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Historical Distribution of European beech (*Fagus sylvatica* L.) in southwestern France: Evidence from macrofossil soil charcoal analysis



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1. Introduction

In Europe, most boreal and temperate species distributions were constrained to Quaternary glacial refugia during the last glacial maximum (LGM 26,500-19,000 yr BP) (Bennet et al., 1991; Willis and Vittaker, 2000; Hampe and Jump, 2011). Evidence based on pollen stratigraphies (Huntley and Birks, 1983) and phylogeographical surveys (Taberlet et al., 1998; Hewitt, 2000), suggested the three southern Mediterranean peninsulas: Iberian, Italian and Balkan as the main glacial refugia of most boreal and temperate European tree species. However, recent evidence, such as megafossil (Kullman, 2002), macrofossil (Willis and van Andel, 2004), and integrated researches combining fossil and genetic data (Magri et al., 2006; Parducci et al., 2012), suggested that distributional ranges of trees during the LGM were more extensive and included many local areas of small populations in central and eastern Europe persisting in so-called 'cryptic' (Stewart and Lister, 2001; Birks and Willis, 2008), 'northerly' (Stewart and Lister, 2001; Bhagwat and Willis, 2008), 'peripheral' (Holderegger and Thiel-Egenter, 2009) or 'micro' (Rull, 2009) refugia.

Beech (*Fagus sylvatica* L.) is one of the most abundant, widespread and economically important species in Europe (von Wuehlisch, 2008) covering about 12 million ha (Muhs & von Wuehlisch, 1993) and occupying a wide range of habitats with different soil types (Ellenberg, 1996; Peters, 1997). It is a monoecious and late succesional deciduous tree, with a long life span of *ca.* 300 years (Ellenberg, 1996), growing season \geq 140 days (Peters, 1997), and atmospheric humidity requirements (E Silva, 2010). Current beech distribution spreads from the Cantabrian Mountains in the west to the Carpathians and Balkan Mountains in the east and from Sicily in the south to southern Sweden and Norway in the north (von Wuehlisch, 2008).

Based on paleoecological and genetic evidence, a model of postglacial beech expansion was proposed by Magri et al. (2006). This model suggested that beech spread continuously and irreversibly from scattered nuclei during 10,000 years over the late and post glacial period. The rate of beech spread was affected by various factors, including climate and human activity (Huntley et al., 1989; Magri, 2008; Timbal and Ducouso, 2010; E. Silva et al., 2011), as well as others such as the geographical constraints (Svenning and Skov, 2007), slow dispersal and establishment rates (Gardner and Willis, 1999), and interspecific competition (Magri, 2008).

Historical presence of beech stands in southwestern France (*Landes de Gascogne* and surrounding area) is not included in this model, most likely because beech is virtually absent from this region in the current vegetation maps at the country or even regional scale (*i.e.* 1/200,000) (Badeau et al., 2004; Timbal and Ducouso, 2010). However, local isolated beech stands in this region were formally documented only recently (Timbal and Ducouso, 2010). Beech stands are restricted to wet microenvironments within this dry region and are thus distributed as small isolated patches forming riparian forest galleries benefiting from local increased soil moisture and

atmospheric humidity with respect to the regional matrix.

The historical presence of beech in southwestern France is suggested by indirect proxies. A floristic model predicts a wider range than is currently occupied by beech in southwestern France (E. Silva et al., 2011). A modelling study based on climatic parameters and species ecological niche (Svenning et al. 2008) suggested the potential for a putative beech glacial refugium in this region. Finally, Tarze et al. (2009) found *ca.* 6100 toponyms (names of places established for centuries or millennia) related to beech throughout the region which could indicate greater regional beech abundance in the recent past. However, direct paleoecological information from southwestern France is scarce and limited to a few unpublished palynological studies (Galop, 2005, 2006) because the area is largely devoid of suitable paleostratigraphical study sites. Moreover, rigorous detection of cryptic historical beech stands by this “classical” paleoecological proxy would be difficult if these stands remained small and isolated as expected for cryptic refugia (Rull, 2009). Pollen can be transported from long-distances and thus expresses a regional scale floristic composition unsuitable to detect local microrefugia.

Our objectives are i) to assess the presence of a cryptic glacial refugium for beech in southwestern France, and ii) to uncover the glacial and postglacial history at each of the current beech stands by testing whether these stands have natural (relicts) or anthropogenic (recent) origin. In this study, we used macrofossil analysis of charcoal in mineral soils. Based on botanical identification and radiocarbon (^{14}C) accelerator mass spectrometry (AMS) dating of charcoal macrofossils buried in mineral soil (Thinon, 1992), this novel paleoecological approach has proven useful for reconstructing fire and vegetation histories at the stand scale where no other paleoecological proxies were available (Talon et al., 2005, de Lafontaine and Payette, 2011, 2012). Over the past 15 years, it was used successfully to reconstruct Holocene history in North American forests (Talon et al., 2005; Fesenmyer and Christensen, 2010; de Lafontaine and Payette 2011, 2012), French Alps (Talon et al., 1998; Carcaillet, 2001) and German Jurassic Mountains (Poschlod and Baumann, 2010).

2. Material and methods

2.1. Study sites

Eleven beech stands from the Landes de Gascogne area were studied: Cazats (CAZ), Ciron A (CIRA), Ciron B (CIRB), Ciron C (CIRC), Curton (CUR), Escource (ESC), Laveyron (LAV), Mas d’Agenais (AGE), Roquefort (ROQ), Villenave (VIL) (Fig. 1). Landes de Gascogne is characterized by aeolian coversands of *ca.* 13,000 km² in southwestern France. The area is delimited by the Atlantic Ocean to the west, the Garonne River to the north and east, the Adour and

Midouze Rivers to the south. Coversands originated from three depositional phases, separated by paleosols, corresponding to the Late Pleniglacial (between 15,000 and ~23,000 yr BP), the Younger Dryas (*ca.* 12,000 yr BP) and Little Ice Age (*ca.* between 1350 and 1850 AD) (Bertran et al., 2009, 2011). Although they are uncommon, geological outcrops from calcareous, clay and loamy Tertiary (Oligocene and Miocene) deposits are locally present (Klingebliel and Legigan, 1985).

Table 1 shows a description of the various edaphic features, topographies, vegetation types and stand types.

Table 1

Characteristics of each sampling sites

Sites	Soil		Topo graphy	Vegetation Type	Stand Type
	Type	Texture			
AGE	Brown earth (brunisol)	Loamy	Flat	Mature beech-oak (<i>Quercus robur</i> L. and <i>Q. petraea</i> (Matt.) Liebl.) forest with hornbeam (<i>Carpinus betulus</i> L.)	Forest patch on a plateau
CAZ	Brown earth (brunisol)	Loamy	Slope	Mature beech-oak (<i>Quercus robur</i> L. and <i>Q. petraea</i> (Matt.) Liebl.) forest with hornbeam (<i>Carpinus betulus</i> L.)	Riparian forest gallery
CIRA	Calcareous sand	Sandy (stony)	Slope	Mature beech forest with lime tree (<i>Tilia cordata</i> Mill.)	Riparian forest gallery
CIRB	Calcareous sand	Sandy (stony)	Slope	Mature beech forest with lime tree (<i>Tilia cordata</i> Mill.)	Riparian forest gallery
CIRC	Calcareous sand	Sandy (stony)	Slope	Mature beech forest with lime tree (<i>Tilia cordata</i> Mill.)	Riparian forest gallery
CUR	Brown earth (brunisol)	Clay	Flat	Maritime pine (<i>Pinus pinaster</i> Aiton) plantation established <i>ca.</i> 5 years ago which replaces a mature beech forest with hornbeam	Pine plantation on a plateau
ESC	Regosol	Sandy	Slope	Mature beech individuals in a stand dominated by oak (<i>Quercus robur</i> L. and <i>Q. petraea</i> (Matt.) Liebl.) and holly (<i>Ilex aquifolium</i> L.)	Riparian forest gallery
LAV	Brown earth (brunisol)	Loamy	Flat	Mature beech-oak (<i>Quercus robur</i> L. and <i>Quercus petraea</i> (Matt.) Liebl.) forest with hornbeam (<i>Carpinus betulus</i> L.)	Forest patch on a plateau
ROQ	Regosol	Sandy	Slope	Mature beech forest with lime tree (<i>Tilia cordata</i> Mill.)	Riparian forest gallery
SYM	Regosol	Sandy	Flat	Disturbed zone with many introduced exotic species introduced	Forest patch in a parkland
VIL	Regosol	Sandy	Flat	Mature beech-oak (<i>Quercus robur</i> L. and <i>Q. petraea</i> (Matt.) Liebl.) forest	Riparian forest gallery

