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Shedding light on the effects of climate and anthropogenic pressures on the disappearance of *Fagus sylvatica* in the Italian lowlands: evidence from archaeo-anthracology and spatial analyses

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HIGHLIGHTS

- *Fagus sylvatica* inhabited the Italian Peninsula lowlands in the late Holocene.
- Climate and anthropogenic pressure affected the loss of *F. sylvatica* from the Italian Peninsula lowlands.
- Climate had a more uniform effect on *F. sylvatica* presence in Italy regardless of the elevation.
- Anthropogenic pressure mostly affected the presence of beech in lowland areas placed <300 m a.s.l.

GRAPHICAL ABSTRACT
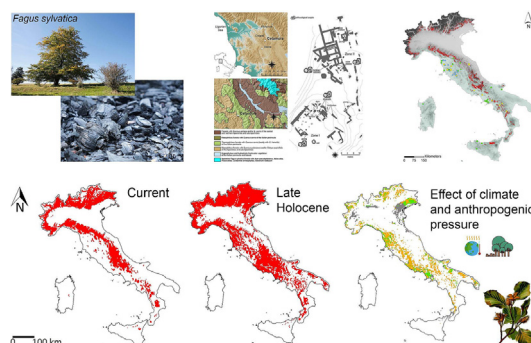
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ABSTRACT

Fagus sylvatica is one of the most representative trees of the European deciduous broadleaved forests, yet the impact of changing climatic conditions and anthropogenic pressures (anthromes) on its presence and distribution in the coastal and lowland areas of the Mediterranean Basin has long been overlooked.

Here, we first analysed the local forest composition in two different time intervals (350–300 Before Current Era, BCE and 150–100 BCE) using charred wood remains from the Etruscan site of Cetamura (Tuscany, central Italy). Additionally, we reviewed all the relevant publications and the wood/charcoal data obtained from anthracological analysis in *F. sylvatica*, focusing on samples that date back to 4000 years before present, to better understand the drivers of beech presence and distribution during the Late Holocene (LH) in the Italian Peninsula. Then, we combined charcoal and spatial analyses to test the distribution of beech woodland at low elevation during LH in Italy and to evaluate the effect of climate change and/or anthrome on the disappearance of *F. sylvatica* from the lowlands.

We collected 1383 charcoal fragments in Cetamura belonging to 21 woody taxa, with *F. sylvatica* being the most abundant species (28 %), followed by other broadleaved trees. We identified 25 sites in the Italian Peninsula with beech charcoals in the last 4000 years. Our spatial analyses showed a marked decrease in habitat suitability of *F. sylvatica* from LH to the present (ca. 48 %), particularly in the lowlands (0–300 m above sea level, a.s.l.) and at higher altitudes (>900 m a.s.l.). In the lowland areas, where *F. sylvatica* has disappeared, climate had a more uniform effect on beech distribution patterns across the entire elevation range analysed, whereas climate + anthrome and anthrome alone influenced 69 % and 84 % of the lowland areas, respectively.

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Our results highlight the advantage of combining different approaches, such as charcoal analysis and spatial analyses, to explore biogeographic questions about the past and current distribution of *F. sylvatica*, with important implications for today's forest management and conservation policies and practices, as well as for future research projects.

1. Introduction

Fagus sylvatica L. (European beech) is one of the most representative trees in the European deciduous broadleaved forests (Fang and Lechowicz, 2006). It is widespread across Europe, where it can be found from Sicily to southern Scandinavia and from the Iberian Peninsula to the southeast of the Carpathians (Caudullo et al., 2017). Pollen records and genetic data suggest that this species has spread across Europe from small scattered populations left after the last glacial event and is currently experiencing its maximum post-glacial spread (Magri, 2008; Petit et al., 2001).

F. sylvatica is a mesophilous and shade-tolerant tree, therefore its occurrence is strongly influenced by rainfall and temperature. In fact, it requires a humid atmosphere with precipitation well distributed throughout the year and well-drained soils; it tolerates severe winter cold, but it is sensitive to spring frost (Lebourgeois et al., 2005; Hacket-Pain et al., 2016). Thus, in northern and central Europe, beech is limited to the lowlands and the hills, where it represents the most successful tree of temperate forests (Leuschner et al., 2006; Bolte et al., 2007). In southern Europe, summer water shortage restricts beeches to the moist temperate and submediterranean montane zone characterised by frequent fogs, low probabilities of drought and limited late spring frosts (Piovesan et al., 2005; Pezzi et al., 2008). *F. sylvatica* dominates the forests in areas with annual mean temperatures between 4 and 8 °C and with average monthly temperatures of the coldest month ranging between -7 to -3 °C; however, provided that annual rainfall amounts exceed 1000 mm, it grows very well also when the temperature is close to 0 °C (Quézel and Médail, 2003).

The beech forests located in the Italian Peninsula (excluding the Alps and the Po Valley) represent the southernmost edge of the species' distribution range within the Mediterranean Basin. Here, the typically Mediterranean macrobioclimate along the coast features unfavourable conditions, while the hinterland, with increasing altitude, is progressively characterised by the more advantageous conditions of the Submediterranean to Temperate macrobioclimate (Pesaresi et al., 2017). In fact, the Apennine range is one of the main refuge areas of the species, and still hosts some of the most representative and almost pure stands of *F. sylvatica*, mostly located between 1000 and 2000 m above sea level (a.s.l.). Currently, beech forests cover a surface of ca. 10,351 km^2 (ca. 10 % of the total forest cover: Gasparini and Tabacchi, 2011) in Italy and for this specific reason, *F. sylvatica* can be considered one of the most important hardwood species, especially from an ecological and a socio-economic perspective. Due to its high energetic potential, beech is also coppiced for firewood and charcoal (von Wühlisch, 2008).

Along the Apennines, two major types of beech forest have been identified (Fig. S1): 1) high-elevation (from 1500 to 2000 m a.s.l.) forests, characterised by beech dominance and a species-poor herbaceous understory (De Sillo et al., 2012); 2) mountain forests (from 1000 to 1500 m a.s.l.), where some evergreen species, like *Ilex aquifolium*, *Taxus baccata* and *Abies alba*, may co-occur in the tree layer (Bianchi et al., 2011). Beyond these two main areas, scattered high-elevation and mountain beech forests also occur outside the canonical Apennine range on several isolated low mountains along the sea board characterised by supra- or even meso-Mediterranean thermotype conditions (Fig. S1 and Table S1, Pesaresi et al., 2017). Here beeches grow on poor and thin soils, usually facing a significant summer water deficit, and co-occur with mesophilous forest trees such as *Acer opalus*, *A. pseudoplatanus* and *C. betulus*.

Outside the Apennine range, thermophilous beech stands are present, at lower elevations between 400 and 800 m a.s.l. in the transition zone between the Mesomediterranean and Mesotemperate thermotype belts (Fig. S1 and Table S1, Pesaresi et al., 2017).

Below 400 m a.s.l., the Mediterranean climate sets clear limits to the tolerance of beech to water stress and high temperatures, making it vulnerable to competition with drought-tolerant tree species. Yet, the foothills host plenty of extra-zonal beech wood nuclei or isolated beech trees (Fig. S1 and Table S2). Many of these stands take advantage of particularly favourable pedological (e.g., volcanic soils) and microclimatic (e.g., borders of inner lakes or valleys subject to thermal inversion, N-facing slopes with frequent flow of cool-humid air from the sea) local conditions that prevent or strongly mitigate summer drought (Sabbatini et al., 2011; Saracino, 2013; Elisei, 2015). These lowland beech stands are part of forest ecosystems whose canopy shows a higher number of co-occurring (co-dominant) tree species. In fact, *F. sylvatica* is associated with mesophilous (*Quercus cerris*, *Q. petraea*, *Q. robur*, *Carpinus betulus*, *Castanea sativa*, *Acer pseudoplatanus* and *Ulmus glabra*) and thermophilous (*Q. pubescens* and *Q. frainetto*, *Fraxinus ornus* and *F. oxycarpa*, *Acer campestre* and *Ostrya carpinifolia*) deciduous trees, and even with few evergreen mesophilous trees like *Ilex aquifolium* and *Taxus baccata* (Abbate et al., 2003).

Analyses focused on lacustrine pollen sequences provide a complex picture of the fluctuations (shrinkage and rise) that affected *F. sylvatica* along the Italian Peninsula. During the Early Holocene optimum, characterised by higher average temperatures and rainfall precipitations at their highest (Giraudi et al., 2011; Magny et al., 2013), beech spread from its glacial refuges (e.g., Lucanian Apennines: Joannin et al., 2012) around 11,000 calibrated years Before Present (cal. yrs BP), and from lower reliefs of central Italy ca. 9400–9000 cal. yrs BP (Magri, 1999). During this optimum, beech took part to mixed forests with deciduous oaks, and many other trees (genera *Betula*, *Carpinus*, *Ulmus*, *Corylus*, and *Tilia*). Around 6000–5500 cal. yrs BP (Guido et al., 2013; Savelli et al., 2013; Branch and Marini, 2014) *F. sylvatica* completed its spread and colonization along the Italian Peninsula.

Interestingly, the currently so-called "heterotopic" beech stands (outside the Apennines) apparently became isolated in recent times. Indeed, during the last 4000 years, i.e., from Mid to Late Holocene (hereafter LH), the pollen sequences show that beech is mostly restricted to the mountainous areas of the central and southern Apennines, stressing the relict character of the current small, isolated populations at low elevations (Magri et al., 2015).

In the last thousand years, the Mediterranean Basin has experienced a gradual warming and redistribution of precipitation regimes (Luterbacher et al., 2012). Therefore, the progressive shrinkage and disappearance of *F. sylvatica* in the LH pollen sequences at lower elevations has been mainly ascribed to shifting climatic conditions, hinting at a warmer climatic phase (Mariotti Lippi et al., 2007). However, the low resolution of many pollen analyses does not allow to clearly distinguish between shifts in vegetation cover due to anthropogenic impact or/and climate change, especially during the last 3000 years (Peyron et al., 2013; Zanchetta et al., 2013; Sadori et al., 2016). Instead, although the deposition of archaeological charcoals is not a continuous process, archaeo-anthracology provides a higher spatial resolution than pollen and reliable hints on the local presence of the identified tree taxa (Figueiral and Mosbrugger, 2000).

The use of spatial analyses in palaeoecology and palaeobiogeography has grown substantially in the last two decades due to the development of robust theoretical and methodological frameworks and the increasing availability of palaeoecological and palaeoclimatic data. In palaeobotany,

spatial analyses have been used to estimate the past potential distribution of several plant species (e.g., Di Pasquale et al., 2020; Poli et al., 2022) and predict the consequences that climate change and human impact could have in the future on their distribution (Svenning et al., 2011; Varela et al., 2011).

