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1

8000 years of vegetation history in the northern Iberian Peninsula inferred from the palaeoenvironmental study of the Zalama ombrotrophic bog (Basque-Cantabrian Mountains, Spain)

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This paper focuses on pollen, spores, non-pollen palynomorphs (NPPs), and certain geochemical elements from the ombrotrophic blanket bog of Zalama (Basque-Cantabrian Mountains, northern Iberian Peninsula), with the support of a robust chronology based on 17 AMS ^{14}C dates. The main results related to the last 8000 years show that, during the early middle Holocene, pines and deciduous forests were the most extensive tree formations. At the beginning of the succession, pines reach 44%, showing probably some regional abundance, while after 7600 cal. a BP, deciduous forests were particularly abundant. From *ca*. 6500 cal. a BP the diagram shows the first anthropogenic evidence, linked with the new economic practices related to the Neolithic of the Basque-Cantabrian Mountains. From 3300 cal. a BP the expansion of *Fagus sylvatica* is particularly clear, becoming since then one of the dominant forests in this region. We also discuss the Holocene evolution of other noteworthy plant communities in south-western Europe, such as *Taxus baccata*, *Juglans* and shrublands.

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Different aspects of peatlands have long been studied in the scientific literature from two basic perspectives: i) their function as "islands of biodiversity", i.e. refuges of particularly vulnerable species, and ii) the use of peatlands as palaeoenvironmental archives. These natural deposits can be interpreted from many different viewpoints, and their contribution is essential for a proper understanding of past climatic, biotic, and cultural records (Barber 1993; Lappalainen 1996; Chambers *et al*. 2010; de Jong *et al*. 2010). In this sense, ombrotrophic bogs, such as the Zalama peat bog presented in this work, are especially noteworthy deposits. Their water regime and nutrient supply are derived directly and exclusively from precipitation (Lindsay 1995). As a result, they are oligotrophic and usually highly acidic environments, ensuring overall good preservation of organic matter (Pontevedra-Pombal *et al*. 2006, 2013). These characteristics are critical in making ombrotrophic peatlands excellent palaeoenvironmental archives which yield data on global climate changes as well as on the impact of mining, agriculture, and livestock.

The area surrounding the Zalama peat bog is also of biogeographical interest because it acts as the border between the Eurosiberian and Mediterranean regions. The existence of several mountain barriers parallel to the coastline limits the progressive arrival of Atlantic influences, favouring complex and rich floristic variability (Aseginolaza *et al.* 1996). Therefore, this mountain region currently has a rich variety of landscapes, where floristic elements typical of the moist conditions of the Atlantic area coexist with species better adapted to the continental climate on the northern Spanish plateau. It is also a relatively unknown region from the palaeoenvironmental standpoint due to the scarcity of palaeobotanical studies (Iriarte 2008; Pérez-Díaz *et al.* 2015). The only the palynological research available until now has been conducted in the nearby peat bog of Los Tornos (Peñalba 1989, 1994; Muñoz-Sobrino *et al*. 2005) and the archaeobotanical studies (pollen, charcoal, seeds) of some archaeological sites located in the bottom of the valleys, such as El Mirón (Iriarte 2012; Peña-Chocarro 2012; Zapata 2012), Cotobasero (Zapata 2002), La Boheriza (Iriarte 1995), and La Cabaña (Iriarte 1999). In short, all these factors, i.e. its nature as an ombrotrophic bog, its geographical location, and the scarcity of palaeobotanical research in this area, make the Zalama peat bog extremely valuable for evaluating the landscape, climate conditions, and human pressure during the Holocene.

In this paper, we discuss the Holocene evolution of the vegetation in the Basque-Cantabrian region over the last 8000 years. For this, we present a high-resolution study of pollen grains, spores, and non-pollen palynomorphs, as well as geochemical data of trace elements from the ombrotrophic bog of Zalama (Basque-Cantabrian Mountains, northern Iberian Peninsula), this being probably the most south-westerly recorded example of a blanket bog in Europe (Heras & Infante 2005).

Study area

The study site is the peat bog of Zalama (43º8´6´´ N, 3º24´35´´ W, 1330 m a.s.l.), located in the vicinity of a peak of the same name, in the south-westernmost corner of the Basque-Cantabrian Mountains (Ordunte Mountains, Basque Country, northern Iberian Peninsula). It is located on a gentle, domed hill on the watershed between the Cantabrian and Mediterranean hydrographic areas (Fig. 1A). This blanket bog is located near the main summit and is unaffected by water movement in streams or overland flow. The peat rests directly on periglacial deposits with quartzite fragments and therefore there is no other organic soil horizon (Fig. 1B) (Heras & Infante 2004). Originally covering an area of 5 ha, it has been badly affected by fires used by cattle breeders to control pastures (Heras & Infante 2005). Today the burnt area is occupied by bare rock and mineral soil. The blanket bog still covers 2.5 hectares (Heras & Infante 2004), and today is under a major restoration process (Aguirre-Pascual 2011). The predominant geological bedrock is made up of Lower and Upper Cretaceous sedimentary rocks (Middle and Upper Albian-Lower Cenomanian) and sandstones with abundant quartz grains (Garrote *et al*. 1992).

The peat bog is located in an Atlantic climatic area. The nearest weather station (Cerroja) is located 10 km to the north. In 2014 the measurements indicated an average yearly precipitation of 1341 mm for a total of 185 rainy days, and a mean annual temperature of 13.7 ºC (Euskalmet 2011). However, this station is located at a much lower elevation (677 m a.s.l.), while at higher elevations rainfall is presumably heavier. It is also important to note the frequent mist on the nearby peaks even in summer, due to the orographic barrier of the Basque-Cantabrian Mountains to the moist air from the Bay of Biscay. This constant moisture throughout the year is essential for the good preservation of the peat bog.

The current vegetation of the peat bog is composed of a dense peaty moorland purely of ombrotrophic characteristics, dominated by *Calluna vulgaris*, with abundant heath peatlands (*Erica tetralix*), dry heaths (*Erica cinerea*), *Molinia caerulea*, *Daboecia cantabrica*, *Sphagnum rubellum*, *Juncus squarrosus*, *Ulex gallii*, and *Eriophorum vaginatum* (Uribe-Etxebarria *et al*. 2006). There are also communities of *Pteridium aquilinum*, a heliophilous fern that sometimes grows on bogs (Fig. 1C). In the vicinity, the current forests are restricted to lower elevations (Bariego & Gastón 2002), with acidophilous beech forests composed of *Fagus sylvatica*, *Ilex aquifolium*, *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Blechnum spicant*, *Veronica officinalid*, and *Euphorbia dulcis* on the northern slopes. The southern slopes, where the insolation is greater, have *Quercus pyrenaica* forests with *Pseudoarrhenatherum longifolium*, *Pteridium aquilinum*, *Arenaria montana*, and *Potentilla erecta*, as well as scattered Scots pine (*Pinus sylvestris*) stands on the sunny slopes (Aseginolaza *et al*. 1996).

