Journal of Vegetation Science ▮▮ (2014)

Late Holocene persistence of *Abies alba* in low-mid altitude deciduous forests of central and southern Italy: new perspectives from charcoal data

Gaetano Di Pasquale, Emilia Allevato, Anna Cocchiararo, Daniela Moser, Marco Pacciarelli & Antonio Saracino

Keywords
Anthropic relic; Apennines; Archaeology; Charcoal analysis; Human impact; Mediterranean mountains; Potential natural vegetation; Timber and fuel; Undisturbed forest vegetation; Vegetation history

Nomenclature
Pignatti (1982).

Received 23 July 2013
Accepted 15 December 2013
Co-ordinating Editor: Sally Woods

Di Pasquale, G. (gaetano.dipasquale@unina.it), **Allevato, E.** (Corresponding author, eallevat@unina.it) & **Saracino, A.** (a.saracino@unina.it): Department of Agriculture, University of Naples Federico II, Via Università 100, Portici, 80055, Italy
Cocchiararo, A. (anna.cocchiararo @gmail.com) & **Pacciarelli, M.** (marco.pacciarelli@unina.it): Department of Humanistic Studies, University of Naples Federico II, Via Nuova Marina 3, Naples 80134, Italy
Moser, D. (dmoser@gshdl.uni-kiel.de): Institute for Ecosystem Research, Palaeoecology, Christian-Albrechts-University Kiel, Olshausenstrasse 75, Kiel 24118, Germany

Abstract

Questions: Pollen data for *Abies alba* Mill., a key European tree species, show broad occurrence in the Italian peninsula in the early to mid-Holocene diffusion (until ca. 6000 yr ago) along the Italian peninsula and a strong decline/local extinction starting ca. 5000 yr ago. This decline has been attributed to climate change. Recently, high-resolution pollen studies, mainly in northern Italian sites claim that *A. alba* disappearance was mainly due to human impact. We examined the presence of *A. alba* in archaeological sites of southern and central Italy in order to trace the late Holocene history (last 3000 yr) of this tree and enhance understanding of its role in pre-anthropic vegetation and of human involvement in its decline.

Location: Central and southern Italy.

Methods: Anthracological analysis was conducted in six archaeological layers at the archaeological site of Trebbio-Spinellina (800–600 BC, Sansepolcro, Tuscany). A critical analysis of wood/charcoal literature relevant to *Abies* in central and southern Italy was used to corroborate the results of Trebbio-Spinellina. Charcoal records from archaeological sites have been compared with the current distribution of *A. alba*.

Results: At Trebbio-Spinellina, *A. alba* charcoal is present in all contexts examined, together with mesophilous broad-leaf taxa (*Quercus* deciduous, *Carpinus betulus*, *Ostrya carpinifolia*, *Corylus avellana*). A low charcoal percentage of *Fagus sylvatica* and *Taxus baccata* is also found; evergreen taxa are mainly represented by *Quercus ilex* with occasional shrubs (i.e. *Viburnum*, *Cistus*, *Erica*). In the literature, we identified several peninsular and insular Italian archaeological sites showing charcoal evidence of *Abies*, accompanied by deciduous oaks, mainly *Q. cerris*, and other broad-leaf mesophilous trees, dating from the Iron Age to the Middle Ages. All sites, except one, lie at less than 600 m a.s.l., and far from present-day *A. alba* communities.

Conclusion: Results call for a reworking of the prevailing paradigm of *A. alba* as a relic mountain species. Indeed, *A. alba* once grew at lower altitudes than currently and was associated with deciduous oaks, mainly *Q. cerris*, and other mesophilous broad-leaf trees. This evidence calls into question the suitability of the Potential Natural Vegetation (PNV) concept usually applied in the floristic approach. The recent population decline is attributable to human activity rather than to climate change. Finally, the persistence of *A. alba* until the late Holocene calls into question the assumptions that it is a relic species with no potential to expand its spatial range.

Doi: 10.1111/jvs.12196

Introduction

Abies alba Mill. is a south-central European mesophilous, shade-tolerant, late-successional tree species with several scattered populations in the western Mediterranean regions, in northeast Spain, southern France and Italy (Quézel & Médail 2003). In southern France, it grows on calcareous or calcareous–dolomitic soils down to 500 m a.s.l., associated with *Quercus ilex* (Quézel & Médail 2003); in the Iberian Peninsula, it occurs mainly above 1200 m a.s.l. (Peguero-Pina et al. 2007); in Corsica, *A. alba* grows in scattered locations mainly associated with *Fagus sylvatica* between 800 and 1500 m a.s.l. (Gamisans 1999); and in central and southern Italy, several small and isolated populations grow at highest elevations in the Apennine chain, mainly above 1000 m a.s.l.

Abies alba is genetically differentiated into five regional types (Balkans, northern Italy, southern Italy, southern France and southern Spain) that closely correspond to palaeoecological evidence for its refugial areas (Willis & McElwain 2002). Molecular analysis also indicates that southern and northern Italian population are genetically separated (Konnert & Bergmann 1995; Vendramin et al. 1999; Liepelt et al. 2010). This evidence corroborates earlier observations of Giacobbe (1950) who, on the basis of morphological and ecological features, hypothesized the existence of an 'Apennine' variety. Recent tree ring studies have confirmed the existence of Southern Apennines ecotypes with a strong adaptation to summer drought (Carrer et al. 2010) and a higher resistance to *Heterobasidion abietinum* root disease (Puddu et al. 2003).

At the northern edge of the Central Apennines, dendroecological analyses have shown that in the last century *A. alba* exhibited a progressive adaptation to more xerothermic conditions in response to climate warming (Gallucci & Urbinati 2009); in the extreme south of its range this tree seems to be less affected by drought because it has reduced biological activity during the summer months (Freni 1955; Santini & Martinelli 1991).

Pollen data indicate, for the early Holocene, a wide diffusion of this species and a strong decline/local extinction starting in the middle Holocene and developing asynchronously over its range. In the Northern Apennines, after a period of dominance at most sites, the *Abies* decline occurred asynchronously between ca. 6500 yr cal. BP and 3000 yr cal. BP (e.g. Watson 1996; Cruise et al. 2009; Vescovi et al. 2010a,b; Guido et al. 2013), while in the coastal sector of northern Tuscany and Liguria (Colombaroli et al. 2007; Bellini et al. 2009) similar decreases occurred between 7000 cal. yr BP and 5000 cal. yr BP. Further south, on the Colline Metallifere, *A. alba* was widespread until about 7000 cal. yr BP and decreased around 6500 cal. yr BP (Drescher-Schneider et al. 2007). Apart from Watson's data (1996), all the cited papers refer to the presence of *A. alba* outside the Apennines at middle altitudes and sub-coastal areas. Pollen data from Latium testify to an early extinction of *A. alba* at the beginning of the Last Glacial Period (Follieri et al. 1998) and it never reappears in this region during the Holocene (Mercuri et al. 2002).

In southern Italy, *A. alba* pollen data indicate a different history. The record of Lago di Monticchio documents a middle Holocene *Abies* expansion not recorded elsewhere in central Italy and a decline starting at ca. 3000 cal. yr BP (Watts et al. 1996; Allen et al. 2002). A late decline has also been observed at Lago Trifoglietti in northern Calabria (Joannin et al. 2012).

The Holocene history of *A. alba* is based mainly on pollen studies, and climate change has been the hypothesized cause of its decline (Sadori et al. 2011). Recently, several scholars suggested human pressure (e.g. Allen et al. 2002; Joannin et al. 2012; Guido et al. 2013) and forest fires (Tinner et al. 1999; Vescovi et al. 2010a) as the driving force of *A. alba* depletion. A recent synthesis based on a sound pollen data set and macrofossils highlights the strong role of anthropization, whereas climatic simulations based on pollen-independent palaeoclimatic records emphasize the low impact of climate on *A. alba* decline (Tinner et al. 2013). Pollen data from central-southern Italy fail, however, to explain *A. alba* history for the last 3000 yr because of the low spatial detail and the lack of matching analyses of human history; therefore, the transition from pristine to anthropic vegetation remains unknown.