The past and current distribution range of *F. sylvatica* in Europe has been widely studied using various tools such as geostatistics, ecological modelling and remote sensing applications (e.g., Caudullo et al., 2017; Mauri et al., 2017; Poli et al., 2022) or palaeobotanical data (Magri et al., 2006, 2015; Magri, 2008). The main objectives of this study are to explore the current and past presence of *F. sylvatica* in mixed low altitude forest stands and to reconstruct the potential causes of its progressive disappearance in the Italian Peninsula, characterised by Mediterranean and Submediterranean macrobioclimatic conditions, through charcoal data and spatial analyses. We first analysed the charcoal material collected at the Etruscan site of Cetamura (Tuscany, central Italy). In fact, charcoal analysis at archaeological sites represents a very effective tool to reconstruct past vegetation history and dynamics at the local scale (Figueiral and Mosbrugger, 2000). Cetamura provided a special opportunity to gain insights into the LH history of mixed beech forests in the Italian peninsula, under limiting Mediterranean conditions, and to investigate the factors triggering the changes in forest composition in two different time intervals, i.e. 350–300 Before Current Era (BCE, ca. 2300 cal. yrs BP) and 150–100 BCE (ca. 2100 cal. yrs BP). Additionally, we reviewed all the relevant publications containing archaeo-anthracological data testifying the presence of *F. sylvatica* during the last 4000 yrs in the Italian Peninsula. Then, we combined charcoal and spatial analyses to test the distribution patterns of beech at low elevation during LH in Italy and to shed light on the effects of climate change and/or anthrome on the disappearance of *F. sylvatica* from the lowlands.

2. Materials and methods

2.1. Charcoal analyses

2.1.1. Study area

The archaeological site of Cetamura (Long. 696604 E, Lat. 4818482 N, WGS84/UTM zone 32N) is located at 695 m a.s.l. in the top wine-producing region of Chianti, between Florence and Siena (Fig. 1a). According to the Gaiole weather station (TOS11000087, 5 km from Cetamura, 360 m a.s.l.; Long. 695939 E, Lat. 4814376 N, WGS84/UTM zone 32N; annual interval: 2005–2020; data source: http://www.sir.toscana.it/), the local mean minimum temperature in the coldest month (January) is -0.5 °C, while the mean maximum in the warmest month (July) is 31 °C. Average annual rainfall is ca. 850 mm (unevenly distributed throughout the year). The bioclimate of Cetamura is characterised by a lower supratemperate thermotype and a lower humid ombrotype (Pesaresi et al., 2017).

The forest surrounding Cetamura is dominated by *Q. cerris* (Fig. 1b), often co-occurring with other broadleaved trees such as *Q. pubescens* and *Ostrya carpinifolia*, and with evergreen *Q. ilex* on rocky and steep slopes (Casini and De Dominicis, 1996). In this area, we also found shrubs and small trees such as *Erica scoparia*, *E. arborea*, *Cytisus scoparius*, *Crataegus monogyna* and *Juniperus communis*. Scattered old chestnuts (*Castanea sativa*) are also present.

2.1.2. Archaeo-anthracological analysis

The anthracological analysis of the charred wood remains from Cetamura involved samples from 11 stratigraphic layers, framed into five different archaeological contexts (Table 1). This term is used to indicate the presumed function of the excavated contexts in each settlement phase. Identification of the samples follows the numbering of the layers and the archaeological contexts classified in the excavation report. In accordance with the current methodology, contexts were carefully selected considering the origin of the charred wood deposits (Théry-Parisot et al., 2010). In archaeological horizons, scattered and dispersed charcoals result from long-term accumulated fuelwood consumption, accounting for the entire – or almost the entire – supply area characteristic of a time period.

Scattered charcoal, present in occupation levels, votive features and refuse pits, allowed to carry out a composite and diachronic characterization of the past vegetation landscape. The research considered two different time intervals, i.e. 350–300 BCE and 150–100 BCE.

The archaeological sediments were filtered through a flotation machine with mesh-size sieves of 4.2 and 0.5 mm. Considering the exponential trend of charred wood fragmentation, charcoal remains with a diameter > 2 mm were preferred for the sake of a more rapid and accurate identification (Asouti and Austin, 2005; Figueiral and Mosbrugger, 2000). Charcoal fragments were identified through an incident light microscope working with $100\times$, $200\times$, and $500\times$ magnification, by using some of the most important wood atlases (Schweingruber, 1990; Vernet et al., 2001) and a reference collection stored at the Plant and Wood Anatomy Lab of the University of Naples Federico II. Taxonomic identification reached the species or genus level thanks to the good state of preservation of the fragments. In some cases, grouped taxonomic references have been used according to the anatomical type, such as *Ostrya/Carpinus* or deciduous *Quercus* type. Occasionally, bad conservation or vitrification did not allow us to identify the samples, or the identification process was only possible on the sub-family level (e.g., Maloidaeae, Prunoideae, Schweingruber, 1990). Botanical nomenclature follows Pignatti (1982).

To ensure robust analyses, we selected 200–300 dispersed charcoal remains per archaeological contexts (Table 1). Remains have been counted and the percentage frequency of each taxon calculated on the total amount per time interval.

2.1.3. Review of archaeo-botanical data

We reviewed the archaeo-botanical literature concerning *F. sylvatica* wood/charcoal found in low areas (below 600 m a.s.l.) in the archaeological sites of Italian Peninsula (proper excluding Alps and Po Valley), spanning from the Middle/Late Bronze Age (1950 BCE; ca. 3900 cal. yrs BP) to the 19th century CE and ranging in Mediterranean and Submediterranean macrobioclimatic belts (Fig. S1, Table S3). When indicating prehistorical and historical dates and time intervals (BCE/CE), we also add cal. yr BP to ease the comparison of palaeoecological data in the literature. We georeferenced all the data collected from the literature by using QGIS 2.12.3-Lyon and obtained a final dataset of 25 sites where charcoal and plant parts of *F. sylvatica* were found in the past (Fig. S1, Table S3).

2.2. Spatial analyses

2.2.1. Training and projection areas

As training area, we considered all the European territories included within the known distribution of *F. sylvatica* according to the European Forest Genetic Resources Program (http://www.euforgen.org/species/fagus-sylvatica/; von Wühlisch, 2008) and Caudullo et al. (2017) (Fig. S2) to avoid truncated beech niche estimations (Barbet-Massin et al., 2010). Our projection area included only Italy (Fig. S2). We focused our spatial analyses on the distribution of *F. sylvatica* in two time periods: 1) current (1979–2013 CE); and 2) LH (4200–300 cal. yrs BP).

2.2.2. Presence records

Current and LH presence records for *F. sylvatica* were extracted from the EU-Forest dataset (https://figshare.com/collections/A_high-resolution_pan-European_tree_occurrence_dataset/3288407, Mauri et al., 2017) and Magri et al. (2006), respectively. To avoid redundancy, spatially autocorrelated points were removed from the current and LH datasets using the Spatially Rarefy Occurrence Data tool of the SDMtoolbox v. 2.4 (Brown et al., 2017) in ArcGIS v. 10.8 (http://www.esri.com/software/arcgis). The Average Nearest Neighbour and Moran's I statistics were used to test the independence in a random distribution of the remaining presence records (e.g., Ancillotto et al., 2019; Sanjo Jose and Nameer, 2020; Ali et al., 2021). After spatial autocorrelation analysis of our datasets, to generate Ecological Niche Models (hereinafter ENMs) we used only fully independent presence records falling within the *F. sylvatica* native range as
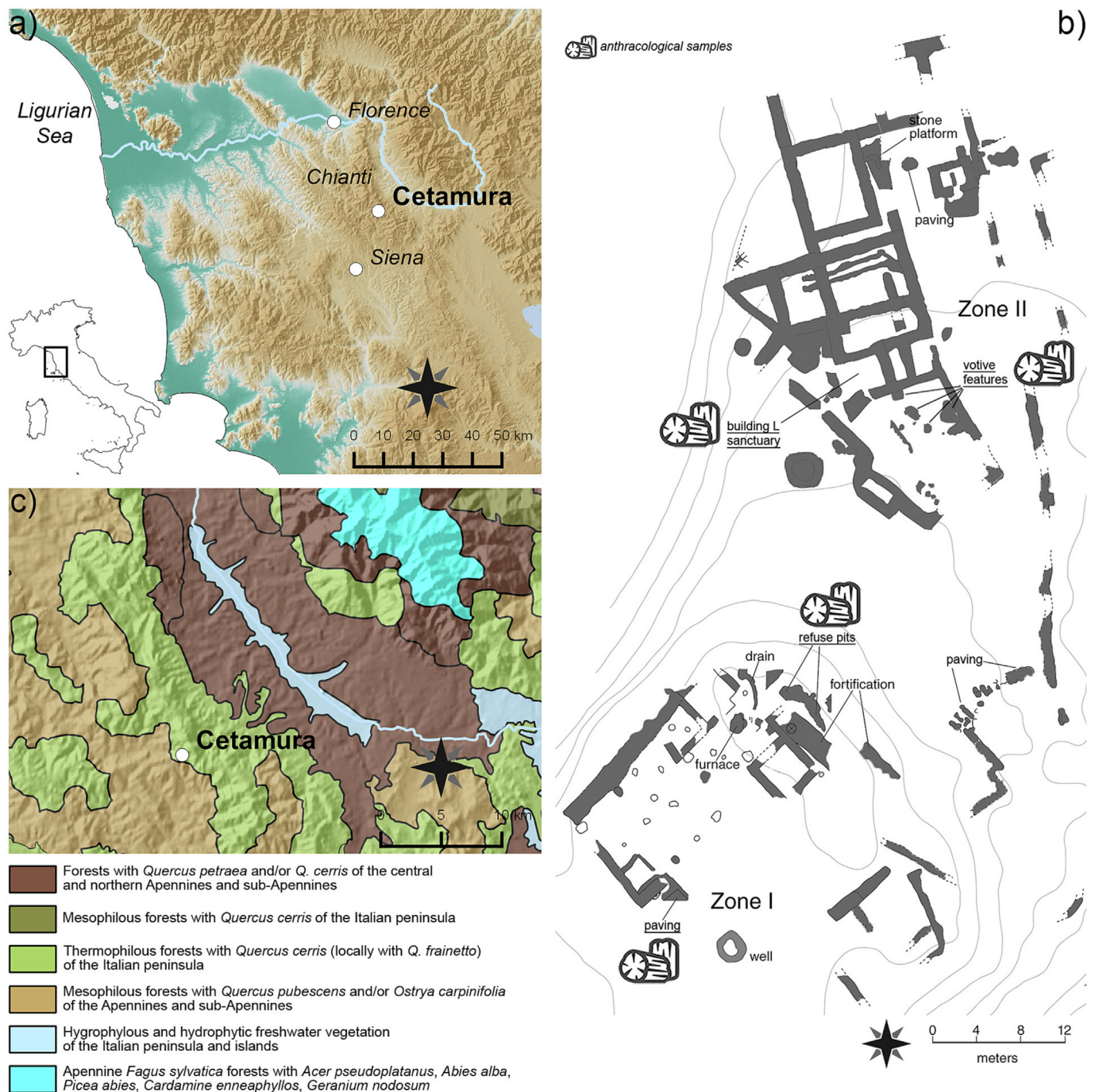
Fig. 1. Location of the archaeological site of Cetamura in the Chianti area (a). Potential natural vegetation map in the area of Cetamura (b, source: http://sinva.minambiente. it/geoserver/VA/vt_serie_di_vegetazione/wms&l=it; legend from Blasi et al., 2017) and the map of the archaeological site of Cetamura with the point where we collected anthracological samples.
(c, from de Grummond, 2011, modified).

described by Caudullo et al. (2017). The final datasets used in the current and LH analyses included 1148 and 123 beech occurrences, respectively (Table S4 and S5).