Materials and methods

Coring and sampling

The core was taken using a Wardenaar corer (10x10x100 cm; Wardenaar 1987) for the first 100 cm and a Russian peat sampler (GYK type, 50 cm length; 5 cm in diameter) for the rest. The coring point was located in the centre of the peat bog where a core with a total length of 232 cm was extracted (Table 1). Contiguous sampling was performed in the uppermost 30 cm, where samples were taken every centimetre. The rest of the core samples were taken every 2 cm. Two surface samples were also taken at the peat-vegetation interface. All together, a total of 131 samples were analysed.

Chronology

Selected peat samples were sent to Angström Laboratory of Uppsala University (Sweden) and Centro Nacional de Aceleradores of Sevilla University (Spain) for radiocarbon dating, in order to establish patterns of bog development. Chronology was based on 17 accelerator mass spectrometry (AMS) radiocarbon dates on peat material (Table 2). The dates were calibrated using CALIB 7.1 radiocarbon calibration program with the IntCal13 curve (Reimer *et al.* 2013). An age/depth model (Fig. 2) was produced using Clam 2.2 software (Blaauw 2010), applying a smooth spline solution. Confidence intervals of the calibrations and the age/depth model were calculated at 95% (2σ) with 1000 iterations. The calendar scale was cal. a BP. The ages of the base of the core represent 8000 calibrated years of peat accumulation.

Pollen and NPPs analyses

A total of 131 samples (1 cm^3) were used for the palynological study. All the palynological samples were chemically treated following Girard & Renault-Miskovsky (1969), with the samples being concentrated in a high-density Thoulet solution (Goeury & de Beaulieu 1979). Small aliquots of the residues were mounted in glycerine jelly, sealed with *Histolaque*. Pollen and spores were identified according to Faegri & Iversen (1989), Moore *et al*. (1991) and Reille (1999). Non-pollen palynomorphs were identified according to van Geel (1978, 2001, 2006), van Geel *et al.* (1981, 1989, 2003) and Cugny (2011). In each sample a minimum of 500 terrestrial pollen grains were counted. Cyperaceae, aquatics, and spores were excluded from the pollen sum to avoid over-representation (Wright & Patten 1963). The pollen diagram (Fig. 3) was produced using the Tilia 2.0 and TGView programs (Grimm 1992, 2004). Local pollen assemblage zones (LPAZ) were constructed on the basis of agglomerative constrained cluster analysis of incremental sum of squares (CONISS) with square-root-transformed percentage data (Grimm 1987).

Elemental geochemistry

Mineral contribution to the bogs can be assessed using reference lithogenic elements present in rocks and soils. It can be assumed that variations in the trace elements in the ombrotrophic peat profile reasonably reflect fluctuations in the deposition of atmospheric soil dust (ASD) (Shotyk 1996; Pontevedra-Pombal *et al*. 2013). Titanium (Ti) and vanadium (V) are such elements. The total content of these elements was determined in the peat as a proxy of soil erosion. We performed a statistical normalization of the element content (Z-scores, calculated by dividing the difference between the element content of each sample and the average value of the whole core by the standard deviation) which minimizes differences due to local effects (i.e. due to differences in the geological composition) and results in a relative scale of variation in enrichment to identify periods of elevated values.

In Teflon vessels an aliquot of 0.300 g of each sample was digested (180 ºC – 5 – 1000 W and 180 ºC – 10 – 1000 W) by microwave (Milestone, Ethos1 plus) using a mixture of 8 ml HNO_3 69% (PlasmaPURE-Scp Science) and 2 ml of HF 48% (Sigma Aldrich). Due to high organic matter content, the addition of H_2O_2 was required. Then, the digested sample was flushed in a final volume of 25 ml with 2.5% H_3BO_3 (Sigma Aldrich). The sample was filtered and stored in plastic tubes in the cold and dark until analysed by quadrupole inductively coupled plasma-mass emission spectrometry (ICP-MS) using a Varian 820-MS. Routinely, 10% of the samples were analysed in duplicate. All calibration standards were prepared as samples from multi-element solutions. For both elements, the correlation coefficients of the calibration lines were equal or superior to 0.999. All measured elements were above the detection limits, while the blank sample values were below. To assess the precision and accuracy of analytical procedures and to check the calibration, we used five internationally certified reference materials (CRMs). Element recoveries in CRMs were consistent with the certified values (Table 3). CRMs and blanks were inserted into every sample batch.

Results

Pollen zonation

The pollen-percentage diagram was divided into two main local pollen-assemblage zones (LPAZ) (Fig. 3) using CONISS. The subzone ZAL-1 was in turn divided into three sub-zones (ZAL-1a, ZAL-1b and ZAL-1c). The diagram provides insight into the vegetation history of the Basque-Cantabrian Mountains from 8000 cal. a BP to the present, both at the local and regional scale.

Zone ZAL-1a (231-166 cm depth, 7975-6463 cal. a BP). The oldest section of this LPAZ (231-208 cm, 7975-7585 cal. a BP) shows that the main arboreal taxon was *Pinus* (44-34%). Other taxa such as deciduous *Quercus* and *Corylus* have a secondary role (<20%). Shrubs reached noteworthy values, mainly *Erica* and *Calluna*. Poaceae registered the lowest values in the entire sequence (<10%). Hygrophilous taxa reached 5-8% of the total pollen. The rest of this LPAZ (208-166 cm, 7585-6463 cal. a BP) was characterized by the decline of pines, which decreased to 22%. Deciduous *Quercus* and *Corylus* percentages rose to 27 and 19%, respectively. Both shrubs (*Erica* and *Calluna*) and hygrophilous taxa (Cyperaceae, monolete and trilete ferns) were substantially represented.

Zone ZAL-1b (166-106 cm, 6463-4789 cal. a BP). This LPAZ showed lower values for tree pollen (<65%), with mesophilous taxa as the main components. Deciduous *Quercus* exceeded 26%, with *Corylus* in a secondary position (maximum values of 18%). *Pinus* decreased (13-18%) and *Juglans* reappeared. *Taxus* appeared at this LPAZ with very low values. Shrub percentages declined, with *Erica* and *Calluna* as the main taxa. Herbs increased markedly (maximum values of 32%), with Poaceae as the main taxon (22%). This area is also characterized by higher percentages of Cardueae, Chenopodiaceae, *Dipsacus fullonum*, *Plantago major/media*, *P. lanceolata* and *Urtica dioica*, but with low values (<2%).

Sordaria reached maximum values of 2%. Hygrophilous taxa showed lower values, almost all Cyperaceae.

