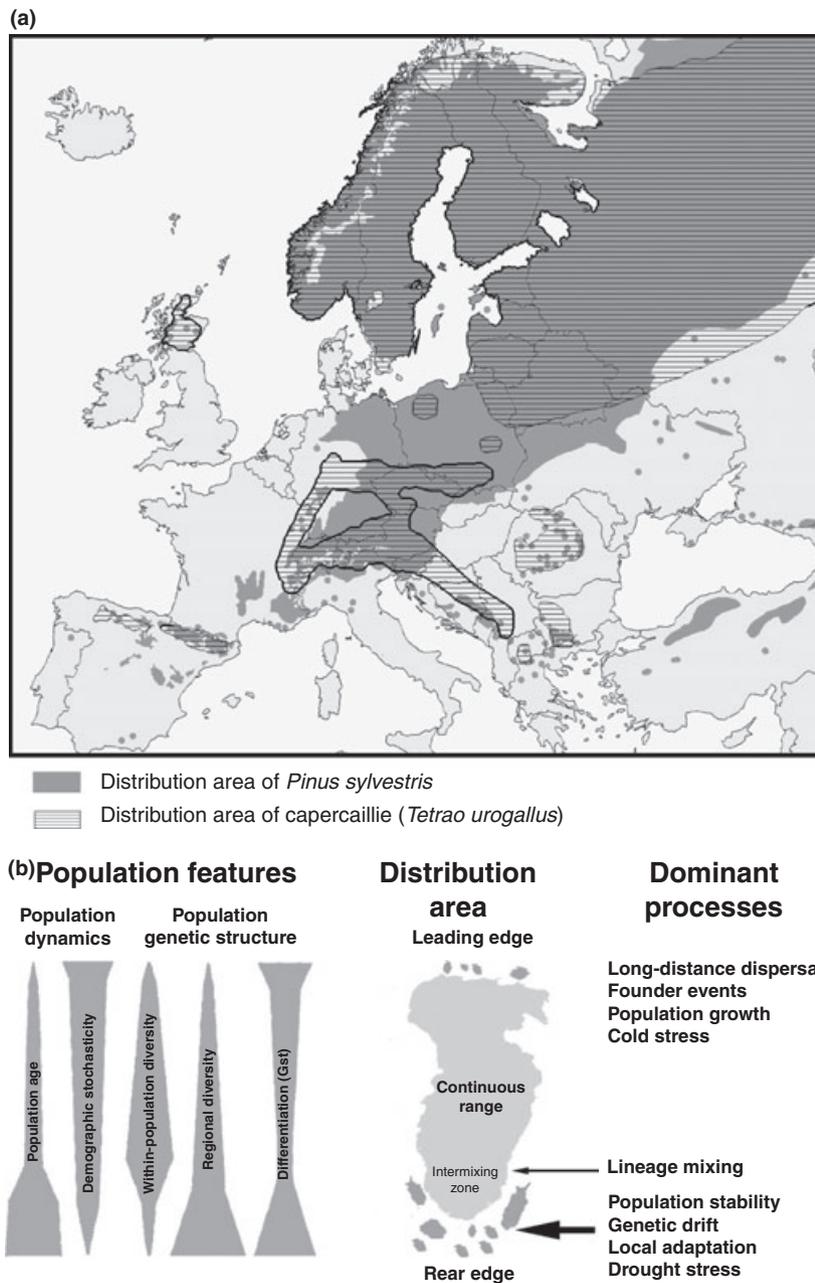
(a)

Distribution area of *Pinus sylvestris*

Distribution area of capercaillie (*Tetrao urogallus*)

(b)Population features

Distribution area

Dominant processes

Population dynamics

Population genetic structure

Population age

Demographic stochasticity

Within-population diversity

Regional diversity

Differentiation (Gst)

Leading edge

Long-distance dispersal
Founder events
Population growth
Cold stress

Continuous range

Intermixing zone — Lineage mixing

Population stability
Genetic drift
Local adaptation
Drought stress

Rear edge

Figure 5 (a) Distributions of *Pinus sylvestris* and *Tetrao urogallus*, from Mátyás *et al.* (2004) and Storch (2000). Besides being the main food resource of the capercaillie (*Tetrao urogallus*), *P. sylvestris* is the dominant taxon over most of its range. The Cantabrian Range is an exception, probably owing to the recent local decline and scarcity of the species. (b) The populations of both species show the typical genetic differentiation of rear-edge populations at low latitudes. Redrawn from Hampe & Petit (2005).

Implications for management and conservation

The palaeobotanic and genetic data available suggest that the persistence of rear-edge populations at the low-latitude margins is crucial in the long-term conservation of genetic diversity (Hampe & Petit, 2005). These populations do not have to be the source of long-distance post-glacial recolonizations (see Hewitt, 2000; Petit *et al.*, 2003) (as is the case for *P. sylvestris* and *T. urogallus*), but they maintain a valuable genetic resource, and have played a key role in the conservation of biodiversity over the Quaternary. These populations could be even more important if climate change reshuffles the geographic distribution of flora and fauna.

In today's Iberian Peninsula, *P. sylvestris* has its westernmost limit in the Serra do Gerês (Portugal) and Sierra de Gredos (Spain), and its southernmost in the Sierra Nevada and Sierra de Baza (Spain). The persistence of these stands is probably related to the longevity and resistance of the adult trees, as their ability to regenerate seems to be severely reduced. These populations are highly fragmented, and several studies have already pointed out their biological decline as a result of climatic, biotic, and anthropogenic factors (Hódar *et al.*, 2003; Castro *et al.*, 2004; Rubiales *et al.*, 2007). In north-western Iberia the stands at Lillo and Velilla del Río Carrión seem to be the only viable populations with any mid-term chance of survival.

The capacity of *P. sylvestris* to persist in marginal stands remains uncertain. Certainly, the longevity of the individuals may, to some extent, make up for their low reproductive ability, allowing stands to endure long periods without recruitment (García & Zamora, 2003). Furthermore, the heterogeneity of Iberian environments, which allowed the existence of refugia, guarantees the availability of potential niches for the species without the need for long-distance migration – although these may already be occupied. However, simulations restrict the potential area of the species in Iberia to a few enclaves under the scenarios of climate change projected by the Intergovernmental Panel on Climate Change (IPCC) (Benito *et al.*, in press). Thus, the extinction of its populations at the regional scale is very possible – the same has been noted for numerous species worldwide (Thomas *et al.*, 2004). Conservation strategies are therefore urgently needed to detect valuable stands, and measures should be adopted (taking into account the influence of man) to monitor the population dynamics of this species.

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