2.2.3. Environmental predictors

To analyse the current and LH potential distribution of *F. sylvatica*, we considered a set of 19 bioclimatic variables extracted from the PaleoClim database (Brown et al., 2018, http://www.paleoclim.org/), the elevation from the WorldClim database v. 2.1 (https://www. worldclim.org/data/worldclim21.html, Fick and Hijmans, 2017) and the anthropogenic land-use estimates for the Holocene database

(hereafter anthrome, https://easy.dans.knaw.nl/ui/datasets/id/easy-dataset:74467/tab/2, Klein Goldewijk et al., 2017).

The bioclimatic variables were derived from the monthly mean temperature (or minimum and maximum temperature, depending on their availability) and precipitation values. The elevation variable was derived from the Shuttle Radar Topography Mission (https://www2.jpl. nasa.gov/srtm/). Anthrome was obtained using gridded global estimates of human population density and land use from the History Database of the Global Environment v. 3.2.1 (HYDE). HYDE is an internally consistent combination of updated historical population estimates and land use. Categories include cropland, distinguishing irrigated and rain-fed crops (other

Table 1
Sampled anthracological levels correlated with the time interval, corresponding archaeological contexts and number of analysed charcoals. BCE = Before Current Era.

Time interval (BCE)	Archaeological contexts	Sampled layers	Charcoals (N)
150–100	Zone II, Building L, Sanctuary	58N/0.10.1	213
	Zone II, Votive Feature 1	54N/0.19.6	254
		54N/0.26.2	32
	Zone II, Votive Feature 2	50N/0.14.1	176
		50N/0.18.2	4
		50N/0.18.3	70
		50N/0.20.1	12
350–300	Zone I, Paving	9N/21W.7.1	77
		9N/21W.13.1	83
		9N/21W.13.5	129
	Zone I, Refuse Pits	24N/12W.57.8	333

than rice) and irrigated and rain-fed rice fields. Pasture lands were included in the model, too, and divided into more intensively grazed pastures, converted rangeland and non-converted natural (extensive) rangeland. Population is represented by maps of total, urban, and rural population, population density and built-up area. The bioclimatic and elevation variables represent continuous, ratio-scaled data, while anthrome is a categorical, discrete variable.

The bioclimatic and elevation variables were downloaded at a resolution of 2.5 arc-minutes (~5 km), while anthrome had a resolution of 5 arc-minutes (~10 km). This latter variable was converted to the 5 km resolution using the resample tool in ArcGIS in order to have all the predictors at the same spatial resolution. While the bioclimatic variables were selected in the current (Karger et al., 2017) and LH (Fordham et al., 2017) time frames, we used the same layer of elevation for the current and LH models considering that this factor did not change in the two time periods. Contrarily, for anthrome, we chose the years that fall in the middle of the current and LH time periods, i.e., anthrome 2000 BCE and anthrome 0 BCE, respectively.

We clipped the variables on the training and projection areas through the tool "clip" in ArcGIS and converted them into tif files using the package SDMtoolbox v. 2.4 (Brown et al., 2017). The predictors used in our models were selected according to the scientific literature (e.g., Durrant et al., 2016; Poli et al., 2022). Additionally, we excluded the co-linear variables based on the results of the Variance Inflation Factor (Zuur et al., 2010). This led to a final set of nine predictors used for both training and projection models in the current and LH time periods: annual mean temperature (°C), temperature seasonality (°C), annual precipitation (mm/year), precipitation of the driest month (mm/month), precipitation seasonality (%), precipitation of the warmest quarter (mm/three months), precipitation of the coldest quarter (mm/three months), elevation (m) and anthrome (for further details on the anthrome categories used in this study see https://easy. dans.knaw.nl/ui/datasets/id/easy-dataset:74467/tab/2, readme_release_HYDE3.2.1.txt files).

2.2.4. Ecological niche models

We explored the current and LH potential distribution of *F. sylvatica* using ENMs in an ensemble forecasting approach through the package biomod2 (v. 3.4.6, Thuiller et al., 2020), a widely used modelling platform in spatial ecology (e.g., Raffini et al., 2020; Kuiper et al., 2020; Bosso et al., 2022), in R version 4.0.2. To generate our models, we considered four algorithms (Thuiller et al., 2009): 1) Maximum Entropy Models (MAXENT); 2) Generalized Boosted Models (GBM); 3) Random Forests (RF; for further details, see Thuiller et al., 2009); and 4) Artificial Neural Network (ANN). MAXENT used presence-only data, while GBM, RF and ANN required both presence and absence data, thus five sets of 1000 background points were randomly placed over the study area to increase the precision of calibrated models. As in other studies (e.g., Smeraldo et al., 2020; Tulowiecki, 2020), GBMs were developed with the maximum number of trees set to 5000, threefold cross-validation procedures to select the optimal number

of trees to be kept, and a value of seven as the maximum depth of variable interactions. RF models were fitted by growing 750 trees with half the number of available predictors sampled for splitting at each node. MAXENT models were fitted with a maximum value of 1000 iterations. To avoid model overfitting, we developed MAXENT models applying species-specific settings selected using the "ENMeval" R package (e.g., Fourcade et al., 2018). This approach runs successively several MAXENT models using different combinations of parameters to select the settings that optimize the trade-off between goodness-of-fit and overfitting. We set ENMeval to test regularization values between 0.5 and 4, with 0.5 steps, as well as the following feature classes: linear, linear + quadratic, hinge, linear + quadratic + hinge, linear + quadratic + hinge + product and linear + quadratic + hinge + product + threshold, which correspond to the default ENMeval settings. We then selected the parameters that scored lower Akaike Information Criteria values.

The current and LH datasets of *F. sylvatica* presence records were randomly split into a 70 % sample, used for the calibration of the model, and the remaining 30 % was used to evaluate model performance. The data splitting procedure was repeated 10 times and the evaluation values averaged. The relative importance of the predictors was calculated from the ensemble model using the specific functionality available in the biomod2 package (Jiguet et al., 2010). Model averaging was performed by weighting the individual model projections by their AUC scores, a method shown to be particularly robust (Marmion et al., 2009). Then, the final potential distribution was obtained by averaging the projections from the 10 replicated ensemble models generated through the sub-sampling procedure excluding models with AUC <0.75. The average final map obtained had a logistic output format with suitability values from 0 (unsuitable habitat) to 1 (suitable habitat). The final map was then binarised into presence-absence values using a threshold that maximises sensitivity (the percentage of correctly predicted presence) and specificity (the percentage of correctly predicted absence; Fielding and Bell, 1997). This threshold has been widely used (e.g., Algar et al., 2009; Dubuis et al., 2011) and is among the most accurate ones (Liu et al., 2005). Further details are available in Appendix A.

To explore the effect of climatic changes and human impact on the current and LH distribution of *F. sylvatica* in the training and projection areas, we generated six models using a combination of the elevation, climate and anthrome predictors as follows: 1) current distribution using elevation, climate and anthrome (hereinafter CECA); 2) current distribution using elevation and climate (hereinafter CEC); 3) current distribution using elevation and anthrome (hereinafter CEA); 4) LH distribution using elevation, climate and anthrome (hereinafter LHECA); 5) LH distribution using elevation and climate (hereinafter LHEC); and 6) LH distribution using elevation and anthrome (hereinafter LHEA). To be brief, in this manuscript we showed and discussed only the results of the most complete models, i.e., CECA and LHECA. The models CEC, CEA, LHEC and LHEA were used to detect the weight of each environmental predictor or their combination (elevation + climate, elevation + climate + anthrome, and elevation + anthrome) affecting the potential distribution of *F. sylvatica* present in the past but currently extinct.

Environmental similarity and dissimilarity between the training and projection areas was tested using the Multivariate Environmental Similarity Surfaces (MESS) generated by MAXENT software v. 3.4.4 (https:// biodiversityinformatics.amnh.org/open_source/maxent/, Phillips et al., 2006).

We assessed the predictive performances of CECA and LHECA by measuring the Area Under the receiver operating characteristic Curve (AUC; Fielding and Bell, 1997) and the True Skill Statistic (TSS; Allouche et al., 2006).

2.2.5. Field validation

To further assess the accuracy of the LHECA model, we used the independent dataset of past *F. sylvatica* presence obtained from the review of the archaeo-botanical data (Fig. S1 and Table S3) to achieve field validation (e.g., Westwood et al., 2020; Konowalik and Nosol, 2021). We calculated the distance between the beech archeo-botanical data and the LHECA

binary map by using the "Near" tool in ArcGIS v. 10.8. In order to do this, we converted the past records and the LHECA binary map into a point feature. As suggested in the ArcGIS Help section, we selected the geodetic methods to calculate all the distances to consider the curvature of the spheroid and correctly deal with data near the dateline and poles. Then, we assigned a score of 0 (poor prediction), 0.5 and 1 (good prediction) depending on whether the past records fell at a greater distance from 5 km, in a distance range from 0 to 5 km and inside (0 distance) the presence pixel of the LHECA binary map, respectively. We chose the threshold of 5 km in relation to the resolution of the environmental predictors used to run the models. Finally, we calculated a mean value and assessed the performance of our LHECA model following the slightly modified method by Konowalik and Nosol (2021). Three performance classes were considered: poor (0–0.335), medium (0.336–0.665) and good (0.666–1).

2.2.6. Niche analyses

Using the CECA and LHECA final binary maps and their environmental predictors (elevation, climate and anthrome), we analysed the current and LH ecological niches of *F. sylvatica* in Italy following the slightly modified method of spatial Principal Components Analysis (sPCA) described in Santos et al. (2014). We added all the environmental predictors in the "Principal components" tool in ArcGIS v. 10.8. We extracted the values of the first two principal components for each grid cell that resulted to be suitable in the CECA and LHECA binary maps. We calculated a convex hull to delimit *F. sylvatica* environmental space from the binary maps included in this study and measured their individual areas and the area of overlap between species' niches. We extracted the PCA1 and PCA2 values for the current niche, the niche obtained from the overlap between current and LH, and LH niche of the *F. sylvatica* and visualised/measured them on a map to explore the spatial differences among them in Italy. To do this, we converted the PCA1 and PCA2 values into a point feature and used the "Erase" tool in ArcGIS v. 10.8 to obtain the individual beech niches. These procedures were performed for CECA and LHECA to compare the current and past niches of *F. sylvatica*.

2.2.7. Effect of the environmental predictors on the potential distribution of *F. sylvatica* present in the past but currently extinct

We explored the amount of the potentially suitable surface of *F. sylvatica* present in the past but currently lost and the effect of the environmental predictors on the change of beech habitat suitability from the LH to the present day. Firstly, we obtained the lost suitable surface of *F. sylvatica* by subtracting the binary map of CECA to LHECA. To do this, we converted both CECA and LHECA binary maps into point features and obtained the difference between their outputs by using the "Erase" tool in ArcGIS v. 10.8. Secondly, we used the LHEC and LHEA binary maps to understand whether and to what extent variables like elevation + climate, elevation + climate + anthrome, and elevation + anthrome affected the areas where *F. sylvatica* was present in the LH and has currently disappeared. To show the results of this analysis the elevation range was subdivided as follows: 0–300 m, 300–600 m, 600–900 m and >900 m a.s.l.