An understanding of the recent history of *A. alba* is relevant for conservation/restoration strategy planning. To promote specific actions devoted to ensuring this species' long-term conservation, the Natura 2000 network (European Habitat Directive 92/43/ECC) has identified the following habitats with the presence of *A. alba* in the Apennines: Priority Habitat *9220 'Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*' and Priority Habitat *9510 'Southern Apennine *Abies alba* forests'. In addition, in southern Italy, *A. alba* persists or is locally extinct in the last decades in the Habitat 9210 'Apennine beech forests with *Taxus* and *Ilex*,' and in Habitat 91M0 'Pannonian-Balkan turkey oak-sessile oak forests'.

A recent debate has called into question the phytosociological approach to detecting pre-anthropic vegetation types and thus the Potential Natural Vegetation (PNV; Carrión & Fernández 2009; Chiarucci et al. 2010; Farris et al. 2010; Loidi et al. 2010; Loidi & Fernández-González 2012; Somodi et al. 2012). For example, on the Canary Islands recent pollen analyses show that before human settlement vegetation was dominated by *Quercus–Carpinus*

Doi: 10.1111/jvs.12196

together with *Pinus canariensis* (de Nascimento et al. 2009). In this case, the prevailing concept of PNV implies that the pre-anthropic (mature phase or climax) vegetation was the so-called laurel forest; thus, the supposed PNV emerges as a clear cultural construct (Carrión & Fernández 2009).

In fact, in sites with a long human history, the phytosociological approach yields scenarios with restricted predictive power and lacks a long-term perspective (Willis & Birks 2006). The difficulty in defining the potential range of a species and its related vegetation types on the basis of field ecological observations (e.g. vegetation surveys, relevès) is especially relevant for *A. alba*, which is particularly affected by human pressure (Tinner et al. 2013; Büntgen et al. 2014).

The goal of this work was to contribute to the late Holocene history of *A. alba* in central and southern Italy by means of archaeological charcoal (charred wood) data. Charcoal analysis in archaeological contexts is considered a good proxy for palaeoecological studies because charcoal resulting from long-term human activities and processes is useful for reconstructing past local vegetation (Figueiral & Mosbrugger 2000). Moreover, these data have a more local resolution than pollen and a better match with cultural history, which can be made because charcoal originates directly from human activities (Chabal et al. 1999). In this context, we present the first charcoal data from the archaeological site of Trebbio-Spinellina (Fig. 1; Tiber Valley, central Italy) dated to the Iron Age, in addition to reviewing the wood/charcoal data from central and southern Italy to better understand the late Holocene *A. alba* distribution and the human role in defining the present-day geographic pattern of this species.

The Trebbio-Spinellina archaeological site lies in the Upper Tiber Valley between Sansepolcro and Città di Castello (300 m a.s.l.). Between 800 and 600 BC, Umbrian populations inhabited the site, which includes both residential and productive areas. The Tiber River was the boundary line between the Umbrian people (hydrographic left, east side) and the Etruscans (hydrographic right, west side), and archaeological data suggest that exchanges did not occur between these two populations (Colonna 1986). Therefore, the area of wood collection had to be localized to the lower slopes of the Alpe della Luna (Fig. 1), which today is covered by a mixed deciduous mesophilous forest dominated by *Quercus cerris* (300–700 m a.s.l.) and at higher altitude by *Fagus sylvatica* woods. Cultivated fields and urban agglomerations mainly cover the floodplain.

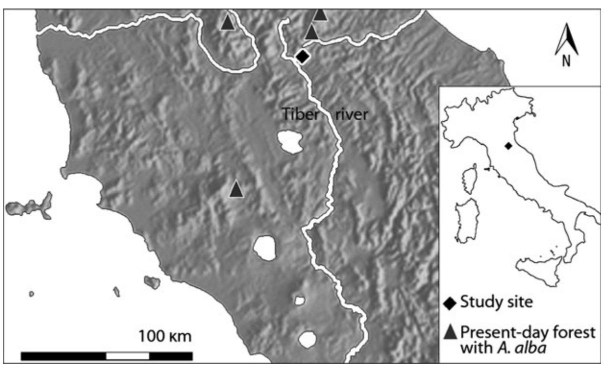


Fig. 1. Map of the study site. Archaeological site of Trebbio-Spinellina and nearby present-day *Abies alba* forests. The Tiber River represents the boundary line of the wood catchment area located at its hydrographic left (east side).

Methods

Anthracological analysis was carried out at the site of Trebbio-Spinellina (Fig. 1), where sediment samples were collected in three archaeological contexts from six layers labelled following the stratigraphic sequence and the archaeological interpretation of the context: layers 364, 376, 378 and 379 from a waste dump, layer 375 from a living surface, and layer 414 from a ditch. The layers are all dated to the 6th century BC.

Charcoal fragments, sorted in the fraction over 4.0 mm, were identified under an incident light microscope working between 100× and 1000× magnification, with reference both to wood atlases (Greguss 1955, 1959; Schweingruber 1990) and to our reference collection. Wood anatomy features of *Abies* do not allow identification to species level (Schweingruber 1990), but in this study, the taxonomic attribution to *A. alba* is consistent with the evidence that *A. alba* is the only *Abies* species occurring in mainland Italy during the past 200,000 yr (Lang 1994). At least 250 charcoal fragments were analysed in each layer, and taxa percentages were calculated from the total of fragments analysed (Chabal et al. 1999).

The paper is further based on a critical review of the literature relevant to *Abies* wood/charcoal from peninsular and insular Italian archaeological sites (Alps are excluded) spanning from the late Middle Bronze Age to the Middle Ages (Fig. 3). For comparison, a spatially detailed map of the present geographic distribution of *A. alba* along the A-pennines has been drawn by merging Habitat *9220 and Habitat *9510 sites included in the Natura 2000 network. Additional data come from field observations carried out by the authors in the last decades along the Apennine chains (for geographical coordinates, see Appendix S1). Sites reforested with *A. alba* were not considered.

We also evaluated the lower altitudinal limits for the species as the minimum elevation where *A. alba* saplings or adult trees grow. The minimum elevations of *A. alba* populations and altitudes of archaeological sites were plotted together against latitude values (Fig. 5).

Results

Charcoal analysis

At Trebbio-Spinellina, *A. alba* charcoal occurs in all contexts examined (Fig. 2) and ranges from 39% up to 65% of the total of charcoal fragments analysed. Archaeological characterization of the recovery contexts suggests that *A. alba* was being used for both woodworking and fuel. Deciduous taxa are well represented (i.e. *Quercus* deciduous, *Carpinus betulus*, *Ostrya*, *Corylus avellana*), while riparian species (*Populus*, *Salix*) are scarce; low percentages of *Fagus sylvatica* and *Taxus baccata* are also present in the waste dump, and evergreen taxa are mainly represented by *Quercus ilex* with a few shrubs (i.e. *Juniperus*, *Viburnum*, *Cistus* and *Erica*).

Literature review

We sought to collect all archaeobotanical citations relevant to *Abies* wood/charcoal along the Italian Peninsula, Sicily and Sardinia, but the list is probably not complete and underestimates the number of archaeological sites where *Abies* wood/timber was used. In Italy, anthracological data are scarce and most data are published in the grey literature, which is often difficult to trace. However, these data provided several examples of evidence of *Abies,* employed for timber as well as for fuel purposes, from the Bronze Age to the Middle Ages, spanning from Sicily to northern Tuscany (Fig. 3).