Zone ZAL-1c (106-50 cm, 4789-2251 cal. a BP). This zone had increasing values of tree pollen, reaching 68%, the main contributor being *Corylus* (27%). Other mesophilous taxa that maintained a continuous and significant presence were deciduous *Quercus* (16-25%). In this LPAZ, *Fagus* occurred for the first time in the succession at 3900 cal. a BP. Pine-pollen percentages exhibited a decreasing trend. Among the shrubs, *Erica* and *Calluna* were best represented. Herbs displayed a significant presence (21-31%), with Poaceae as the main taxon (maximum 25%). Cichorioideae and Fabaceae also displayed an increasing trend. From 4000 cal. a BP, Cyperaceae, Monolete, and Trilete ferns showed an increasing trend. Among non-pollen palynomorphs, *Sordaria* reached a maximum peak of 5.2% at 3460 cal. a BP.

Zone ZAL-2 (50-0 cm, 2251-0 cal. a BP). The diagram reflects several noteworthy changes. Regarding tree pollen, this zone is characterized by increasing values of *Fagus*. At the beginning, its trend was upwards, and it reached high percentages (13%). However, from 900 cal. a BP its values began to decline. Here, *Corylus* and deciduous *Quercus* maintained a noteworthy presence. The shrubs showed significant growth, *Calluna* and *Erica* increasing to reach their maximum percentages in the entire succession (25 and 19%, respectively). Among herbs, Poaceae continued as the main taxon, while the rest of the taxa registered values of <3%. Hygrophilous taxa increased their values. *Pteridium aquilinum* reappeared at that time, and the main non-pollen palynomorph was *Sordaria* (4.5%).

Geochemical record

The mean, standard deviation, and maximum and minimum concentrations of Ti and V and ash content are summarized in Table 4. The values found were comparable to those found in bogs throughout Europe (Shotyk *et al*. 2002; Coggins *et al*. 2006; Cloy *et al*. 2011; Allan *et al*. 2013; Pontevedra-Pombal *et al*. 2013). Ti and V concentrations were significantly correlated ($r = 0.948$; $p < 0.0001$; $N = 129$), and both closely followed the ash content ($r = 0.837$ and 0.828 respectively; $p < 0.001$; $N = 129$), suggesting that the inorganic content of the peats was supplied by atmospheric soil dust. The ash content and concentrations of lithogenic elements (Ti and V) showed a similar trend (Fig. 4) during the bog development. Background values were not exceeded until after 4000 cal. a BP. From then on, the three geoindicators gradually increased to the present. The increase detected in the last 500 years is attributable to greater soil erosion resulting from agricultural and industrial intensification or to climatic changes over the last millennium (Le Roux *et al*. 2004; Zaccone *et al*. 2008; Pontevedra-Pombal *et al*. 2012).

Discussion

Pines vs. deciduous forests in the Basque-Cantabrian Mountains (8000-6500 cal. a BP)

The oldest part of the Zalama pollen record shows the highest values of pine pollen of the entire succession, reaching maximum of 44% (Fig. 3). These values are not sufficient to support the presence of large pine forests in the local environment of the site. It is known that most pines, due to high pollen production and good dispersal ability, have a larger pollen-dispersal area than do other species (Poska & Pidek 2010). According to studies of modern pollen rain in some well-developed pine forests, composed mainly of *Pinus sylvestris*, we infer the presence of large pine forests only when the values reach 60% (López-Sáez *et al*. 2013). Accordingly, we suggest at this time the presence of regional pine forests, or perhaps the presence of scattered trees near the site, but in any case mature forests. The significance of our data is that they indicate the presence of pine forests in the study area during the middle Holocene, although these forests do not have a phytosociological characterization in the literature of northern Spain (Rivas-Martínez 1987). One compelling question is what species of pines were present in the environment in the last eight millennia. Although we could not distinguish between them and we retrieved no macro-remains, we suggest that the vast majority of pine pollen in the core originated from *Pinus sylvestris* because it is the only species remaining today in the area surrounding the peat bog (Aseginolaza *et al*. 1996). In this area, the 19th-century authors Willkomm & Lange (1861), following the works of Planelles (1852) and Olazábal (1856), stressed in the nature of relict Scots pine forests in the Cantabrian Mountains (Rubiales *et al*. 2010, 2012). Similarly, Catón-Santaren & Uribe-Etxebarria (1980), Ruiz-Urrestarazu (1989) and Aseginolaza *et al.* (1996) point to the presence of relict *Pinus sylvestris* forests in the Basque Country, hardly altered by anthropogenic activities in the last millennium. In any case, we cannot completely rule out the contribution of other pines, such as *Pinus nigra*, macrofossils of which have been found in several deposits of the northern plateau (García-Amorena *et al*. 2011).

According to the data from Zalama peat bog, from 7585 cal. a BP, pines suffered a major setback parallel to the development of deciduous forests in the Basque-Cantabrian Mountains. The reasons for this phenomenon are likely climatic. The increased precipitation and temperature in the early middle Holocene, which has been detected in lakes, bogs, marine sediments and speleothems in northern Iberian Peninsula (Santos *et al*. 2000; Roucoux *et al*. 2001; Moreno *et al.* 2011; Stoll *et al*. 2013), resulting in tree recolonization, caused an early decline of pine forests across the northern Iberian Peninsula. This phenomenon was sharper and more sudden in the Atlantic areas of northern Iberia, as demonstrated by Muñoz-Sobrino (2001), Muñoz-Sobrino *et al.* (2007) and Rubiales *et al*. (2008, 2011, 2012). Deciduous taxa, especially *Quercus*, *Corylus,* and sometimes *Betula*, in this temperate and humid climate had certain advantages that allowed them to compete successfully against coniferous formations which survived in other areas. Pines, therefore, remained in such regions as the more continental, dry inland areas of the southern slopes of the Cantabrian Range, less suitable for the competition of hardwoods (Muñoz-Sobrino 2001; Rubiales *et al.* 2008, 2011; Muñoz-Sobrino *et al*. 2012). From these times, ~7585 cal. a BP, deciduous trees formed the dominant forests in the environs of the Zalama bog. Above all, hazel and deciduous *Quercus* started to play a major role in local forests. Deciduous *Quercus* had already gained terrain since the decline of pines, and became one of the dominant Holocene forest taxa. Hazel was also a foremost species in the wet mesophylous forest of the northern Iberian Peninsula, where it formed part of mixed deciduous formations.

