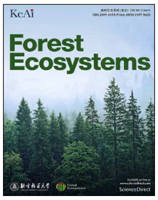
Forest Ecosystems 14 (2025) 100345

Contents lists available at ScienceDirect

Forest Ecosystems

journal homepage: www.keaipublishing.com/cn/journals/forest-ecosystems



Causes of co-existence of cool-temperate *Fagus* and warm-loving evergreen *Quercus* forests in central Italy during the Holocene thermal maximum

Giorgia Beffa [a,b,*], Erika Gobet [a,b], Sevil Coşgun [a,b,c], Riccardo Dotta [a], Luc Hächler [b,d], Marina Alexandra Morlock [b,e,f], Laura Sadori [g], Patrick Schläfli [a,b], Christoph Schwörer [a,b], Lieveke van Vugt [a,b], Hendrik Vogel [b,e], Paul David Zander [b,d,h], Martin Grosjean [b,d], Willy Tinner [a,b]

[a] *Institute of Plant Sciences, University of Bern, Bern 3013, Switzerland*
[b] *Oeschger Centre for Climate Change Research, University of Bern, Bern 3012, Switzerland*
[c] *Eidg. Forschungsanstalt WSL, Birmensdorf 8903, Switzerland*
[d] *Institute of Geography, University of Bern, Bern 3012, Switzerland*
[e] *Institute of Geological Sciences, University of Bern, Bern 3012, Switzerland*
[f] *Department of Ecology and Environmental Sciences, Umeå University, Umeå 90736, Sweden*
[g] *Dipartimento di Biologia Ambientale, Sapienza University of Rome, Rome 00185, Italy*
[h] *Climate Geochemistry Department, Max Planck Institute for Chemistry, Mainz 55128, Germany*

ARTICLE INFO

Keywords:
Palaeoecology
Plant–climate interactions
Biodiversity
Climate warming
Mediterranean
Continuous time series

ABSTRACT

Mediterranean forest communities are particularly diverse but at risk due to their sensitivity to global warming. Understanding the long-term vulnerability of Mediterranean vegetation to climate change is crucial for conservation and management purposes. Studies on past changes of forest communities in response to climate change at ecologically meaningful resolutions (i.e., decadal time scales) are therefore essential, but still very rare. The Holocene thermal maximum (HTM; ca. 10,000–5,000 cal years before the present (BP)) may be used to study species and community responses to warmer conditions than during recent decades. We performed high-resolution multiproxy palaeoecological analyses on sediments from crater Lake Mezzano in central Italy to reconstruct vegetation, diversity, and fire dynamics between 8,450 and 7,050 cal years BP. Ordination, cross-correlation, and species-response analyses were used to investigate the response of Mediterranean forest communities to HTM climate warming, human impact, and fire. Vegetational changes prior to 7,450 cal years BP were driven by climate. *Fagus sylvatica* spread into mixed deciduous oak forests during the Early Holocene in response to declining seasonality (cooler summers and warmer winters). Subsequently, *Fagus sylvatica* declined and evergreen *Quercus ilex* expanded after 8,200 cal years BP when the climate became warmer. Although reduced, *Fagus sylvatica* remained important together with deciduous oaks. The co-existence of *Fagus sylvatica* and evergreen *Quercus* forests is extremely rare today. Human impact significantly affected forest vegetation after 7,450 cal years BP, when Neolithic agricultural activities became important, ultimately extirpating these special communities but fostering the overall biodiversity. However, their past occurrence in several central Italian calderas during the HTM suggests that these environments provided habitats that permitted the thriving of cool-temperate forests of *Fagus sylvatica* under mesomediterranean conditions, with summers ca. 1–2 °C warmer than today. Cool and moist calderas may thus become increasingly important for maintaining Mediterranean mesophilous forest species under global warming conditions.

1. Introduction

The Mediterranean realm is known to be one of the world's main biodiversity hotspots, yet one of the most threatened due to its sensitivity to climate change (Myers et al., 2000; Cuttelod et al., 2009). The Italian peninsula lies at the center of the Mediterranean and presents a

---

[*] Corresponding author. Institute of Plant Sciences, University of Bern, Bern 3013, Switzerland.
E-mail address: giorgia.beffa@unibe.ch (G. Beffa).

Peer review under the responsibility of Editorial Office of Forest Ecosystems.

https://doi.org/10.1016/j.fecs.2025.100345
Received 10 March 2025; Received in revised form 7 May 2025; Accepted 7 May 2025

large variety of landscapes hosting numerous plant species typical of different European biomes, spanning from arctic-alpine to subtropical vegetation types (Pignatti, 1997, 1998; Blasi et al., 2018; Lang et al., 2023), which are expected to undergo major compositional and distributional shifts as a consequence of ongoing global warming (Dobrowski et al., 2021). From an ecological perspective, species and community displacements are expected to occur particularly in warm and dry habitats where plant species characteristics of temperate ecosystems are already growing close to their heat or drought tolerance threshold (Piovesan et al., 2008; Peñuelas et al., 2017; Morales-Molino et al., 2021; Del Martinez Castillo et al., 2022; Machado Nunes Romeiro et al., 2022). Due to their low drought tolerance, beech forests are currently restricted to elevations above ca. 800–1,800 m a.s.l. in the Apennines and elsewhere in the Mediterranean (Horvat et al., 1974; Díaz-Gonzalez and Peñas, 2017; Pignatti et al., 2017). There, *Fagus sylvatica* faces significant threats due to the increasing frequency of drought events (Piovesan et al., 2008; Morales-Molino et al., 2021; Frei et al., 2022). However, palaeoecological evidence (Magri et al., 2015; Buonincontri et al., 2023) suggests that, in the past, beech forests also thrived in the mesomediterranean Italian lowlands in competition with evergreen oaks (Buonincontri et al., 2023). Today, the co-occurrence of *Fagus sylvatica* with *Quercus ilex* is extremely rare in the Italian lowlands below ca. 800 m a.s.l. (Cavalli and Drosera, 1989; Scoppola and Caporali, 1998; Croce et al., 2008; Di Pietro et al., 2010; Spicciarelli et al., 2011). Although above 800 m a.s.l. to uppermost elevations of 1,000–1,200 m a.s.l., the two species can co-occur in human-disturbed, transitional vegetation settings (e.g., Bartolo et al., 1990; Chirici et al., 2014), the Mid Holocene co-dominance of *Fagus sylvatica* and *Quercus ilex* in lowland forests remains ecologically enigmatic.

Detailed observation of past vegetation dynamics under varying climatic conditions is essential to get better insights into current and future scenarios of plant communities' composition and biodiversity. The reconstruction of past vegetation dynamics at ecologically meaningful (annual to decadal) temporal scales requires continuously sampled, high-resolution palaeoecological time series, which unfortunately are only very rarely available. Of particular interest are periods of past rapid climate change or with warmer climatic conditions than today. The Holocene thermal maximum (HTM) lasted approximately 10,000−5,000 cal years before the present (BP) and was characterized by higher summer temperatures than the recent industrial period in the northern hemisphere, probably as a consequence of higher orbitally-forced summer insolation (Wanner et al., 2008; Samartin et al., 2017; Fischer et al., 2018; Cartapanis et al., 2022; Lang et al., 2023). Climate models, marine records, and pollen-independent proxies such as fossil chironomid assemblages show that in the Mediterranean realm, during the HTM, summer temperatures were on average ca. 1–2 °C warmer than those of the past ca. 30 years (Fischer and Jungclaus, 2011; Samartin et al., 2017; Marriner et al., 2022). Major changes in plant community composition characterized the HTM. Because it is plausible to assume that they were mainly caused by warmer summer temperatures, vegetation reorganizations may re-occur under future global warming. Thus, the HTM period may be regarded as an analogue for projected warmer conditions (Fischer et al., 2018). Nevertheless, this analogy is only approximate as it does not consider important factors, such as divergent drivers of global warming (Williams and Jackson, 2007) and human pressure (Mercuri et al., 2013). When interpreting past vegetation dynamics, it is important to disentangle climate and human impact, although this is not always unproblematic, given that they may act together and land use may also be influenced directly by climate change (van Geel and Mauquoy, 2010; Woodbridge et al., 2014; Rey et al., 2019). However, predicting the consequences of possible displacement scenarios of mesophilous Mediterranean forest species may markedly benefit from integrating highly resolved multiproxy palaeoecological time series disclosing the causes and mechanisms of forest species and community responses to past climate change.

Our continuous high-resolution study (8,450–7,050 cal years BP) from central Italy has the goal of reconstructing decadal-scale vegetation dynamics during the period of the HTM when forest gradually shifted from a natural to an anthropogenically disturbed state in response to the first Neolithic agriculture. The primary goal of our study is to investigate the long-term ecology of the formerly widespread, today almost extinct co-existence of beech and evergreen oak forests under warm HTM conditions. This period allows us to study the transition from primeval forests to early land use, focussing on various degrees of human impact, from absent to moderate. We are particularly interested in disentangling the effect of climate, fire, and first human impact on forest vegetation dynamics and species diversity using continuously sampled, high-resolution data. Such a procedure allows us to disclose the causes of the marked forest composition and structure changes observed in central Italy during the Early and Mid Holocene, thereby enhancing our understanding of the sensitivity and vulnerability of these particular Mediterranean forest communities to climatic and land use changes. Our study of past vegetation dynamics in response to climate and land use changes may help to better assess future ecological responses to global warming and human pressure. Specifically, it may provide novel insights for maintaining future forest diversity through management, conservation, and restoration strategies.

2. Material and methods

2.1. Study site

Lago di Mezzano (42°36′42.0″ N, 11°46′12.0″ E, 452 m a.s.l., 0.5 km^2, 31 m water depth) is a maar lake located in central Italy in the caldera of Latera, which is part of the Vulsini volcanic complex along with the nearby Lago di Bolsena and the artificially dried-out lake Lagaccione (Fig. 1). Lago di Mezzano was formed about 100,000 years ago following a phreatomagmatic eruption and is mainly surrounded by volcanic bedrock (Giraudi, 2004). The caldera of Latera is located ca. 30 km east of the Tyrrhenian Sea and ca. 50 km west of the Apennines. The climate is Mediterranean with warm summers and mild winters. At the nearby weather station of Pitigliano (ca. 9 km from Lago di Mezzano at 300 m a.s.l.), the mean annual temperature of the past thirty years (1993–2023) is 15.2 °C, August mean temperature 24.2 °C, and January mean temperature 6.9 °C (SIR Toscana, 2024). Mean annual rainfall of ca. 910 mm results in rather humid climatic conditions in the area (Baldi et al., 2004), with mean precipitation during the three driest months (June–August) amounting to 117 mm in total (SIR Toscana, 2024), leading to slight summer aridity (Blasi, 1994). Our study site in the caldera of Latera and its surroundings are located in the transition from submediterranean or supramediterranean deciduous mixed oak forests to mesomediterranean vegetation with occasional occurrences of *Quercus ilex* trees (Blasi, 1994; Lang et al., 2023). Nowadays, the hilly landscape is characterized by pastures and cereal fields surrounding the lake. The north-facing slopes are covered by mixed deciduous oak forests dominated by *Quercus cerris* with rare specimens of *Fagus sylvatica*. These rare individuals occur hundreds of meters below the montane belt in which *Fagus sylvatica* dominates or co-dominates at altitudes >800–1,000 m a.s.l. (Pignatti et al., 2017). Other tree and shrub species such as *Quercus pubescens*, *Carpinus betulus*, *Corylus avellana*, *Ruscus aculeatus*, *Acer campestre*, *Ostrya carpinifolia*, *Castanea sativa*, *Fraxinus ornus*, *Acer opalus*, *Prunus avium*, *Cornus mas*, *Rosa canina*, *Prunus spinosa*, and *Ligustrum vulgare* also occur. Few specimens of the evergreen species *Quercus ilex* are found in the south-facing areas of the caldera pointing to the proximity of our site to the mesomediterranean deciduous and evergreen mixed oak woodlands (Lang et al., 2023). *Alnus glutinosa*, *Populus alba*, and *Salix* sp. are present at the lake shore.

2.2. Temperature recording in the caldera of Latera

We installed four temperature recorders (onset HOBO pendant temperature data loggers) near Lago di Mezzano in August 2022. Three

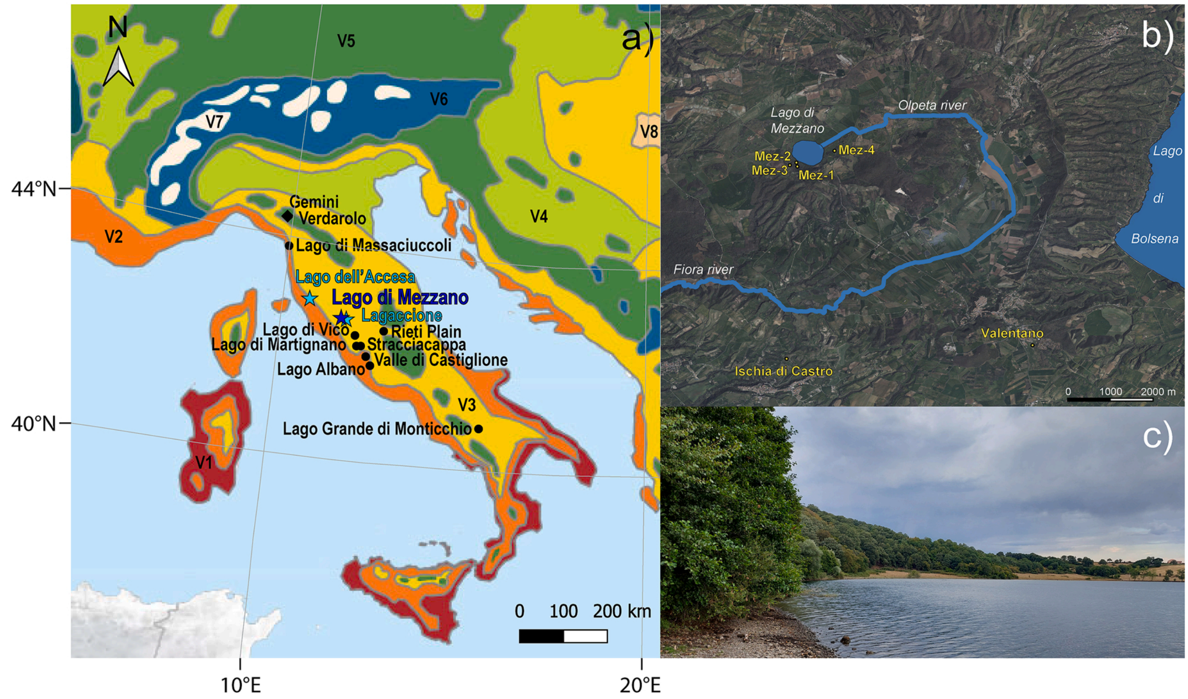


Fig. 1. **(a)** Map showing the location of the study site. Lago di Mezzano (blue star), important nearby lake sediment sites (light blue stars), and other sites discussed in the article. Background colors in the map represent different vegetation types (Lang et al., 2023): red (V1) = thermomediterranean evergreen mixed oak and olive-carob woodlands, orange (V2) = mesomediterranean deciduous and evergreen mixed oak woodlands, yellow (V3) = submediterranean and supra-mediterranean mostly deciduous mixed oak forests, light green (V4) = temperate central and eastern European deciduous mixed oak forests, dark green (V5) = temperate western, central, and southeastern European mixed beech and beech-fir forests, dark blue (V6) = montane and subalpine conifer forests, white (V7) = alpine dwarf shrub, meadow, and tall herb vegetation above treeline and light pink (V8) = eastern European forest steppes. **(b)** Satellite map of the caldera of Latera with temperature loggers and climate station's locations (Tulumello, 2023). **(c)** Photograph of Lago di Mezzano (view from the southern shore towards the northwest).