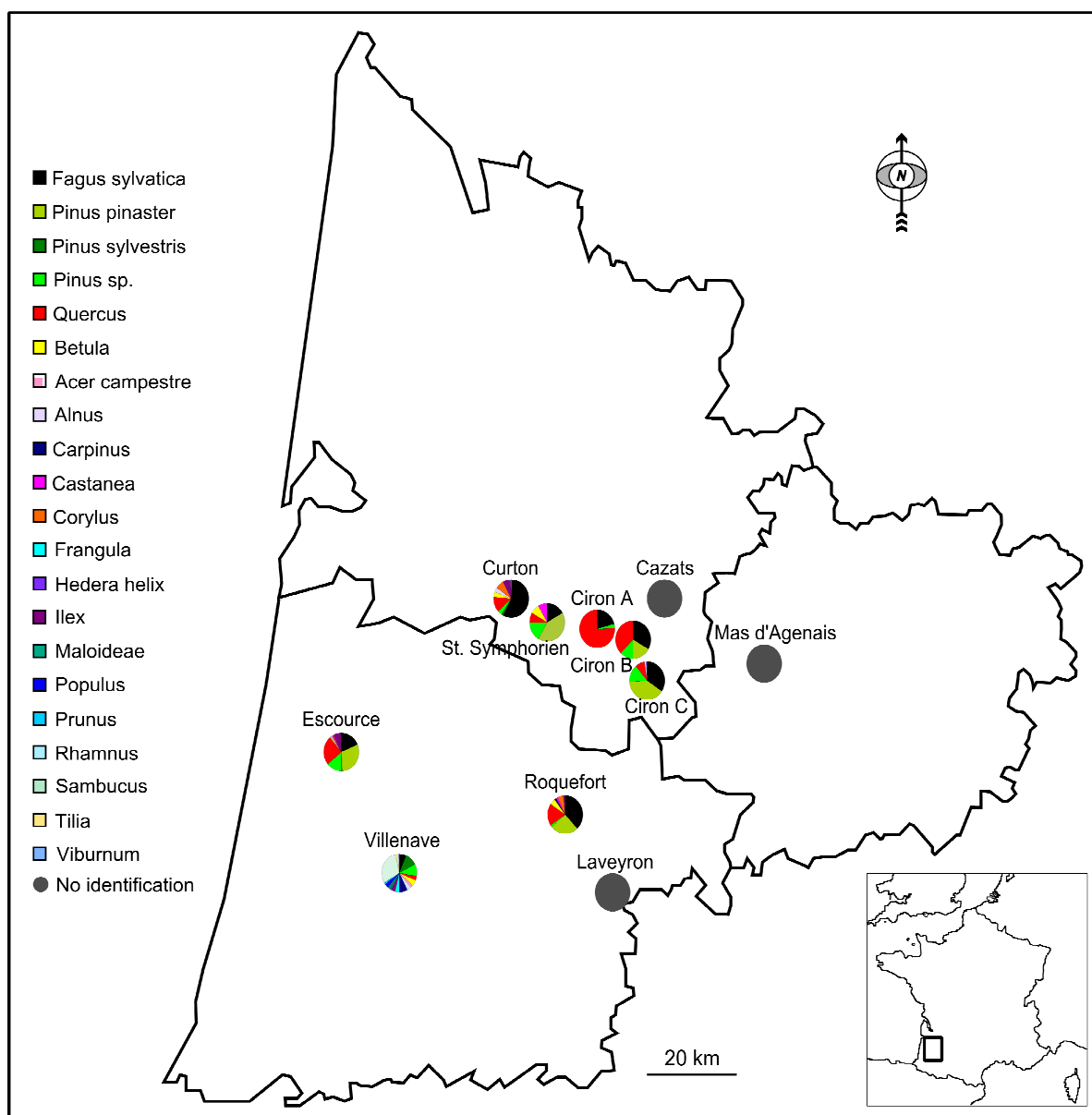


Fig.1. Location of sampling sites in *Landes de Gascogne* and surrounding areas, southwestern France. Pie-charts show the relative abundance of each taxa in the macrofossil assemblage of eight sampling sites.

2.2. Charcoal extraction

A plot (50 m x 10 m) was established at each of the beech stands. Charcoal samples were extracted from 25 soil cores, 24 cores distributed every 5 m along the perimeter and 1 core in the middle of the plot. Litter and organic topsoil was removed and mineral soil cores of 750 cm³ were collected from the 15 cm mineral soil surface using a soil auger.

At the laboratory, a macrofossil charcoal treatment for paleoecological studies was used Thinin (1992). First, to disperse the soil aggregates of samples, sandy soil cores were immersed in a solution of sodium hydroxide (NaOH 1%) for 12 h, while clay, loamy and calcareous soil cores in

sodium phosphate (Na_2PO_4 2.5%) for 24 h. Second, samples were washed with running water in sieves with mesh sizes of 4 mm and 2 mm using a vibratory wet sieve shaker (Retsch, Germany). Third, charcoal particles from local origin ($\text{Ø} \geq 2$ mm) (Ohlson and Tryterud, 2000) were manually extracted under a binocular microscope (Olympus, Japan), and the morphological type (black, permineralised, vitrified, white [bincho-tan]) was recorded. All charcoal particles were dried either in a stove at 60°C (Heraeus Hanau, Germany) for 8 h or at room temperature for at least three weeks, and weighed using an analytical balance (Sartorius, Germany).

2.3. Botanical identification of charcoal particles

Based on wood anatomy characteristics and biogeographic distribution of species, all charcoal macrofossil particles from seven samples sites: CIRA, CIRB, CIRC, ESC, ROQ, SYM, VIL, and particles ≥ 0.5 mg from CUR, were identified to the smallest possible taxonomic rank under an optical microscope (Olympus, Japan) mounted with episcopic light source. Note that due to time constraints, charcoal particles from the remaining plots were not included in this analysis, but they will be identified after the Master's defence. For taxonomic identification purpose, we compared charcoal macrofossils with a charred wood reference of Landes species. To prepare the charcoal references, a dry metal cauldron containing radial wood disks from twenty-nine species of Landes area, was filled with white-sand and heated on a gas stove to maximal temperature for 7 hours. Charcoal pieces produced were cooled at room temperature, cleaned and recorded (available at INRA-UMR BIOGECO, Amasifuen Guerra unpublished). We also used a wood anatomy guide from central Europe (Schoch et al., 2004), and a charcoal identification guide from southwestern Europe (Vernet et al., 2001), to help with charcoal identification.

2.4. Radiocarbon dating

Eighty individual charcoal particles from nine study sites: CAZ (8), CIRA (8), CIRB (11), CIRC (7), CUR (18), ESC (7), ROQ (8), SYM (5), and VIL (8) were sent for radiocarbon dating using the Accelerator Mass Spectrometry (AMS) technique to the Poznań Radiocarbon Laboratory (Foundation of the Adam Mickiewicz University, Poznan, Poland). Note that charcoal particles from the remaining sites (AGE and LAV) will be radiocarbon dated once their taxonomic identification will be completed. To select charcoal particles for radiocarbon dating we used the same criteria employed by Talon et al. (2005) and de Lafontaine and Payette (2011, 2012): dry weight ≥ 2.5 mg (lower limit for radiocarbon dating), botanical identification (focusing on beech but including other species), spatial distribution (avoiding many dates from the same soil core) and randomness. We used calibration dataset IntCal09.14C (Heaton et al., 2009) implemented in the software CALIB 6.1.1 (Stuiver et al., 2005) for calibrating radiocarbon dates (yr BP) to calibrated

years BP (cal yr BP). Software CALIBomb (Hua and Barbetti, 2004) was used to calibrate modern ^{14}C dates (after 1950 AD).

2.5. Reconstruction of beech history

At each sites where radiocarbon dates were available, the determination of fire events was based on the cumulative probabilities analysis (Meyer et al.,1992) using the ‘sum probabilities’ option in CALIB 6.1.1 (Stuiver et al., 2005) to plot the probability that a given event occurred at a particular time (Fesenmyer and Christensen, 2010; de Lafontaine and Payette, 2011, 2012). This method sums the probabilities of all dates and therefore takes into account the uncertainties inherent to radiocarbon dating. A methodological error of soil charcoal analysis is that the radiocarbon age of a charcoal fragment corresponds to the time when the wood that comprises charcoal was produced and not to the actual age of a fire event; as a result radiocarbon age may be several centuries older than the actual date of the fire which produced charcoal. This “inbuilt age” error could be more important in sites with infrequent fires (Gavin, 2001). Consequently, for each species, we corrected the “inbuilt age” error by accounting for its life span using the “Sample Age Span” option implemented in CALIB 6.1.1.