Notably, *Juglans* also expanded its presence at this time. It was documented at the beginning of the sequence (ZAL-1), but between 6460 and 5500 cal. a BP (low part of ZAL-2) it became more abundant, though with low values (<2%). Walnut has usually been considered an introduced species in Western Europe during the late Holocene (Beug 1975), but research in the last few decades have provided sufficient data to demonstrate its indigenous nature in the Iberian Peninsula (Sánchez-Goñi 1988; Carrión & Sánchez 1992; Ramil-Rego *et al*. 2000; Da Silva Oliveira 2012; Mercuri *et al*. 2013), as in the case of the Zalama pollen record. In addition, some development of riparian communities (*Alnus*, *Fraxinus*, and *Salix*) can be detected in the diagram, probably at a regional scale. This, together with the increase in fern spores (monolete and trilete) and Ranunculaceae, confirms the onset of more humid conditions in this period. This pattern is not an isolated event but a regional trend, involving the entire Atlantic area of northern Spain, as has been demonstrated in other deposits, such as Los Tornos (Peñalba 1989) and Pozo do Carballal (Muñoz-Sobrino *et al*. 1997) peat-bog pollen records. In Enol Lake, the multi-proxy climatic reconstruction suggests favourable temperatures and the presence of highly stable forested landscapes at 8700-4650 cal a. BP (Moreno *et al*. 2011).

First anthropogenic evidence (~ 6500-3300 cal. a BP)

In addition to the regression of pines and the progressive advance of deciduous forests, other changes in the landscape were detected by 6500 cal. a BP in the Zalama pollen record. The most notable are related to the first evidence of human impact ~6460 cal. a BP. From then on, the pollen diagram reflects some decrease in forests and their replacement by open areas, mainly pastures of Poaceae and other synanthropic taxa (*Plantago lanceolata*, *P. major/media*, *Urtica dioica*, Caryophyllaceae, Chenopodiaceae, and Cichorioideae; Fig. 3). These elements, together with the coetaneous appearance of coprophilous fungi (*Sordaria*) suggest nearby pastures and certain types of pastoral pressure (Behre 1981; Sjögren 2006; López-Sáez & López-Merino 2007; Sjögren & Lamentowicz 2008). In addition, the presence of pyrophilous taxa (*Asphodelus albus*) and carbonicolous fungi (*Chaetomium* sp.) appears to reflect the use of fire as a tool for opening spaces by early farming communities (van Geel 1978; Kuhry 1985).

These first pieces of evidence of human impact on forests are related to early cattle raising in the Basque-Cantabrian Mountains. The northern area of the Iberian Peninsula in general and the Basque-Cantabrian Mountains in particular, have been considered marginal areas for Neolithic farming (Zapata & Peña-Chocarro 2013). However, in the last decade several archaeological findings, supported mainly by archaeobotanical research, have refuted these assumptions (Zapata 2002, Zapata *et al*. 2004). In fact, such evidence can be explained by the profusion in the region of archaeological sites precisely dated to the Early Neolithic (end of the 8th and first half of 7th millennia ago) such as Los Canes, Los Gitanos, El Mirón, Kobaederra, Pico Ramos, Lumentxa, Arenaza, Herriko Barra and Marizulo (Zapata *et al.* 1997, 2007; Alday & Mujika 1999; Arias & Altuna 1999; Zapata 2002; Iriarte *et al.* 2004; Arias 2005; Peña-Chocarro *et al.* 2005; Ontañón *et al.* 2013). This phenomenon of increased human impact is detected also in nearby pollen records of Monte Areo (López-Merino *et al*. 2010) and Pena Veira peat bogs (Ramil & Aira 1993). This intensity of human impact (forest clearance and burning) 6500 years ago has been also recorded in other regions of northern Spain such as Galicia, by clear signs of erosion, cumulic soil formation, and the appearance of stone and charcoal lines (Kaal *et al*. 2008).

This anthropogenic evidence indicates some reduction in Zalama peat bog between 4800 and 3400 cal. a BP, this being manifested in the interruption of continuous curves of different taxa such as

Sordaria, *Urtica dioica*, *Plantago lanceolata*, *Dipsacus fullonum*, Cichorioideae, Chenopodiaceae, and *Aster* (Fig. 3). This phase of less human pressure during the Copper and Early Bronze Ages is also reflected by the expansion of hazel, which prospered because of its pioneering nature (Costa-Tenorio *et al*. 2005), and occupied certain areas previously devoted to pasture. This episode is part of a long-term climatic phase of global cooling (Magny & Haas 2004), which has also been recorded in the north-western Iberian Peninsula (Fábregas *et al*. 2003).

Another noteworthy phenomenon during this time is the beginning of the continuous curve of *Taxus*. This plant was not identified previously, but ~6000 cal. a BP it makes its appearance in the Zalama pollen record with a continuous curve until 3000 cal. a BP. Its presence is not prominent (<2%) but its appearance at this time is remarkable. Although it is an anemophilous tree, its pollen production and dispersal rate are very low. Some studies show a meagre representation in surface samples taken near the tree, reflecting that even extremely low pollen values (1-2%) must attest to the local presence of this genus (Heim 1970; Norýskiewicz 2003). The increase in the use of yew wood is detected at some archaeological sites located in northern Iberia dated in the Early Neolithic, such as El Mirón, Aizpea, and other archaeological sites in the Sierra de Cantabria (Zapata 2001, 2012; Ruiz-Alonso 2014). However, from the charcoal record alone it is difficult to determine the real significance of *Taxus* in the landscape. Indeed, wood macro-remains linked to human settlements can be used as indicators of the presence of this genus, rather than a quantitative estimate of the prevalence of *Taxus* in the landscape (Pérez-Díaz *et al*. 2013; Uzquiano *et al*. 2014). From 6000 cal. a BP the first continuous curves of yew pollen are recorded in many deposits located in the northern Iberian Peninsula, particularly in some well-dated peat bogs such as Zalama and nearby Los Tornos in the Basque-Cantabrian Mountains as well as in other pre-Pyrenean bogs such as Atxuri and Belate (Peñalba 1989; Pérez-Díaz *et al.* 2015). They all have continuous pollen values spanning a quite similar chronology, between 6000 and 2700 cal. a BP. In another pollen record, Saldropo (Peñalba 1989, 1994), no continuous values were recorded, but rather only isolated occurrences 5000-2750 cal. a BP.

The expansion of Fagus and the current landscape status (3300 cal. a BP-present day)

In this last phase, the forests in this area underwent a major change, a transformation led by the expansion of a single taxon: *Fagus*. Its first appearance in the Zalama pollen record was dated to 3900 cal. a BP with sporadic, discontinuous, and low values. However, from 3300 cal. a BP the pollen diagram shows the presence of a continuous curve of this new element, and from 3000 cal. a BP its values exceed 1%, reaching a maximum of 13% (Fig. 3). Therefore, beech forests were one of the main vegetation communities in the late Holocene of the Basque-Cantabrian Mountains and nearby regions such as the western Pyrenees and Cantabrian Region (Table 5).