3. Results

3.1. Charcoal analyses

3.1.1. Archaeo-anthracological analysis

We collected 1383 charcoal fragments (622 = 300–350 BCE and 761 = 150–100 BCE) in Cetamura, assigned to 21 different taxa (Table 2).

3.1.1.1. Time interval: 350–300 BCE. The charcoal data of this period are related to the ritual activities in the sanctuary of the Gods of Fate and Fortune, located in Zone I (Fig. 1c) during the reoccupation of Cetamura. *F. sylvatica* (28.6 %) was the most frequent taxon, followed by other broadleaved trees such as *Quercus* cf. *cerris* (8.2 %), *Ostrya carpinifolia* (7.4 %) and *Q.* cf. *pubescens* (6.4 %). *Carpinus* sp. (3 %), *Cornus* sp. (3 %) and *Fraxinus* cf. *ornus* (1.3 %) were present at lower frequencies (Fig. 2). None of the evergreen taxa, *Q.* cf. *ilex* and *Erica* sp., exceeded 1.5 %.

3.1.1.2. Time interval: 150–100 BCE. In this period, the sanctuary was rebuilt and re-used. Charcoal in the main building resulted from the ritual

Table 2

Charred wood remains from Cetamura according to the time interval. For each taxon, the number of charcoal fragments in the archaeological contexts, the total amount in each time interval, and the respective percentages are reported. BCE = Before Current Era.

Taxa/time interval	350–300 BCE						150–100 BCE							
	Zone I Paving		Zone I Refuse Pits		Total		Zone II Building L Sanctuary		Zone II Votive Feature 1		Zone II Votive Feature 2		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Acer cf. *campestre*	0	0	3	0.9	3	0.5	0	0	0	0	0	0	0	0
Acer cf. *monspessulanum*	3	1.0	4	1.2	7	1.1	0	0	0	0	0	0	0	0
Acer sp.	5	1.7	0	0	5	0.8	0	0	3	1.0	0	0	3	0.4
Carpinus sp.	0	0	19	5.7	19	3.1	61	28.6	10	3.5	4	1.5	75	9.9
Cornus sp.	8	2.8	11	3.3	19	3.1	0	0	0	0	0	0	0	0
Erica sp.	0	0	8	2.4	8	1.3	0	0	3	1.0	0	0	3	0.4
Fabaceae	15	5.2	13	3.9	28	4.5	0	0	1	0.3	45	17.2	46	6.0
Fagus sylvatica	60	20.8	118	35.4	178	28.6	0	0	72	25.2	98	37.4	170	22.3
Fraxinus ornus	0	0	8	2.4	8	1.3	0	0	4	1.4	0	0	4	0.5
Juniperus sp.	0	0	0	0	0	0	0	0	0	0	4	1.5	4	0.5
Maloideae	0	0	3	0.9	3	0.5	0	0	0	0	0	0	0	0
Ostrya carpinifolia	19	6.6	27	8.1	46	7.4	0	0	25	8.7	0	0	25	3.3
Ostrya/Carpinus	12	4.2	29	8.7	41	6.6	37	17.4	0	0	0	0	37	4.9
Prunoideae	0	0	2	0.6	2	0.3	0	0	0	0	0	0	0	0
Quercus cf. *cerris*	40	13.8	11	3.3	51	8.2	48	22.5	61	21.3	21	8.0	130	17.1
Quercus cf. *ilex*	4	1.4	5	1.5	9	1.4	24	11.3	9	3.1	29	11.1	62	8.1
Quercus petraea/robur	0	0	0	0	0	0	0	0	2	0.7	4	1.5	6	0.8
Quercus cf. *pubescens*	24	8.3	16	4.8	40	6.4	12	5.6	26	9.1	5	1.9	43	5.7
Deciduous *Quercus*	19	6.6	8	2.4	27	4.3	0	0	46	16.1	30	11.5	76	10.0
Quercus sp.	58	20.1	13	3.9	71	11.4	11	5.2	20	7.0	12	4.6	43	5.7
Ulmus sp.	0	0	3	0.9	3	0.5	0	0	3	1.0	8	3.1	11	1.4
Undetermined	22	7.6	32	9.6	54	8.7	20	9.4	1	0.3	2	0.8	23	3.0
Total	289	100	333	100	622	100	213	100	286	100	262	100	761	100
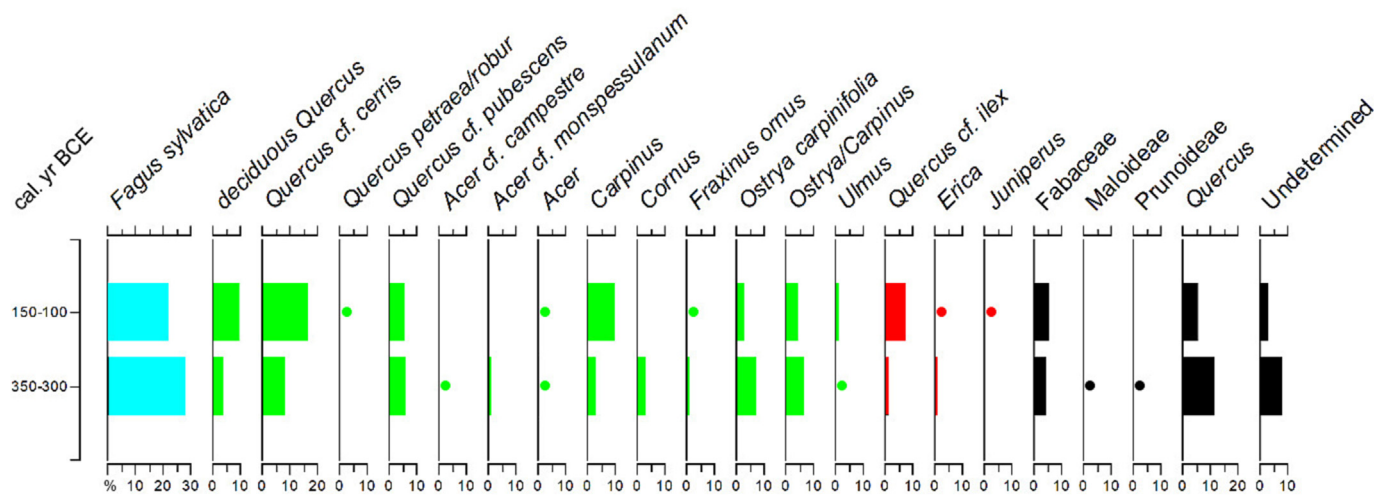
Fig. 2. Charcoal analysis diagram of charred wood remains from Cetamura. On the y-axis, time intervals (calibrated years Before Current Era, BCE) are indicated. On the x-axis, the percentages of each taxon, calculated over the total amount of charcoal remains analysed in each time interval, are reported. The coloured bars group the taxa as follows: deciduous (green); sclerophyllous (red); *Fagus sylvatica* (turquoise). The black bars indicate the taxa that could only be identified at the family, subfamily or genus level. Solid circles represent relative percentage values <1 %.

fires (Fig. 1c, Zone II). Here, *F. sylvatica* counted for 22.3 % of the remains, while *Q.* cf. *cerris* and *Carpinus* sp. represented 17.1 % and 9.9 % of the analysed material, respectively. *Q.* cf. *pubescens* (5.7 %) and *Ostrya carpinifolia* (3.3 %) were also recorded. The presence of the Mediterranean evergreen *Q. ilex* increased to 8.1 % compared to the previous time interval (Fig. 2).

3.1.2. Review of archaeo-botanical data

We identified 25 sites characterised by beech charcoals in the Italian peninsula in the last 4000 years BP. The elevation of the archaeological sites with *F. sylvatica* wood/charcoal/plant remains ranged between 2 and 600 m a.s.l. (Fig. S1 and Table S3). In these settlements, *F. sylvatica* was mainly used as fuelwood (Table S3). Interestingly, 19 sites (76 %) fell within areas that are characterised by Mediterranean macrobioclimatic conditions (Table S3). All the references analysed in this study are reported in Tables S1, S2 and S3.

3.2. Spatial analyses

3.2.1. Current potential distribution range of F. sylvatica

The analysis of the contribution of each variable showed that the annual mean temperature, temperature seasonality and elevation were the main drivers of the CECA model for *F. sylvatica* in the training area (Fig. S3). In particular, *F. sylvatica* is more likely to occur where the annual mean temperature ranges between 8 and 12 °C, the temperature seasonality between 4 and 8 °C and the elevation is higher than 1000 m a.s.l. (mean = 1076 m; SD = 467 m). In the projection area, the current model predicted a suitable area of 73,829 km^2 and high probability of occurrence of *F. sylvatica* especially in the Alps, the Apennines, the highest mountains of eastern Sicily and even a small area in central Sardinia (Fig. 3a and c). The MESS analysis indicated that Italy showed high environmental similarity with respect to the training area (positive values) (Fig. S4a). CECA models showed AUC of 0.907 (mean) ± 0.045 (SD) and TSS of 0.682 (mean) ± 0.034 (SD).

3.2.2. LH potential distribution range of F. sylvatica

Our LHECA results suggested that the temperature seasonality, precipitation of warmest quarter and elevation mostly affected the LH distribution of *F. sylvatica* in the training area. A higher probability of presence was observed in areas with temperature seasonality ranging between 5 and 7 °C, high values of the precipitation of warmest quarter (>500 mm) and elevation below 400 m a.s.l. or above 1000 m a.s.l. (mean = 815 m a.s.l.; SD = 693 m a.s.l.) (Fig. S5). The LHECA model predicted a suitable surface of 143,092 km^2 and high probability of potential distribution of *F. sylvatica*

in several areas in northern, central, and southern Italy, northeastern Sicily and a small area in inner Sardinia (Fig. 3b and d). Also in this case, the MESS analysis indicated that Italy showed high environmental similarity with respect to the training area (positive values) (Fig. S4b). LHECA models showed AUC of 0.941 (mean) ± 0.047 (SD) and TSS of 0.769 (mean) ± 0.038 (SD).

3.2.3. Field validation

A total of 25 archaeological sites (19 scattered along the Italian Peninsula, 4 in Sicily and 1 in Sardinia) bearing wood/charcoal data referred to *F. sylvatica* were analysed (Fig. S1, 4a and 4b, and Table S3). The distance between these sites and the LHECA binary map ranged from a minimum of zero km (12 points) to a maximum of 103.2 km (Fig. 4b). Other seven sites distributed in the central and southern Italic Peninsula from Tuscany to Apulia showed a distance ranging between 1.7 km and 6.6 km (Fig. 4b). Our data from Cetamura (Tuscany) fell within an area that is potentially suitable for beech in the LH (Fig. 4b). Comparing the archaeological distribution with the LH binary map of *F. sylvatica* and the distance of each site from the closest stand of *F. sylvatica*, we identified 13 sites (ID 4, 6, 8, 9, 11–19) that fall inside the LH potential range of beech and seven sites (ID 1–3, 5, 7, 10, 20) that fall within a distance range of 2 and 7 km from the LH stand of *F. sylvatica*. Among all the analysed sites, the points in Sicily and Sardinia showed the highest distance (>58 km) from the closest suitable stand of *F. sylvatica* (Fig. 4b). The field validation showed that archaeo-botanical records obtained the following scores: 18 records = 1; 2 records = 0.5; and 5 records = 0. The final mean value was 0.8 (good prediction).