Abies alba distribution on the Apennines

A detailed map of present-day native populations (Fig. 4; for geographical coordinates see Appendix S1) permits the comparison of the geographic position of archaeological sites with the position of *A. alba* native populations and evaluation of the topographic distance between them. *A. alba* grows with several scattered populations along the whole Apennine chain. The most northern site is Monte Nero, belonging to the Emilian Apennine (Borghetti & Vignali 1988), while the most southern site is at Gambarie, located on the Aspromonte chains (Ciancio et al. 1985); in

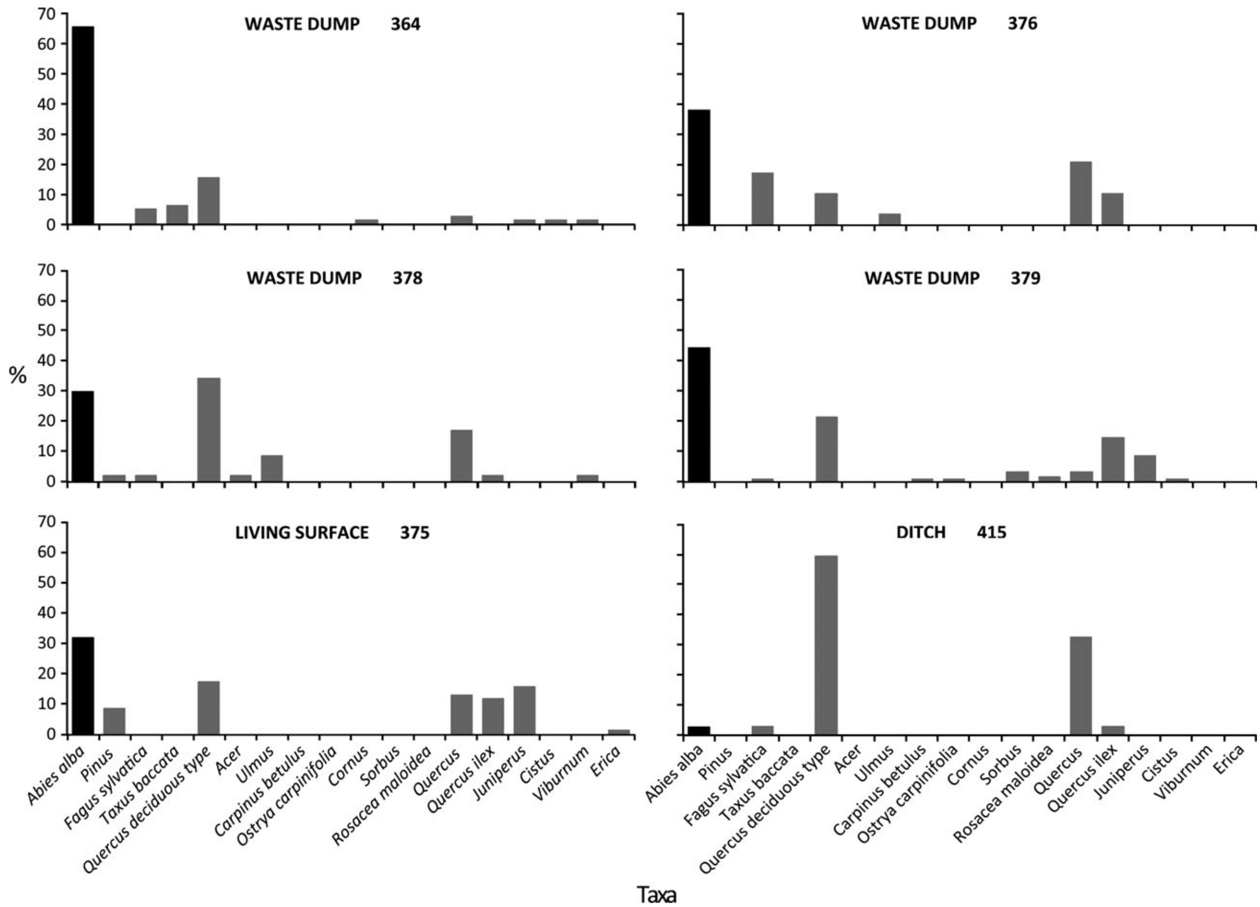
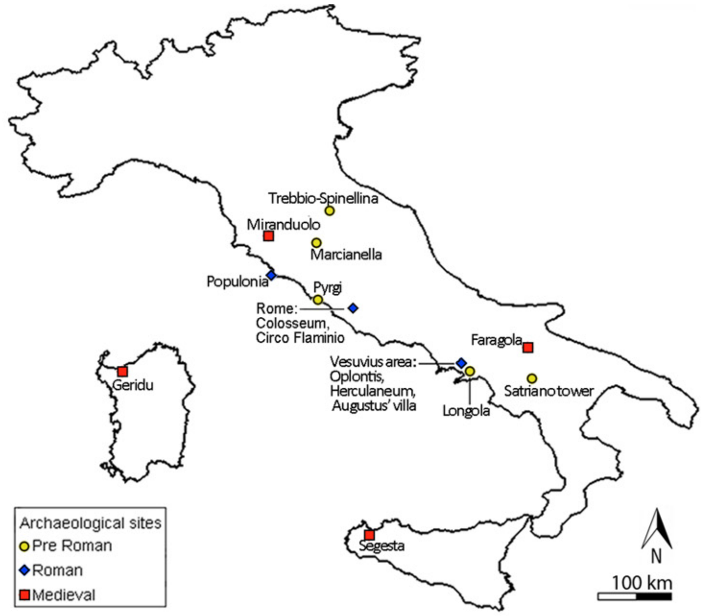


Fig. 2. Results of charcoal analysis. Taxon percentages are calculated from the total of analysed charcoal fragments in each layer.



Site		Geographical coordinates		Elevation m. a.s.l.	Supposed use of the fir wood	Archaeological dating	Reference
Trebbio-Spinellina	San Sepolcro (AR)	43°32'77"N	12°08'49"E	300	Building structures, fuel	6^{th} cent. BC	This article
Miranduolo	Chiusdino (SI)	43°7'11"N	11°4'48"E	500	Unknown	11^{th} - 12^{th} cent. AD	Di Pasquale et al. 2008
Marcianella	Chiusi (SI)	43°00'56"N	11°56'41"E	350	Fuel	3^{rd} cent. - 2^{nd} cent BC	Di Pasquale 2003
Populonia	Piombino (LI)	42°59'17"N	10°29'25"E	160	Building structures	2^{nd} - 1^{s}t cent. BC	Di Pasquale & Terzani 2006
Pyrgi	Cerveteri (Roma)	42°0'53"N	11°57'50"E	0	Unknown	ca 270 BC	Coccolini & Follieri 1980
Colosseum	Roma	41°53'24"N	12°29'32"E	20	Artefacts	4^{th} cent. BC	Follieri 1975
Circo Flaminio	Roma	41°53'33"N	12°28'38"E	16	Poles	2^{nd} cent. BC	Sadori et al. 2007
Faragola	Ascoli Satriano (FG)	41°12'17"N	15°33'59"E	420	Fuel	7^{th} cent. AD	Caracuta et al. 2012
Augustus' Villa	Somma Vesuviana (NA)	40°52'33"N	14°25'26"E	130	Building structures	BC 363 - BC 3 (^{14}C date of *Abies* charcoal)	Allevato et al. 2012
Herculaneum	Ercolano (NA)	40°48'21"N	14°20'50"E	12	Building structures	Before 79 AD	Moser et al. 2012
Longola	Poggiomarino (NA)	40°47'41"N	14°34'27"E	30	Poles and boards	16^{th} - 17^{th} cent. BC	Heussner 2008; Fioravanti et al. 2010
Geridu	Sorso (SS)	40°46'50"N	8°34'24"E	150	Unknown (little barked branches)	12^{th} cent. AD	Deiana pers. comm.
Oplontis	Torre Annunziata (NA)	40°45'25"N	14°27'10"E	5	Building structrures and frames	Before 79 AD	Moser et al. 2013
Satriano tower	Satriano (PZ)	40°34'10"N	15°38'18"E	980	Building structures	7^{th} cent. BC	Novellis 2008
Segesta	Calatafimi Segesta (TP)	37°56'24"N	12°50'15"E	350	Unknown (little barked branches)	12^{th}-13^{th} cent. AD	Castiglioni & Rottoli 1997

Fig. 3. Quoted sites where *Abies* charcoal/wood has been identified. Sites are listed according to their geographic location from north to south; archaeological dating refers to *Abies* charcoal.