It is currently accepted that the present Iberian beech forests originated from populations located in several refuge areas, according to the growing number of palaeobotanical finds in ancient chronologies and genetic studies (Martínez-Atienza & Morla-Juaristi 1992; Rodriguez-Guitián *et al*. 1996; Ramil-Rego *et al*. 2000; Costa Tenorio *et al*. 2005; Magri *et al*. 2006; López-Merino *et al*. 2008; Magri 2008). From those regions, located mainly in the northern Iberian Peninsula, *Fagus* expanded during the late Holocene. The causes of the expansion of beech can be summarized by two main non-mutually exclusive factors: climatic and anthropogenic forcing (Galop *et al*. 2004; Bradshaw & Lindbladh 2005; Tinner & Lotter 2006; Giesecke *et al*. 2007; López-Merino *et al*. 2008; Magri 2008; Valsecchi *et al*. 2008; Muñoz-Sobrino *et al*. 2009; Bradshaw *et al*. 2010; Bradley *et al*. 2013).

Regarding the prevailing climate conditions in this area, the palynological record of Zalama appears to manifest some increase in effective moisture by rising values of *Corylus* and fern spores since 3300 cal. a BP. Similarly, other regional studies, such as the multiproxy analysis of the Enol Lake, suggest a wetter climate with more humid conditions between 4650 and 2200 cal. a BP (Moreno *et al*. 2011). Such conditions would be optimal for *Fagus* development.

The other agent perhaps involved in this process, human disturbances, caused open landscapes due to agropastoral activities, which could have favoured *Fagus* regeneration (Iversen 1973; Watts 1973; Björkman 1999). This would have allowed them to form mixed forests with other deciduous tree formations, and later monospecific beech forests.

In the succession of Zalama, from 3400 cal. a BP (Middle Bronze Age), the pollen diagram shows renewed anthropization, after a certain abandonment phase mentioned above (4800-3400 cal. a BP). This is manifested by some intensification in local pastoral activities and some indicators of disturbances associated with fire and overgrazing (*Chaetomium* sp. and *Asphodelus albus*). This phase coincides with surpassing, for the first time in the Zalama record, background levels of lithogenic elements, represented by their z-scores (Fig. 5), indicating greater soil erosion. Passing this first buffering threshold may be an indirect sign of the aforementioned deforestation, but also of the intensity in the direct impact of the increased use of soil resources, coinciding with the more abundant cereal pollen and coprophilous fungi spores (Fig. 3). The beginning of these erosive crises has been detected in soils, peatlands, and archaeological sites around the north-western Iberian Peninsula (Fábregas *et al*. 2003). In Zalama bog, the ash content and V and Ti concentrations began to increase before any remarkable sign of forest decline. This characteristic has also been detected in other studies, suggesting that lithogenic geoindicators are more sensitive to small changes in the landscape than pollen is (Hölzer & Holzer 1998; Martinez-Cortizas *et al*. 2005). This phenomenon of increasing anthropization by 3400 cal. a BP occurred at the same time as the continuous curve of *Fagus* (Fig. 3). Thus it seems probable that the expansion of beech was favoured by anthropogenic disturbances, as seen in other parts of Europe such as the French Pyrenees (Galop & Jalut 1994; Jalut *et al*. 1998) or even within the Iberian Peninsula (Ramil-Rego *et al*. 2000; Martínez-Cortízas *et al*. 2005; López-Merino *et al*. 2008). The emergence of beech in the vegetation of the Basque-Cantabrian Mountains significantly affected other existing forest communities. The mixed deciduous forests dominated by *Quercus* and *Corylus*, suffered a significant setback at this time because of the great competition of beech in disturbed environments.

The emergence of *Fagus* coincides also with the decline of *Taxus* ~3000-2700 cal. a BP. This decline does not appear to be due to a single factor but rather to the concurrence of different elements, both natural and human, which encouraged this regressive dynamics in the late Holocene. Among the major causes, several biological, environmental, and anthropic factors can be noted: e.g. increasing anthropic pressure, exclusive competition with other tree species (mostly *Fagus*), and self-regeneration problems (Iszkulo 2010; Linares 2013). Other elements harmed by the expansion of beech were the conifers. Pines, which displayed a regressive trend throughout the Holocene, also suffered a significant setback at that time, and almost disappeared from the pollen record of the Zalama peat bog (Fig. 3).

In addition to the beech forest formations, other elements now played a major role at a local scale, i.e. shrubs. From 2250 cal. a BP these thickets showed an increasing trend, with a greater representation of *Calluna vulgaris* and *Erica*. This coincidence with other notable evidence of human impact (some deforestation, anthropogenic communities, and grasslands) may indicate its origin in the perturbations derived from the extension of grazing areas related to the expanding use of this pastoral setting. In Zalama bog, this phase of retreat in trees, expansion of *Fagus* and shrubs, and in general, anthropization of the landscape is synchronous with a dramatic increase in ASD deposition (Fig. 5), which marks the beginning of intensifying soil erosion. Besides consistency with biotic markers of agriculture and grazing, this erosive phase was also coeval with the onset of iron metallurgy in the Cantabrian-Pyrenean area, the development of which led to extensive deforestation (Etxezarraga 2004). The same erosive phase was recorded in polycyclic soils and peatlands in NW Iberia including dense lines of charcoal, gravel and stones, and growing palaeopollution (van Mourik 1986; Martínez-Cortizas *et al*. 2005; Costa-Casais *et al*. 2009; Pontevedra-Pombal *et al*. 2013; Silva-Sánchez *et al*. 2014). These shrublands have dominated the landscape at a local scale until the present in our study area. The main components of the landscape near the bog are currently *Calluna vulgaris* and *Erica tetralix*. This phenomenon of heathland expansion is commonplace in the north-western Iberian Peninsula for this period (e.g. Allen *et al*. 1996; Muñoz Sobrino *et al*. 1997, 2001; Morales-Molino *et al*. 2011, 2013, 2014).

Conclusions

The study of the raised ombrotrophic bog of Zalama contributes to the knowledge of the evolution of the landscape in the northern Iberian Peninsula during the Holocene. Its location on the border between the Eurosiberian and Mediterranean regions offers added value, reflecting the history of vegetation dynamics, climatic conditions, and anthropogenic activities in a deposit of special biogeographical interest.

The beginning of the succession (8000 cal. a BP) is characterized by pine forests, showing the importance of pine woods in the south-western European landscape in the early middle Holocene. The new climatic conditions triggered the *Pinus sylvestris* retreat in this area, dated in Zalama from 7600 cal. a BP. In this context, rising temperatures and greater precipitation favoured the development of deciduous forest (oak, hazel, birch), much better adapted to the new conditions. Since then, pines have been restricted to the more continental and drier areas on the southern slopes of the area.

Palaeobotanical data show that yew has been present in several places in the northern Iberian Peninsula since at least the Pleistocene. However, higher values are documented during the middle Holocene. From 8000 cal. a BP, significant use of yew wood appears in archaeological contexts. From 6000 cal. a BP, yew expands somewhat, according to its increasing presence in the pollen records. This phase lasted several millennia, until the late Holocene, when yew populations underwent a regression around 3000 cal. a BP.