3.2.4. Niche analysis

sPCA showed a striking overlap between the current and LH *F. sylvatica* niches. In fact, the overlap of Current in the LH and that of LH in the Current, was ca. 85 % and ca. 54 %, respectively (Fig. 5).

3.2.5. Effect of environmental predictors on the potential distribution of lost F. sylvatica stands

We observed a decrease in habitat suitability of *F. sylvatica* in Italy from LH to current of 69,263 km^2 (48 %) (Fig. 6a), mainly affecting the lowland areas (Fig. 6a). Here, climate + anthrome and anthrome alone were the main variables affecting the shrinkage of beech suitable areas, while the climate variable only seems to have affected the innermost Italian stands (Fig. 6b).

Climate, climate + anthrome, and anthrome influenced an area of 41,350 km^2, 15,424 km^2 and 12,483 km^2, respectively. Taking into
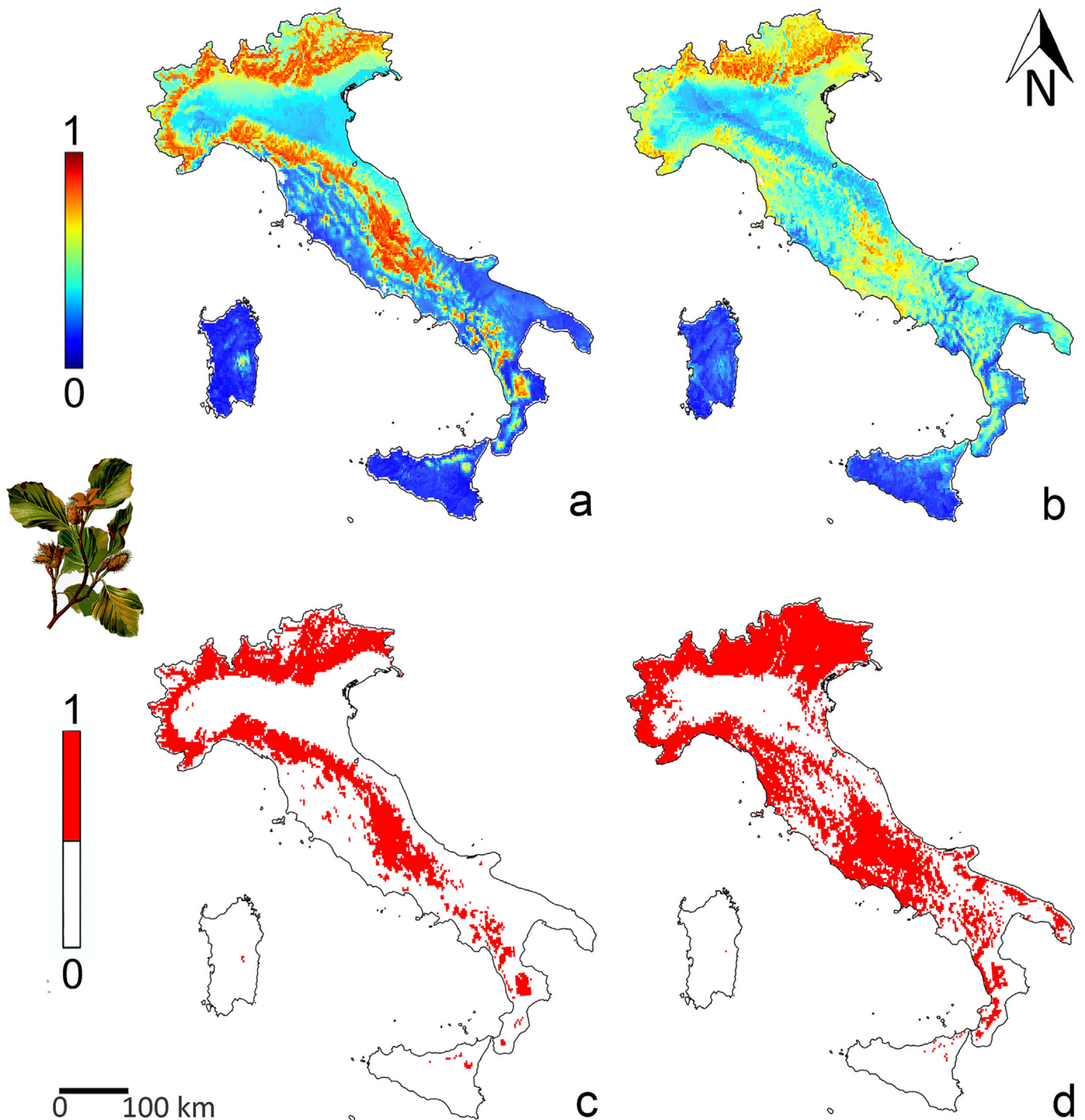
Fig. 3. Current (a and c) and LH (b and d) continuous (up) and binary (down) maps of habitat suitability for *F. sylvatica* in the projection area. Continuous value close to 1 indicate area with high probability of *F. sylvatica*'s presence, close to 0 suggest low probability of *F. sylvatica*'s presence. Binary maps: red areas = presence; white areas = absence.

consideration the combination of climate + anthrome, the most affected stands of *F. sylvatica* were those located in the lowlands (0–300 m a.s.l.) and those at higher elevation (>900 m a.s.l.) (Fig. 7a), while only climate and anthrome mostly affected areas <600 m a.s.l. Considering the percentage of relative frequency, we noticed that on the one hand, the climate affected more homogeneously the beech distribution patterns across the whole elevation range, while, on the other hand, climate + anthrome, and anthrome alone influenced 69 % and 84 % of the lowland areas, respectively (Fig. 7b).

4. Discussion

4.1. Analysis of the Cetamura charcoals

The gathering of the wood material found in the archaeological sites clearly follows the 'principle of least effort' adopted by local dwellers, i.e., the taxa found in the charcoal assemblage typically reflect the most common occurrences in the territory close to the site, although the over abundance of some species could also depend on the specific technical
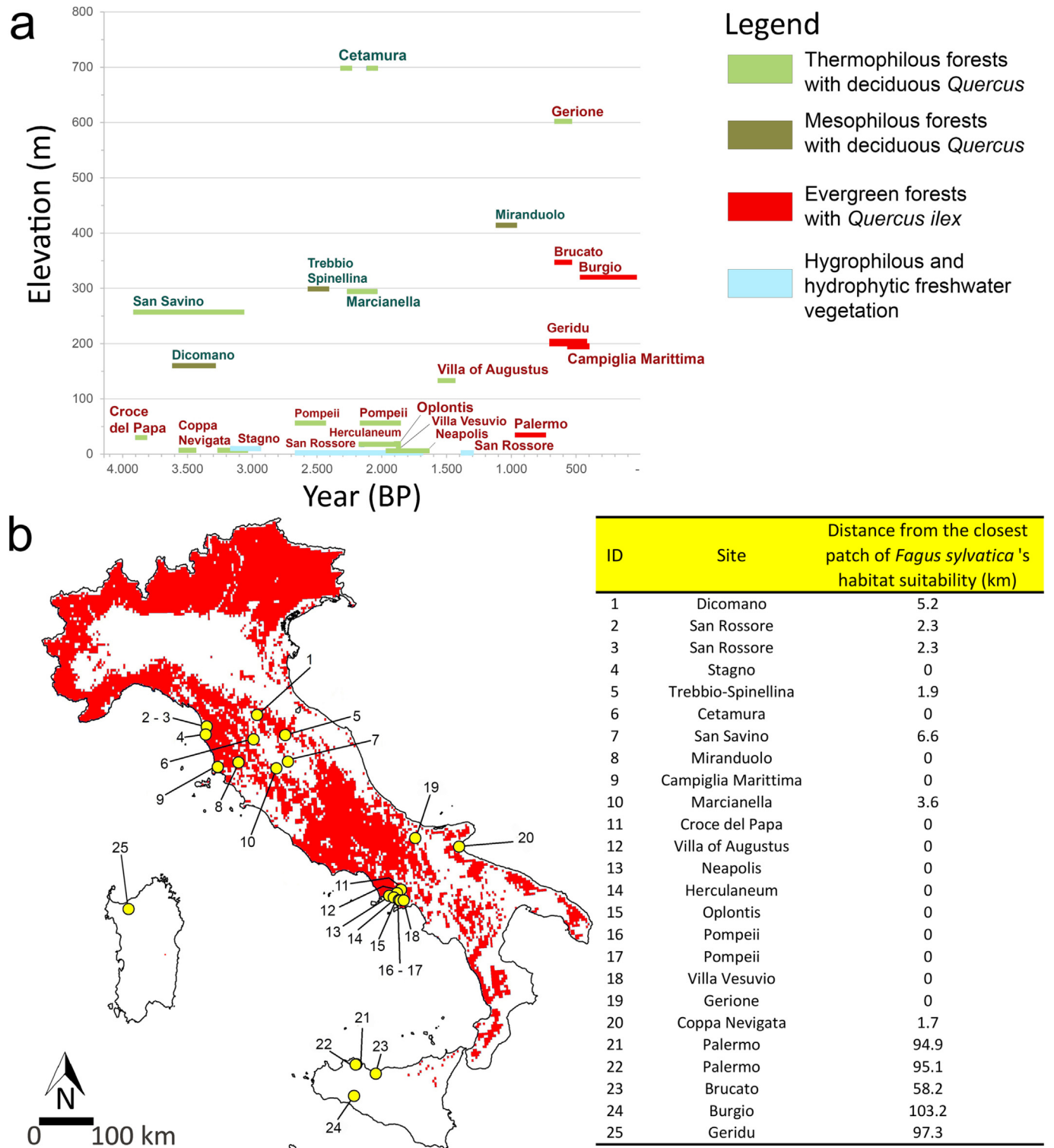
Fig. 4. Elevation (m a.s.l.) and time interval (calibrated years Before Present) of the archaeological sites used for the near analysis. For each locality the current forest vegetation patterns are provided with colour bars (a, source: http://sinva.minambiente.it/geoserver/VA/vt_serie_di_vegetazione/wms&l=it; legend: Blasi et al., 2017). LH binary map of *F. sylvatica* (white areas = absence; red areas = presence) and sites (yellow dots) where beech charcoal was found; the distance of each site from the closest stand of *F. sylvatica* is indicated in the table (b).

properties of the wood itself (e.g., Théry-Parisot and Meignen, 2000; Marston, 2009). The charcoal records of Cetamura suggested the presence of a mixed forest where beech co-occurred with thermophilous broadleaved deciduous trees (mainly *Q.* cf. *cerris*, *Carpinus* sp., *Q.* cf. *pubescens* and *Ostrya carpinifolia*) and evergreen sclerophyllous trees

(*Q.* cf. *ilex*). The dominance of *F. sylvatica* firewood could have been encouraged by the higher quality of beech wood for fuel.