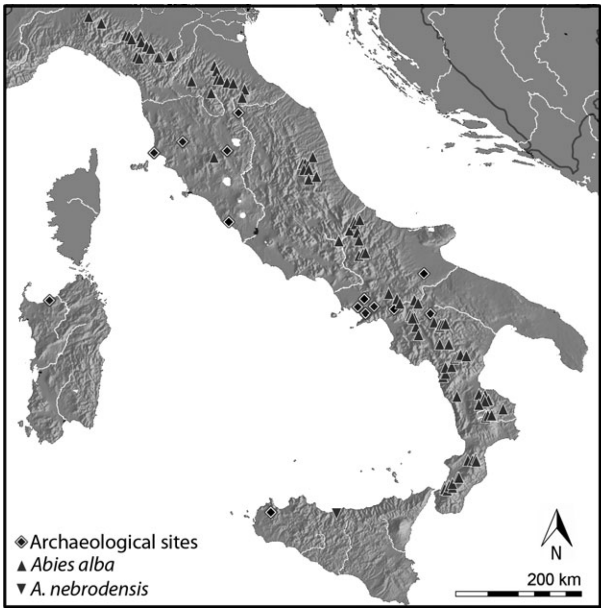


Fig. 4. Current distribution of *Abies alba* and archaeological sites where *Abies* charcoal has been identified (Italy, Alps excluded).

Sicily, *A. alba* is represented by the vicariant species *A. nebrodensis* (Morandini et al. 1994). The Gran Sasso and Laga massifs host the most eastern populations. In addition to the Apennine chains, *A. alba* grows on the Monte Amiata and on the Alpi Apuane. The topographic distance of the mainland archaeological sites from the nearest fir population ranges between 10 and 90 km.

The lower altitudinal limits of native *A. alba* populations along the Apennine range between 600 and 1600 m a.s.l. In contrast, the archaeological sites where *Abies* charcoal was found are mainly located at low altitudes, even in coastal and sub-coastal areas (15–500 m a.s.l.; Fig. 5).

Discussion

Charcoal data from Trebbio-Spinellina

Wood collection in prehistory/protohistory was normally carried out following the 'principle of least effort'; thus, in the areas situated closest to the settlements, the taxa found in a charcoal assemblage generally reflect their occurrence in the vegetation surrounding the site (Asouti & Austin 2005). Archaeological interpretations of the recovery contexts of the Trebbio-Spinellina site allow the inference that *A. alba* was used there both as building timber and fuel. Use for fuel strongly suggests a close supply area (Chabal 1997). On the whole, charcoal data suggest a vegetation type characterized by species that are today considered to be Mediterranean mountain taxa such as *A. alba* and *Fagus sylvatica*, co-occurring with species of the mixed deciduous forest (*Acer*, *Ulmus*, *Ostrya carpinifolia*, *Carpinus betulus* with deciduous *Quercus* prevailing) and finally by *Q. ilex* and a few evergreen shrub species. Also remarkable is the presence of *Taxus baccata*, whose distribution along the Apennine chains today is fragmented into small populations.

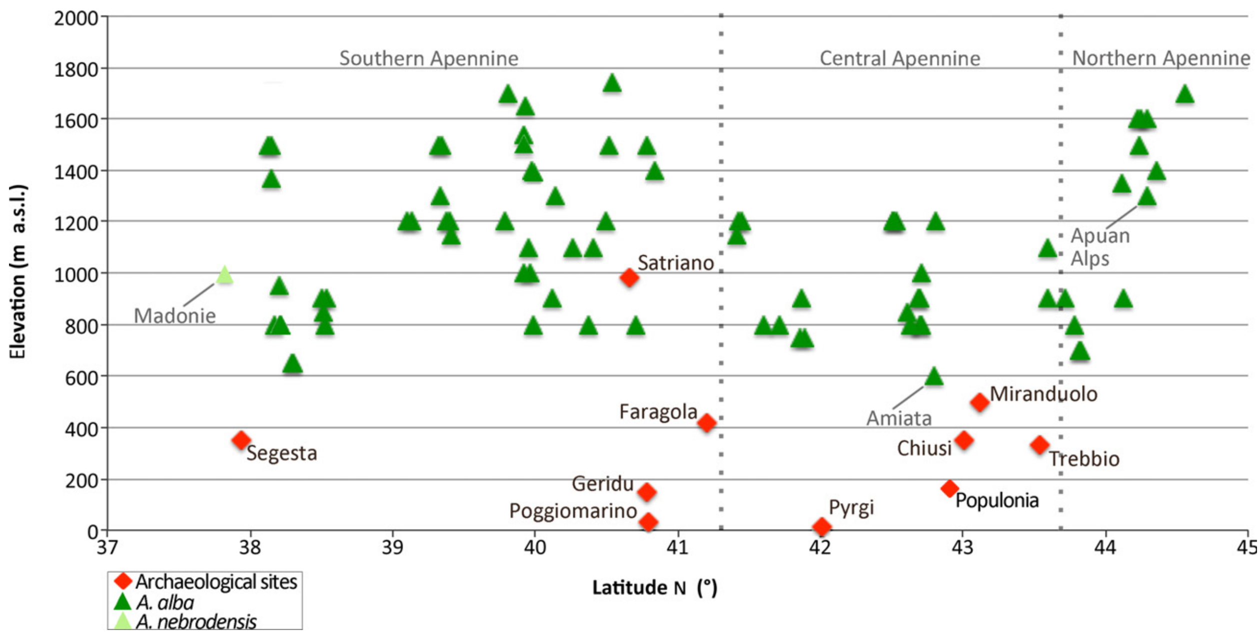


Fig. 5. Geographic location of sites with native populations of *Abies alba* and cited archaeological sites. The lowest limit of *Abies* is the minimum elevation where natural regeneration and/or adult *A. alba* trees growing isolated or in groups are detected.

Journal of Vegetation Science
Doi: 10.1111/jvs.12196

This conifer shares with *F. sylvatica* the same oceanic bioclimate and consequently grows mainly in thermophilous (low elevation) Mediterranean beech woodlands. Anthropogenic pressure has relegated it to the understorey and/or confined it to cliffs (Piovesan et al. 2009).

Charcoal assemblage suggests that *A. alba* trees were present in mixed mesophilous deciduous forests at the same altitude of the archaeological site or a little higher. This evidence highlights a strong discrepancy with the altitudinal belts where *A. alba* currently grows (Fig. 5), as well as with the current forest types classifications. More broadly, these data suggest a different altitudinal distribution of the species than that proposed by current vegetation belt classifications; Quézel & Médail (2003), for example, consider *A. alba* as a mountain tree having its ecological optimum between 1200 and 1600 m a.s.l. (étage montagnard), according to latitude. The reconstructed forest vegetation suggested by our charcoal data more closely resembles to some present forests where *A. alba* grows mixed with mesophilous deciduous taxa currently found at much lower elevations, starting from 600 m a.s.l. For example, near Monte Amiata, *A. alba* grows next to *Q. ilex* in mixed deciduous forests of *Q. cerris* (Arrigoni et al. 1990); in the Molise Apennine, *A. alba* is mainly associated with *Q. cerris*, *Acer campestre*, *Carpinus betulus* and *Fagus sylvatica* (Di Martino 1996), and in the Lucanian Apennines, *A. alba* is mixed with *Q. cerris* (Nolè et al. 2003).