The first anthropogenic disturbances are noted in Zalama peat bog during the middle Holocene. From 6460 cal. a BP, pasturelands increasingly occupy some open areas in this mountain range. The presence of anthropogenic taxa and coprophilous fungi points to the new productive economic activities related to the first crop raising and animal husbandry in the Basque-Cantabrian Mountains.

In the late Holocene the biggest change in the vegetal landscape was the expansion of beech forests. The spread of beech forests in Zalama is documented from 3300 cal. a BP, at a very similar time as in other areas of the northern Iberian Peninsula. Anthropogenic perturbations may have favoured this phenomenon.

The geochemical record of Zalama Bog suggests that the carrying capacity of the soil was definitely exceeded in the late Holocene, beginning a sequence of erosive phases coetaneous with deforestation and the expansion of anthropic spaces and widespread shrublands.

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TABLE AND FIGURE CAPTIONS

Figure 1. Study area. A. Map indicating the location of the peat bog of Zalama (white star) and the other sites mentioned in the text (black points), B. Image of the peat bog of Zalama (Patxi Heras), C. Image of *Pteridium aquilinum*, D. Aerial view of the peat bog of Zalama.

Figure 2. Age-depth model of Zalama peat bog.

Figure 3. Palynological diagram of the peat bog of Zalama.

Figure 4. Trend of atmospheric soil dust geoindicators in different periods of the development of Zalama bog. Periods: 1000 to 500 cal. a BP (Late Middle Ages); 1500 to 1000 cal. a BP (Early Middle Ages); 2000 to 1500 cal. a BP (Late Antiquity and Roman times); 3000 to 2000 cal. a BP (Late Bronze - Iron Age); 4000 to 3000 cal. a BP (Bronze Age).

Figure 5. Distribution of Ti and V trace elements overtime and the main changes in the vegetal landscape in the late Holocene record of Zalama peat bog.

Table 1. Morpho-stratigraphy of the peat section at Zalama peat bog. VP= von Post scale (von Post, 1937); IP= sodium pyrophosphate index (Lynn *et al*. 1974; Soil Survey Staff 1975).

Table 2. AMS-radiocarbon data with 2σ range of calibration from Zalama peat bog.

Table 3. V and Ti values from the peat bog of Zalama. The asterisk is reference value.

Table 4. Inorganic ash (%), titanium and vanadium (mg kg^{-1}) content in Zalama bog.

Table 5. Chronology of the expansion of *Fagus* in northern Iberia.

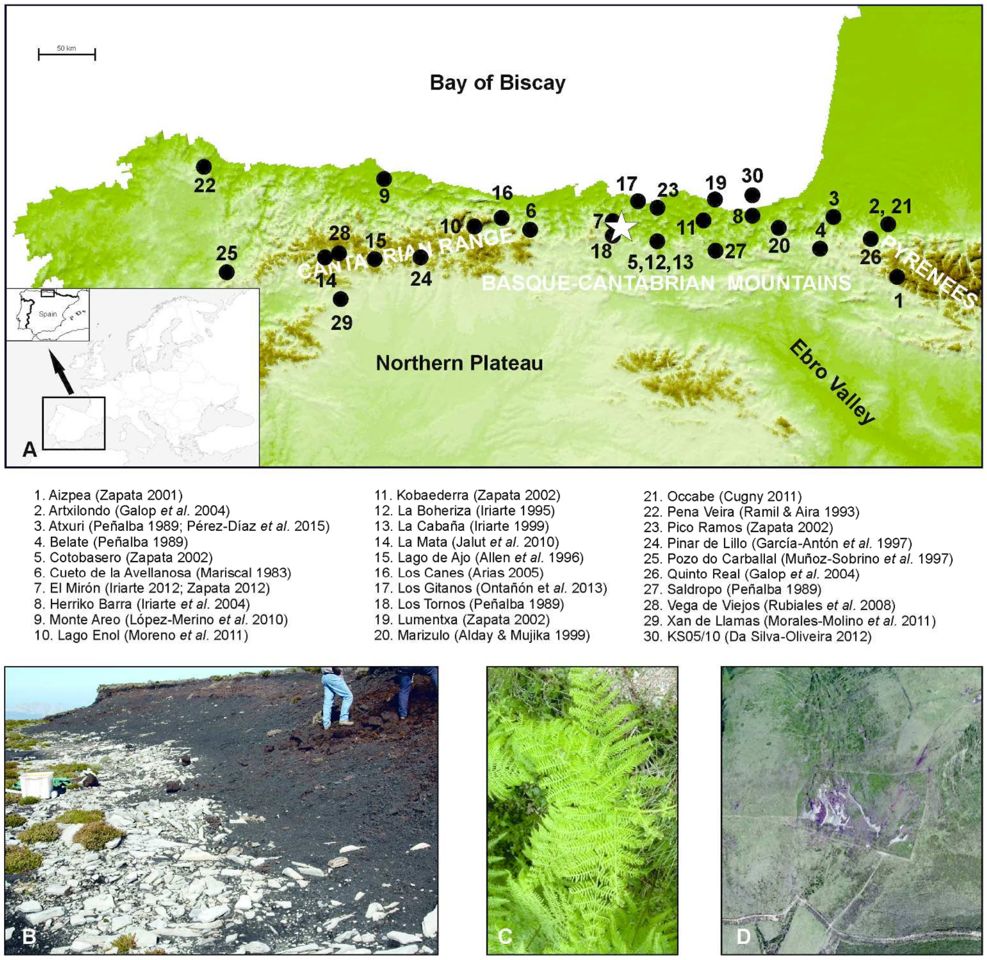

Figure 1. Study area. A. Map indicating the location of the peat bog of Zalama (white star) and the other sites mentioned in the text (black points), B. Image of the peat bog of Zalama (Patxi Heras), C. Image of Pteridium aquilinum, D. Aerial view of the peat bog of Zalama.
202x196mm (300 x 300 DPI)