loggers were placed on the north-facing slope at different altitudes (Mez-1, 42°36′28″ N, 11°46′0″ E, 496 m a.s.l.; Mez-2, 42°36′32″ N, 11°45′59″ E, 484 m a.s.l.; Mez-3, 42°36′29.4″ N, 11°45′52.3″ E, 543 m a.s.l.) close to the few *Fagus sylvatica* trees still existing in the caldera of Latera, while the fourth recorder was positioned in the deciduous oak forest located in the plain on the north-eastern side of the lake (Mez-4, 42°36′44.2″ N, 11°46′38.2″ E, 462 m a.s.l.). We installed the temperature loggers in the shade, at about 1–2 m above the ground, and temperatures were measured for 365 days at 2-h intervals. Data were averaged and mean monthly temperatures were compared with measurements from two meteorological stations located at comparable altitudes within a 7-km radius from Lago di Mezzano, outside the caldera of Latera: Valentano

Table 1
Radiocarbon dates, calibrated, and modeled ages.

No.	Laboratory code	Depth (cm)	Material	^{14}C age (years BP)	Median age (cal years BP)	Age, 2σ (cal years BP)	Age (cal years BP) in diagram[a]
1	BE-13828.1.1	683–683.5	*Fagus sylvatica* bud scale	6125 ± 30	7005	7153–6857	6982
2	BE-13827.1.1	684.5–685	Leaf fragments (cf. *Quercus* sp.)	6160 ± 30	7062	7180–6944	7014
3	BE-13285.1.1	685–685.5	Bud scales indet, charred leaf fragments	6270 ± 90	7174	7408–6940	7025
4	BE-16570.1.1	699.5–700	Leaf fragments indet	6390 ± 25	7309	7413–7205	7303
5	BE-16571.1.1	710.5–711	*Fagus sylvatica* bud scale, leaf fragments indet	6650 ± 50	7526	7620–7432	7519
6	BE-16572.1.1	718–718.5	Leaf fragments indet	6845 ± 30	7672	7744–7600	7658
7	BE-16573.1.1	718.5–719	Bud scales indet, leaf fragments indet	6820 ± 45	7648	7728–7568	7665
8	BE-16574.1.1	722–722.5	Bud scales indet, seed fragment indet	6920 ± 45	7747	7855–7639	7721
9	BE-16575.1.1	729–729.5	*Fagus sylvatica* bud scales, bud scale indet	6995 ± 45	7825	7949–7701	7839
10	BE-16576.1.1	736–736.5	Bud scales indet, leaf fragment indet	7110 ± 45	7939	8037–7841	7963
11	BE-16577.1.1	742–742.5	Bud scale indet, leaf fragments indet	7255 ± 45	8087	8203–7971	8097
12	BE-16578.1.1	742.5–743	*Fagus sylvatica* bud scale, leaf fragments indet	7250 ± 25	8088	8198–7978	8106
13	BE-16579.1.1	744–744.5	Bud scale indet	7290 ± 25	8106	8194–8018	8135
14	BE-16580.1.1	749–749.5	Bud scales indet	7450 ± 60	8266	8398–8134	8240
15	BE-16581.1.1	756.5–757	*Fagus sylvatica* bud scale	7600 ± 60	8397	8529–8265	8396
16	BE-16314.1.1	853–855	Leaf and seed fragments, wood	8360 ± 100	9340	9596–9084	9340[b]

Note.
[a] OxCal P-sequence (1–15).
[b] date 16 not in the P-sequence.

(494 m a.s.l.) and Ischia di Castro (468 m a.s.l.; Tulumello, 2023).

2.3. Coring and chronology

We retrieved eight parallel sediment cores from the deepest and central parts of Lago di Mezzano in May 2019 and September 2020. We visually parallelized the cores according to the lithostratigraphy. The core parallelization was refined using X-ray fluorescence (XRF) and hyperspectral imaging (HSI) data to obtain a 1,191 cm long master sequence. For this study, we focus on a continuous section from 687.5 to 758.5 cm, spanning from ca. 8,450 to 7,050 cal years BP. We present a chronology based on 15 radiocarbon dates measured on short-lived terrestrial plant macrofossils (Table 1). The age-depth model (Fig. 2) was developed using Bayesian approaches (OxCal 4.4, P-Sequence; Bronk Ramsey, 1994, 1995, 2001; Bronk Ramsey et al., 2001) and the IntCal 20 calibration curve (Reimer et al., 2020). One additional radiocarbon date (sample 16: BE-16314.1.1; Table 1 and Fig. 2) was measured at a depth of 853 cm (9,340 cal years BP) to allow comparison with other sites located in the study region.

2.4. Palynological and charcoal analyses

We collected 143 continuous sediment samples with a volume of 0.5 cm^3, every 0.5 cm (9.6 ± 1.1 years per sample) for pollen, spores, algae, and microscopic charcoal analyses. *Lycopodium* tablets were added to the samples before the treatment to allow the estimation of concentration (particles·cm^{-3}) and influx (particles·cm^{-2}·$year^{-1}$; Stockmarr, 1971). The samples were treated using chemical (HCl, KOH, HF, and acetolysis) and physical (500 μm sieving, decanting) standard methods (Moore et al., 1991). Pollen and spores were identified by means of palynological keys and atlases (e.g., Moore et al., 1991; Reille, 1992; Beug, 2004) and the reference collection of the Institute of Plant Sciences of the University of Bern, Switzerland. Cerealia t. (t. = type) pollen grains were differentiated into *Avena* t., *Hordeum* t., and *Triticum* t. following Beug (2004). We counted a minimum terrestrial pollen sum of 500 grains per sample, excluding pollen of aquatic plants and spores of fungi, ferns, and mosses. In the same slides we used for pollen determination, we also quantified charcoal particles with a size >10 μm, which are referred to as microscopic charcoal as a proxy of regional burning following Tinner and Hu (2003) and Finsinger and Tinner (2005). Sediment samples with an average volume of 8 cm^3 were taken every 0.5 cm and sieved with a mesh width of 200 μm to find short-lived terrestrial plant macrofossils for radiocarbon dating. The sieved material was used to quantify macroscopic charcoal particles >600 μm as a proxy of local burning following Adolf et al. (2018).

2.5. Biogeochemical analyses

Full methodological descriptions of XRF element and HSI pigment analyses are provided in Beffa et al. (2024). For the purpose of this study, we utilize the elements titanium (Ti) and iron (Fe) as indicators for terrigenous detrital sediment delivery from the watershed (Peterson et al., 2000; Haug et al., 2001) and phosphorus (P) as indicator for sedimentary nutrient retention under oxic water column conditions (Makri et al., 2021) and nutrient enrichment (Corella et al., 2012). We adopted the HSI $RABD_{845}$ index (bacteriopheophytin (Bphe)) as an indicator for the presence of anoxygenic phototrophic purple sulfur bacteria and hypolimnetic anoxia (Yurkov and Beatty, 1998; Butz et al., 2015; Zander et al., 2021), while the HSI $RABD_{655–685max}$ index (total chlorophylls and colored diagenetic products (TChl)) indicates the presence of algae bearing green pigments and in-lake primary productivity (Leavitt and Hodgson, 2002; Zander et al., 2021). Anoxia and lake stratification may result from either deep-water conditions, warm temperatures, or environmental stability with closed forest and low wind mixing (Makri et al., 2021) or a combination thereof. Anoxia may also lead to reductive dissolution and low sequestration rates of sedimentary Fe and P, and recycling of nutrients (internal loadings) sustaining high aquatic primary production (here TChl; Tu et al., 2021).

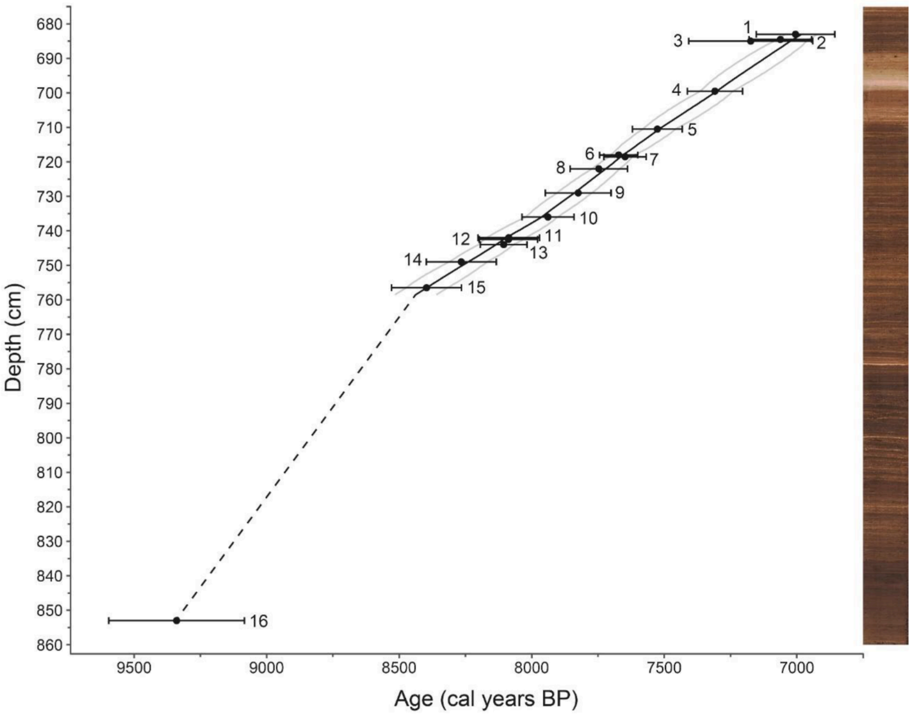


Fig. 2. Age depth model and sediment picture of Lago di Mezzano. Black points represent the calibrated ages of ^{14}C dated terrestrial plant macrofossils with 95% (2σ) error bars (IntCal20, Reimer et al., 2020). The black line is the P-sequence (Bayesian approach) modeled chronology (OxCal, Bronk Ramsey, 1994; 1995, 2001; Bronk Ramsey et al., 2001). Grey lines show the 95% (2σ) confidence interval of the model. The dashed line is a linear interpolation to the calibrated radiocarbon date 16. Dates are numbered according to Table 1.

2.6. Numerical methods

Zonation—We defined statistically significant local pollen assemblage zones (LPAZs) using the optimal sum of square partitioning (Birks and Gordon, 1985) combined with the broken-stick method (Bennett, 1996) using the software R (R Core Team, 2022).

Palynological richness—To evaluate the richness of past plant species around Lago di Mezzano we used rarefaction analysis, based on a constant minimum counting sum of 508 pollen grains per sample, to estimate palynological richness (PRI; Birks and Line, 1992) and the probability of interspecific encounter (PIE; Hurlbert, 1971) as a measure of evenness (e.g., Lepori et al., 2005; Lestienne et al., 2020). PIE allows evaluating taxa dominance as it indicates the probability that two randomly chosen individuals in a sample are from the same taxon.

Ordination analysis—To investigate ecological gradients present in our pollen data, we carried out ordination analyses using Canoco 5 (ter Braak and Šmilauer, 2012). First, we performed a detrended correspondence analysis (DCA) to establish if linear or unimodal ordination models are better suited to the data. The first axis of the DCA measured 1.2 standard deviation units (SD units; Lepš and Šmilauer, 2003). Therefore, we decided to continue with two linear models, principal component analysis (PCA) and redundancy analysis (RDA). Two climatic and environmental variables were chosen as explanatory variables for the RDA: microscopic charcoal influx as a proxy for regional fires and chironomid-inferred mean July air temperature anomalies (°C) (averaged from the Gemini and Verdarolo sediment records; Samartin et al., 2017). To average the original data from Gemini and Verdarolo, we followed the procedure of Heiri et al. (2015). In a second step, the original, individual records of Gemini and Verdarolo, as well as the sea surface temperature anomalies (SST; Marriner et al., 2022) and the macroscopic charcoal influx, were passively added to the RDA as supplementary variables for comparison purposes.

Species response curves—To understand the response of selected important taxa to environmental drivers such as fires and temperature, we used generalized additive models (GAMs) following Colombaroli et al. (2010) and Morales-Molino et al. (2021). GAMs were fitted using Canoco 5 (ter Braak and Šmilauer, 2012) assuming a Poisson distribution curve and a maximum of two degrees of freedom (i.e., polynomial order of the fitted function) following a stepwise selection based on the Akaike Information Criterion (AIC). Choosing the model with the lowest AIC value allowed us to identify the most parsimonious model that improves the null model (i.e., in which the environmental variables have no effect on the species values). Specifically, we analyzed the response of *Fagus*, *Quercus ilex* t., *Quercus pubescens* t., and *Corylus* to macro- and microscopic charcoal-inferred local and regional fire activity and mean chironomid-inferred July air temperature changes (Samartin et al., 2017). We tested the robustness of the relationship with temperature using another Mediterranean temperature record, the annual SST anomalies from Marriner et al. (2022).