Other wood/charcoal evidence of *A. alba* from the Bronze to the Iron Age (1700–200 BC)

Abies alba charcoals have been found in several other archaeological sites where it was used both for timber and fuel. For example, between the 3rd and 2nd centuries BC, *A. alba* was mainly associated with deciduous oak in southern Tuscany, where its wood is common in the charcoal assemblage of the Etruscan site of Marcianella (Figs 3 and 5). In this period, the site was a small centre for pottery production (Pucci & Mascione 2003), and *A. alba* was used for fuel in the furnaces for ceramics (Di Pasquale 2003). The present vegetation surrounding the site is characterized by scattered small woodlands dominated by deciduous *Quercus* (*Q. cerris* and *Q. pubescens*). The nearest silver fir populations grow at Bocca Trabaria (Fig. 4) 70 km north, and on Monte Amiata, 30 km south (Fig. 4).

In the Etruscan site of Pyrgi (Fig. 3), the ancient harbour of Cerveteri, located 50 km north of Rome, wood remains from a votive well dating to the 3rd century BC attest to a significant use of *A. alba* (Coccolini & Follieri 1980). The nearest source area could be located at ca. 90 km away from the site (Fig. 4). Although *A. alba* is nearly absent in the Holocene pollen records of this region (Lago di Vico, Magri & Sadori 1999; Lagaccione, Magri 1999; Lago Albano e Lago Nemi, Mercuri et al. 2002), F. Spada (pers. comm., University of Rome La Sapienza) notes evidence in this area of a cultic significance of *A. alba* woods in the Archaic Etruscan age.

Also of interest are the data from the wetland site of Longola Poggiomarino in southern Italy. This late Bronze–Iron Age settlement is located in the Sarno plain, not far from Mt. Vesuvius (Figs 3 and 5). Identification of 3000 poles and planks shows that *A. alba* was mainly selected for shaped boards. Again, *Q. cerris* and *Q. robur* are also present and constitute the most used trees. *Ulmus*, *Fraxinus*, *Alnus*, *Fagus sylvatica*, *Salix*, *Acer* and *Abies* represent together about 10% of the samples identified (Heussner 2008; Heussner et al. 2008). The provenance of the wood was probably the area surrounding the site, suggesting that *A. alba* grew locally mixed with broad-leaved trees.

More southwards, in the Greek settlement of Torre di Satriano in Lucania (Fig. 3), *A. alba* was employed in the 7th century BC as building material, but above all as single fuelwood in the furnaces (Novellis 2008). *A. alba* was found in this location's charcoal assemblages mainly accompanied by *Q. cerris*. At present, *A. alba* is absent in the mesophilous *Q. cerris* forest close to the site, and the nearest silver fir populations are at a distance of ca. 12 km (Fig. 4) at relatively low altitudes (Fig. 5).

In the Lucanian Apennines, the mountains surrounding the Cistercian monastery of S. Maria del Sagittario (745 m a.s.l.) are described as having been, in AD 1600, covered by large forests of oaks, mainly *Q. cerris*, and *A. alba* (Angelini 1988). Today, *Q. frainetto* and *Q. cerris* woods grow around the monastery ruins, while *A. alba* survives in the oak wood of the lateral valley of the Rubbio torrent. Only 45 km northwards, *A. alba* still grows in the *Q. cerris* woods of Laurenzana. Overall, charcoal assemblages seem to indicate a mixed forest where *A. alba* was mainly associated with *Q. cerris* and other deciduous broad-leaf species.

Wood/charcoal evidence of *A. alba* in the Roman Age (100 BC–AD 500)

Evidence for use of *A. alba* is highest during the Roman Age (Allevato et al. 2010). Several classical literary sources point out that *A. alba* is an excellent timber for construction, emphasizing its superiority over other tree species (see Di Bérenger 1865; Meiggs 1982). However, archaeobotanical data from the western Mediterranean are not reported in Fig. 5 as evidence of a local presence of fir because of the long-distance trade routes characterizing the Roman economic network (Meiggs 1982).

The most abundant evidence of *A. alba* as building timber comes from the Vesuvius region (Fig. 3) and the ancient town of Herculaneum. Herculaneum was destroyed by the AD 79 Vesuvius eruption, but unlike

Pompeii, because of differences in the burial effects of the eruption, charred wood belonging to building structures and furniture has been well preserved. Unsystematic research carried out at the site (Caramiello et al. 1992; Fioravanti & Gallotta 2005) suggested that *A. alba* was a common timber for building structures; it also appears to have been used for furniture (Mols 2002). More systematic analysis shows that *A. alba* was the most widely used timber (60% of timber samples and ca. 80% of beams; Moser et al. 2012). Even at Oplontis in the Villa of Poppea (Fig. 3), *A. alba* was used extensively not only for large beams but also for frames, windows, doors, pivots and hinges (Moser et al. 2013). On the northern side of Monte Vesuvius, evidence of *A. alba* for building structures comes from a Roman villa (Fig. 3; Allevato et al. 2012). Kuniholm (2002), using dendrochronological investigations, hypothesized that *A. alba* timber in the Vesuvius area came from the eastern Alps. However, new tree ring data support that an Apennine provenance of the Herculaneum silver fir timber is also possible (Moser et al. 2012).

Finally, outside of the Campania region, in the area of Rome, several wooden poles made with *A. alba* and dated to the 2nd century BC have been found at the Circo Flaminio (Sadori et al. 2007), and artefacts dated to the 4th century AD have been found at the Colosseum (Follieri 1975). At Populonia (southern Tuscany; Fig. 3), *A. alba* was used to shape the planks of a roof dated to the 1st century BC (Di Pasquale & Terzani 2006). These data confirm the great exploitation of *Abies* as described by classical authors, and suggest wide diffusion of this tree through the Italian peninsula.

Charcoal data in the Middle Ages (AD 700–1300)

Charcoal/wood data for the Middle Ages are quite scarce due to the reduced number of archaeological excavations. Nevertheless, *A. alba* timber continued to be present, again in contexts seemingly incoherent with the present distribution of this tree.

In Tuscany, at the Medieval site of Miranduolo, located 400 m a.s.l. at the edges of the Colline Metallifere (Figs 3 and 5), *Abies* charcoal is present in addition to the prevailing *Castanea sativa* and deciduous *Quercus* in one context dated to the 11th to 12th century AD (Di Pasquale et al. 2008). In the same region, in the more coastal sector, at Populonia, *Abies* charcoal fragments were also found in contexts dated to the 13th century AD (Di Pasquale & Terzani 2006).

At Faragola in southern Italy, on the Daunian sub-Apennine at 250 m a.s.l (Figs 3 and 5), *A. alba* was still used extensively in the 7th century AD for fuel in metalworking as well as for building timber (Caracuta et al. 2012). Again, in addition to *Abies*, taxa belonging to the mixed deciduous forest such as deciduous *Quercus*, *Acer* and *Carpinus* are present in the assemblages. Areas where *A. alba* currently grows are more than 50 km from the site (Fig. 4).