The floristic composition of the forest community of Cetamura suggested by charcoal remains resembles some low elevation mixed deciduous forest stands with beech still occurring in Chianti (380 m a.s.l.) at ca. 40 km
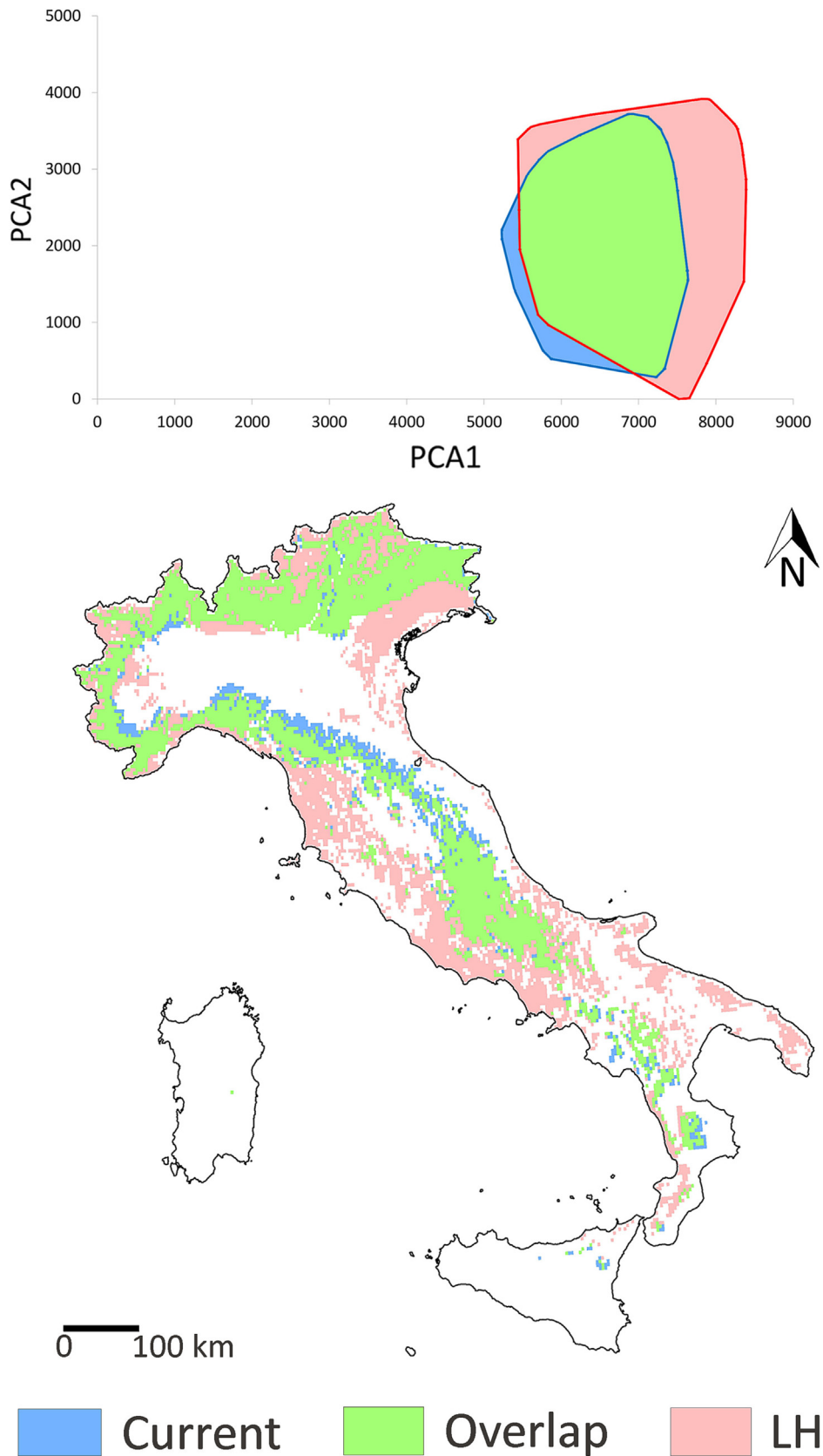
Fig. 5. *F. sylvatica*'s niches (current, overlap and LH) in the projection area: spatial Principal Components Analysis (upper panel) and map (lower panel).

from Cetamura (Table S1, ID 4). Several extra-zonal stands of few or isolated beech trees are also recorded in *Castanea sativa* forests of this region at ca 340 m a.s.l. (Table S2, ID 3).

Interestingly, this mixed broadleaved forest type has also been noticed close to the northern Tyrrhenian Sea coastline, namely in the Colline Pisane (Table S1, ID 6, 7, Table S2, ID 4, 5) and in the Colline Metallifere (Table S1,
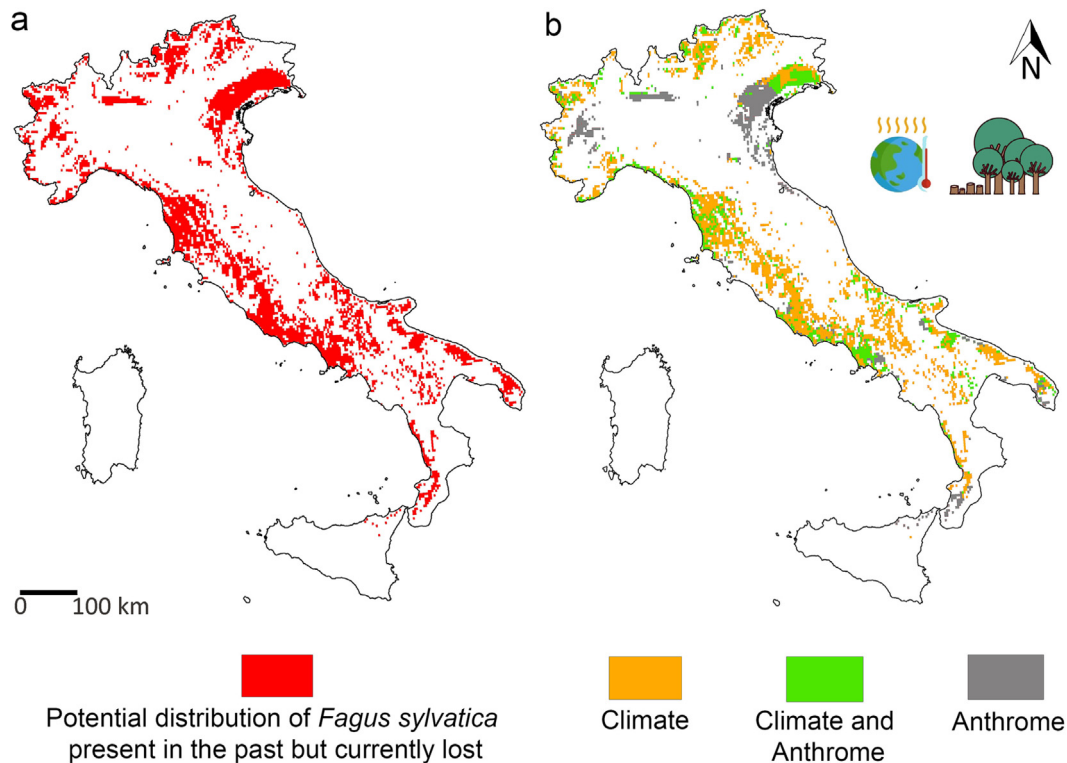
Fig. 6. Potential distribution of *F. sylvatica* present in the past but currently lost (a) and areas that were affected by the climate, climate + anthrome, and anthrome variables (b).

ID 7, 8, 11–20, Table S2, ID 1, 2, 6–8, 11, 12). In mountain areas ranging from ca. 30 to 60 km east-southeast of Cetamura. *F. sylvatica* grows between ca. 400 and 1000 m a.s.l. together with *Q. cerris*, *Acer* spp., *Carpinus* sp., *O. carpinifolia*, *F. ornus* and to a lesser extent *Q. ilex*. In this area of the Apennines, monospecific beech forests start at around 800–900 m a.s.l. (Arrigoni, 1998). Therefore, the data of Cetamura suggest that mixed deciduous forest stands with beech were more widespread in the past in the Chianti hills, at least before the Roman Age (ca. 2300–2050 cal. yrs BP). The sanctuary of Cetamura required large amounts of fuelwood for 200 years, and people likely took advantage of the mixed deciduous forest close to the site. It is worth noting the rise of *Q. ilex* around the end of the 2nd century BCE; as holm oak is a very drought-tolerant and extremely resistant to clearcutting, its increase might be a direct consequence of progressive clearance of the forest cover, whereas *F. sylvatica* decreases. Our data support the Negri's hypothesis (Negri, 1927) that, prior to Etruscan colonization, central Italy was covered by an almost continuous mixed mesophilous broadleaved forest across a significant altitudinal gradient, where beeches coexisted with *Quercus pubescens*, *Q. cerris*, *Q. robur*, *Carpinus* sp., *Fraxinus excelsior*, *Alnus glutinosa*, and other deciduous trees. Instead, in the following centuries, the overexploitation of local forest resources caused the disappearance of beech below 800 m a.s.l., so that the "extra-zonal" mixed deciduous forest stands with *F. sylvatica* are the last remnant fragments of this extinct forest type.

4.2. Review of archaeo-botanical data

In addition to Cetamura, available data from a total of 24 archaeological sites located below 600 m a.s.l. spanning a period of ca. 4000 years (from the Early Bronze to the Modern Age) were surveyed. During the considered time lapse, *F. sylvatica* was more widespread in low-middle elevation forest communities across the central and southern Italian peninsula, emphasising the relict and scattered distribution pattern of present extrazonal stands, currently disconnected from the high-altitude beech forests.

The considered archaeo-botanical records also pointed out that *F. sylvatica* usually co-occurred with thermophilous deciduous trees like

Q. cerris, *Q. pubescens*, *Carpinus* sp. and *O. carpinifolia* (Fig. 4 and S1, Table S3) in most sites located close to the LH potential distribution of *F. sylvatica*, and especially in Tuscany, Campania, and Apulia (Table S3, ID 1–6, 8–20). Furthermore, charcoal data recorded the presence of *F. sylvatica* in plain and lowland forests associated with several mesophilous (*Quercus robur* and *Q. petraea*) and thermophilous (*Acer campestre*, *Ulmus* spp. and *Carpinus* sp.) deciduous trees (Table S3, ID 4, 7, 16, 17 and 20).

It is believed that beech tolerance in low-altitude forests strongly depends on the reduction of stress factors such as water shortage and high temperatures. The Mid and Late Holocene were characterised by rapid climatic excursions involving a progressive "Mediterraneisation" of climate, with longer periods of warmer and drier conditions (Sadori et al., 2011; Giraudi et al., 2011; Peyron et al., 2011). A reduced seasonal contrast and lower precipitation favoured the dynamism of xero- and meso-thermophilous species and, in specific periods, the spread of sclerophyllous and evergreen forests (Peyron et al., 2011; Mercuri and Sadori, 2014).