Cross-correlation analyses—To identify the relationship as well as leads and lags between fire (micro- and macroscopic charcoal influx), browsing or grazing (percentages and influx of *Sporormiella* dung spores), cultivation (percentages and influx of Cerealia sum pollen), and the resulting vegetation changes including biodiversity (proxies PRI and PIE), we calculated cross-correlations (Green, 1981; Clark et al., 1989; Dodson, 1990; Tinner et al., 1999; Lang et al., 2023) using the program R (R Core Team, 2022). The time window ranges from 8,450 to 7,050 cal years BP and includes 143 samples (1 sample = 9.6 ± 1.1 years). We calculated cross-correlations coefficients at ±30 lags, which corresponds to ±288 years, i.e., less than ¼ of the sample size (Bahrenberg et al., 2008). To exclude major trends from the time series, all data were linearly de-trended. The correlation significance was estimated by calculating ±2 standard error (SE) of the Pearson correlation coefficients, which corresponds to a two-sided significance level (α) of 5% (Tinner et al., 1999; Bahrenberg et al., 2008).

3. Results

3.1. Temperature variations inside and outside the caldera of Latera

From August 2022 to July 2023, the warmest month in the caldera of Latera was July with an average of 23.9 °C, while the coldest month was January with an average of 6.4 °C. This also emerged from measurements at Ischia di Castro and Valentano, which recorded mean monthly temperatures of 25.9 and 24.8 °C in July 2023 and mean monthly temperatures of 6.8 and 6.3 °C in January 2023, respectively (Tulumello, 2023). The temperature difference during the warmest month at comparable altitudes clearly shows lower summer temperatures in the caldera (−2 °C) than those measured at Ischia di Castro and Valentano, probably caused by the pooling of cold air in the crater basin (Fig. S1; Pastore et al., 2022).

3.2. Lithology and chronology

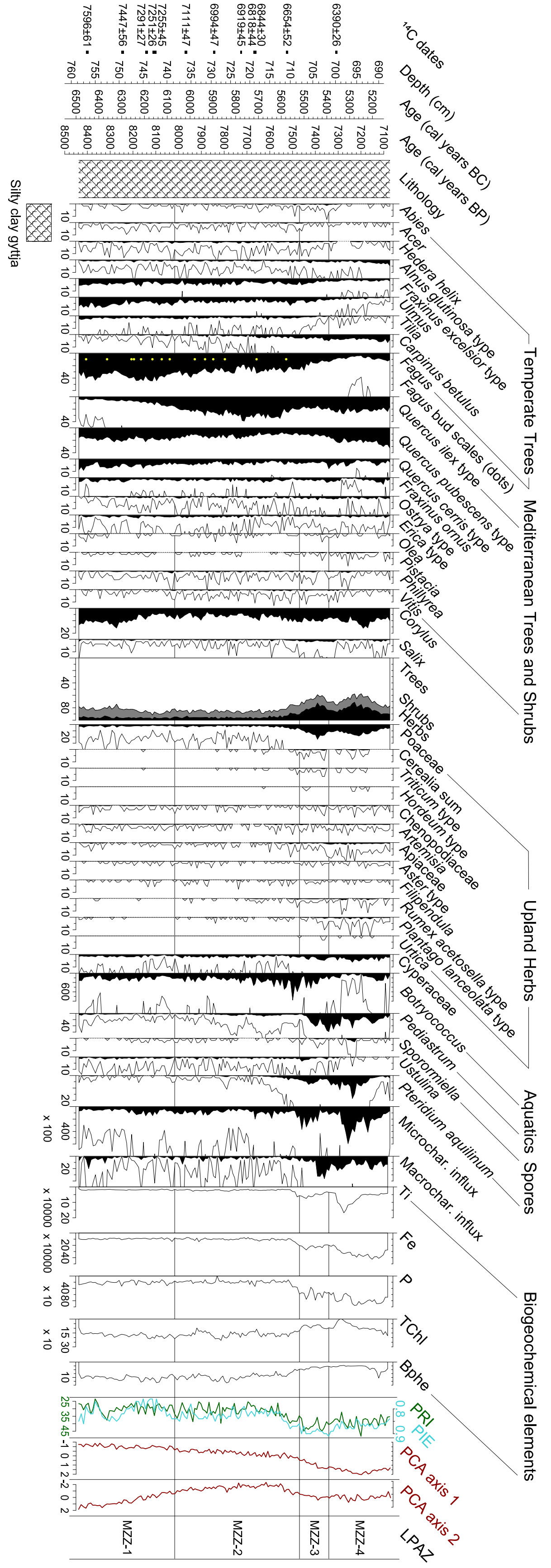
The sediments consist of silty clay gyttja throughout the sequence (Figs. 2 and 3), with decreasing organic content and increasing proportions of bright silty and clayey materials towards the top (Figs. 2 and 3, 7,500–7,100 cal years BP). Bayesian approaches allowed us to reduce the mean dating uncertainty (2σ) to ±64 cal years for the period of interest 8,450–7,050 cal years BP (Fig. 2).

3.3. Pollen, charcoal, and biogeochemical analyses—vegetation, fire, and environmental history

Our high-resolution pollen sequence is divided into four statistically significant pollen zones (LPAZs) that indicate important changes in the composition of the regional vegetation around Lago di Mezzano. Pollen and microscopic charcoal particles deposited in small to medium-sized lakes are usually considered to derive from extra-local to regional sources, as they can be transported by wind over intermediate distances (up to ca. 20–50 km; Conedera et al., 2006; Seppä, 2007; Conedera et al., 2009; Liu et al., 2022), whereas the heavier macrofossils and macroscopic charcoal particles provide a local signal (Birks, 1980; Adolf et al., 2018).

During the first two LPAZs (Fig. 3), MZZ-1 and MZZ-2 (8,450–7,450 cal years BP), tree pollen shows values > 80% and arboreal pollen (AP) > 95%, suggesting the presence of closed forests around the lake. The occurrence of *Fagus sylvatica* bud scales (14 pieces in 880 years) shows that this cool-temperate tree species was present locally near the lake. This is also supported by pollen data, since at the beginning of our sequence, in MZZ-1 (8,450–8,000 cal years BP), *Fagus* pollen shows the highest percentage values in the record with two maxima around 8,400 and 8,200 cal years BP (ca. 45%), whereas *Quercus pubescens* t. (15%–20%) and *Corylus* (9%–15%) have lower values. This percentage-based interpretation is supported by influx values (e.g., *Fagus* with ca. 12,000 pollen grains·cm^{-2}·year^{-1}; Fig. S2(a)) and indicates the dominance of beech in the forests of this time. *Quercus ilex* t. (7%), *Quercus cerris* t. (5%), *Ulmus* (5%), and *Fraxinus excelsior* t. (4%) were also important trees. After ca. 8,200 cal years BP, pollen of evergreen oaks (*Quercus ilex* t.) increases, already reaching 18% towards the end of MZZ-1 (ca. 8,000 cal years BP), while *Fagus sylvatica* pollen percentages decrease to 27%. *Corylus* pollen percentages markedly decline from 16% around 8,250 cal years BP to 4% around 8,100 cal years BP, suggesting a shift towards darker forests (tree pollen > 90%, AP > 95%). During MZZ-1, the first pollen grains of crops and weeds occur, e.g., *Triticum* t. at about 8,150 cal years BP and *Plantago lanceolata* t. at 8,400–8,200 cal years BP. Microscopic charcoal influx is low (average 5,160 particles·cm^{-2}·year^{-1}) but starts to increase at around 8,200 cal years BP (ca. 9,430 particles·cm^{-2}·year^{-1}), while macroscopic charcoal influx remains low (ca. 3 particles·cm^{-2}·year^{-1}), suggesting increasing regional but low local fire activity.

In MZZ-2 (8,000–7,450 cal years BP), *Quercus ilex* t. pollen



(caption on next column)

Fig. 3. Selected pollen percentages, spores, micro-, and macroscopic charcoal influx (particles·cm^{-2}·year^{-1}), lithology, element counts from XRF analysis (Ti, Fe, P; cts) and HSI analysis (total aquatic productivity TChl and hypolimnetic anoxia Bphe; µg·g$^{-1}_{\text{dry sediment}}$) of Lago di Mezzano. Samples were taken contiguously every 0.5 cm. Water plants, ferns, and other spores are excluded from the total terrestrial pollen sum. PRI, PIE, and PCA scores of axes 1 and 2 are also shown. The yellow dots indicate the *Fagus* bud scales. Empty curves show 10 × exaggeration.

percentages markedly increase to > 35%, whereas those of *Fagus*, *Q. pubescens* t., *Corylus*, *Ulmus*, and *F. excelsior* t. slightly decrease. The pollen data suggest that forests around the lake were co-dominated by mesophilous deciduous *F. sylvatica* and evergreen *Q. ilex* or *Q. coccifera*, species belonging to the cool-temperate and mesomediterranean vegetation types, respectively. During this LPAZ anthropogenic indicator taxa such as *Plantago lanceolata* t., *Rumex acetosella* t., Cerealia sum, and *Triticum* t. increase, while *Quercus ilex* t. suddenly stops increasing to decrease to 15% at ca. 7,550 cal years BP. Micro- and macroscopic charcoal show low influx values (on average 8,625 micro- and 3 macroparticles·cm^{-2}·year^{-1}, respectively), indicating low fire activity. From 8,450 to 7,450 cal years BP (MZZ-1 and MZZ-2), PRI and PIE show constant low values, suggesting rather low species diversity. During this period, high Bphe and TChl values in combination with low Ti, Fe, and P values point to stable environmental conditions (low erosion, closed forest) with a strongly stratified water column (hypolimnetic anoxia) and high in-lake productivity because of efficient P cycling (Peterson et al., 2000; Haug et al., 2001; Tu et al., 2021; Zander et al., 2022).

During MZZ-3 (from 7,450 to 7,350 cal years BP) and MZZ-4 (7,350 to 7,050 cal years BP), AP drops twice below 80%, at about 7,450 cal years BP and again at 7,250 cal years BP, suggesting forest openings. *F. excelsior* t., *Ulmus*, *Tilia*, *Abies*, *Acer*, and *Hedera* decline together with *Fagus* (the latter from 27% to 4%). Conversely, *Q. pubescens* t. and *Corylus* increase together with herbaceous taxa such as Poaceae, Apiaceae, and *Aster* t. and anthropogenic indicators such as Cerealia sum, *Triticum* t., *Hordeum* t., *P. lanceolata* t., *R. acetosella* t., *Urtica*, and the dung spore *Sporormiella*, suggesting arable and pastoral farming activities that diminished at around 7,150 cal years BP. Micro- and macroscopic charcoal as well as *Pteridium aquilinum* fern spores also show high values, indicating that fire was likely used to open the forest for agricultural purposes. Markedly increasing *Pediastrum* values suggest a change in the lake water conditions during this period. *Ustulina* spores decline as well, probably as a consequence of reduced dead wood availability. During these two LPAZs, PRI and PIE values are higher, indicating increasing biodiversity in response to early land use.

A striking increase of Ti and Fe suggests high clastic erosional input, likely due to vegetation opening during MZZ-4 (Peterson et al., 2000; Haug et al., 2001). High sedimentary P values are probably the result of P removal from the water column, likely by soil-sourced Fe-oxides in a well-mixed lake (oxic conditions; low Bphe), causing lower in-lake production (low TChl; Makri et al., 2021; Tu et al., 2021; Zander et al., 2022). The subsequent decrease in erosion (decreasing Ti), re-establishment of anoxia (high Bphe), lower Fe and P sequestration in sediments, and efficient P cycling with high aquatic primary production (TChl) occurred when forests recovered and fire activity declined, likely in response to reduced agricultural activities (Peterson et al., 2000; Haug et al., 2001; Tu et al., 2021; Zander et al., 2022).

3.4. Numerical analyses – vegetation ecology

3.4.1. Ordinations

PCA axis 1 explains 41.6% of the total variance within the data, whereas PCA axis 2 explains 11.9%. If ordered along the age scale, PCA axis 1 is highly correlated with herbs and palynological diversity (PRI and PIE), likely summarizing the transition from closed forest to diverse and open vegetation (Fig. 3). PCA axis 2 mirrors the course of *Q. ilex* t. pollen percentages, highlighting the importance of this Mediterranean evergreen broadleaved tree for forest development around Lago di Mezzano. This interpretation is supported by the alignment of the species and sample scores (Fig. S3).

Both climatic and environmental RDA variables significantly influence the variance within the dataset for the period 8,450–7,050 cal years BP (Fig. 4). Chironomid-inferred mean July air temperature anomalies explain 37.3% and microscopic charcoal influx 18.7% of the total variance. Both explanatory variables are positively correlated with anthropogenic indicators such as *Plantago lanceolata* t. and *Rumex acetosella* t., herbaceous taxa such as Poaceae and Cichorioideae and heliophilous taxa such as *Ostrya* t. and *Carpinus betulus*. Interestingly, mean July air temperature anomalies are also positively correlated with the evergreen Mediterranean taxon *Quercus ilex* t., which is confirmed by the linkage with warm SST (Fig. 4). The two environmental variables are negatively correlated with *Fagus*, *Ulmus*, *Tilia*, *Fraxinus excelsior* t., *Quercus cerris* t., *Acer*, and *Hedera helix*. Taken together this suggests that human impact and fire activity under warm climatic conditions reduced the populations of these temperate taxa, while Mediterranean *Q. ilex* benefited from high summer temperatures, but not (or less) from high fire activity and human disturbance.

3.4.2. *Species response curves*

GAMs show that *Fagus* responded negatively to increasing regional and local fire activity, whereas *Corylus* and *Q. pubescens* t. were slightly advantaged (Fig. 5). *Q. ilex* t. reached the highest abundance at intermediate disturbance levels but responded negatively to very high regional and local fire activity. This suggests that *Q. ilex* was favored by fires only if they were not too frequent or intense (Colombaroli et al., 2009). GAMs also suggest that high summer (chironomids) and annual (SST) temperatures promoted evergreen *Q. ilex*. *Fagus* conversely, responded negatively to increasing temperatures (Fig. 5), probably indicating less competitiveness under warmer climatic conditions. *Q. pubescens* t. and *Corylus* increased with the highest temperatures, but this may have resulted from human and fire impact coinciding with temperature peaks.