Charcoal particles are not stratified in soils (Carcaillet, 2001; Fesenmyer and Christensen, 2010) because taphonomical processes (*e.g.* tree uprooting events, colluvial erosion, freeze-thaw cycles, and biotic activity) continually rework the soil profile. Consequently, a random sampling of charcoal particles for radiocarbon dating does not reflect the actual fire history of a site. For this reason, we computed an asymptotic accumulation curves from the ^{14}C data to estimate by extrapolation the expected maximum number of fire events occurring at each site. In biodiversity studies, an asymptotic accumulation curve is defined from a cumulative number of ‘species’ found within a defined area, as a function of some measure of the sampling effort expended to find them (Soberón and Llorente, 1993; Colwell and Coddington, 1994). Our use of the asymptotic accumulation curves allowed us to estimate how many fire events were missed in each reconstruction of local fire history. Accumulation curves were obtained plotting the number of recorded fire events [$F(n)$] as a function of the number of radiocarbon dated charcoal particles (n), and then extrapolating an expected number of fire events ($Fmax$) by fitting an asymptotic, negative exponential function

$$F(n) = Fmax (1 - e^{-Kn})$$

where the asymptote, $Fmax$, is the estimated expected number of fire events at each site, and K is a fitted constant that controls the shape of the accumulation curve (Holdridge et al., 1971; Soberón and Llorente, 1993). The Asymptotic Exponential B 2D formula implemented in an online curve fitting web site (zunzun.com) was used to calculate equation parameters. The difference between

Fmax and the number of recorded fire events corresponds to an estimation of the number of fire events missed by our sampling. Note that accumulation curve remains an extrapolation procedure and should be interpreted as a relative appreciation of the completeness reconstructions of local fire history, and does not indicate the true number of fire events. Finally, a regional fire history was computed by pooling together the radiocarbon dates from all sites and proceeding as it was done for each local site.

2.6. *Historical forest composition*

Botanical assemblages were inferred from taxonomical identifications and radiocarbon dates of charcoal particles of six beech stands: Ciron A, Ciron B, Ciron C, Curton, Escource and Roquefort. Only seven taxa were used to reconstruct historical floristic composition. Historical presence of the target species (beech), of companion species (oak, birch and holly), of emblematic species from Landes de Gascogne (maritime pine), and of currently regionally absent species (Scots pine and an unidentified pine [likely also Scots pine]) were evaluated. A visual comparison of the past floristic compositions was made between the six sampling sites to assess mainly the historical occurrence of beech and a regional historical floristic composition was made by polling local data across southwestern France.

3. Results

3.1. *Charcoal abundance and floristic composition*

Soil charcoal particles were recorded at all 11 sampled sites from southwestern France (Fig. 2; $n = 3024$ particles in total) in plots with various soil types, topography, floristic communities, and disturbance degree varying from mature forests to recent plantations. The number of charcoal particles was variable between plots. The highest amount of charcoal particles ($n = 982$) was recorded at AGE. By contrast, CIRB ($n = 33$) and SYM ($n = 19$) presented the lower amount charcoal particles (Fig. 2). Charcoal particles showed obvious morphological differences that were recorded as black, permineralised, vitrified and white charcoal (bincho-tan). The relative abundance of the different charcoal morphotypes was variable between sampling sites (Fig. 2), and apparently related to substrate. Permineralised ($n = 1932$) and black ($n = 989$) charcoal particles were the more abundant morphotypes in the macrofossil assemblages of southwestern France. Black charcoal was clearly most abundant in plots established on sandy (ESC, SYM, VIL) and calcareous substrate (CIRA, CIRB, CIRC). By contrast, permineralised charcoal particles were more abundant in clay (CUR) and loamy (CAZ, LAV, AGE) soils. Vitrified ($n = 36$) charcoal was uncommon in the Landes de Gascogne area whereas white charcoal ($n = 67$) was associated to a single site (ROQ)

The floristic composition of the charcoal recovered at eight sampling sites was determined from 1166 taxonomic identifications, representing 39 % of the complete charcoal record (Fig. 1). Overall, 21 taxa were identified. The floristic composition varied between plots (CIRA, n = 3; CIRB, n = 4; CIRC, n = 6; CUR, n = 9; ESC, n = 10; ROQ, n = 9; SYM, n = 6; VIL, n = 16). Beech and oak were recorded at all eight plots. Three species: beech (n = 240), oak (n = 131), maritime pine (n = 103), had highest relative abundance. Only at VIL did charcoal particles from elder (*Sambucus* sp.) have the highest relative abundance. Taxonomical identification of charcoal particles from CAZ, AGE and LAV will be completed after my Master's defence.

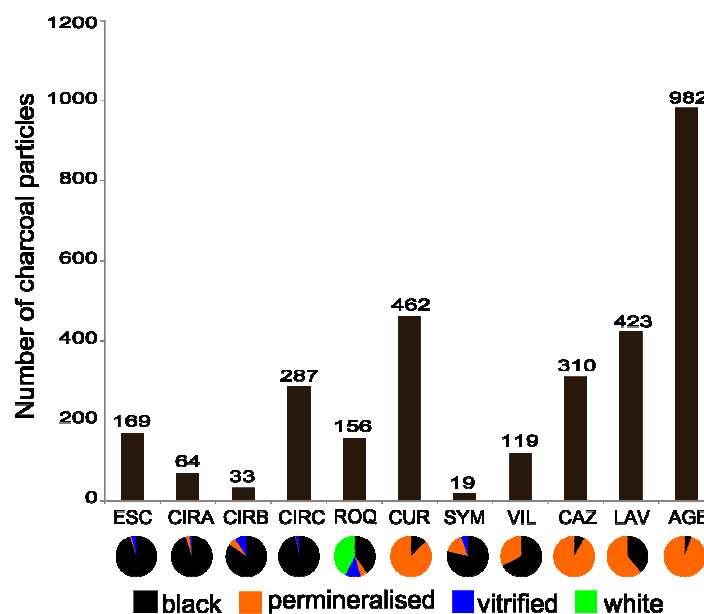


Fig.2. Number of charcoal particles recovered at each sampling sites. Pie-charts show the relative abundances of each morphotype in the macrofossil charcoal assemblage.

3.2. Beech stands fire histories

So far we have received radiocarbon dating results from 50 individual charcoal particles from six sampling sites (listed in Appendix 1). Radiocarbon dating of the remaining 30 charcoal particles is still in progress at the Poznan Radiocarbon Laboratory and results are expected by September 2012. Radiocarbon dates span the last *ca.* 44,000 years (from 43,930 to 13 cal yr BP). Note however that there is a hiatus between 30,000 and 14,000cal yr BP.

At Ciron A, 8 radiocarbon dates corresponded to 5 fire events, between 3779 and 59 cal yr BP. According to the accumulation curve, we might have missed one fire event (Fig. 3A; Fig. 4A). At Ciron B, 9 radiocarbon dates between 43,930 and 13 cal yr BP corresponded to 6 historical fire

events. The accumulation curve indicated that 2 fire events could have been missed (Fig. 3B; Fig. 4B). At Ciron C, 7 radiocarbon dates were recorded, and 2 of them corresponded to modern dates (after 1950 AD). The remaining 5 radiocarbon dates corresponded to 2 fire events, between 916 and 13 cal yr BP. The accumulation curve clearly indicated that we identified all the fire events expected by the extrapolation (Fig. 3C; Fig. 4C). At Curton, we recorded 7 fire events from 11 radiocarbon dates between 13,183 and 346 cal yr BP. The accumulation curve suggested that we might have missed 3 fire events (Fig. 3D; Fig. 4D). At Escource, 7 radiocarbon dates were recorded, 2 corresponded to modern dates (after 1950 AD), and the remaining 5 corresponded to 4 distinct fire events between 32,617 and 21 cal yr BP. The accumulation curve indicated that one fire event may have been missed (Fig. 3E; Fig. 4E). At Roquefort, 8 radiocarbon dates were recorded, 2 corresponded to modern dates (after 1950 AD), and 6 between 5736 and 136 cal yr BP corresponded to 4 fire events. According to the extrapolation from accumulation curve, we identified all the fire events expected (Fig. 3F; Fig. 4F).