Finally, two pieces of evidence are remarkable for their geographic location: Geridu (Fig. 3; NW Sardinia) and Segesta (Fig. 3; W Sicily). In the medieval village of Geridu, a few charcoal fragments of *Abies* were found in the collapse of a roof, along with a small branch of *Abies* still retaining its bark (A. Deiana, pers. comm.). *A. alba* is absent in Sardinia, and the provenance of this wood could be Corsica. At Segesta, barked small branches of *Abies* were recovered in contexts functionally related to the furnaces dated to 12th–13th centuries AD. Although wood anatomy does not permit identification to species level, the authors hypothesize that the charcoal could be identified as *A. nebrodensis* (Castiglioni & Rottoli 1997). Today, *A. nebrodensis* consists of a relict population of 23 mature trees located on the Madonie Mts. between 1400 and 1650 m a.s.l., where it grows at the lower elevation mixed with *Q. ilex*, *Arbutus unedo*, *Ilex aquifolium*, *Juniperus* sp., *Cistus* and *Phillyrea* sp. (Ducci et al. 1999). Also in the previous case, the presence of small barked branches is not consistent with a distance of more than 200 km from the present location of these trees. This evidence could be attributed to a specific use, which is unfortunately difficult to infer, but could once again attest to the strong human pressure on *Abies*.

Past ecology and new perspectives

Overall, for the recent Holocene, charcoal data have documented, throughout peninsular Italy, evidence of *A. alba* at lower altitudes than at present (Fig. 5). The high spatial definition of this proxy allows confirmation that *A. alba* was growing in low-middle altitude forest communities associated with deciduous species, mainly *Q. cerris*, at least until the Middle Ages. This evidence would support the validity of the scenario proposed by Tinner et al. (2013), in which, under low human pressure, *A. alba* would be capable of co-occurring with thermophilous species. Simulation models of dynamic vegetation also showed that under low disturbance, this tree would have persisted and even expanded in the late Holocene (Henne et al. 2013; Tinner et al. 2013).

Interestingly, around the mid-20th century, some Italian forest ecologists indicated the optimum for *A. alba* on the Apennines as lying between the upper belt of the mesophilous *Q. cerris* forest and the lower belt of the thermophilous Mediterranean *F. sylvatica* forest (Giacobbe 1950; Susmel 1959; see also Fig. 4 in Tichy 1962); at present, this vegetation type survives in a few areas of the Central and Southern Apennines and here a good natural regeneration of *A. alba* has been documented (Nolè et al.

Journal of Vegetation Science
Doi: 10.1111/jvs.12196

2003). Despite that, today the majority of phytosociologists consider *A. alba* a typical tree of the higher elevation mountain belt, and its potential to form forests in suitable meso-xeric lowlands is neglected.

From this point of view, this work enriches the recent debate about the validity of the PNV concept usually applied in the floristic approach (Carrión & Fernández 2009; Chiarucci et al. 2010; Farris et al. 2010; Loidi et al. 2010; Loidi & Fernández-González 2012; Somodi et al. 2012), revealing the weakness of this method. Indeed, the phytosociological approach refers vegetation units to existing patterns of mature vegetation and does not consider that vegetation is dynamic and may continuously change from and into modern analogue assemblages of species (Chiarucci et al. 2010). More generally, palaeoecological data of the Quaternary demonstrate that plants did not migrate as parts of intact associations in response to the Holocene warming, but rather as individual species, 'the resulting associations of historic times being therefore ephemera of habitat, climate, and opportunity' (Colinvaux et al. 1997).

Today, the existence of communities similar to those detected with our charcoal data could still be possible where the human impact is low. Forest management and biodiversity conservation strategies should consider, therefore, a wider number of sites and forest typologies suitable for reintroducing *A. alba* beyond its present distribution range on the Apennines. In this context, it is noteworthy that if *A. alba* decline took place very recently as a consequence of human activities, it is not appropriate to consider current distribution as determined by climate but rather as an 'anthropic relic' of over-exploitation. More broadly, the occurrence of very recent 'no-present-analogue' communities (*sensu* Williams & Jackson 2007) suggests the possibility of their return in a not-far-distant future, and this is why late Holocene archaeo-palaeobotanical data can be a significant starting point of knowledge for forest restoration projects.

Acknowledgements

We are grateful to Laura Sadori and an anonymous referee for very constructive and helpful comments on the article. We also thank the co-ordinating Editor for careful reading of our article and useful comments for its improvement. This work was partially funded by the NURSE project granted to A. S. at the Department of Agriculture, University of Naples Federico II.

References

Allen, J.R.M., Watts, W.A., Mc Gee, E. & Huntley, B. 2002. Holocene environmental variability – the record from Lago Grande di Monticchio, Italy. *Quaternary International* 88: 69–80.

Allevato, E., Russo Ermolli, E., Boetto, G. & Di Pasquale, G. 2010. Pollen–wood analysis at the Neapolis harbour site (1st–3rd century AD, southern Italy) and its archaeobotanical implication. *Journal of Archaeological Science* 37: 2365–2375.

Allevato, E., Buonincontri, M., Vairo, M., Pecci, A., Cau, M.A., Yoneda, M., De Simone, G.F., Aoyagi, M., Angelelli, C. ··· Di Pasquale, G. 2012. Persistence of the cultural landscape in Campania (Southern Italy) before the AD 472 Vesuvius eruption: archaeoenvironmental data. *Journal of Archaeological Science* 39: 399–406.

Angelini, G. 1988. *Il disegno del territorio. Istituzioni e cartografia in Basilicata. 1500–1800*. Editori Laterza, Roma, Bari, Italy.

Arrigoni, P.V., Mazzanti, A. & Ricceri, C. 1990. Contributo alla conoscenza dei boschi della Maremma grossetana. *Webbia* 44: 121–149.

Asouti, E. & Austin, P. 2005. Reconstructing woodland vegetation and its exploitation by past societies, based on the analyses and interpretation of archaeological wood charcoal macro-remains. *Environmental Archaeology* 10: 1–18.

Bellini, C., Mariotti-Lippi, M. & Montanari, C. 2009. The Holocene landscape history of the NW Italian coasts. *The Holocene* 19: 1161–1172.

Borghetti, M. & Vignali, G. 1988. L'abete bianco nei boschi di Monte Nero. *L'Italia Forestale e Montana* 5: 311–328.

Büntgen, U., Tegel, W., Kaplan, J.O., Schaub, M., Hagedorn, F., Bürgi, M., Brázdil, R., Helle, G., Carrer, M. (····) & Liebhold, A. 2014 Placing unprecedented recent fir growth in a European-wide and Holocene-long context, *Frontiers in Ecology and the Environment* 12: 100–106.

Caracuta, V., Fiorentino, G., Turchiano, M. & Volpe, G. 2012. Processi di formazione di due discariche altomedievali del sito di Faragola: il contributo dell'analisi archeobotanica. *Post-Classical Archaeologies* 2: 225–245.

Caramiello, C., Fioravanti, M., Griffa, A., Macchioni, N., Uzielli, L. & Zeme, A. 1992. Analysis and preservation of ligneous material from the Herculaneum excavations: problem and initial results. *Allionia* 31: 47–59.

Carrer, M., Nola, P., Motta, R. & Urbinati, C. 2010. Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos* 119: 1515–1525.

Carrión, J.S. & Fernández, S. 2009. The survival of the 'natural potential vegetation' concept (or the power of tradition). *Journal of Biogeography* 36: 2202–2203.

Castiglioni, E. & Rottoli, M. 1997. I macroresti vegetali. In: Molinari, A. (ed.) *Segesta II. Il Castello e la Moschea (Scavi 1989 1995)*, pp. 235–249. Flaccovio, Palermo, Italy.

Chabal, L. 1997. *Forêts et sociétés en Languedoc (Néolithique final, Antiquité tardive): l'anthracologie, méthode et paléoécologie*. Editions de la Maison des sciences de l'homme, Paris, France.

Chabal, L., Fabre, L., Terral, J.-F. & Théry-Parisot, I. 1999. L'anthracologie. In: Ferdière, A. (ed.) *La Botanique*, pp. 43–104. Edition Errance, Paris, France.