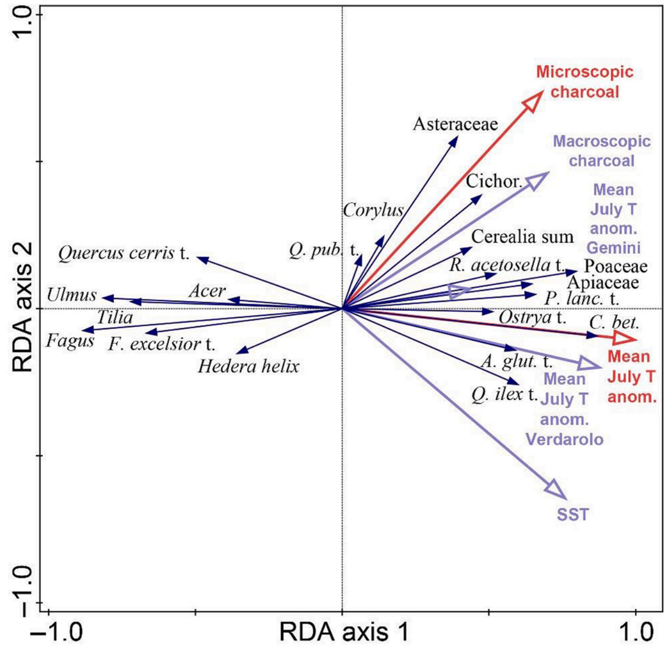


Fig. 4. RDA of selected species (blue arrows) and two explanatory variables (red arrows) for the period 8,450–7,050 cal years BP: chironomid-inferred mean July air temperature anomalies (°C) (averaged from Gemini and Verdarolo records; Samartin et al., 2017) influence 37.3% of the data variance and microscopic charcoal influx (particles·cm^{-2}·year^{-1}) influences 18.7% of the data variance. Purple arrows: mean July air temperature anomalies (°C) from Gemini and Verdarolo (Samartin et al., 2017), SST (Marriner et al., 2022), and macroscopic charcoal influx (particles·cm^{-2}·year^{-1}) as supplementary explanatory variables. Abbreviations: Cichor. = Cichorioideae, *P. lanc.* t. = *Plantago lanceolata* t., *R. acetosella* t. = *Rumex acetosella* t., *A. glut.* t = *Alnus glutinosa* t., *C. bet.* = *Carpinus betulus*, *F. excelsior* t. = *Fraxinus excelsior* t., *Q. pub.* t. = *Quercus pubescens* t., *Q. ilex* t. = *Quercus ilex* t.

3.4.3. *Time-series analysis*

Cross-correlations disclose leads and lags between fire (micro- and macroscopic charcoal influx), browsing or grazing (*Sporormiella* dung spores percentages and influx), cultivation (Cerealia sum pollen percentages and influx), and the resulting vegetation (pollen %) and biodiversity changes (PRI and PIE; Fig. 6). Trees and herbs show maximum negative, respectively maximum positive correlation with microscopic charcoal at lag +2 (ca. 19 years after a fire), suggesting that in the region small and short-lived grassland species were promoted by fire on the expense of long-lived and tall woody plants. *Sporormiella* dung spore percentages show a maximum positive correlation with microscopic charcoal influx at lag +2 (ca. 19 years after a regional fire), likely indicating the use of fire to establish pastures. Conversely, *Sporormiella* dung spores influx shows a significant negative correlation with Cerealia sum pollen percentages at lag −8 (ca. 75 years before a cultivation peak) and significant positive correlations with Cerealia sum pollen percentages at lag 0. This may suggest reduced (forest) grazing before and increased grazing with the start of cultivations around Lago di Mezzano. Pollen percentages of trees show a maximum negative correlation with Cerealia sum influx at lag 0, conversely, herbs show a maximum positive correlation with Cerealia sum influx at lag 0, confirming that forest disruption and the creation of open land by fire was a result of land use. Taken together agricultural activities were a main driver of fire and vegetation changes already during the earliest Neolithic together with climate change, as emphasized by the GAM results. Pollen percentages of trees vs. PRI and PIE reach maximum negative correlation at lag 0, whereas pollen percentages of shrubs vs. PRI show maximum positive correlation at lag −4 (ca. 40 years before a major expansion of shrubs) and pollen percentages of herbs vs. PRI and PIE show maximum positive correlation at lag 0. This indicates that biodiversity (PRI and PIE; Fig. 3) was related to vegetation structure, increasing when open land enlarged in response to human disturbance (e.g., fire, grazing, and browsing).

4. Discussion

4.1. *Vegetation dynamics under different climates in the caldera of Latera*

Before human societies started to significantly influence plant communities, climate and other environmental (e.g., soils, disturbance) and biotic factors (e.g., competition, facilitation, dispersal) were the main drivers of vegetation dynamics (Birks and Berglund, 2018; Lang et al., 2023). During the Late Glacial and the Holocene, major climate changes were associated with important shifts in vegetation structure and composition (Vescovi et al., 2007; Di Rita et al., 2015; Masi et al., 2018; Lang et al., 2023). After the onset of the Holocene at ca. 11,700 cal years BP to ca. 10,000 cal years BP summers were warm and dry and seasonality was higher than today (Laskar et al., 2004), which probably prevented mesophilous *Fagus sylvatica* from spreading. Cold and frosty winters on the other hand probably hindered the expansion of *Quercus ilex* at most sites in Italy. During this period, *Corylus*, deciduous *Quercus*, and *Pinus* were the dominant taxa in the region (Sadori, 2018).

After ca. 10,000 cal years BP seasonality started to decrease (Laskar et al., 2004). Slightly cooler and moister summers as well as milder winters with less (late) frost may have allowed beech forests to expand on moist and sheltered areas of the caldera of Latera (Sadori, 2018). *F. sylvatica* is an oceanic mesophilous species adapted to low-temperature variations that prefers cool, humid summers, and cold winters. In

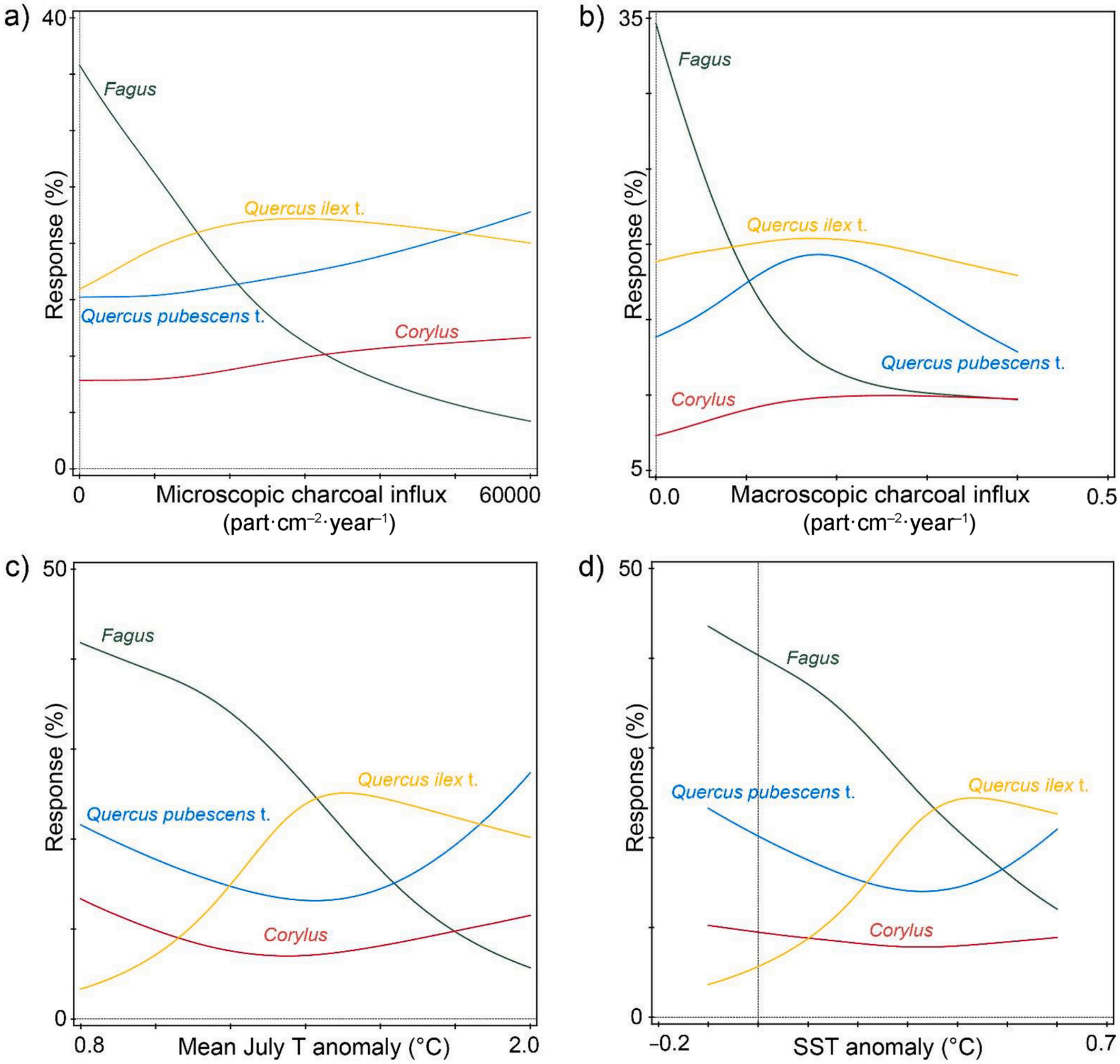


Fig. 5. Response curves of the main pollen taxa for the period 8,450–7,050 cal years BP to **(a)** microscopic charcoal influx as proxy for regional fire activity, **(b)** macroscopic charcoal influx as proxy for local fire activity, **(c)** chironomid-inferred mean July air temperature anomalies relative to the mean temperature of the period 1 to 1,850 AD (stacked for two sites; Samartin et al., 2017) and **(d)** SST (Marriner et al., 2022) anomalies relative to the average of Mediterranean temperature Holocene reconstructions.

comparison to other temperate species, it is very sensitive to harsh winter frost, late frost, and summer drought (Pignatti, 2005; Ellenberg, 2009). Nowadays, *F. sylvatica* is widespread in Southern and Central Europe. South of the Alps beech forests usually occur above ca. 800–1,000 m a.s.l., where high summer temperatures and drought are not a limiting factor (San-Miguel-Ayanz et al., 2016). There, *F. sylvatica* often grows together with *Abies alba* (Pignatti et al., 2017; Lang et al., 2023), deciduous *Quercus*, other temperate tree species, and *Ilex aquifolium* (e.g., in Sicily; Tinner et al., 2016). Occasionally, *F. sylvatica* may occur below ca. 800–1,000 m a.s.l. in the submediterranean and meso-mediterranean vegetation belts, where microclimatic and soil conditions are particularly favorable, e.g., in cool calderas or other topographic depressions (Buonincontri et al., 2023). On the basis of the ecological preferences of the species, we, therefore, assume that after 10,000 cal years BP, *F. sylvatica* and other cool-temperate deciduous trees probably grew abundantly on north-facing slopes around Lago di Mezzano, with cooler and more humid microclimate, while submediterranean deciduous *Quercus* forests with *Corylus avellana* undergrowth were distributed in more sun-exposed areas and where spring or winter frost occurrence was high.

After ca. 8,200 cal years BP evergreen *Quercus*, probably *Q. ilex*, became co-dominant with *F. sylvatica* and deciduous *Quercus* in the caldera of Latera. *Q. ilex* is well adapted to climatic conditions characterized by dry summers and humid, mild winters, but is very sensitive to winter frost (Pignatti et al., 2017). Thus, continuing decreasing Mid Holocene seasonality (Laskar et al., 2004) implying declining winter frost occurrences (Colombaroli et al., 2008; Lang et al., 2023; Ganz et al., 2024) probably allowed its spread in the Lago di Mezzano area. In addition, decadal to centennial-scale periods with particularly warm and dry summers (Vinther et al., 2006; Magny et al., 2007; Giraudi et al., 2011; Samartin et al., 2017; Sadori, 2018; Marriner et al., 2022) likely advantaged warm-loving *Q. ilex* on the expense of cool-temperate *F. sylvatica* (Fig. 5). We assume that *Q. ilex* partly displaced the submediterranean deciduous oak forests and *Corylus avellana* to the shadier and wetter areas previously occupied by temperate beech forests. *F. sylvatica* and other temperate trees, being less competitive under warmer and drier summer conditions, declined (Figs. 3 and 7).