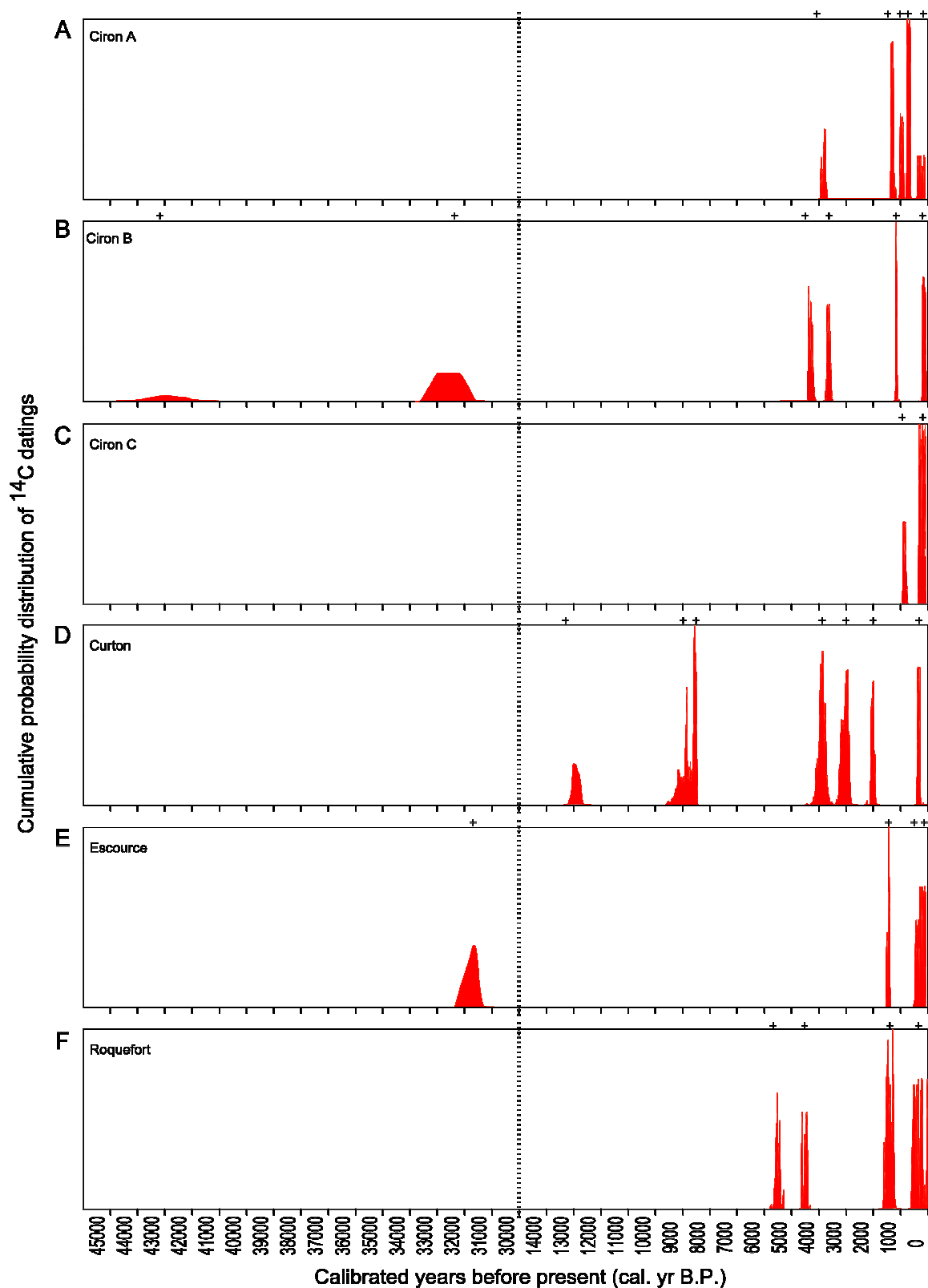


Fig.3. Stand-scale fire histories. Histograms represent cumulated probability of the calibrated ¹⁴C dates. '+' indicates different calibrated radiocarbon dates. Dotted vertical bar breaks the time scale between 30,000 and 14,000 calibrated years before present.

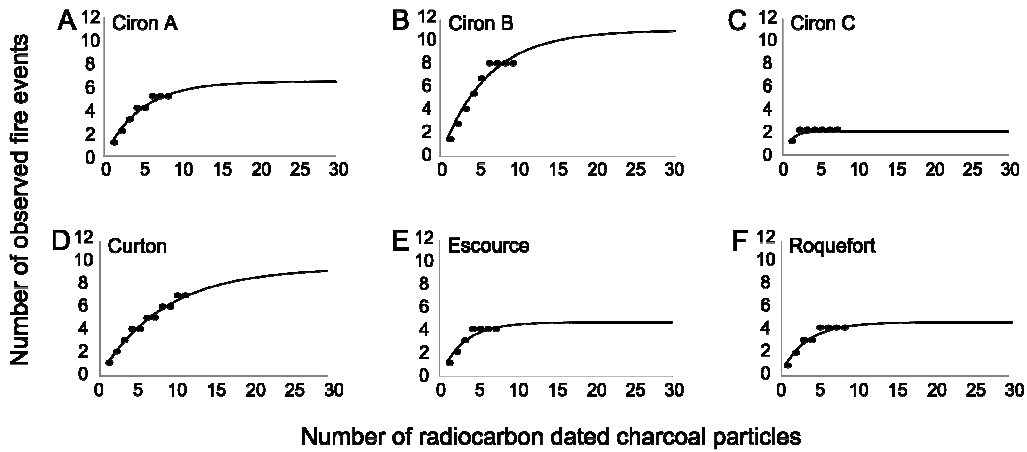


Fig.4. Accumulation curves of the number of fire events recorded based on calibrated ^{14}C dated charcoal particles. Extrapolation curves were fitted using an asymptotic, negative exponential function.

3.3. Regional-scale fire history

At the regional southwestern France scale, we analysed results from 50 radiocarbon dates, 6 corresponded to modern dates (after 1950 AD) and 44 between 43,930 and 13 cal yr BP. Six periods of fire activities were identified (Fig. 5). The oldest fire period from a single radiocarbon date was identified between 43,930 and 40,704 cal yr BP, followed by a hiatus *ca.* 7000 cal yr BP. Two radiocarbon dates made possible to detect a second fire period between 33,200 and 31,162 cal yr BP, which was followed by the longest hiatus of *ca.* 18,000 cal yr BP. A third small fire period from 13,183 to 12,662 was identified through a single radiocarbon date. From four radiocarbon dates, a fourth period of fire between 9927 and 8420 cal yr BP was detected. After a hiatus of *ca.* 3000 cal yr BP, a fifth period characterised by recurrent fire activity between 5736 and 2975 cal yr BP was recognised from 9 radiocarbon dates. Finally, from 27 radiocarbon dates, a sixth recent period between 2135 and 13 cal yr BP was identified.

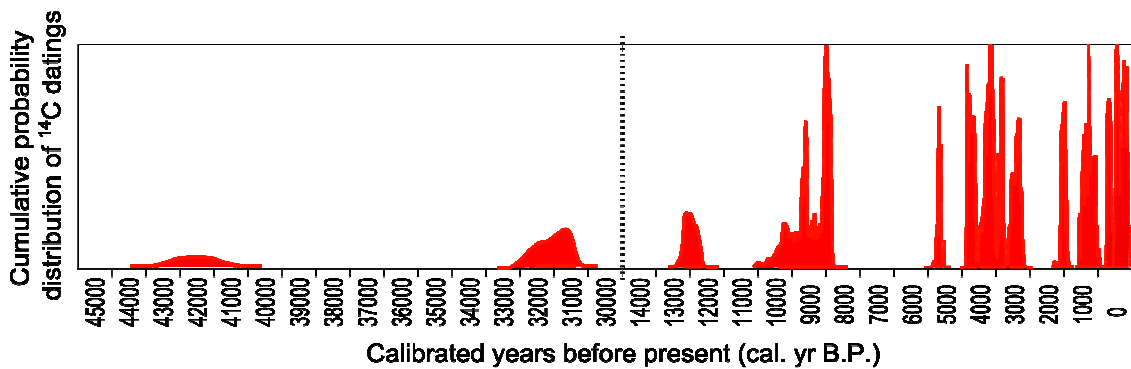


Fig.5. Regional fire history. Histograms represent cumulated probability of the calibrated ^{14}C dates. Dotted vertical bar breaks the time scale between 30,000 and 14,000 calibrated years before present.