Chiarucci, A., Araújo, M.B., Decocq, G., Beierkuhnlein, C. & Fernández-Palacios, J.M. 2010. The concept of potential natural vegetation: an epitaph? *Journal of Vegetation Science* 21: 1172–1178.

Ciancio, O., Iovino, F., Menguzzato, G. & Mirabella, A. 1985. L'Abete (*Abies alba* Mill.) in Calabria: possibilità e limiti di diffusione e ridiffusione. *Annali dell'Istituto Sperimentale per la Selvicoltura – Arezzo* 16: 7–249.

Coccolini, G. & Follieri, M. 1980. I legni dei pozzi del tempio A nel santuario etrusco di Pyrgi. *Studi etruschi* 48: 277–291.

Colinvaux, P.A., Bush, M.B., Steinitz-Kannan, M. & Miller, M.C. 1997. Glacial and postglacial pollen records from the Ecuadorian Andes and Amazon. *Quaternary Research* 48: 69–78.

Colombaroli, D., Marchetto, A. & Tinner, W. 2007. Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). *Journal of Ecology* 95: 755–770.

Colonna, G. 1986. Il Tevere e gli Etruschi. *Archeologia Laziale* 7: 90–97.

Cruise, G.M., Macphail, R.I., Linderholm, J., Maggi, R. & Marshall, P.D. 2009. Lago di Bargone, Liguria, N Italy: a reconstruction of Holocene environmental and land-use history. *The Holocene* 19: 987–1003.

de Nascimento, L., Willis, K.J., Fernández- Palacios, J.M., Criado, C. & Whittaker, R.J. 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography* 36: 499–514.

Di Bérenger, A. 1965. *Studii di archeologia forestale*. Ristampa a cura di Accademia Italiana di Scienze Forestali e della Direzione Generale dell'Economia Montana e delle Foreste, Firenze, Italy.

Di Martino, P. 1996. *Storia del paesaggio forestale del Molise*. Iresmo/Lampo, Campobasso, Italy.

Di Pasquale, G. 2003. I carboni di Chiusi: una ipotesi di ricostruzione del paesaggio forestale. In: Pucci, G. & Mascione, C. (eds.) *Manifattura ceramica etrusco-romana a Chiusi. Il complesso produttivo di Marcianella vol. 1*, pp. 315–320. Edipuglia srl, Bari, Italy.

Di Pasquale, G. & Terzani, M. 2006. Archeobotanica a Populonia: primi risultati e prospettive della ricerca. In: Aprosio, M. & Mascione, C. (eds.) *Materiali per Populonia 5*, pp. 283–291. ETS, Pisa, Italy.

Di Pasquale, G., Di Falco, G. & Moser, D. 2008. Analisi archeobotaniche. In: Valenti, M. (ed.) *Miranduolo in Alta Val di Merse (Chiusdino - SI)*, pp. 323–347. All'Insegna del Giglio, Firenze, Italy.

Drescher-Schneider, R., de Beaulieu, J.-L., Magny, M., Walter-Simonnet, A.-V., Bossuet, G., Millet, L., Brugiapaglia, E. & Drescher, A. 2007. Vegetation history, climate and human impact over the last 15,000 years at Lago dell'Accesa (Tuscany, central Italy). *Vegetation History and Archaeobotany* 16: 279–299.

Ducci, F., Proietti, R. & Favre, J.-M. 1999. Allozyme assessment of genetic diversity within the relic Sicilian fir *Abies nebrodensis* (Lojac.) Mattei. *Annals of Forest Science* 56: 345–355.

Farris, E., Filibeck, G., Marignani, M. & Rosati, L. 2010. The power of potential natural vegetation (and of spatial-temporal scale): a response to Carrión & Fernández (2009). *Journal of Biogeography* 37: 2211–2213.

Figueiral, I. & Mosbrugger, V. 2000. A review of charcoal analysis as a tool for assessing Quaternary and Tertiary environments: achievements and limits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164: 397–407.

Fioravanti, M. & Gallotta, G.P. 2005. I legni di più frequente impiego in epoca romana. In: Caneva, G. (ed.) *La biologia vegetale per i beni culturali, conoscenza e valorizzazione*, vol 2, pp. 22–25. Nardini editore, Firenze, Italy.

Follieri, M. 1975. Resti vegetali macroscopici nel collettore ovest del Colosseo. *Annali di Botanica* 34: 123–141.

Follieri, M., Giardini, M., Magri, D. & Sadori, L. 1998. Palynostratigraphy of the last glacial period in the volcanic region of central Italy. *Quaternary International* 47–48: 3–20.

Freni, C. 1955. Andamento del ritmo vegetativo in *Abies alba* Mill. dell'Aspromonte. *Annali dell'Accademia Italiana di Scienze Forestali* 20: 135–154.

Gallucci, V. & Urbinati, C. 2009. Growth dynamics and climatic sensitivity of Silver fir (*Abies alba* Mill.) in the European important site (SIC) at the Alpe della Luna - Bocca Trabaria (PU - Italy). *Forest@* 6: 85–99.

Gamisans, J. 1999. *La végétation de la Corse*. Edisud, Aix-en-Provence, France.

Giacobbe, A. 1950. L'ecologia dell'Abete bianco. Nota III - Caratteri floristici e climatici dell'Abete bianco. *Archivio Botanico* 26: 129–149.

Greguss, P. 1955. *Identification of living gymnosperms on the basis of xylotomy*. Akadémiai Kiadó, Budapest, Hungary.

Greguss, P. 1959. *Holzanatomie der europäischen Laubhölzer und Sträucher*. Akadémiai Kiadó, Budapest, Hungary.

Guido, M.A., Menozzi, B.I., Bellini, C., Placereani, S. & Montanari, C. 2013. A palynological contribution to the environmental archaeology of a Mediterranean mountain wetland (North West Apennines, Italy). *The Holocene* 11: 1517–1527.

Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O. & Tinner, W. 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecology* 28: 819–833.

Heussner, U. 2008. Cronologia assoluta della tarda Età del Bronzo e della prima Età del Ferro a Longola/Poggiomarino. In: Guzzo, P.G. & Guidobaldi, M.P. (eds.) *Nuove ricerche archeologiche nell'area vesuviana (scavi 2003–2006). Atti Del Convegno Internazionale, Roma 1-3 Febbraio 2007*, pp. 489–491. L'Erma di Bretschneider, Roma, Italy.

Heussner, U., Kastenmeier, P. & Pappalardo, M.T. 2008. Dendrocronologia: utilizzo e lavorazione delle specie arboree a Longola. In: Guzzo, P.G. & Guidobaldi, M.P. (eds.) *Nuove ricerche archeologiche nell'area vesuviana (scavi 2003-2006). Atti Del Con-*

vegno Internazionale, Roma 1–3 Febbraio 2007, pp. 576–578. L'Erma di Bretschneider, Roma, Italy.

Joannin, S., Brugiapaglia, E., de Beaulieu, J.-L., Bernardo, L., Magny, M., Peyron, O., Goring, S. & Vannière, B. 2012. Pollen-based reconstruction of Holocene vegetation and climate in southern Italy: the case of Lago Trifoglietti. *Climate of the Past* 8: 1973–1996.

Konnert, M. & Bergmann, F. 1995. The geographical distribution of genetic variation of silver fir (*Abies alba, Pinaceae*) in relation to its migration history. *Plant Systematics and Evolution* 196: 19–30.

Kuniholm, P.I. 2002. Dendrochronological investigation at Herculaneum and Pompeii. In: Jashemski, W.F. & Meyer, F.G. (eds.) *The Natural History of Pompeii*, pp. 235–239. Cambridge University Press, Cambridge, UK.

Lang, G. 1994. *Quartäre Vegetationsgeschichte Europas*. Methoden und Ergebnisse, Fischer, Jena, Germany.