The reconstructed vegetation dynamics reveal an uncommon coexistence of moisture-loving, cool-temperate *Fagus* and drought-tolerant, warm-loving evergreen *Quercus* forests, a combination now

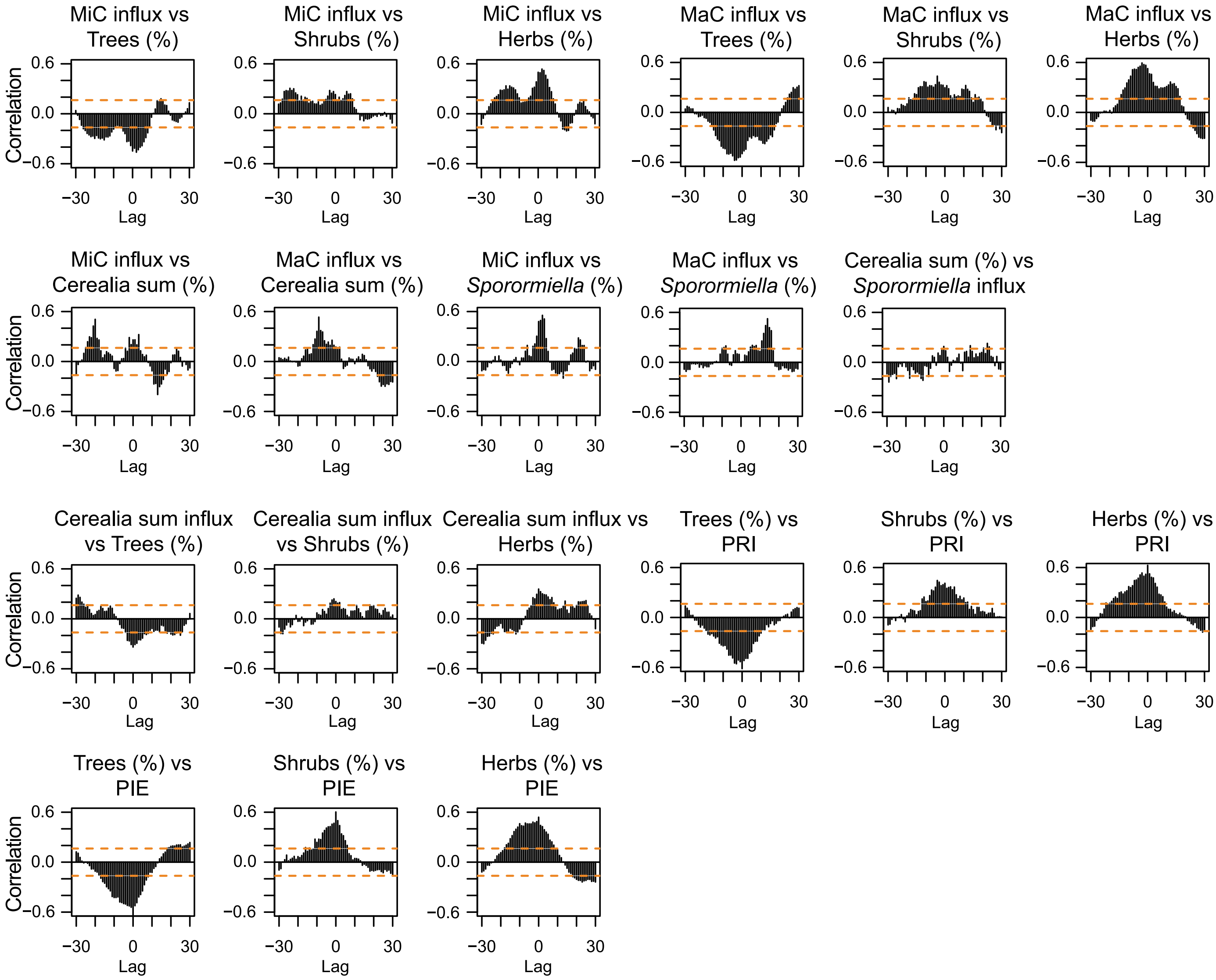


Fig. 6. Cross-correlation between micro- and macroscopic charcoal influx (particles·cm^{-2}·year^{-1}), Cerealia sum pollen percentages and influx (particles·cm^{-2}·year^{-1}), *Sporormiella* spore percentages and influx (particles·cm^{-2}·year^{-1}), trees, shrubs, and herbs pollen percentages and palynological diversity (PRI and PIE) from Lago di Mezzano (8,450–7,050 cal years BP). MiC = microscopic charcoal, MaC = macroscopic charcoal. All variables were de-trended. 1 lag corresponds to 9.6 ± 1.1 years (mean ± standard deviation). The orange dashed lines mark the significance level ($p < 0.05$).

only very exceptionally found in the Mediterranean realm (Buonincontri et al., 2023). The existing mixed occurrences are very fragmented, so little is known about their ecology. In the caldera of Latera the former and now extinct co-existence of beech and holm oak lowland forests might be explained by special local environmental conditions. *F. sylvatica* is very rare today in the caldera of Latera, as reflected by very low pollen percentages (0.2%) in the lake sediment surface sample. *Q. ilex* is more abundant but still reaches only 4.2% of the surface sediment. The significantly higher abundance of these two tree species in the Early and Mid Holocene unambiguously documents that the HTM forest composition has no local modern analogue. However, the current location of various relict individuals of *F. sylvatica* close to the bottom of the caldera on humid, cool, and shady slopes as well as the presence of *Q. ilex* in the warmest and sunniest areas (today mostly converted to fields) may reveal their former habitats during the Early and Mid Holocene. A similar situation documented in the ecological literature at elevations below 800 m a.s.l. occurs at the Monticchio lakes in the Monte Vulture caldera (Spicciarelli et al., 2011). However, the underlying causes remain ambiguous. At Monticchio, small *Q. ilex* stands grow on sunny slopes above and below the *F. sylvatica* forest near the caldera bottom, thus creating intriguing vegetational patterns in which elements of mesic forests co-exist with isolated mesomediterranean tree stands. More generally, unrelated to the co-occurrence of *Q. ilex* and *F. sylvatica*, the vegetation distribution in calderas is often influenced by thermal inversions (Ai-liang, 1981; Pastore et al., 2022) with cold-loving species growing at lower elevations than warm-loving ones.

4.2. *Comparison with other sites in central Italy*

Past climate reconstructions are often based on proxies showing broad-scale and long-term events (e.g., Vinther et al., 2006; Giraudi et al., 2011; Samartin et al., 2017) that in many cases do not capture minor regional variations or microclimatic conditions. Nevertheless, microclimatic conditions are essential to understanding the vegetation history at a specific site or at similar sites in a specific region (Stoutjesdijk and Barkman, 2014). We assume that during the HTM under warmer and drier summer conditions than today, microclimatic conditions allowed *Fagus sylvatica* to co-dominate with *Quercus ilex* in the forests of the caldera of Latera, ca. 300–500 m below the current altitudinal range of the species in the Apennines (Pignatti et al., 2017).

This assumption is corroborated by similar HTM *Fagus* occurrences around other crater lakes in central Italy such as nearby Lagaccione (Magri, 1999), Lago di Vico (Magri and Sadori, 1999), Stracciacappa (Giardini, 2007), Lago di Martignano (Kelly and Huntley, 1991), Valle di Castiglione (Di Rita et al., 2013), and Lago Albano (Lowe et al., 1996), and in depression areas such as the Rieti Plain (Ricci Lucchi et al., 2000). At most of these sites (Fig. 1; Lang et al., 2023), however, *Fagus* was less important than in the calderas of Lago di Mezzano and Lagaccione, while deciduous *Quercus* was more prominent. Warmer and drier climatic conditions may have promoted deciduous *Quercus* at lower latitudes and altitudes at the sites Stracciacappa, Lago di Martignano, Valle di Castiglione, and Lago Albano. However, at Lago di Vico at 510 m a.s.l. and thus at a similar elevation as Lago di Mezzano, deciduous *Quercus* rather than *Fagus* was dominant, perhaps because of the larger size of the lake and thus of its wider pollen catchment area (Magri and Sadori, 1999). Interestingly, outside the rather moist and cool calderas, e.g., at Lago di Massaciuccoli, a lagoon at the Mediterranean Sea, or at Lago dell'Accesa, a karstic lake at 157 m a.s.l., the temperate conifer *Abies alba*, which is more drought-resistant than *F. sylvatica* (Ellenberg, 2009), was associated with *Q. ilex* during the HTM (e.g., Drescher-Schneider et al., 2007; Colombaroli et al., 2007, 2008, 2009; Tinner et al., 2013). However, in the caldera of Monte Vulture, around the Monticchio lakes, *Abies alba* grew alongside *Q. ilex* during the Mid Holocene as well (Allen et al., 2002), suggesting that the moistening and cooling effect of calderas might be less pronounced at lower, warmer latitudes.

At Lago di Mezzano, *Q. ilex* expanded ca. 1,800 years later than

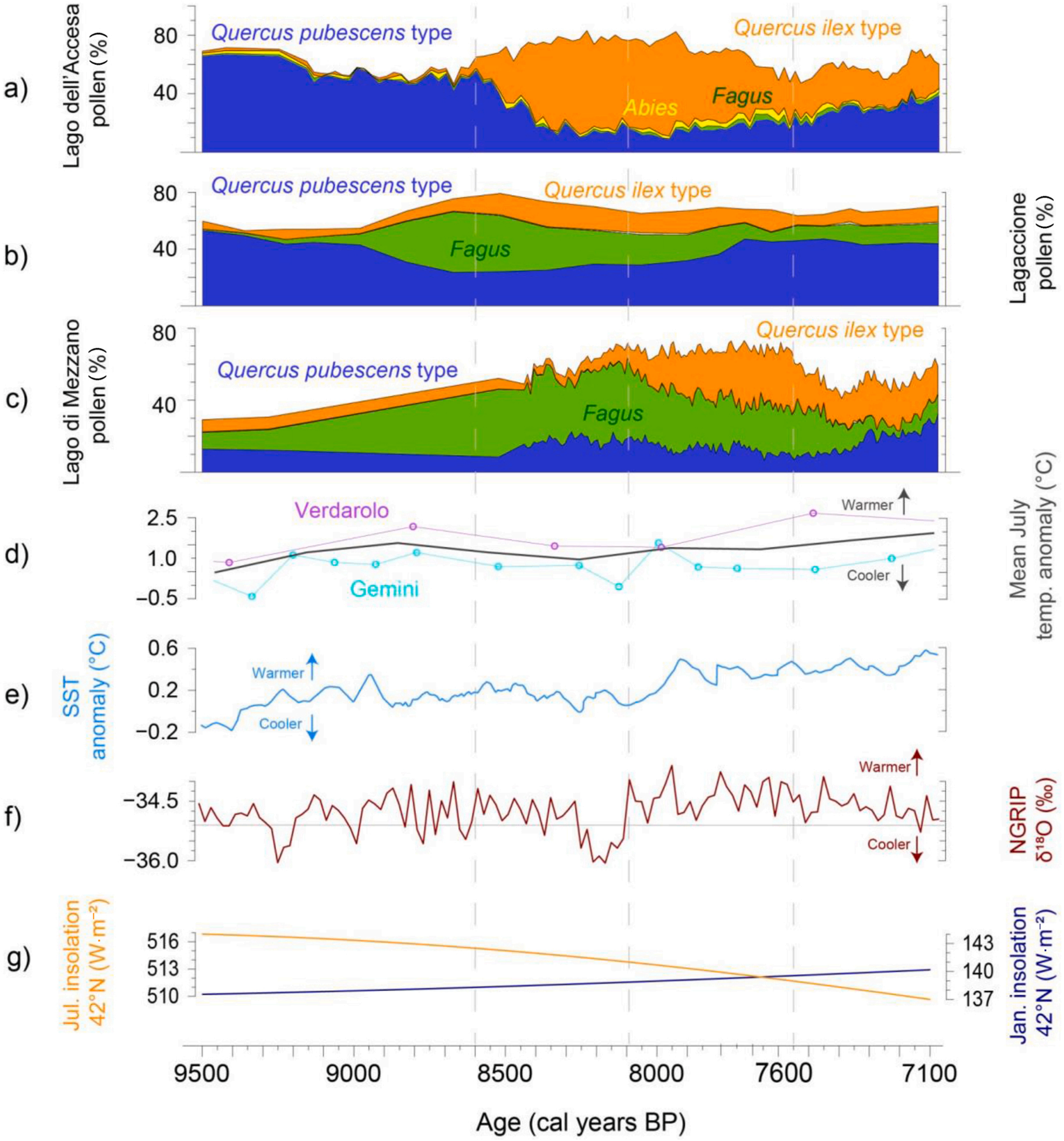


Fig. 7. Comparison of selected pollen percentages (*Fagus*, *Quercus ilex* t., and *Quercus pubescens* t.) from **(a)** Lago dell'Accesa (Colombaroli et al., 2008), **(b)** Lagaccione (Magri, 1999), and **(c)** Lago di Mezzano with independent climate proxies and reconstructions: **(d)** mean July air temperature anomalies relative to the mean temperature of the period 1 to 1,850 AD based on chironomids (Lago Verdarolo and Lago Gemini Inferiore; Samartin et al., 2017), **(e)** SST (Marriner et al., 2022) anomalies relative to the average of Mediterranean temperature Holocene reconstructions, **(f)** δ^{18}O NGRIP (Vinther et al., 2006) and **(g)** July (orange) and January (blue) insolation curves for 42° N (Laskar et al., 2004). Vertical dashed lines show times of important vegetation changes at Lago dell'Accesa and at Lago di Mezzano. Changes at ca. 8,000 and 7,500 cal years BP define statistically significant LPAZ boundaries at Lago di Mezzano (Fig. 3).

Fagus, i.e., after 8,200 cal years BP (Figs. 3 and 7). Similar expansion dynamics were observed at Lago dell'Accesa (Tuscany; Colombaroli et al., 2008), at Lagaccione, at other central Italian crater lakes, and in the Rieti Plain. However, the timing of the mass expansion at these sites varied substantially between ca. 11,500 and 8,200 cal years BP (Fig. 7). Congruently, at warmer sites currently located in the meso-mediterranean belt (Kelly and Huntley, 1991; Lowe et al., 1996; Giardini, 2007; Colombaroli et al., 2008; Di Rita et al., 2013), the increase of *Q. ilex* was more pronounced than at cooler and moister sites currently located in the submediterranean or supramediterranean belt (Magri and Sadori, 1999; Ricci Lucchi et al., 2000). This points to regional latitudinal or altitudinal temperature and/or moisture effects shaping the past central Italian *Q. ilex* population dynamics (Fig. 7). This regional finding also applies to the European scale, given that after 10,000 cal years BP, during the Mid and Late Holocene, when conditions became less continental and generally warmer, *Q. ilex* spread elsewhere in Italy, in central and eastern Iberia as well as in the Balkans north of Greece (Lang et al., 2023).