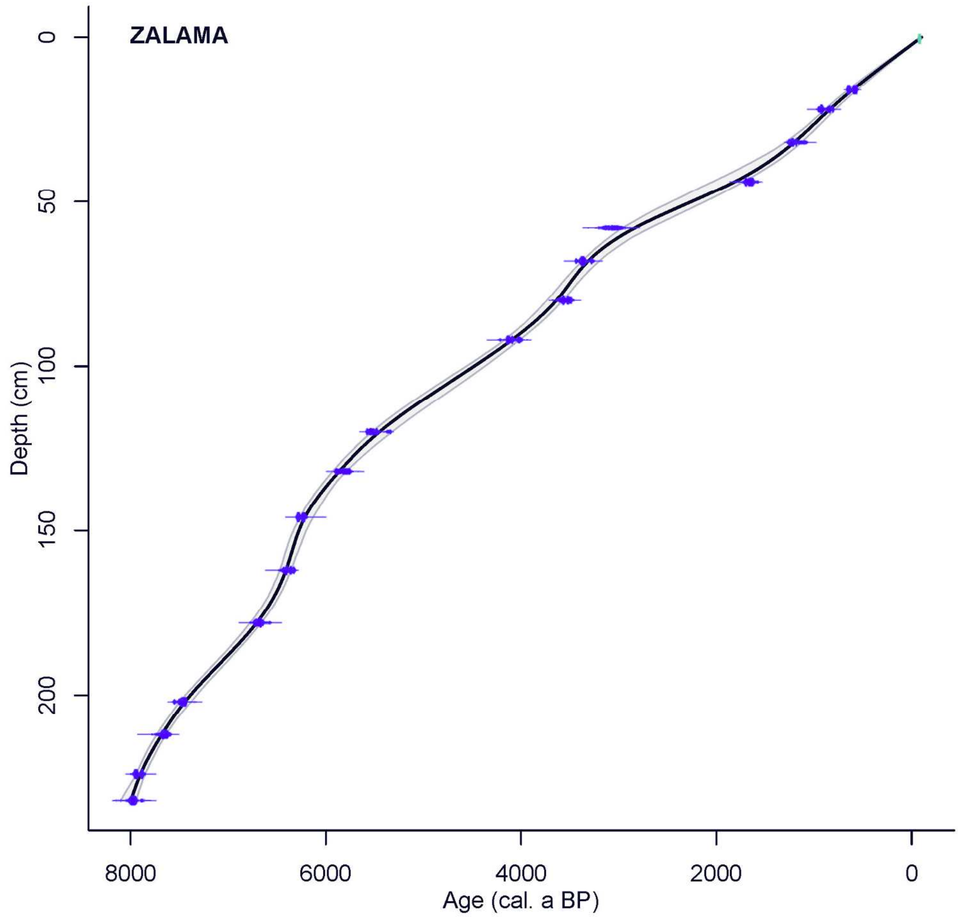

Figure 2. Age-depth model of Zalama peat bog.
182x170mm (300 x 300 DPI)

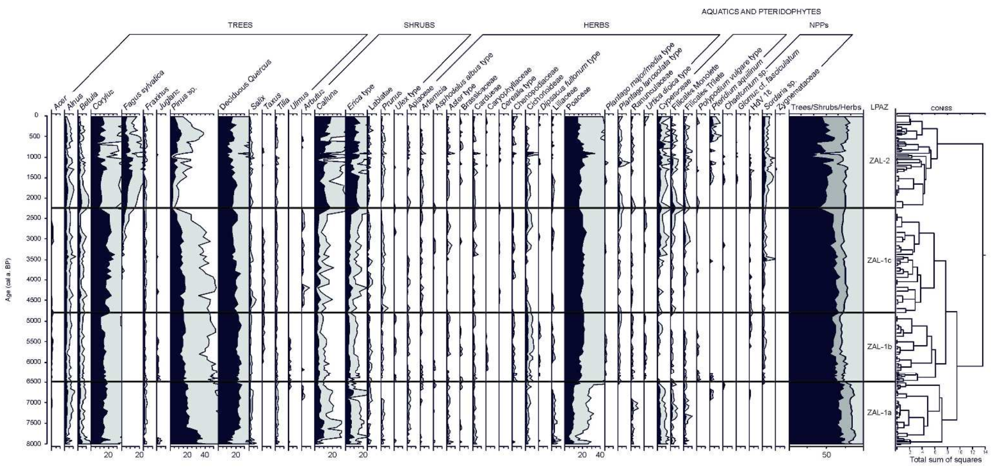

Figure 3. Palynological diagram of the peat bog of Zalama.
272x127mm (300 x 300 DPI)

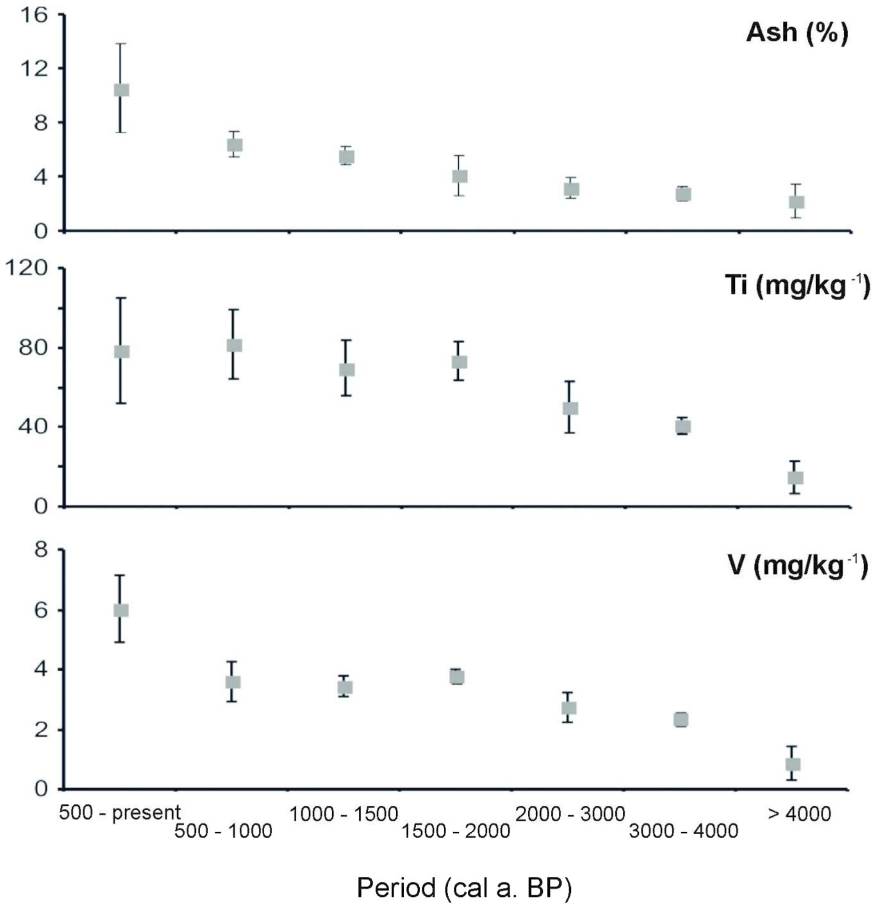

Figure 4. Trend of atmospheric soil dust geoindicators in different periods of the development of Zalama bog. Periods: 1000 to 500 cal. a BP (Late Middle Ages); 1500 to 1000 cal. a BP (Early Middle Ages); 2000 to 1500 cal. a BP (Late Antiquity and Roman times); 3000 to 2000 cal. a BP (Late Bronze - Iron Age); 4000 to 3000 cal. a BP (Bronze Age).
153x152mm (300 x 300 DPI)