3.4. *Stand – scale floristic composition histories*

Eight radiocarbon dates from Ciron A (beech, $n = 7$; oak, $n = 1$) were analysed. The oldest charcoal found at CIRA was beech dated between 3779 and 3612 cal yr BP. Beech charcoal was also recorded between 1288 and 1168 cal yr BP, and again after 888 cal yr BP (Fig. 6A). From Ciron B, nine charcoal particles (beech, $n = 6$; maritime pine, $n = 1$; pine, $n = 1$; oak, $n = 1$) were radiocarbon dated. We found the most ancient beech charcoal particles of this study: first between 43,930 and 40,704 cal yr BP and later between 33,200 and 31,536 cal yr BP. Pine and oak charcoals were dated at 4765 – 4616 and 4091 – 3900 cal yr BP, respectively. Another beech was dated between 1349 and 1280 cal yr BP. Finally, recent charcoal particles from maritime pine and beech dated after 227 cal yr BP (Fig. 6B). The most recent radiocarbon assemblages of the six sampling sites was from Ciron C. Seven charcoal particles were dated (beech, $n = 5$; oak, $n = 1$; maritime pine, $n = 1$). Two dates corresponded to modern ages (after 1950 AD), 6 were more recent than 225 cal yr BP, and one beech charcoal date was recorded between 916 and 760 cal yr BP (Fig. 6C). From Curton, 11 charcoal particles were radiocarbon dated (beech, $n = 7$; pine, $n = 2$; holly, $n = 1$; birch, $n = 1$). The oldest radiocarbon date from this stand was a pine (likely Scots pine) recorded between 13,183 and 12,662 cal yr BP. Another pine (probably Scots pine) was dated between 9927 and 9006 cal yr BP. Charcoal from holly was dated between 9144 and 8773 cal yr BP. Oldest beech radiocarbon date at Curton was between 8786 and 8412 cal yr BP, and was contemporary to a birch radiocarbon date between 8603 and 8420. Finally, six radiocarbon dates between 4438 and 346 cal yr BP indicated continuous presence of beech during the last four millennia (Fig. 6D). From Escource, 7 charcoal particles were dated (beech, $n = 4$; Scots pine, $n = 1$; maritime pine, $n = 1$; birch, $n = 1$). Beech charcoal was recent (between 495 and 21 cal yr BP) or modern (after 1950 AD) but a Scots pine was dated between 32,617 and 31,162 cal yr BP (Fig. 6E). From Roquefort, 8 charcoal particles (beech, $n = 6$; birch, $n = 1$; oak, $n = 1$) were radiocarbon dated, and the two more ancient beech were recorded at 5457 – 5736, and 4527 – 4658 cal yr BP. Also, beech charcoal more recent than 224 cal yr BP and modern (after 1950 AD) were recorded (Fig. 6F)

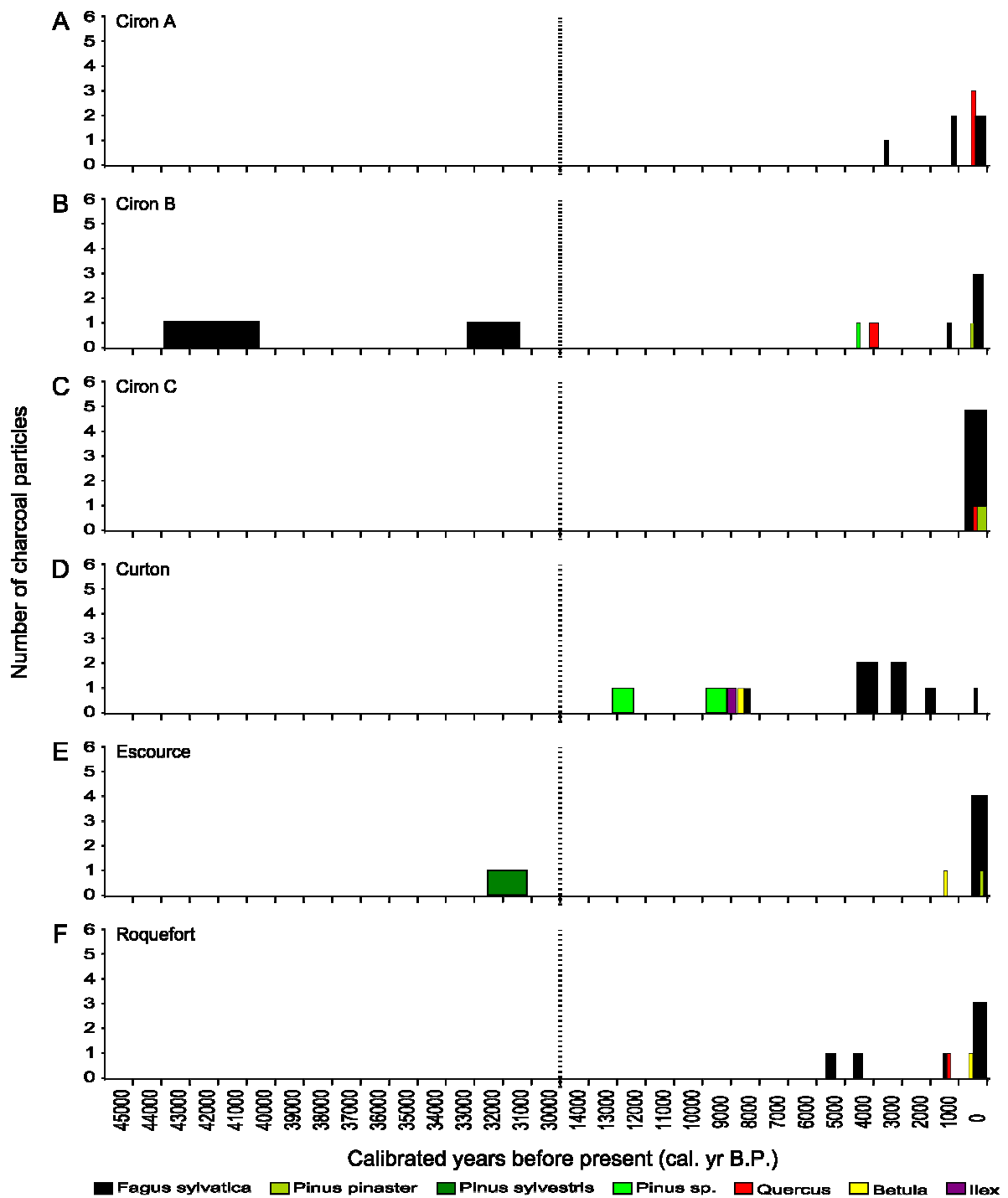


Fig.6. Stand-scale vegetation histories. Width of histogram bars illustrates range of calibrated ^{14}C dates (2 sigma). Dotted vertical bar breaks the time scale between 30,000 and 14,000 calibrated years before present.

3.5. Regional – scale floristic composition history

In southwestern France, radiocarbon dating indicated that beech was present in different periods over the last *ca.* 44,000 cal yr BP. Beech was recorded in 5 of the 6 fire periods identified in southwestern France (Fig. 7). Recent beech charcoals corresponding to the last 1000 cal yr BP and modern age (after 1950 AD) were the most abundant. Species currently present in beech stands such

as beech, oak, birch and holly were radiocarbon dated over the last 9000 cal yr BP. Maritime pine, which is currently very abundant in Landes de Gascogne, was radiocarbon dated since the last 300 cal yr BP. By contrast, radiocarbon dates from Scots pine were recorded at 31,000 cal yr BP and charcoal particle from an unidentified pine, which is more likely to be a Scots pine, was radiocarbon dated at *ca.* 12,500, 9500 and 4500 cal yr BP.