4.3. Land use activities

Despite the presence of people in the region around Lago di Mezzano since the Palaeolithic (Petitti, 2012), the timing of the first vegetational reorganizations in response to human impact remains unclear. Our new high-resolution data show that sporadic human cultivation activities, which, however, did not significantly alter the surrounding vegetation, began in the region around the lake at about 7,850 cal years BP (Fig. 3). Increasing abundances of pollen of crops and weeds such as Cerealia (including *Triticum* t. and *Hordeum* t.), *Plantago lanceolata* t., *Rumex acetosella* t., *Urtica*, and *Sporormiella* dung fungi spores, suggest a marked rise of human activities at about 7,450 cal years BP. This shift was accompanied by increasing soil erosion and changes in lake biogeochemistry and mixing regimes (Lotter, 2001; Zander et al., 2021; Beffa et al., 2024). Forest disruption by slash-and-burn activities, browsing, and grazing (Figs. 3 and 6), likely weakened wind sheltering, leading to the mixing of the lake and the establishment of oxic conditions. This, in turn, promoted P removal from the water column through adsorption of PO_4 onto Fe-(oxy-)hydroxides and their preservation after burial, thereby promoting reduced in-lake primary production (Fig. 3; Makri et al., 2021; Tu et al., 2021; Zander et al., 2022). Our human impact reconstructions are consistent with the extraordinary archaeological findings from the lakeshore site La Marmotta on Lago di Bracciano (Fugazzola Delpino et al., 1993), ca. 80 km south-east of Lago di Mezzano. The shores of the lake were inhabited by farmers during the Early Neolithic between ca. 7,640 and 7,210 cal years BP (Fugazzola Delpino and Tinazzi, 2010; Caruso Fermé et al., 2021, 2023; Mazzucco et al., 2022). The archaeological data document the existence of a Neolithic community exhibiting well-developed expertise in navigation, farming, crafting, and construction. Among the most significant finds are sickles containing well-preserved pollen grains trapped within the building materials, suggesting remarkable arable farming activities during the earliest Neolithic (Mazzucco et al., 2022; Arobba et al., 2024). In agreement with these findings, our results show that vegetation structure and composition in the Lago di Mezzano area underwent unexpectedly strong anthropogenic transformations already during the Early Neolithic. Evergreen holm oak forests were opened at first around 7,550 cal years BP. About 100–300 years later, at 7,450–7,300 cal years BP, temperate trees such as *Fagus sylvatica*, *Abies alba*, *Acer*, *Fraxinus excelsior*, *Ulmus*, *Tilia*, and the evergreen liana *Hedera helix*, declined markedly as well, leaving space for meadows and fields. Disruptions of natural vegetation promoted open land plant diversity at the expense of tree diversity, which decreased (Fig. 6; Colombaroli and Tinner, 2013; Giesecke et al., 2014). High fire activity and increasing land use occurred when summer temperatures and drought increased (Figs. 3 and 7; Magny et al., 2007; Zanchetta et al., 2007; Vannière et al., 2008; Samartin et al., 2017). Warm temperatures and summer drought may have induced populations to settle near the lake (Sadori et al., 2004; Rey et al., 2019), where water was always available. Ultimately, warmer and drier climatic conditions may have favored the introduction of farming in central Italy, facilitating the disruption of the dense primeval forests and therefore the shift from Mesolithic gathering to Neolithic production economies. Towards the end of this first forest opening phase, at about 7,300 cal years BP, Mediterranean vegetation (e.g., *Quercus ilex* t., *Quercus cerris* t. and *Fraxinus ornus* t.) recovered more quickly than temperate trees (e.g., *Fagus*, *F. excelsior* t., *Ulmus*, and *Tilia*), possibly because of its better adaptation to fires and high temperatures (Figs. 3 and 5). During the second very pronounced forest opening phase (7,300–7,050 cal years BP), regional fire activity reached its apex and many temperate species such as *Fagus*, *Ulmus*, *Tilia*, and *Abies* collapsed, whereas evergreen and deciduous *Quercus* became dominant, creating a new vegetation type which was more comparable with today's highly humanized Mediterranean forest communities (Chiappini, 1988; Blasi and Biondi, 2017; Pignatti et al., 2017; Lang et al., 2023). During the following millennia, until the end of the HTM around 5000 years ago, *F. sylvatica* recovered to reach peak values between 15% and 20% when land use declined, to repeatedly decrease to values of ca. 5% when Neolithic farming became more intense (Beffa et al., 2024). Conversely, *Q. ilex* remained rather stable at 10%–15% during the remaining HTM.

5. Conclusions

Our new palaeoecological data point to a high climate sensitivity of Mediterranean vegetation. Temperature and moisture alterations released strong community shifts, which can be explained by the climatic niches of the species. The responses of *Quercus ilex* as likely the most warm-loving tree in the study area and of *Fagus sylvatica* as the most drought-intolerant tree were among the most drastic, while ecologically intermediate deciduous *Quercus* and *Corylus avellana* responded more moderately (Fig. 5). This finding emphasizes that species growing at the edges of their climatic niches may respond considerably to subtle changes of, e.g., a few °C (Fig. 5). Increasing heat and summer drought in central and southern Europe has led to significant *F. sylvatica* growth reduction (Jump et al., 2006; Piovesan et al., 2008) and diebacks (Schuldt et al., 2020; Frei et al., 2022; Klesse et al., 2022) in recent years. The persistence of beech-dominated forests may therefore become increasingly difficult at their range edge (Braun et al., 2021; Del Martinez Castillo et al., 2022; Langer and Bußkamp, 2023; Rukh et al., 2023). Our palaeoecological reconstructions emphasize the climate sensitivity of *F. sylvatica*. Once certain heat and/or drought thresholds are reached, beech forests may rapidly decline (Figs. 4 and 5). On the other hand, the palaeoecological evidence and today's occurrence of relict *F. sylvatica* stands in the caldera of Latera at mean July temperatures around 25 °C and under reduced summer precipitation shows that beech forests may grow in humid depressions and calderas even under warm Mediterranean conditions. The extraordinary and widespread co-existence of *F. sylvatica* and *Q. ilex* forests during the HTM in Mediterranean Italy implies that Central European beech forests may persist in cool and moist habitats, e.g., in topographic depressions, even if *Q. ilex* should massively spread north of the Alps in response to strong climate warming, as anticipated by vegetation modeling (e.g., Overpeck et al., 2003; Bugmann et al., 2014; Buras and Menzel, 2019).

Farming activities started at ca. 7,850 cal years BP but significantly affected vegetation only after ca. 7,450 cal years BP. First land use led to an increase in ecosystem heterogeneity and therefore to major shifts in the spatial distribution of biodiversity. The local disappearance of tall, late-successional tree species was offset by an increase in short-lived open-land species that led to an overall increase in species richness. Among the tree species, *F. sylvatica* was particularly affected by human impact (Figs. 3, 5 and 7). Hence, to foster its spread or recovery, restoration measures reducing anthropogenic disturbance (e.g., grazing, fire, cutting) would be needed. Similar conclusions were reached by a recent study emphasizing that *F. sylvatica* stands were widespread in the

Mediterranean Italian lowlands before being strongly reduced by human disturbance during the Late Holocene (Buonincontri et al., 2023).

On the basis of the past co-existence of dissimilar vegetation communities such as Mediterranean evergreen oak and temperate mesophilous beech forests during the HTM, we conclude that, if protected against excessive human disturbance, calderas and other topographic depressions may serve as cold and humid refugia (Dobrowski, 2011; Ashcroft and Gollan, 2013; Gubler et al., 2018) in an increasingly hot and dry Mediterranean landscape to maintain biodiversity.

CRediT authorship contribution statement

Giorgia Beffa: Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Erika Gobet:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Sevil Coşgun:** Writing – review & editing, Investigation. **Riccardo Dotta:** Investigation. **Luc Hächler:** Writing – review & editing, Investigation. **Marina Alexandra Morlock:** Writing – review & editing, Investigation. **Laura Sadori:** Writing – review & editing. **Patrick Schläfli:** Writing – review & editing. **Christoph Schwörer:** Writing – review & editing. **Lieveke van Vugt:** Writing – review & editing, Investigation. **Hendrik Vogel:** Writing – review & editing, Supervision. **Paul David Zander:** Writing – review & editing, Investigation. **Martin Grosjean:** Writing – review & editing, Supervision. **Willy Tinner:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Data availability

Data will be made 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.

Funding and Acknowledgements

We acknowledge the Soprintendenza Archeologia, Belle Arti e Paesaggio per l'area metropolitana di Roma, la provincia di Viterbo e l'Etruria meridionale, and the Comune di Valentano for coring permissions at Lago di Mezzano. We thank Willi Tanner, Erwin Tanner, Peter Ruprecht, Yunuén Temoltzin Loranca, Kathrin Ganz, Yannick Hunziker, and Carolina Senn for helping with field work, Marco Conedera and Boris Vannière for valuable discussions on forest and fire dynamics, Walter Finsinger for valuable scientific input, Petra Boltshauser-Kaltenrieder for helping with the determination of macrofossils, Scarlett Pérez for macrofossils preparation for radiocarbon dating, Sönke Szidat for radiocarbon dating, César Morales-Molino and Jacqueline F. N. van Leeuwen for support with pollen analysis, Azzurra Pistone for helping to collect the temperature loggers and two anonymous reviewers for their constructive comments. This study was funded by the Swiss National Science Foundation (SNF 200020_182084).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100345.

References

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J. F.N., Bigler, C., Connor, S.E., Gałka, M., La Mantia, T., Makhortykh, S., Svitavská-Svobodová, H., Vannière, B., Tinner, W., 2018. The sedimentary and remote-sensing reflection of biomass burning in Europe. Glob. Ecol. Biogeogr. 27, 199–212. https://doi.org/10.1111/geb.12682.

Ai-liang, J., 1981. Temperature inversion and vegetation inversion in xishuangbanna, southwestern Yunnan, People's Republic of China. Mt. Res. Dev. 1, 275. https://doi.org/10.2307/3673065.

Allen, J.R., Watts, W.A., McGee, E., Huntley, B., 2002. Holocene environmental variability—the record from Lago Grande di Monticchio, Italy. Quat. Int. 88, 69–80. https://doi.org/10.1016/S1040-6182(01)00074-X.

Arobba, D., Caramiello, R., Morandi, L.F., Gibaja, J.F., Mineo, M., Mazzucco, N., 2024. Pollen analysis of neolithic adhesives and comparative experimental archaeology: insights from La Marmotta (Lake Bracciano, Rome). J. Archaeol. Sci. 165, 105970. https://doi.org/10.1016/j.jas.2024.105970.

Ashcroft, M.B., Gollan, J.R., 2013. Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: understanding factors that promote microrefugia. Agric. For. Meteorol. 176, 77–89. https://doi.org/10.1016/j.agrformet.2013.03.008.

Bahrenberg, G., Giese, E., Mevenkamp, N., Nipper, J., 2008. Statistische Methoden in der Geographie - Band 2: Multivariate Statistik. Borntraeger, Stuttgart, Germany.

Baldi, M., Crisci, A., Genesio, L., Piani, F., Meneguzzo, F., Dalu, G.A., El Asmar, T., 2004. Remote climate processes underlying summer drought events in the Mediterranean. Balwois Conference 2004, Ohrid, FY Republic of Macedonia, pp. 1–12.

Bartolo, G., Brullo, S., Minissale, P., Spampinato, G., 1990. Contributo alla conoscenza dei boschi a *Quercus ilex* della Sicilia. Acta Bot. Malacit. 15, 203–215.

Beffa, G., Gobet, E., Hächler, L., Isola, I., Morlock, M.A., Sadori, L., Schläfli, P., Rey, F., van Vugt, L., Vogel, H., Zander, P.D., Zanchetta, G., Grosjean, M., Tinner, W., 2024. A novel, continuous high-resolution palaeoecological record from central Italy suggests comparable land-use dynamics in Southern and Central Europe during the Neolithic. Holocene 34, 1009–1024. https://doi.org/10.1177/09596836241247302.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytol. 132, 155–170. https://doi.org/10.1111/j.1469-8137.1996.tb04521.x.

Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, Munich, Germany.

Birks, H.H., 1980. Plant macrofossils in Quaternary lake sediments. Adv. Limnol. 15.

Birks, H.J.B., Gordon, A.D., 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London.

Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from quaternary pollen-analytical data. Holocene 2, 1–10. https://doi.org/10.1177/095968369200200101.

Birks, H.J.B., Berglund, B.E., 2018. One hundred years of quaternary pollen analysis 1916–2016. Veget. Hist. Archaeobot. 27, 271–309. https://doi.org/10.1007/s00334-017-0630-2.

Blasi, C., 1994. Fitoclimatologia del Lazio. Fitosociologia 27, 5–30.

Blasi, C., Biondi, E., 2017. La flora in Italia. Ministero dell'Ambiente e della Tutela del Territorio e del Mare. Sapienza Università Editrice, Roma.

Blasi, C., Capotorti, G., Copiz, R., Guida, D., Mollo, B., Smiraglia, D., Zavattero, L., 2018. Terrestrial Ecoregions of Italy. Map and Explanatory Notes. Global Map S.r.l., Firenze, Italy.

Braun, S., Hopf, S.-E., Tresch, S., Remund, J., Schindler, C., 2021. 37 Years of forest monitoring in Switzerland: drought effects on *Fagus sylvatica*. Front. For. Glob. Change 4, 765782. https://doi.org/10.3389/ffgc.2021.765782.

Bronk Ramsey, C., 1994. Analysis of chronological information and radiocarbon calibration: the program OxCal. Archaeol. Comput. Newsl. 41, 11–16.

Bronk Ramsey, C., 1995. Radiocarbon calibration and analysis of stratigraphy: the OxCal Program. Radiocarbon 37, 425–430.

Bronk Ramsey, C., 2001. Development of the radiocarbon calibration program OxCal. Radiocarbon 43, 355–363.

Bronk Ramsey, C., van der Plicht, J., Weninger, B., 2001. 'Wiggle matching' radiocarbon dates. Radiocarbon 43, 381–389.

Bugmann, H., Brang, P., Elkin, C., Henne, P., Jakoby, O., Lévesque, M., Lischke, H., Psomas, A., Rigling, A., Wermelinger, B., Zimmermann, N.E., 2014. Climate change impacts on tree species, forest properties, and ecosystem services. CH2014-Impacts, toward Quantitative Scenarios of Climate Change Impacts in Switzerland. OCCR, FOEN, MeteoSwiss, C2SM, Agroscope and ProClim 79–88. Bern, Switzerland.

Buonincontri, M.P., Bosso, L., Smeraldo, S., Chiusano, M.L., Pasta, S., Di Pasquale, G., 2023. 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. Sci. Total Environ. 877, 162893. https://doi.org/10.1016/j.scitotenv.2023.162893.

Buras, A., Menzel, A., 2019. Projecting Tree species composition changes of european forests for 2061–2090 under RCP 4.5 and RCP 8.5 scenarios. Front. Plant Sci. 9, 1986. https://doi.org/10.3389/fpls.2018.01986.

Butz, C., Grosjean, M., Fischer, D., Wunderle, S., Tylmann, W., Rein, B., 2015. Hyperspectral imaging spectroscopy: a promising method for the biogeochemical analysis of lake sediments. J. Appl. Remote Sens. 9, 096031. https://doi.org/10.1117/1.JRS.9.096031.

Cartapanis, O., Jonkers, L., Moffa-Sanchez, P., Jaccard, S.L., de Vernal, A., 2022. Complex spatio-temporal structure of the Holocene thermal maximum. Nat. Commun. 13, 5662. https://doi.org/10.1038/s41467-022-33362-1.