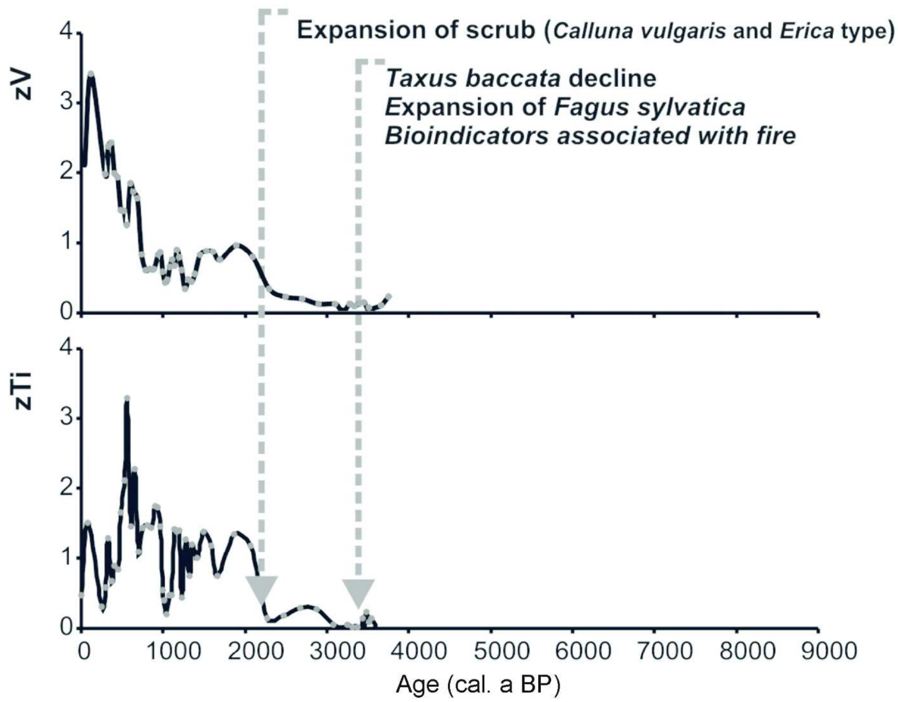

Figure 5. Distribution of Ti and V trace elements overtime and the main changes in the vegetal landscape in the late Holocene record of Zalama peat bog.
172x137mm (300 x 300 DPI)

Depth (cm)	Morpho-stratigraphic features	VP	IP
0-6	Vegetation-peat interface	H1	-
6-12	Brown, dry and compact peat	H2	Fibric
12-18	Brown to dark brown, dry and compact peat	H4	Hemic – Fibric
18-32	Reddish brown peat	H2	Fibric
32-48	Dark brown peat	H5	Sapric - Hemic
48-86	Blackish brown peat. Charcoal fragments	H7	Sapric
86-94	Brown to dark brown peat	H4	Hemic – Fibric
94-112	Dark brown peat	H5	Hemic
112-120	Dark brown peat. Wood fragments	H6-7	Sapric
120-160	Reddish fibrous peat with *Sphagnum* remains	H2	Fibric
160-224	Grey-black peat	H7-8	Sapric
224-232	Grey-black peat with very fine quartz sands Minerogenic phase	H9	Sapric

Sample	Material	Depth interval (cm)	Lab. code	Age (^{14}C a BP)	Age range (^{14}C cal. a BP)	Calendar age a BP; average probability
ZAL 10	Peat	15-16	CNA626	635±30	553-665	599
ZAL 16	Peat	21-22	CNA627	990±40	796-963	902
ZAL 26	Peat	31-32	Ua-41646	1245±34	1073-1272	1199
ZAL 34	Peat	42-44	CNA628	1755±30	1565-1736	1661
ZAL 41	Peat	56-58	CNA629	2920±50	2925-3212	3065
ZAL 46	Peat	66-68	Ua-41647	3142±34	3324-3447	3368
ZAL 52	Peat	78-80	Ua-41648	3321±31	3475-3633	3548
ZAL 58	Peat	90-92	CNA630	3740±30	3984-4157	4097
ZAL 72	Peat	118-120	Ua-41650	4757±41	5328-5589	5511
ZAL 78	Peat	130-132	Ua-41651	5076±40	5734-5914	5817
ZAL 85	Peat	144-146	Ua-41652	5454±38	6190-6306	6251
ZAL 93	Peat	160-162	CNA631	5615±35	6309-6466	6387
ZAL 101	Peat	176-178	Ua-41653	5858±38	6597-6753	6680
ZAL 113	Peat	200-202	Ua-41654	6561±47	7420-7566	7470
ZAL 118	Peat	210-212	Ua-41655	6826±47	7582-7750	7658
ZAL 124	Peat	222-224	CNA632	7095±35	7846-7981	7932
ZAL 128	Peat	230-232	Ua-35895	7150±50	7852-8053	7973

Certificated Reference Material	N	V (mg kg^{-1}) certified	V (mg kg^{-1}) measured	Ti (%) certified	Ti (%) measured
NIST – Montana Soil (2710a)	3	82±9*	86±3	0.311±0.007	0.307±0.053
NIST – Coal Fly Ash (1633c)	3	286.2±7.9	283±5.4	0.724±0.030	0.726±0.0410
NIST – Coal (1632b)	3	14*	17±1.5	0.045±0.002	0.043±0.012
NIST – Apple Leaves (1515)	3	0.26±0.03	0.25±0.08		
NIST – Peach Leaves (1547)	3	0.37±0.03	0.39±0.09		

	Average	SD	Min.	Max.
Ash	4.60	5.55	0.80	42.46
Ti	38.98	31.64	6.90	157.17
V	2.30	1.98	0.17	11.37

Region	Site	Altitude (m a.s.l.)	Date of the expansion of *Fagus*	References
Western Pyrenees	Occabe	1300	~4500 cal. a BP	Cugny (2011)
	Artxilondo	1100	~4500 cal. a BP	Galop *et al.* (2004)
	Atxuri	500	~4200 cal. a BP	Peñalba (1989); Pérez-Díaz *et al*. (2015)
	Quinto Real	910	~4000 cal. a BP	Galop *et al.* (2004)
	Belate	847	After 3335-2955 cal. a BP	Peñalba (1989)
Basque-Cantabrian Mountains	Saldropo	625	~4150-3645 cal. a BP	Peñalba (1989)
	Los Tornos	920	After 2965-2715 cal. a BP	Muñoz-Sobrino *et al.* (2005)
	Zalama	1330	~3300-3000 cal. a BP	This study
Cantabrian Region	Cueto de la Avellanosa	1320	~3000 cal. a BP	Mariscal (1983)
	Enol lake	1070	~3500 cal. a BP	Moreno *et al.* (2011)
	Lago de Ajo	1570	~3200 cal. a BP	Allen *et al.* (1996)