Liepelt, S., Mayland-Quellhorst, E., Lahme, M. & Ziegenhagen, B. 2010. Contrasting geographical patterns of ancient and modern genetic lineages in Mediterranean *Abies* species. *Plant Systematics and Evolution* 284: 141–151.

Loidi, J. & Fernández-González, F. 2012. Potential natural vegetation: reburying or reboring? *Journal of Vegetation Science* 23: 596–604.

Loidi, J., del Arco, M., Pèrez de Paz, P.L., Asensi, A., Díez Garretas, B., Costa, M., Díaz González, T., Fernández-González, F., Izco, J. ··· Sánchez-Mata, D. 2010. Understanding properly the 'potential natural vegetation' concept. *Journal of Biogeography* 37: 2209–2211.

Magri, D. 1999. Late Quaternary vegetation history at Lagaccione near Lago di Bolsena (central Italy). *Review of Palaeobotany and Palynology* 106: 171–208.

Magri, D. & Sadori, S. 1999. Late Pleistocene and Holocene pollen stratigraphy at lago di Vico, central Italy. *Vegetation History and Archaeobotany* 8: 247–260.

Meiggs, R. 1982. *Trees and Timber in the Ancient Mediterranean World*. Oxford University Press, Oxford, UK.

Mercuri, A.M., Accorsi, C.A. & Bandini Mazzanti, M. 2002. The long history of Cannabis and its cultivation by the Romans in Central Italy, shown by pollen records from Lago Albano and Lago di Nemi. *Vegetation History and Archaeobotany* 11: 263–276.

Mols, S.T.A.M. 2002. Identification of the woods used in the furniture at Herculaneum. In: Jashemski, W.F. & Meyer, F.G. (eds.) *The Natural History of Pompeii*, pp. 225–234. Cambridge University Press, Cambridge, UK.

Morandini, R., Ducci, F. & Menguzzato, G. 1994. *Abies nebrodensis* (Lojac) Mattei - Inventario 1992. *Annali Istituto Sperimentale per la Selvicoltura* 22: 5–51.

Moser, D., Heussner, U., Kastenmeier, P., Nelle, O. & Di Pasquale, G. 2012. Local or global? Methods to solve the problem of silver fir timber circulation during the Roman Age. In: Vezzalini, G. & Zannini, P. (eds.) *Atti del VII Convegno Nazionale di Archeometria, 22th –24th February 2012 Modena*, pp. 302–311. Pàtron Editore, Modena, Italy.

Moser, D., Allevato, E., Clarke, R.J., Di Pasquale, G. & Nelle, O. 2013. Archaeobotany at Oplontis: woody remains from the Roman Villa of Poppaea (Naples, Italy). *Vegetation History and Archaeobotany* 22: 397–408.

Nolè, A., Saracino, A. & Borghetti, M. 2003. Microclima luminoso, rinnovazione naturale e distribuzione spaziale di *Abies alba* Mill, nell'Abetina di Laurenzana, Basilicata. *L'Italia Forestale e Montana* 58: 7–21.

Novellis, D. 2008. Tra abeti, querce e campi coltivati: dati archeobotanici preliminari da Torre di Satriano. In: Osanna, M. & Serio, B. (eds.) *Progetti di archeologia in Basilicata. Banzi e Tito*, pp. 131–136. Edipuglia, Bari, Italy.

Peguero-Pina, J.J., Camarero, J.J., Abadía, A., Martín, E., González-Cascón, R., Morales, F. & Gil-Pelegrín, E. 2007. Physiological performance of silver-fir (*Abies alba* Mill.) populations under contrasting climates near the south-western distribution limit of the species. *Flora* 202: 226–236.

Pignatti, S. 1982. Flora d'Italia, vol 1, 2, 3. Edagricole, Bologna, Italy.

Piovesan, G., Presutti Saba, E., Biondi, F., Alessandrini, A., Di Filippo, A. & Schirone, B. 2009. Population ecology of yew (*Taxus baccata* L.) in the Central Apennines: Spatial patterns and their relevance for conservation strategies. *Plant Ecology* 205: 23–46.

Pucci, G. & Mascione, C. (eds.) 2003. *Manifattura ceramica etrusco-romana a Chiusi. Il complesso produttivo di Marcianella vol 1*. Edipuglia srl, Bari, Italy.

Puddu, A., Luisi, N., Capretti, P. & Santini, A. 2003. Environmental factors related to damage by *Heterobasidion abietinum* in *Abies alba* forests in Southern Italy. *Forest Ecology and Management* 180: 37–44.

Quézel, P. & Médail, F. 2003. *Ecologie et biogéographie des forêts du bassin Méditerranéen*. Elsevier, Paris (Collection Environnement), France.

Sadori, L., Giardini, M. & Masi, A. 2007. Il paesaggio urbano e suburbano della Roma imperiale. *Atti della Società dei Naturalisti di Modena* 138: 255–272.

Sadori, L., Jahns, S. & Peyron, O. 2011. Mid-Holocene vegetation history of the central Mediterranean. *The Holocene* 21: 117–129.

Santini, A. & Martinelli, N. 1991. Indagine dendroecologica sull'abete bianco (*Abies alba* Mill.) di Serra San Bruno (CZ). *Giornale Botanico Italiano* 125: 895–906.

Schweingruber, F.H. 1990. *Anatomie europäischer Hölzer/Anatomy of European Woods*. Verlag Paul Haupt, Bern, Switzerland.

Somodi, I., Molnár, Z., Ewald, J.. 2012. Towards a more transparent use of the potential natural vegetation concept – an answer to Chiarucci et al. *Journal of Vegetation Science* 23: 590–595.

Susmel, L. 1959. Ecologia, biologia e possibilità attuali di coltivazione dell'abete bianco (*Abies alba* Mill.) nell'Appennino Centro Meridionale. *Annali dell'Accademia Italiana di Scienze Forestali* 8: 165–202.

Tichy, F. 1962. *Die Wälder der Basilicata und die Entwaldung im 19. Jahrhundert. Vorgänge, Ursachen und Folgen. Heidelberger Geo-*

graphische Arbeiten, Heft 8. Keysersche Verlagbuchhandlung, Heidelberg, Germany.

Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B. & Conedera, M. 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87: 273–289.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G. ··· Valsecchi, V. 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs* 83: 419–439.

Vendramin, G.G., Degen, B., Petit, R.J., Anzidei, M., Madaghiele, A. & Ziegenhagen, B. 1999. High level of variation at *Abies alba* chloroplast microsatellite loci in Europe. *Molecular Ecology* 8: 1117–1126.

Vescovi, E., Ammann, B., Ravazzi, C. & Tinner, W. 2010a. A new Late-glacial and Holocene record of vegetation and fire history from Lago del Greppo, northern Apennines, Italy. *Vegetation History and Archaeobotany* 19: 219–233.

Vescovi, E., Kaltenrieder, P. & Tinner, W. 2010b. Late-Glacial and Holocene vegetation history of Pavullo nel Frignano (Northern Apennines, Italy). *Review of Palaeobotany and Palynology* 160: 32–45.

Watson, C.S. 1996. The vegetational history of the northern Apennines, Italy: information from three new sequences and a review of regional vegetational change. *Journal of Biogeography* 23: 805–841.

Watts, W.A., Allen, J.R.M., Huntley, B. & Fritz, S.C. 1996. Vegetation history and climate of the last 15,000 years at Laghi di Monticchio, southern Italy. *Quaternary Science Reviews* 15: 113–132.

Williams, J.W. & Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.

Willis, K.J. & Birks, H.J.B. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314: 1261–1265.

Willis, K.J. & McElwain, J.C. 2002. *The Evolution of Plants*. Oxford University Press, Oxford, UK.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Geographical coordinates of present-day *Abies alba* native populations.

Journal of Vegetation Science
Doi: 10.1111/jvs.12196