Almost all our archaeological beech occurrence records (apart those from Sicily and Sardinia) were found close to the LH distribution of *F. sylvatica* and date back to, ca. 3700–3000 cal. yrs BP (Table S3, ID sites 1, 4, 7, 11 and 20), ca. 2300–1400 cal. yrs BP (Table S3, ID sites 2, 3, 5, 6, 10, 12–18) and ca. 1100–600 cal. yrs BP (Table S3, ID sites 8, 9, 19), in line with the warmer and drier climatic phases of the LH, characterised by lower lake stands in the Italic peninsula (Giraudi et al., 2011; Sadori et al., 2015). However, the presence of *F. sylvatica* is commonly associated with plant remains belonging to mesophilous (*Quercus robur/ petraea*) and thermophilous (*Q. cerris*, *Q. pubescens*, *Acer campestre*, *Ulmus* spp. and *O. carpinifolia*) deciduous species. This observation seems to contradict the above-mentioned sclerophyllisation process of the forest vegetation cover.

In their review of Mid-Holocene vegetation history in the central Mediterranean, Sadori et al. (2011) underlined that during the transition from the Mid-Holocene to the LH, the overlap of human impact with a climate aridification trend culminated around 4000 yr BP (Early Bronze Age). The inland Tyrrhenian regions, located in Mediterranean and more cool
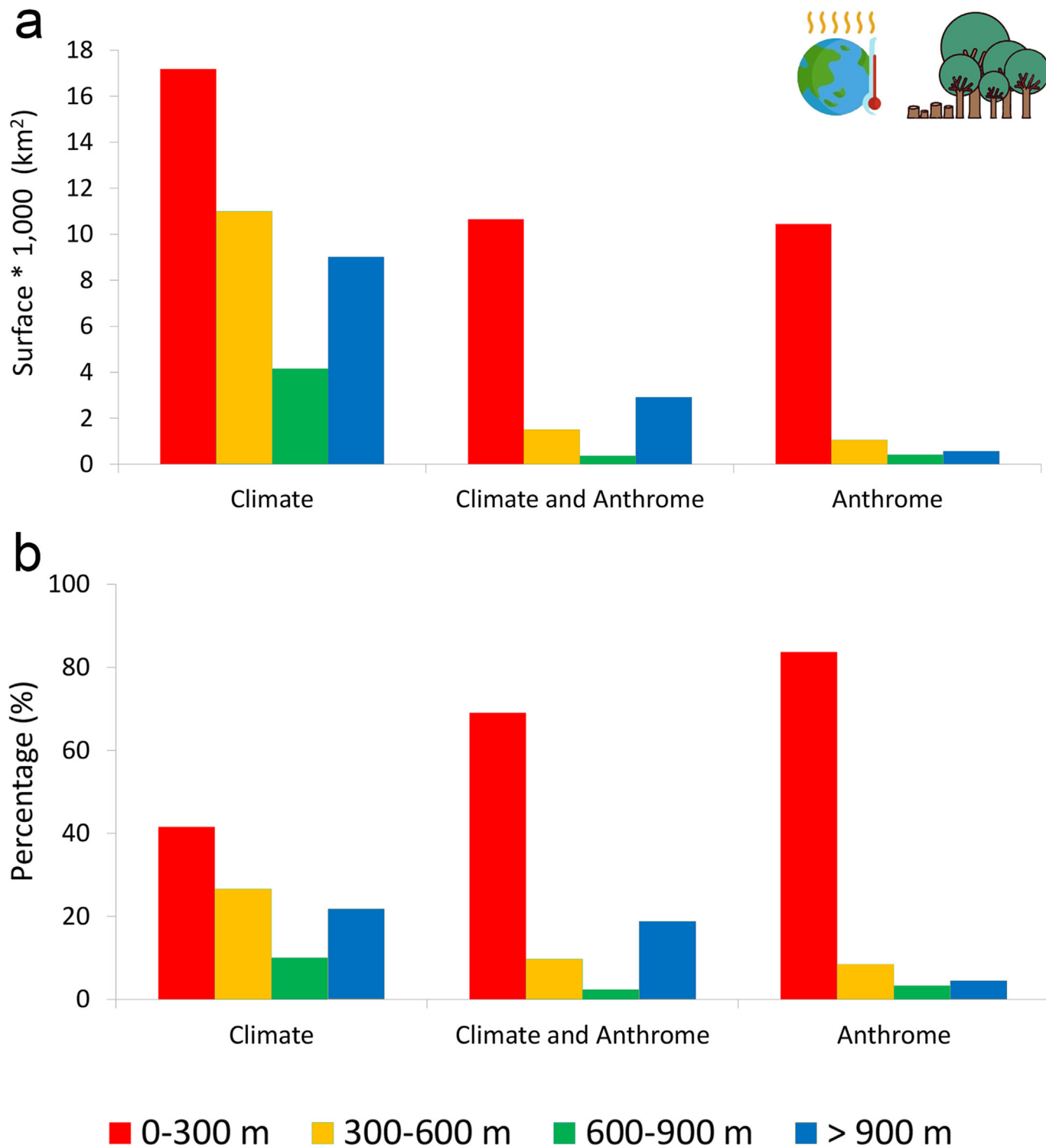
Fig. 7. Potential distribution of *F. sylvatica* present in the past but currently extinct (a) and percent of the relative frequency of the impact of the variables climate, climate + anthrome, and anthrome at different elevations (b).

and humid climatic conditions, were less affected by this mid-Holocene "Mediterraneisation" (Sadori et al., 2011), influencing the presence of beech trees, for example, in the Submediterranean Tuscan and Umbria hills (Fig. S1, Table S3, ID sites 1 and 7). However, it is important to highlight that the archaeological presence of *F. sylvatica* remains was recorded after 4000 yr BP along the Tyrrhenian and Adriatic seaboard in several Bronze Age sites, suggesting the enduring presence of *F. sylvatica* in regions subject to fully Mediterranean bioclimatic conditions (Fig. S1, Table S3, ID

sites 4, 11 and 20). In particular, on the east coast of the Ligurian Sea and in the Campania Plain, beech remains are attested also during the Roman Warm Period at ca. 2300–1400 cal. yr BP (Fig. S1, Table S3, ID 2, 3, 12–18). Therefore, climate may have not played a decisive role in the history of Italian low-altitude beech stands. The anthracological data are, indeed, in agreement with the niche analyses, indicating the influence of climate + anthrome, and anthrome, 69 % and 84 % respectively, in the lowland areas up to an altitude of 300 m a.s.l.

After ca. 3600 cal. yr BP, human impact became evident in the Italian peninsula with fire and forest clearance in the Middle Bronze Age (Sadori, 2018; Moser et al., 2017; Stoddart et al., 2019) as a result of a dramatic population increase during the Bronze and Iron Ages (ca. 3800–2800 cal. yr BP) that cannot be correlated with climatic changes (Palmisano et al., 2021).

Until the Final Bronze/Early Iron Age (ca. 3000 cal. yr BP), archaeological sites with *F. sylvatica* remains showed the presence of light-demanding species, suggesting the occurrence of forest communities with a (relatively) open canopy (Table S3, ID sites 1, 4, 7, 11, 20). Cultivated tree species are also recorded, confirming the interference of human settlements on the forested areas where the beech was present (Table S3, ID sites 11 and 20). According to archaeological evidence, beech wood is mainly used as fuel (Table S3, ID sites 1, 7, 11 and 20). In fact, beech has a high heating value, whereas it is not durable for timber because it is easily attacked by insects and fungi. More broadly, the thermophilous and mesophilous deciduous forests with *F. sylvatica* were used by the local populations as coppice woods.

The spread of the Roman economy at ca. 2300 cal. yr BP launched a period of intense anthropogenic modifications of the natural habitats (Mercuri and Sadori, 2014). The impact of the classical period on the agrarian and forest landscapes of the Italic peninsula was initially noteworthy, but highly varied close to human settlements. Later, the Roman impact was more pervasive (Stoddart et al., 2019). The presence of beech wood in archaeological sites is more and more related to its use as fuel (Table S3, ID sites 5, 6, 10, 12 and 17), but the presence of timber for building (Table S3, ID sites 10 and 14) and ships (Table S3, ID sites 2, 3 and 13) is recorded, as well as the occurrence of "small" plant remains of beech (Table S3, ID sites 2, 3 and 18). Interestingly, in the same period, the Greek botanist Theophrastus (c. 372-c. 287 BCE), describing the properties of the beech wood, explicitly mentioned both lowland and mountainous provenances, bearing witness that this species also grew at low altitudes at that time (Di Bérenger, 1859-1863).

From the final Iron Age and along the Roman period (ca. 2700–1700 cal. yr BP), our review identified few sites investigating a time lapse long enough to understand the forest cover evolution (Fig. S1, Table S3, ID 2, 3, 6, 16, 17). However, although located in different geographic and macrobioclimatic areas (Fig. S1, ID 2, 3, 16 and 17: Mediterranean; ID 6: Submediterranean), these sites show very similar dynamics.

From the 2nd century BCE to the 79 CE, beech wood was the most important fuel supply in the Roman town of Pompeii in the Campania Plain (Fig. S1, Table S3, ID sites 16 and 17). Here *F. sylvatica* co-occurred with deciduous *Quercus* and other mesophilous taxa (*Carpinus* and *Acer*). During these three centuries, the beech remains show a gradual decrease in favour of thermophilous deciduous trees, sclerophylls, and fruit trees from orchards. To explain this trend, the importation of beech wood based on the current presence of *F. sylvatica* forests above 900 m a.s.l. and 15 km away from Pompeii and "the increased use of fruit and nut woods as kindling, simply because they were available and close by" has been invoked (Veal, 2014).

In the Roman harbour of Pisa at San Rossore (Fig. S1, Table S3, ID sites 2 and 3), between the 1st century BCE and 2nd century CE beech leaves and fruits are the most common remains (Bertacchi et al., 2008) and *F. sylvatica* lumber is used in the mast carling and prow deck in the ship C dated to the 1st cent. BCE–1st cent. CE (Giachi et al., 2003). For the authors beech, and the mixed deciduous forest communities where it grew, initially covered the lower elevations around the Arno Valley. The species gradually declined until its complete disappearance due to forest overexploitation which made this harbour important in the Roman age (Bertacchi et al., 2008; Sadori et al., 2015).

Indeed, Cetamura, Pompeii, and San Rossore (in chronological order) differ in terms of altitude, distance from the coastline and macrobioclimate (Submediterranean at Cetamura and Mediterranean at Pompeii and Pisa-San Rossore). Notwithstanding these differences, these three sites share the same gradual increase in the use (and thus presence) of thermophilous

broadleaved deciduous and evergreen taxa, suggesting a similar pattern of change in the forest vegetation cover.