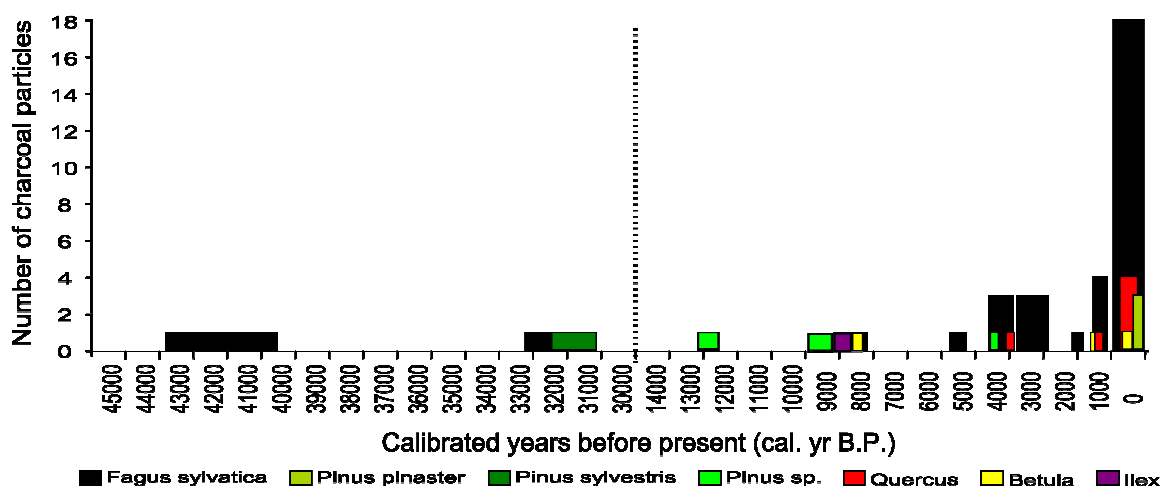


Fig.7. Regional-scale vegetation history. Width of histogram bars illustrates range of calibrated ^{14}C dates (2 sigma). Dotted vertical bar breaks the time scale between 30,000 and 14,000 calibrated years before present.

4. Discussion

In this study, radiocarbon dating of macrofossil soil charcoal was used to reconstruct long-term history of beech stands from southwestern France. The maximal temporal resolution of ^{14}C dating method is *ca.* 40,000 cal yr BP (Kitagawa and van der Plicht, 1998). Our results go back to *ca.* 44,000 cal yr BP, indicating that the macrofossil soil charcoal analysis is limited by radiocarbon methodology and not by charcoal degradation. Indeed, it was shown that charcoal can remain buried in the soil over several millenia without significant degradation due to high stability of its chemical structure and biological inertia (de Lafontaine and Asselin, 2011, 2012). During the last *ca.* 10 years, paleoecological research using macrofossils contributed to a better knowledge of the European glacial refugia because macrofossils allow detection of small plant populations such as those found in LGM cryptic refugia which are unlikely to produce a diagnostic regional pollen spectrum (Willis et al., 2000; Willis and van Andel, 2004). Reliability of soil charcoal as a tool to reconstruct past vegetation and fire history at stand scale is based mainly on three factors. First, high spatial resolution (Talon et al., 2005; Touflan and Talon, 2009) provided by the local origin of

macrofossil charcoals (Olson and Tryterud, 2000). Second, high level of charcoal conservation during millennia in different substrates and despite the influence of various taphonomical contexts such as bioturbation, soil reworking by uprooted trees, freeze-thaw processes (de Lafontaine and Asselin, 2011) makes it possible to distinguish charcoal anatomical characteristics for botanical identification. Third, high temporal resolution provided by the high inert carbon content of charcoal particles which provides the least risk of chemical contamination and ensures a reliable radiocarbon dating (Willis and van Andel, 2004). Thus, macrofossil soil charcoals analysis provides an estimate of the minimum number of past fire events at stand scale (Carcaillet, 1998; Olson and Tryterud, 2000; Talon et al., 2005; Fesenmyer and Christensen, 2010) and represents direct proof of historical plant assemblages on a stand (Talon et al. 2005; de Lafontaine and Payette, 2011, 2012). By contrast, soil charcoal study does not provide a continuous stratigraphic sequence (Carcaillet, 1998, 2001; Willis and van Andel, 2004; Fesenmyer and Christensen, 2010), because soil reworking processes accumulate over centuries and millennia (Carcaillet, 2001). Soil charcoal study rather represents a ‘snapshot’ of the vegetation in a given period of time (Willis and van Andel, 2004), and reconstruction of past vegetation and fire history depends upon the number and variability of radiocarbon dates. Nevertheless, absence of macrofossil soil charcoal for a determined episode of time must be carefully interpreted because several post-fire processes could influence whether macroscopic charcoal is present in the soil at a particular stand (Ohlson and Tryterud, 2000). Thus, lack of evidence (charcoal particles) for a determined period of time does not mean absence of fire events or plant assemblages.

Heterogeneous patterns of soil charcoal distribution in terms of relative abundance, morphotypes and botanical assemblages were found across beech stands from southwestern France. This variability highlights the high spatial resolution of macrofossil soil charcoal analysis. Traditional paleoecological method based on pollen analysis has various limitations in terms of taxonomic (difficult identification of taxa) and spatial (information on regional scale) resolution (Birks and Birks, 2000). Also, a palynological study covering the last 40,000 years is virtually impossible in Landes de Gascogne and surrounding areas because of the lack of suitable sites (*e.g.* lakes and mires) for pollen deposition (Jacobson and Bradshaw, 1981). Macrofossil soil charcoal analysis represents a reliable alternative paleoecological proxy in this region. Relative abundance of charcoal particles varied between beech stands. Number of charcoal particles in a determined stand could depend from various factors such as fire history *per se* (because charcoal is produced during fire events), degree of anthropization (anthropogenic fires could artificially increase the amount of recent and modern charcoal in the assemblage), various taphonomical processes, or even sampling effect. In this study, there was no obvious effect of the environment on the abundance of charcoal (*e.g.* plots on flat topography had both the highest and lowest records of charcoal abundance)

Four distinct morphotypes were recorded in the soil charcoal assemblage. Regular black charcoal, produced from wood carbonized at a continuous high temperature and stopped slowly, was found in all sites but it was more abundant in stands with sandy and calcareous soils. The uncommon white charcoal, formed from wood carbonized at a moderately low temperature followed by a quick rise in temperature and finally by a quick cooling, was related specifically to Roquefort on sandy soil and most likely associated to unique fire event with peculiar burning conditions. Vitrified charcoal, charred wood without visible anatomical structure (Touflan and Talon, 2009) is currently of unknown origin but likely related to the burning conditions (McParland et al., 2010). Such vitrified charcoal was recorded in sites with sandy and calcareous substrate. These three charcoal morphotypes highlight complexity of scenarios (natural or anthropogenic) of how they could have been produced. A fourth morphotype named permineralized charcoal results from a fossilization process whereby soil solution saturated with dissolved minerals is gradually infilling the charcoal cavities (de Lafontaine et al., 2011). This morphotype was clearly more abundant in stands with loamy and clay soils. The smallest size of minerals matters from clay and loamy soils could have facilitated successful impregnation of minerals into the charcoal pieces. In boreal forests, increasing of permineralized charcoal was associated to oldest macrofossil charcoal (older than 5000 cal yr BP) (de Lafontaine et al., 2011). In southwestern France age of charcoal particles was not associated to morphotypes, radiocarbon dates of charcoals pieces were indistinctly variables between morphotypes (*e.g.* some individuals of black charcoal were older than permineralized charcoals).

According to radiocarbon dates from six sampling sites, in southwestern France long term of fire history of beech stands during the last *ca.* 44,000 cal yr BP indicates a natural dynamic of the forest in this region during the Holocene and the last glacial period. It appears that regime of fire was more recurrent during the Holocene, but this is likely sampling artefact due to an overrepresentation of the modern material in the charcoal assemblages. In turn, this might be a consequence of anthropogenic effects on the charcoal record. For example, modern charcoal at Ciron C, Roquefort and Escource indicates fire events after 1950. It is impossible that natural wildfire events occurred at these sites because there is no field evidence of modern wildfire and late-successional beech trees are obviously older than *ca.* 60 yr. Anthropogenic charcoal are recognizable in the radiocarbon dated charcoal record by the fact that fire events appear too close in time to constitute actual stand-scale disturbance. Results from radiocarbon dates demonstrate that beech was present in Landes de Gascogne during almost all the Holocene since *ca.* 9000 cal yr BP. Oak, birch and holly were dated to the same periods of beech occurrence during the Holocene. Since these taxa are still present in current beech stands in the region, it could indicate that structure and composition of beech stands remained somewhat similar at least during the post glacial period.