Caruso Fermé, L., Mineo, M., Ntinou, M., Remolins, G., Mazzucco, N., Gibaja, J.F., 2021. Woodworking technology during the early Neolithic: first results at the site of La MARMOTTA (Italy). Quat. Int. 593–594, 399–406. https://doi.org/10.1016/j.quaint.2020.10.067.

Caruso Fermé, L., Mineo, M., Remolins, G., Mazzucco, N., Gibaja, J.F., 2023. Navigation during the early Neolithic in the Mediterranean area: study of wooden artifacts associated with dugout canoes at La Marmotta (Lago di Bracciano, Anguillara

Sabazia, Lazio, Italy). Quat. Sci. Rev. 311, 108129. https://doi.org/10.1016/j.quascirev.2023.108129.

Cavalli, S., Drosera, L., 1989. Nuove stazioni eterotopiche di *Fagus sylvatica* L. nella Toscana Centrale. Atti della Società toscana di scienze naturali, Memorie, Serie B 9, 257–264.

Chiappini, M., 1988. Guida alla flora pratica della Sardegna. C. Delfino Editore, Sassari, p. 461.

Chirici, G., Fattori, C., Cutolo, N., Tufano, M., Corona, P., Barbati, A., Blasi, C., Copiz, R., Rossi, L., Biscontini, D., Ribera, A., Morgante, L., Marchetti, M., 2014. La realizzazione della carta delle formazioni naturali e semi-naturali e della carta forestale su basi tipologiche della regione Lazio. Forest@ 11, 65–71. https://doi.org/10.3832/efor1204-011.

Clark, J.S., Merkt, J., Muller, H., 1989. Post-glacial fire, vegetation, and human history on the northern alpine forelands, south-western Germany. J. Ecol. 77, 897–925.

Colombaroli, D., Henne, P.D., Kaltenrieder, P., Gobet, E., Tinner, W., 2010. Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. J. Ecol. 98, 1346–1357.

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

Colombaroli, D., Tinner, W., 2013. Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. The Holocene 23, 1625–1634.

Colombaroli, D., Tinner, W., van Leeuwen, J., Noti, R., Vescovi, E., Vannière, B., Magny, M., Schmidt, R., Bugmann, H., 2009. Response of broadleaved evergreen Mediterranean forest vegetation to fire disturbance during the Holocene: insights from the peri-Adriatic region. J. Biogeogr. 36, 314–326.

Colombaroli, D., Vannière, B., Emmanuel, C., Magny, M., Tinner, W., 2008. Fire—vegetation interactions during the Mesolithic—Neolithic transition at Lago dell'Accesa, Tuscany, Italy. The Holocene 18, 679–692.

Conedera, M., Tinner, W., Crameri, S., Torriani, D., Herold, A., 2006. Taxon-related pollen source areas for lake basins in the southern Alps: an empirical approach. Veget. Hist. Archaeobot. 15, 263–272.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., Krebs, P., 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quatern. Sci. Rev. 28, 555–576.

Corella, J.P., Brauer, A., Mangili, C., Rull, V., Vegas-Vilarrúbia, T., Morellón, M., Valero-Garcés, B.L., 2012. The 1.5-ka varved record of Lake Montcortès (southern Pyrenees, NE Spain). Quat. Res. 78, 323–332.

Croce, A., La Valva, V., Motti, R., Nazzaro, R., Strumia, S., 2008. La flora vascolare del Vulcano di Roccamonfina (Campania, Italia). Webbia 63, 251–291.

Cuttelod, A., García, N., Malak, D.A., Temple, H.J., Katariya, V., 2009. The Mediterranean: a biodiversity hotspot under threat. Wildlife in a changing world–an analysis of the 2008 IUCN red list of threatened. Species 89, 9.

Del Martinez Castillo, E., Zang, C.S., Buras, A., Hacket-Pain, A., Esper, J., Serrano-Notivoli, R., Hartl, C., Weigel, R., Klesse, S., Resco de Dios, V., Scharnweber, T., Dorado-Liñán, I., van der Maaten-Theunissen, M., van der Maaten, E., Jump, A., Mikac, S., Banzragch, B.-E., Beck, W., Cavin, L., Claessens, H., Čada, V., Čufar, K., Dulamsuren, C., Gričar, J., Gil-Pelegrín, E., Janda, P., Kazimirovic, M., Kreyling, J., Latte, N., Leuschner, C., Longares, L.A., Menzel, A., Merela, M., Motta, R., Muffler, L., Nola, P., Petritan, A.M., Petritan, I.C., Prislan, P., Rubio-Cuadrado, Á., Rydval, M., Stajić, B., Svoboda, M., Toromani, E., Trotsiuk, V., Wilmking, M., Zlatanov, T., de Luis, M., 2022. Climate-change-driven growth decline of European beech forests. Commun. Biol. 5, 163. https://doi.org/10.1038/s42003-022-03107-3.

Díaz-Gonzalez, T.E., Peñas, A., 2017. The high mountain area of northwestern Spain: the cantabrian range, the Galician-Leonese mountains and the bierzo trench. In: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula. Springer, Cham, pp. 251–321. https://doi.org/10.1007/978-3-319-54867-8.

Di Pietro, R., Azzella, M.M., Facioni, L., 2010. The forest vegetation of the Tolfa-Ceriti Mountains (northern Latium–central Italy). Hacquetia 9, 91–150. https://doi.org/10.2478/v10028-010-0002-2.

Di Rita, F., Anzidei, A.P., Magri, D., 2013. A Lateglacial and early Holocene pollen record from Valle di Castiglione (Rome): vegetation dynamics and climate implications. Quat. Int. 288, 73–80. https://doi.org/10.1016/j.quaint.2011.11.011.

Di Rita, F., Celant, A., Milli, S., Magri, D., 2015. Lateglacial–early Holocene vegetation history of the Tiber delta (Rome, Italy) under the influence of climate change and sea level rise. Rev. Palaeobot. Palynol. 218, 204–216.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x.

Dobrowski, S.Z., Littlefield, C.E., Lyons, D.S., Hollenberg, C., Carroll, C., Parks, S.A., Abatzoglou, J.T., Hegewisch, K., Gage, J., 2021. Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. Commun. Earth Environ. 2, 198. https://doi.org/10.1038/s43247-021-00270-z.

Dodson, J.R., 1990. Fine resolution pollen analysis of vegetation history in the Lough Adoon Valley, Co. Kerry, western Ireland. Rev. Palaeobot. Palynol. 64, 235–245.

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). Veg. Hist. Archaeobot. 16, 279–299. https://doi.org/10.1007/s00334-006-0089-z.

Ellenberg, H., 2009. Vegetation Ecology of Central Europe, fourth ed. Cambridge University Press, Cambridge, UK.

Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. The Holocene 15, 293–297. https://doi.org/10.1191/0959683605hl808rr.

Fischer, N., Jungclaus, J.H., 2011. Evolution of the seasonal temperature cycle in a transient Holocene simulation: orbital forcing and sea-ice. Clim. Past 7, 1139–1148. https://doi.org/10.5194/cp-7-1139-2011.

Fischer, H., Meissner, K.J., Mix, A.C., Abram, N.J., Austermann, J., Brovkin, V., Capron, E., Colombaroli, D., Daniau, A.-L., Dyez, K.A., et al., 2018. Palaeoclimate constraints on the impact of 2 °C anthropogenic warming and beyond. Nat. Geosci. 11, 474–485. https://doi.org/10.1038/s41561-018-0146-0.

Frei, E.R., Gossner, M.M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., Wohlgemuth, T., 2022. European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. Plant Biol. 24, 1132–1145. https://doi.org/10.1111/plb.13467.

Fugazzola Delpino, M.A., Tinazzi, O., 2010. Dati di cronologia da un villaggio del Neolitico Antico. Le indagini dendrocronologiche condotte sui legni de La Marmotta (lago di Bracciano-Roma). Miscellanea in ricordo di Francesco Nicosia. Studia Erudita, Fabrizio Serra Editore (in press).

Fugazzola Delpino, M.A., D'Eugenio, G., Pessina, A., 1993. La Marmotta (Anguillara Sabazia, Roma), Scavi del 1989. Un abitato perilacustre di età neolitica. B. Paletnol. Ital. 84, 181–342.

Ganz, K., van Vugt, L., Gobet, E., Morales-Molino, C., Giagkoulis, T., Ogi, S., Hächler, L., Schaad, E., Zander, P.D., Lloren, R., Dubois, N., Grosjean, M., Vogel, H., Kotsakis, K., Bogaard, A., Hafner, A., Tinner, W., 2024. Holocene climate–vegetation–land use interactions in the mesomediterranean coastlands of northern Greece. The Holocene. https://doi.org/10.1177/09596836241297665.

Giardini, M., 2007. Late quaternary vegetation history at Stracciacappa (Rome, central Italy). Veg. Hist. Archaeobot. 16, 301–316. https://doi.org/10.1007/s00334-006-0037-y.

Giesecke, T., Ammann, B., Brande, A., 2014. Palynological richness and evenness: insights from the taxa accumulation curve. Veg. Hist. Archaeobot. 23, 217–228. https://doi.org/10.1007/s00334-014-0435-5.

Giraudi, C., 2004. Le oscillazioni di livello del Lago di Mezzano (Valentano-VT): variazioni climatiche e interventi antropici. Ital. J. Quat. Sci. 17, 221–230.

Giraudi, C., Magny, M., Zanchetta, G., Drysdale, R.N., 2011. The Holocene climatic evolution of Mediterranean Italy: a review of the continental geological data. The Holocene 21, 105–115. https://doi.org/10.1177/0959683610377529.

Green, D.G., 1981. Time series and postglacial forest ecology. Quat. Res. 15, 265–277.

Gubler, M., Henne, P.D., Schwörer, C., Boltshauser-Kaltenrieder, P., Lotter, A.F., Brönnimann, S., Tinner, W., 2018. Microclimatic gradients provide evidence for a glacial refugium for temperate trees in a sheltered hilly landscape of Northern Italy. J. Biogeogr. 45, 2564–2575. https://doi.org/10.1111/jbi.13426.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. Science 293, 1304–1308. https://doi.org/10.1126/science.1059725.

Heiri, O., Ilyashuk, B., Millet, L., Samartin, S., Lotter, A.F., 2015. Stacking of discontinuous regional palaeoclimate records: chironomid-based summer temperatures from the Alpine region. The Holocene 25, 137–149. https://doi.org/10.1177/0959683614556382.

Horvat, I., Glavač, V., Ellenberg, H., 1974. Vegetation Südosteuropas. Gustav Fischer Verlag, Stuttgart, Germany.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586. https://doi.org/10.2307/1934145.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Glob. Change Biol. 12, 2163–2174.

Kelly, M.G., Huntley, B., 1991. An 11,000-year record of vegetation and environment from Lago di Martignano, Latium, Italy. J. Quat. Sci. 6, 209–224.

Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., Neycken, A., Braun, S., Dubach, V., Gessler, A., Ginzler, C., Gossner, M.M., Hagedorn, F., Queloz, V., Samblás Vives, E., Rigling, A., Frei, E.R., 2022. Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in *Fagus sylvatica*. Sci. Total Environ. 851, 157926. https://doi.org/10.1016/j.scitotenv.2022.157926.

Lang, G., Ammann, B., Behre, K.-E., Tinner, W., 2023. Quaternary Vegetation Dynamics of Europe, first ed. Haupt Verlag, Bern.

Langer, G.J., Bußkamp, J., 2023. Vitality loss of beech: a serious threat to *Fagus sylvatica* in Germany in the context of global warming. J. Plant Dis. Prot. 130, 1101–1115. https://doi.org/10.1007/s41348-023-00743-7.

Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long-term numerical solution for the insolation quantities of the Earth. Astron. Astrophys. 428, 261–285. https://doi.org/10.1051/0004-6361:20041335.

Leavitt, P.R., Hodgson, D.A., 2002. Sedimentary pigments. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Springer, Dordrecht, pp. 295–325. https://doi.org/10.1007/0-306-47668-1_15.

Lepori, F., Palm, D., Brännäs, E., Malmqvist, B., 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? Ecol. Appl. 15, 2060–2071.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data Using CANOCOTM. Cambridge University Press, Cambridge, UK.

Lestienne, M., Jouffroy-Bapicot, I., Leyssenne, D., Sabatier, P., Debret, M., Albertini, P.J., Colombaroli, C., Didier, J., Hély, C., Vannière, B., 2020. Fires and human activities as key factors in the high diversity of Corsican vegetation. The Holocene 30, 244–257. https://doi.org/10.1177/0959683619883025.

Liu, Y., Ogle, K., Lichstein, J.W., Jackson, S.T., 2022. Estimation of pollen productivity and dispersal: how pollen assemblages in small lakes represent vegetation. Ecol. Monogr. 92, 1–19. https://doi.org/10.1002/ecm.1513.

Lotter, A.F., 2001. The palaeolimnology of Soppensee (Central Switzerland), as evidenced by diatom, pollen, and fossil-pigment analyses. J. Paleolimnol. 25, 65–79. https://doi.org/10.1023/A:1008140122230.

Lowe, J.J., Accorsi, C.A., Bandini Mazzanti, M., Bishop, A., van der Kaars, S., Forlani, L., Mercuri, A.M., Rivalenti, C., Torri, P., Watson, C., 1996. Pollen stratigraphy of sediment sequences from lakes Albano and Nemi (near Rome) and from the central Adriatic, spanning the interval from oxygen isotope stage 2 to present day. Mem. Ist. Ital. Idrobiol. 55, 71–98.

Machado Nunes Romeiro, J., Eid, T., Antón-Fernández, C., Kangas, A., Trømborg, E., 2022. Natural disturbances risks in European Boreal and Temperate forests and their links to climate change – a review of modelling approaches. For. Ecol. Manag. 509, 120071. https://doi.org/10.1016/j.foreco.2022.120071.

Magny, M., de Beaulieu, J.-L., Drescher-Schneider, R., Vannière, B., Walter-Simonnet, A.-V., Miras, Y., Millet, L., Bossuet, G., Peyron, O., Brugiapaglia, E., Leroux, A., 2007. Holocene climate changes in the central Mediterranean as recorded by lake-level fluctuations at Lake Accesa (Tuscany, Italy). Quat. Sci. Rev. 26, 1736–1758. https://doi.org/10.1016/j.quascirev.2007.04.014.