According to forest ecological researchers, small gap disturbances enable beech trees to access the canopy and to outgrow anyway deciduous oak saplings (Ligot et al., 2013; Petritan et al., 2017), whereas high frequency and large disturbance on the canopy create conditions of higher light levels and lower water availability, favouring the recruitment and regeneration of shade-intolerant and drought-tolerant deciduous *Quercus* and thermophilous trees (Petritan et al., 2017). Under well-lit conditions and with lower water availability, beech loses its dominant role. Once coppiced, sprouts very slowly, and under water stress conditions it regenerates and grows even less leading to stump death (Piovesan et al., 2005, 2008). Light-demanding and drought-tolerant tree species outcompete the shade-tolerant beech by a much higher resprouting strategy at the adult stage and they persist in disturbed environments predominating in wood cutting (Gesler et al., 2007; Petritan et al., 2017).

Intensive forest uses would have favoured the more thermophilous and strongly suckering species, compromising the renewal of beech and its persistence within local natural forest dynamic processes. In Cetamura, the impact of coppicing facilitated the establishment and spread of typically Mediterranean evergreen species, which are better adapted to higher light levels and lower water availability. In San Rossore and, in our opinion, in Pompeii, the gradual decrease of beech, coincide with an increasing exploitation of secondary fuel wood resources, suggests the disappearance of beech in the mixed mesophilous forests during the Romanization of these territories, that induced the expansion of the towns and the transformation of natural areas into countryside.

The general picture for Holocene dynamics of beech in Italy suggests a progressive increase during the postglacial period until about 2500 cal. yrs BP, when it started declining (Magri, 1998; Magri et al., 2015). Palynological data point to a more wide spread distribution of *Fagus* in the earlier Holocene and in previous interglacial periods, however detecting any possible explanation for the progressive confinement of the beech to the mountainous areas of the Apennines and the Alps in the last thousand years (Magri et al., 2015). Moreover, although the shift in climatic conditions towards warmer phases has been invoked as the main trigger of the progressive shrinkage and disappearance of *F. sylvatica* in the LH pollen sequences at lower altitudes (Mariotti Lippi et al., 2007), this hypothesis has not been supported by further research (e.g., Magri et al., 2015).

Our results are consistent with the Mediterranean forest history synthesis proposed by Birks and Tinner (2016): in the second half of the Holocene the so-called "*Homo sapiens* phase" induced major changes in forest structure and composition. In fact, disturbance-sensitive taxa such as *Fagus* declined after centuries and millennia of coppicing for firewood, charcoal production and grazing in the mixed forests of low altitudes. On the other hand, this tree was also selected by humans for their timber and fruits, involving, probably for the first time, the formation and the subsequent expansion of the current monospecific beech populations present at altitudes exceeding 800–1000 m a.s.l. in southern Europe.

4.3. Persistence, shrinkage, and local extinction: new hypotheses for different fates

Many low altitude beech stands rich in other broadleaved (deciduous and even evergreen) trees occur in West Eurasia, from the Hyrcanian region to Transcaucasia (Denk, 1998) and in fully Mediterranean biogeographical contexts throughout southern Europe, i.e. in southern France (Steinmetz, 2003), southern Balkan Peninsula (Quézel and Médail, 2003), Catalonia (Costa-Tenorio et al., 1998) and Turkey (Akman et al., 1979). In many cases, the subsistence of these beech forest stands clearly depends on local thermal inversion mechanisms. Similar phenomena are also attested in the Italian Peninsula (Tables S1 and S2), such as in the Tuscan Colline Metallifere and Colline Pisane, hosting low altitude beech stands in the meso-Mediterranean belt dominated by *Q. cerris* and *Q. ilex* woods (350 to 700 m a.s.l.), in Campania at Roccamonfina and on Monti Picentini

(300 to 400 m a.s.l.), in the Lucanian Apennines (655 to 800 m a.s.l.) and in the Esino-Frasassi valley (240 to 500 m a.s.l.). Thermal inversion was also invoked to explain the presence of beech 10,200–8900 cal. yrs BP near the volcanic lakes of northern Latium (Magri, 2008). Other heterotopic stands in the southern Apennines, like Monticchio (Allen et al., 2002), lie close to lakes, too.

In other areas, however, intensive logging and timber exploitation may have caused the local extinction of *F. sylvatica* stands, like in the case near Lago Lungo near Rieti (Mensing et al., 2015), where beeches nowadays occur only at 800–900 m a.s.l.

Our models show a particularly significant contraction of beech stands in some coastal and hilly areas, particularly in Campania Plain and in north-eastern Sicily, and suggest the possible extinction of beech in Sardinia in protohistoric or historical times. Since the archaeo-anthracological data available to date on Sicily and Sardinia are still very scarce, we preferred to skip the discussion on the two main Italian islands, which risked being too speculative.

4.4. Current and past distribution of Fagus sylvatica in Italy: evidence from spatial analyses

Our ENMs proved to be considerably performant in estimating the current and past distributions of *F. sylvatica* in Italy, as also shown by model validation. In fact, AUC and TSS values such as the ones that we obtained are among the highest reported for published models (e.g., Kuiper et al., 2020; Salinas-Ramos et al., 2021) and documented a high predictive power of habitat suitability (Elith et al., 2010). Furthermore, our LHECA model showed good prediction performance based on a field validation (Konowalik and Nosol, 2021). In agreement with the other models already published, our current map matched well with the potential distribution of *F. sylvatica* in Italy (e.g., Caudullo et al., 2017; Mauri et al., 2017; Poli et al., 2022). The substantial matching between our models and the maps shown by previous authors represents an encouraging piece of evidence supporting the reliability of the maps of past predicted distribution of *F. sylvatica* in Italy. Currently, beech forests cover a surface of ca. 10,351 km^2 in Italy (Gasparini and Tabacchi, 2011) while our current model predicted a potential suitable area of 73,829 km^2. This is not surprising because it is widely known that the current beech distribution in Italy is very limited with respect to the ecological amplitude of *F. sylvatica* niche. Perhaps the general picture, i.e., the beech's extremely wide distribution range and ecological niche breadth, has made us lose sight of the detail, i.e., the peculiarities of low-altitude stands, while many questions could find clear and unexpected answers by focusing our investigations exclusively on these heterotopic stands, analysing possible gradients and differences in terms of physiology (e.g., water stress-tolerance, sprouting ability), vegetation patterns (structure, dominance and floristic composition) and dynamics, population genetics, etc. All this information could be used to refine future analyses allowing a better understanding about the past, present and future potential distribution of *F. sylvatica*. Furthermore, ENMs do not consider biotic interactions such as competition or other unpredictable factors which might play a role in influencing actual and past distribution (e.g., Di Pasquale et al., 2020). Our spatial analysis, especially at the macroscale (continent or country), may not be able to capture some nuances that are important for the ecology of the species. For example, it is possible that the location of heterotopic stands eludes models based on macro- and meso-climatic data and that more attention should instead be paid to the role played by edaphic factors and local microtopography (Garfì et al., 2021). This could explain some apparent inconsistencies between medium- and large-scale models and what is recorded at small scales. For instance, on the one hand dendroecological surveys suggest an increasing distress of Sicilian beech trees, which tend to anticipate their vegetative activity in May to avoid water shortage(Merlino, 2016), while on the other hand Bazan et al. (2018) highlighted a recent increase in beech forest size in the mountainous sector of the Nebrodi Mts. Perhaps the models also underestimate the important effect of

continuous forest cover (and its destruction). In fact, during the summer dry season the average temperatures measured in the undergrowth of closed forest ecosystems may be up to 10 °C lower than those recorded outside the tree canopy. Hence, closed forest stands still appear to be able to "create on their own" good chances of survival in the medium term even in sites considered suboptimal and particularly vulnerable (Rita et al., 2021).

The use of geospatial technologies (as for example GIS, modelling and remote sensing applications) to reconstruct species and vegetation distribution (e.g., Roberts et al., 2018; Zanon et al., 2018) may enable us to better understand the factors triggering past and future vegetation dynamics (Henne et al., 2015; Takolander et al., 2018) and the historical impacts of varying intensity of land use and anthropogenic pressure (Palmisano et al., 2021; Romano et al., 2021). Insights from joint charcoal and spatial analyses to explore biogeographic questions about past and current of species distribution can inform today's forest management and conservation policies and practices, as well as future research projects (e.g., Di Pasquale et al., 2020).

As far as forest planning is concerned, it worths being considered the strong reforestation process due to the socioeconomic changes that occurred from the end of 19 century in Italy (4,215,000 ha of forest in 1888 vs. 11,778,000 ha today, Agnoletti et al., 2022). On this purpose, especially in the last decades many monospecific coppices were converted into high stands with the idea of renaturalizing and rewilding these forests, also favouring biodiversity. In fact, it is well known that heterogeneous mixed-species stands are of special interest as they fulfil many ecosystem services better than monocultures (Pretzsch, 2019). In our opinion, the study of past vegetation dynamics combining archaeo-anthracological records and spatial analysis can be a valuable tool to derive insights into vegetation legacies and develop new conservation and restoration strategies (Di Pasquale et al., 2014, 2020), as recent similar cross-disciplinary studies have also shown for lake palynological records (Palli et al., 2022). From this perspective our data show that it would be helpful to also consider *F. sylvatica* in the rewilding processes of Mediterranean and Submediterranean areas below 600 m a.s.l. in the Italian peninsula.

5. Conclusions

Our results shed light on how and to which extent the bioclimatic conditions and/or human impact affected the presence and distribution of *F. sylvatica* in the Italian Peninsula during the LH. They indicated that both the climatic conditions and anthrome affected the natural potential of these forests. The charcoal data analyses documented the presence of *F. sylvatica* in several lowland areas during the LH in Italy, showing that these areas played an important role for this ecosystem, beech stands were a very common feature of the Italian forest landscape from 2 m a.s.l. to 800–900 m a.s.l. until recent times and that the rarefaction/disappearance of *F. sylvatica* was mainly due to the (over)exploitation of the forest stands.

ENM projections provided a useful complement to our palaeoecological studies, refining charcoal evidence and offering a less biased picture of the distribution pattern of *F. sylvatica* in the LH. Our results showed that human impacts on beech distribution and presence have strongly influenced the landscape, especially in the coastal and lowland areas and in the areas located at >900 m a.s.l. Climate and anthrome can surely influence the landscape patterns also in different ways (e.g., amount of area and quickness of change) and, for this reason, we suggest to include them in the ENMs focused on the assessment of the distribution range changes that tree species experienced in the past and will face in the future.

Our results highlight the advantage of combining different approaches such as charcoal analysis and spatial analyses to explore biogeographic questions about past and current distribution of *F. sylvatica*, with important implications to inform today's forest management and conservation policies and practices.

CRediT authorship contribution statement

The authors confirm contribution to the paper as follows, **Buonincontri**: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Data Curation, Writing - Original Draft and Writing - Review & Editing; **Bosso**: Methodology, Formal analysis, Validation, Investigation, Data Curation, Writing - Original Draft and Writing - Review & Editing; **Smeraldo**: Methodology and Formal analysis; **Chiusano**: Writing - Original Draft and Writing - Review & Editing; **Pasta**: Investigation, Supervision, Writing - Original Draft and Writing - Review & Editing; **Di Pasquale**: Investigation, Supervision, Writing - Original Draft and Writing - Review & Editing.

All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data is available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162893.

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