Two scenarios were possible regarding the fate of beech in the Landes region during the LGM. Beech disappeared during the LGM and later recolonized the Landes; or beech remained in the region during the LGM but given incomplete sampling effort, direct evidence was not yet found. Charcoal particles from beech and Scots pine were recorded during the last glacial period. However, no direct evidence of beech or Scots pine during the LGM was recorded. Nevertheless, absence of charcoal particles during the LGM does not mean absence of floristic assemblages in this period. During the last glacial period, cold and dry climate characterized the landscape of southwestern France (Bertran et al., 2009, 2011). Scots pine is a species currently restricted to cold (boreal or alpine) climates, and its occurrence during the glacial period supports the fact that forests of southwestern France were affected by cold episodes of the ice ages as expected. Scots pine was recorded in the Landes region just before (ca. 32,000 cal yr BP) and after the LGM (ca. 12,500 cal yr BP) at Escource and Curton, respectively. Beech presence during the last glacial period was recorded at ca. 44,000 cal yr BP; and contemporary to Scots pine just before the LGM at ca. 32,000 cal yr BP, but in a different stand (Ciron B). This could indicate a microclimatic effect at Ciron B buffering adverse glacial climate. Beech is a species relatively resistant to diseases and cold temperature (von Wuehlisch, 2008). It is fostered by important atmospheric humidity, and is limited by drought at its southern range (Jump et al., 2006, Piovesan et al., 2008). Thus, beech is rather affected by drought than cold. Beech stand at Ciron B is characterised by a microclimate with increased atmospheric humidity related to the stream and the slope topography thanks to its location in a karst canyon (Timbal and Ducouso, 2010). It is possible that such microclimate have buffered cold and dry regional climatic conditions during the glacial allowing local persistence of beech at Ciron B during the last glacial period at least since *ca.* 44,000 yr.

Later, during the Holocene beech was found at *ca.* 9000 cal yr BP at Curton. According to palynological analysis, beech in southwestern France was already present at 5700 cal yr BP (Galop, 2005, 2006) and its occurrence in this region was inferred as a result of migration, probably from the Massif Central, around 6800 cal yr BP (Magri et al., 2006, 2008). Our study shows that beech presence in southwestern France is at least 2200 yr earlier. Two hypotheses are possible: beech arrived earlier than expected or it survived the last glacial period in the region. Beech capacity to remain in favourable microclimates under adverse climate (*e.g.* Ciron B) suggests that a scenario invoking regional survival of beech cannot be discarded. Thus, soil charcoal proxy allowed us to recognize regional (cold and dry climate) and local (humid microclimate) signals highlighting the benefits of this paleoecological proxy. Although no charcoal predating mid-Holocene was found at Ciron A, Ciron C and Roquefort, these sites currently have microclimate similar to that of Ciron B (Timbal and Ducouso, 2010). In addition, the oldest radiocarbon date at these three sites corresponded to beech. Consequently one can speculate that these three stands were indeed refugia.

However, because extrapolations from accumulation curves showed that other fires events in these sites are unlikely, the use of another proxy to study historical presence of beech in these stands is necessary. Perhaps studying the genetic structure of the current beech populations could help shed light on the demographic history of these stands.

Finally, our results showing natural dynamic of beech stands at southwestern France suggest a relict origin of these populations. However, in Landes de Gascogne the most emblematic species is maritime pine. In our charcoal records, maritime pine was dated since the last *ca.* 300 cal yr BP. Clearly, this corroborates recent massive anthropogenic introduction of this species in Landes de Gascogne beginning in the 18th century (Demounem and Legigan, 1988). By contrast, all beech dates were older. Thus, maritime pine populations clearly correspond to anthropogenic forests contrary to beech stands of natural, relict origin.

5. Conclusions

Macrofossil soil charcoal analysis allowed us to reconstruct long-term history of beech stands in southwestern France (Landes de Gascogne). Reliability of this paleoecological proxy was based on the capacity to provide historical information on the fire history and composition at the stand-scale over the last *ca.* 44,000 cal yr BP. This information allowed us to infer possible scenarios related to the origin of these beech populations. Likewise, soil charcoal analysis allowed us to recognize regional (cold and dry climate) and local (humid microclimate) signals. Charcoal particles are direct evidence of the presence of beech during the last glacial period. However, no evidence was found during the LGM. Then, two possible scenarios were suggested: beech disappeared during the LGM and later recolonized the Landes; or beech remained in the region during the LGM but direct evidence was not yet found. It is possible that microclimate with increased atmospheric humidity favouring beech in the riparian stand where it was recorded for the glacial period have buffered cold and dry regional climatic conditions during the glacial allowing local persistence of beech at least since *ca.* 44,000 cal yr. BP. In addition, we found direct evidence of beech presence earlier than previously inferred by pollen inferences suggesting that beech population in southwestern France is not only the result of postglacial migration. Thus, although direct proofs are still lacking, a scenario invoking regional beech persistence during the LGM cannot be discarded. Soil charcoal proxy was unable to provide paleoecological information from some beech stands before mid-Holocene. We encourage using other methods such as those based on genetic inferences to clarify history of these beech stands. In contrast to beech stands having a paleoecological history, all radiocarbon dates from maritime pine confirmed its recent plantation in the 18th century.

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Appendix 1 List of radiocarbon dates.

ID	Sample Name	Laboratory N°	Age 14C yr B.P.	Cal BP lower**	Cal BP upper**	Prob.***	Species
01	ESC 4-4-1	Poz-44303	27470 ± 350	31162	32617	1	<i>Pinus sylvestris</i>
02	ESC 6-2-1	Poz-44304	80 ± 35	21	144	0.716	<i>Fagus sylvatica</i>
03	ESC 13-2-1	Poz-46538	350 ± 40	313	495	1	<i>Fagus sylvatica</i>
04	ESC 14-2-2	Poz-45167	1520 ± 30	1341	1424	0.706	<i>Betula</i> sp.
05	ESC 15-2-43	Poz-44305	Modern*	-3	-6	1	<i>Fagus sylvatica</i>
06	ESC 19-2-1	Poz-44306	Modern*	-3	-6	1	<i>Fagus sylvatica</i>
07	ESC 25-2-2	Poz-44307	150 ± 25	168	231	0.353	<i>Pinus pinaster</i>
08	CIRA 3-2-1	Poz-44289	3435 ± 35	3612	3779	0.831	Cf <i>Fagus sylvatica</i>
09	CIRA 7-2-2	Poz-44291	1285 ± 30	1173	1288	1	<i>Fagus sylvatica</i>
10	CIRA 7-2-3	Poz-45171	1270 ± 30	1168	1286	0.948	<i>Fagus sylvatica</i>
11	CIRA 8-2-8	Poz-44292	150 ± 35	59	154	0.331	<i>Fagus sylvatica</i>
12	CIRA 9-2-9	Poz-44293	560 ± 30	589	642	0.518	<i>Quercus</i> sp.
13	CIRA 10-2-7	Poz-46537	615 ± 30	549	656	1	<i>Quercus</i> sp.
14	CIRA 12-2-4	Poz-44294	670 ± 35	627	678	0.546	<i>Fagus sylvatica</i>
15	CIRA 19-2-1	Poz-44295	960 ± 30	795	888	0.683	Cf <i>Quercus</i> sp.
16	CIRB 4-2-1	Poz-45166	180 ± 35	134	227	0.526	<i>Pinus pinaster</i>
17	CIRB 9-2-3	Poz-44282	1395 ± 30	1280	1349	1	<i>Fagus sylvatica</i>
18	CIRB 16-2-1	Poz-45165	4210 ± 40	4616	4765	0.669	<i>Pinus</i> sp.
19	CIRB 17-2-1	Poz-44283	37600 ± 1000	40704	43930	1	<i>Fagus sylvatica</i>
20	CIRB 18-2-2	Poz-44284	3675 ± 35	3900	4091	0.981	Cf <i>Quercus</i> sp.
21	CIRB 19-2-6	Poz-44285	105 ± 30	13	147	0.702	<i>Fagus sylvatica</i>
22	CIRB 20-2-1	Poz-44287	28130 ± 320	31536	33200	1	<i>Fagus sylvatica</i>
23	CIRB 21-2-1	Poz-44288	0 ± 30	34	71	0.752	<i>Fagus sylvatica</i>
24	CIRB 24-2-1	Poz-46536	175 ± 30	136	225	0.547	<i>Fagus sylvatica</i>
25	CIRC 6-2-2	Poz-44296	910 ± 30	760	916	0.972	Cf <i>Fagus sylvatica</i>
26	CIRC 7-2-7	Poz-44297	Modern*	-6	-7	1	<i>Fagus sylvatica</i>
27	CIRC 7-2-12	Poz-45170	Modern*	-6	-7	1	<i>Fagus sylvatica</i>
28	CIRC 15-2-1	Poz-44298	125 ± 30	55	150	0.47	<i>Fagus sylvatica</i>
29	CIRC 20-2-3	Poz-44299	140 ± 30	59	152	0.383	<i>Fagus sylvatica</i>
30	CIRC 20-2-14	Poz-44301	175 ± 30	136	225	0.55	Cf <i>Quercus</i> sp.
31	CIRC 22-2-3	Poz-44302	105 ± 30	13	147	0.702	<i>Pinus pinaster</i>
32	CUR 3-4-1	Poz-44308	310 ± 30	346	463	0.757	<i>Fagus sylvatica</i>
33	CUR 5-2-26	Poz-44309	3770 ± 50	3980	4295	0.99	<i>Fagus sylvatica</i>
34	CUR 6-2-13	Poz-44311	7800 ± 80	8412	8786	0.939	Cf <i>Fagus sylvatica</i>
35	CUR 6-2-28	Poz-46534	3090 ± 80	3071	3470	1	Cf <i>Fagus sylvatica</i>
36	CUR 8-2-17	Poz-46535	2945 ± 35	2975	3218	0.996	<i>Fagus sylvatica</i>
37	CUR 11-2-1	Poz-45164	8090 ± 60	8773	9144	0.931	<i>Ilex</i> sp.
38	CUR 15-2-7	Poz-45163	3780 ± 110	3856	4438	0.997	<i>Fagus sylvatica</i>
39	CUR 21-2-24	Poz-44312	8470 ± 180	9006	9927	0.989	<i>Pinus</i> sp.
40	CUR 21-2-31	Poz-44313	11060 ± 120	12662	13183	1	<i>Pinus</i> sp.
41	CUR 22-2-27	Poz-45162	7750 ± 50	8420	8603	1	<i>Betula</i> sp.
42	CUR 23-2-5	Poz-44314	2075 ± 35	1966	2135	0.965	<i>Fagus sylvatica</i>
43	ROQ 2-2-1	Poz-44315	Modern*	-4	-5	0.67	<i>Fagus sylvatica</i>
44	ROQ 6-2-1	Poz-44316	180 ± 30	136	224	0.559	<i>Fagus sylvatica</i>
45	ROQ 6-2-2	Poz-45168	315 ± 30	346	464	0.765	<i>Betula</i> sp.
46	ROQ 9-2-1	Poz-46539	1535 ± 30	1355	1449	0.595	<i>Quercus</i> sp.
47	ROQ 15-2-1	Poz-44317	4115 ± 25	4527	4658	0.588	Cf <i>Fagus sylvatica</i>
48	ROQ 16-2-3	Poz-44318	1665 ± 35	1513	1634	0.847	Cf <i>Fagus sylvatica</i>
49	ROQ 18-2-3	Poz-44320	4850 ± 70	5457	5736	0.959	Cf <i>Fagus sylvatica</i>
50	ROQ 23-4-1	Poz-44321	Modern*	-4	-6	1	<i>Fagus sylvatica</i>