Magri, D., 1999. Late Quaternary vegetation history at Lagaccione near Lago di Bolsena (central Italy). Rev. Palaeobot. Palynol. 106, 171–208. https://doi.org/10.1016/S0034-6667(99)00006-8.

Magri, D., Sadori, L., 1999. Late Pleistocene and Holocene pollen stratigraphy at Lago di Vico, central Italy. Veget. Hist. Archaeobot. 8, 247–260. https://doi.org/10.1007/BF01291777.

Magri, D., Agrillo, E., Di Rita, F., Furlanetto, G., Pini, R., Ravazzi, C., Spada, F., 2015. Holocene dynamics of tree taxa populations in Italy. Rev. Palaeobot. Palynol. 218, 267–284. https://doi.org/10.1016/j.revpalbo.2014.08.012.

Makri, S., Wienhues, G., Bigalke, M., Gilli, A., Rey, F., Tinner, W., Vogel, H., Grosjean, M., 2021. Variations of sedimentary Fe and Mn fractions under changing lake mixing regimes, oxygenation and land surface processes during Late-glacial and Holocene times. Sci. Total Environ. 755, 143418. https://doi.org/10.1016/j.scitotenv.2020.143418.

Marriner, N., Kaniewski, D., Pourkerman, M., Devillers, B., 2022. Anthropocene tipping point reverses long-term Holocene cooling of the Mediterranean Sea: a meta-analysis of the basin's Sea Surface Temperature records. Earth Sci. Rev. 227, 103986. https://doi.org/10.1016/j.earscirev.2022.103986.

Masi, A., Francke, A., Pepe, C., Thienemann, M., Wagner, B., Sadori, L., 2018. Vegetation history and paleoclimate at lake dojran (FYROM/Greece) during the late glacial and Holocene. Clim. Past 14, 351–367. https://doi.org/10.5194/cp-14-351-2018.

Mazzucco, N., Mineo, M., Arobba, D., Caramiello, R., Caruso Fermé, L., Gassin, B., Guilbeau, D., Ibáñez, J.J., Morandi, L.F., Mozota, M., Pichon, F., Portillo, M., Rageot, M., Remolins, G., Rottoli, M., Gibaja, J.F., 2022. Multiproxy study of 7500-year-old wooden sickles from the lakeshore village of La Marmotta, Italy. Sci. Rep. 12, 14976. https://doi.org/10.1038/s41598-022-18597-8.

Mercuri, A.M., Marignani, M., Sadori, L., 2013. Palynology: the bridge between palaeoecology and ecology for the understanding of human-induced global changes in the Mediterranean area. Ann. Bot. (Rome) 3, 107–113.

Moore, P.D., Webb, J.A., Collison, M.E., 1991. Pollen Analysis. Blackwell Scientific Publications, USA.

Morales-Molino, C., Steffen, M., Samartin, S., van Leeuwen, J.F.N., Hürlimann, D., Vescovi, E., Tinner, W., 2021. Long-term responses of Mediterranean mountain forests to climate change, fire and human activities in the Northern Apennines (Italy). Ecosystems 24, 1361–1377. https://doi.org/10.1007/s10021-020-00587-4.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Overpeck, J.T., Whitlock, C., Huntley, B., 2003. Terrestrial biosphere dynamics in the climate system: past and future. In: Alverson, K.D., Bradley, R.S., Pedersen, T.F. (Eds.), Paleoclimate, Global Change and the Future. Springer, Berlin, pp. 81–103.

Pastore, M.A., Classen, A.T., D'Amato, A.W., Foster, J.R., Adair, E.C., 2022. Cold-air pools as microrefugia for ecosystem functions in the face of climate change. Ecology 103, e3717. https://doi.org/10.1002/ecy.3717.

Peñuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusià, J., Ogaya, R., Carnicer, J., Bartrons, M., Rivas-Ubach, A., Grau, O., Peguero, G., Margalef, O., Pla-Rabés, S., Stefanescu, C., Asensio, D., Preece, C., Liu, L., Verger, A., Barbeta, A., Achotegui-Castells, A., Gargallo-Garriga, A., Sperlich, D., Farré-Armengol, G., Fernández-Martínez, M., Liu, D., Zhang, C., Urbina, I., Camino-Serrano, M., Vives-Ingla, M., Stocker, B., Balzarolo, M., Guerrieri, R., Peaucelle, M., Marañón-Jiménez, S., Bórnez-Mejías, K., Mu, Z., Descals, A., Castellanos, A., Terradas, J., 2017. Impacts of global change on Mediterranean forests and their services. Forests 8, 463. https://doi.org/10.3390/f8120463.

Peterson, L.C., Haug, G.H., Hughen, K.A., Röhl, U., 2000. Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. Science 290, 1947–1951. https://doi.org/10.1126/science.290.5498.1947.

Petitti, P., 2012. Preistoria di un paesaggio: La Caldera di Latera e il territorio circostante. Quaderni/Sistema Museale del Lago di Bolsena 16. Città di Bolsena, Bolsena.

Pignatti, S., 1997. Ecologia del paesaggio. Unione Tipografico-Editrice Torinese (UTET), Torino.

Pignatti, S., 1998. I boschi d'Italia – Sinecologia e biodiversità. Unione Tipografico-Editrice Torinese (UTET), Torino.

Pignatti, S., 2005. Valori di bioindicazione delle piante vascolari della flora d'Italia. Braun-Blanquetia 39, 3–97.

Pignatti, S., Guarino, R., La Rosa, M., 2017. Flora d'Italia, second ed. Edagricole, Bologna.

Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Glob. Change Biol. 14, 1265–1281. https://doi.org/10.1111/j.1365-2486.2008.01570.x.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org. (Accessed 20 October 2022).

Reille, M., 1992. Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41.

Rey, F., Gobet, E., Schwörer, C., Wey, O., Hafner, A., Tinner, W., 2019. Causes and mechanisms of synchronous succession trajectories in primeval Central European mixed *Fagus sylvatica* forests. J. Ecol. 107, 1392–1408. https://doi.org/10.1111/1365-2745.13121.

Ricci Lucchi, M., Calderoni, G., Carrara, C., Cipriani, N., Esu, D., Ferreli, L., Girotti, O., Gliozzi, E., Lombardo, M., Longinelli, A., Magri, D., Nebbiai, M., Ricci Lucchi, F., Vigliotti, L., 2000. Late Quaternary record of the Rieti basin, central Italy: paleoenvironmental and paleoclimatic evolution. Giorn. Geol. 62, 105–136.

Rukh, S., Sanders, T.G.M., Krüger, I., Schad, T., Bolte, A., 2023. Distinct responses of European beech (*Fagus sylvatica* L.) to drought intensity and length – a review of the impacts of the 2003 and 2018–2019 drought events in Central Europe. Forests 14, 248. https://doi.org/10.3390/f14020248.

Sadori, L., 2018. The Lateglacial and Holocene vegetation and climate history of Lago di Mezzano (central Italy). Quat. Sci. Rev. 202, 30–44. https://doi.org/10.1016/j.quascirev.2018.09.004.

Sadori, L., Giraudi, C., Petitti, P., Ramrath, A., 2004. Human impact at Lago di Mezzano (central Italy) during the Bronze Age: a multidisciplinary approach. Quat. Int. 113, 5–17. https://doi.org/10.1016/S1040-6182(03)00077-6.

Samartin, S., Heiri, O., Joos, F., Renssen, H., Franke, J., Brönnimann, S., Tinner, W., 2017. Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. Nat. Geosci. 10, 207–212. https://doi.org/10.1038/ngeo2891.

San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., Tinner, W., Ballian, D., Beck, P., Birks, H.J.B., Eaton, E., Enescu, C.M., Pasta, S., Popescu, I., Ravazzi, C., Welk, E., Abad Viñas, R., Azevedo, J.C., Barbati, A., Barredo, J.I., Benham, S.E., Boca, R., Bosco, C., Caldeira, M.C., Cerasoli, S., Chirici, G., Cierjacks, A., Conedera, M., Da Ronch, F., Di Leo, M., García-Viñas, J.I., Gastón González, A., Giannetti, F., Guerrero Hue, N., Guerrero Maldonado, N., López, M.J., Jonsson, R., Krebs, P., Magni, D., Mubareka, S., Mulhern, G., Nieto Quintano, P., Oliveira, S., Pereira, J.S., Pividori, M., Räty, M., Rinaldi, F., Saura, S., Sikkema, R., Sitzia, T., Strona, G., Vidal, C., Vilar, L., Zecchin, B., 2016. European Atlas of Forest Tree Species. Publications Office of the European Union, Luxembourg.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45, 86–103. https://doi.org/10.1016/j.baae.2020.04.003.

Scoppola, A., Caporali, C., 1998. Mesophilous woods with *Fagus sylvatica* L. of northern Latium (Tyrrhenian Central Italy): synecology and syntaxonomy. Plant Biosyst. 132, 151–168. https://doi.org/10.1080/11263504.1998.10654200.

Seppä, H., 2007. Pollen analysis, principles. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science. Elsevier, Amsterdam, pp. 2486–2497.

SIR Toscana, 2024. DATI/Archivio storico. Servizio Idrologico Regionale, Direzione Difesa del Suolo e Protezione Civile. Pisa, Italy. https://www.sir.toscana.it/consistenza-rete. (Accessed 14 February 2024).

Spicciarelli, R., Autera, M., Battafarano, R., 2011. Misure di Tutela e Conservazione, Report Conclusivo "Monte Vulture," Rete Natura 2000. Unione Europea – Regione Basilicata.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Stoutjesdijk, P., Barkman, J.J., 2014. Microclimate, Vegetation and Fauna. KNNV Publishing, Wageningen, Netherlands.

ter Braak, C., Šmilauer, P., 2012. Canoco Reference Manual and User's Guide: Software for Ordination, Version 5.0. Microcomputer Power, Ithaca, NY, USA.

Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene 13, 499–505. https://doi.org/10.1191/0959683603hl615rp.

Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire ecology and dynamics in southern Switzerland. J. Ecol. 87, 273–289. https://doi.org/10.1046/j.1365-2745.1999.00346.x.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. Ecol. Monogr. 83 (1), 419–439. https://doi.org/10.1890/12-2231.

Tinner, W., Vescovi, E., van Leeuwen, J.F.N., Colombaroli, D., Henne, P.D., Kaltenrieder, P., Morales-Molino, C., Beffa, G., Gnaegi, B., van der Knaap, W.O., La Mantia, T., Pasta, S., 2016. Holocene vegetation and fire history of the mountains of Northern Sicily (Italy). Veg. Hist. Archaeobot. 25, 499–519. https://doi.org/10.1007/s00334-016-0569-8.

Tu, L., Gilli, A., Lotter, A.F., Vogel, H., Moyle, M., Boyle, J.F., Grosjean, M., 2021. The nexus among long-term changes in lake primary productivity, deep-water anoxia, and internal phosphorus loading, explored through analysis of a 15,000-year varved sediment record. Glob. Planet. Change 207, 103643. https://doi.org/10.1016/j.gloplacha.2021.103643.

Tulumello, C., 2023. Fornitura prot.n. 1342103: dati termo-pluviometrici di Bolsena, Ischia di Castro, Marta e Valentano: periodo 2021–agosto 2023. Personal communication via email. Agenzia Regionale Protezione Civile - Regione Lazio, Roma.

van Geel, B., Mauquoy, D., 2010. Peatland records of solar activity. PAGES News 18, 11–12. https://doi.org/10.22498/pages.18.1.11.

Vannière, B., Colombaroli, D., Chapron, E., Leroux, A., Tinner, W., Magny, M., 2008. Climate versus human-driven fire regimes in Mediterranean landscapes: the Holocene record of Lago dell'Accesa (Tuscany, Italy). Quat. Sci. Rev. 27, 1181–1196. https://doi.org/10.1016/j.quascirev.2008.02.011.

Vescovi, E., Ravazzi, C., Arpenti, E., Finsinger, W., Pini, R., Valsecchi, V., Wick, L., Ammann, B., Tinner, W., 2007. Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. Quat. Sci. Rev. 26, 1650–1669. https://doi.org/10.1016/j.quascirev.2007.03.005.

Vinther, B.M., Clausen, H.B., Johnsen, S.J., Rasmussen, S.O., Andersen, K.K., Buchardt, S. L., Dahl-Jensen, D., Seierstad, I.K., Siggaard-Andersen, M.-L., Steffensen, J.P., Svensson, A., Olsen, J., Heinemeier, J., 2006. A synchronized dating of three Greenland ice cores throughout the Holocene. J. Geophys. Res. 111. https://doi.org/10.1029/2005JD006921.

Wanner, H., Beer, J., Bütikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Küttel, M., Müller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M., 2008. Mid- to Late Holocene climate change: an overview. Quat. Sci. Rev. 27, 1791–1828. https://doi.org/10.1016/j.quascirev.2008.06.013.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5, 475–482. https://doi.org/10.1890/070037.

Woodbridge, J., Fyfe, R.M., Roberts, N., Downey, S., Edinborough, K., Shennan, S., 2014. The impact of the Neolithic agricultural transition in Britain: a comparison of pollen-based land-cover and archaeological 14C date-inferred population change. J. Archaeol. Sci. 51, 216–224. https://doi.org/10.1016/j.jas.2012.10.025.

Yurkov, V.V., Beatty, J.T., 1998. Aerobic anoxygenic phototrophic bacteria. Microbiol. Mol. Biol. Rev. 62, 695–724.

Zanchetta, G., Drysdale, R.N., Hellstrom, J.C., Fallick, A.E., Isola, I., Gagan, M.K., Pareschi, M.T., 2007. Enhanced rainfall in the Western Mediterranean during deposition of sapropel S1: stalagmite evidence from Corchia cave (Central Italy). Quat. Sci. Rev. 26, 279–286. https://doi.org/10.1016/j.quascirev.2006.12.003.

Zander, P.D., Żarczyński, M., Vogel, H., Tylmann, W., Wacnik, A., Sanchini, A., Grosjean, M., 2021. A high-resolution record of Holocene primary productivity and water-column mixing from the varved sediments of Lake Żabińskie, Poland. Sci. Total Environ. 755, 143713. https://doi.org/10.1016/j.scitotenv.2020.143713.

Zander, P.D., Wienhues, G., Grosjean, M., 2022. Scanning hyperspectral imaging for in situ biogeochemical analysis of lake sediment cores: review of recent developments. J. Imaging 8, 58. https://doi.org/10.3390/jimaging8030058.