*Modern: after 1950 AD; **Cal BP lower and Cal BP upper indicate lower and upper limits of the calibrated radiocarbon dates intervals (2 sigma), respectively; ***Prob.: probability

Appendix 2 List of charred wood reference species of Landes de Gascogne (available at INRA-UMR BIOGECO) (collectors: G. de Lafontaine, A. Ducouso & C.A. Amasifuen Guerra, 2011)

Collection Number	Family	Species	Common name
001	Sapindaceae	<i>Acer campestre</i> L.	Field maple
002	Sapindaceae	<i>Acer negundo</i> L.	Box elder
003	Aquifoliaceae	<i>Ilex aquifolium</i> L.	Holly
004	Araliaceae	<i>Hedera helix</i> L.	Ivy
005	Betulaceae	<i>Alnus glutinosa</i> (L.) Gaertn.	Black alder
006	Betulaceae	<i>Betula pendula</i> Roth	Common birch
007	Betulaceae	<i>Carpinus betulus</i> L.	Horbeam
008	Betulaceae	<i>Corylus avellana</i> L.	Hazel
009	Adoxaceae	<i>Sambucus nigra</i> L.	Common elder
010	Celastraceae	<i>Euonymus europaeus</i> L.	Spindle tree
011	Cornaceae	<i>Cornus sanguinea</i> L.	Dogwood
012	Cupressaceae	<i>Juniperus communis</i> L.	Common juniper
013	Fabaceae	<i>Cytisus scoparius</i> (L.) Link	Common broom
014	Fabaceae	<i>Robinia pseudoacacia</i> L.	Black locust
015	Fagaceae	<i>Castanea sativa</i> Mill.	Spanish chestnut
016	Fagaceae	<i>Fagus sylvatica</i> L.	Beech
017	Fagaceae	<i>Fagus sylvatica</i> L.	Beech
018	Fagaceae	<i>Quercus pyrenaica</i> Steven	Pyrenean oak
019	Fagaceae	<i>Quercus robur</i> L.	Common oak
020	Pinaceae	<i>Pinus pinaster</i> Aiton	Maritime pine
021	Rhamnaceae	<i>Frangula alnus</i> Mill.	Alder buckthorn
022	Rosaceae	<i>Crataegus monogyna</i> Jacq.	Common hawthorn
023	Rosaceae	<i>Malus sylvestris</i> Mill.	European wild apple
024	Rosaceae	<i>Mespilus germanica</i> L.	Common medlar
025	Rosaceae	<i>Prunus avium</i> (L.) L.	Wild cherry
026	Rosaceae	<i>Prunus spinosa</i> L.	Sloe tree
027	Rosaceae	<i>Sorbus domestica</i> L.	Service tree
028	Rosaceae	<i>Sorbus torminalis</i> Crantz	Wildservice tree
029	Salicaceae	<i>Populus tremula</i> L.	Aspen
030	Malvaceae	<i>Tilia cordata</i> Mill.	Small-leaved lime

RÉSUMÉ

Nous avons utilisé une approche pédoanthracologique pour reconstruire l'histoire paléoécologique de l'ensemble des petites populations de hêtre isolées dans le sud-ouest de la France (Landes de Gascogne). Nos objectifs étaient d'évaluer si le hêtre avait persisté tout au long du dernier maximum d'extension glaciaire dans des refuges cryptiques au sud-ouest de la France et d'essayer de découvrir si ces petites populations de hêtre sont d'origine relique ou anthropique. Le hêtre était présent dans le sud-ouest de la France à différentes périodes au cours des derniers 44,000 cal yr BP. Un hiatus des dates ^{14}C au cours du maximum glaciaire a empêché de retrouver une preuve directe de la persistance de hêtre au cours de cette période. La résolution locale de l'approche employée a permis d'inférer que les microclimats humides locaux aurait pu tamponner le climat glacial contraignant, et que la présence de hêtre à 9000 cal yr BP, soit 2200 ans plus tôt qu'inféré par les études palynologiques suggèrent qu'un scénario impliquant la persistance régionale de hêtre ne peut pas être exclu. La dynamique naturelle de ces forêts fragmentées au cours de l'Holocène et de la dernière période glaciaire suggère une origine reliques des peuplements de hêtre.

RESUMEN

En este estudio utilizamos un método basado en el análisis de partículas de carbón presentes en el estrato mineral del suelo para reconstruir la historia paleoecológica del conjunto de poblaciones aisladas de haya presentes en el suroeste de Francia (Landes de Gascogne). Nuestros objetivos fueron de evaluar si el haya permaneció el último máximo glacial en refugios crípticos en el suroeste de Francia, y explorar si el origen de estas poblaciones es relicto o antrópico. El haya estuvo presente en el suroeste de Francia, en diferentes periodos de los últimos 44,000 años cal yr BP. Sin embargo, no hay evidencia directa de la persistencia de haya durante el último máximo glacial debido a la ausencia de datos ^{14}C en ese periodo. La resolución espacial local del método usado nos permitió inferir que el microclima húmedo de las localidades evaluadas pudo haber amortiguado el clima glacial regional, y que la presencia de haya a 9000 cal yr BP, 2200 años antes de lo revelado por estudios palinológicos, indica que no podemos descartar la presencia de haya en todo el escenario regional. La dinámica natural de estos bosques fragmentados, durante el Holoceno y el último periodo glacial, sugiere un origen relicto de estas poblaciones de haya.