Quaternary Science Reviews 376 (2026) 109830

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

From Neanderthals to *Homo sapiens*: New palaeoecological and tephrocronological data from the MIS3 layers of Grotta-Riparo di Uluzzo C (Apulia, southern Italy)

Juan Ochando [a,b,c,*], Donatella Magri [a], Biagio Giaccio [d], Giovanni Zanchetta [e], Antonino Vazzana [f], Omry Barzilai [g], Francesco Berna [c,h], Gruppo Speleologico Neretino [i], Giulia Marciani [f,c], Andrea Zerboni [j], Sara Silvestrini [f], Enza E. Spinapolice [k], Adriana Moroni [c,l,m], Gabriele Terlato [f], Matteo Romandini [f], Stefano Benazzi [f]

[a] *Department of Environmental Biology, Sapienza University of Rome, Piazzale Aldo Moro 5, 00185 Rome, Italy*
[b] *Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain*
[c] *Department of Physical Sciences, Earth and Environment, University of Siena, Strada Laterina, 8, 53100 Siena, Italy*
[d] *Istituto di Geologia Ambientale e Geoingegneria, Consiglio Nazionale delle Ricerche, Monterotondo, Rome, Italy*
[e] *Department of Earth Science, University of Pisa, via Santa Maria 53, 56126, Pisa, Italy*
[f] *Department of Cultural Heritage, University of Bologna, Via Degli Ariani 1, 48121 Ravenna, Italy*
[g] *Material Culture PaleoLab, School of Archaeology and Maritime Cultures, The University of Haifa, 199 Abba Khoushy Ave, Haifa, Israel*
[h] *Department of Archaeology. Simon Fraser University (SFU) Education Building 9635, 8888 University Drive, Burnaby, B.C. Canada V5A 1S6, Canada*
[i] *Gruppo Speleologico Neretino, Piazza Cesare Battisti, 73048, Nardò, Italy*
[j] *Department of Earth Science "A. Desio', University of Milan, Italy*
[k] *Department of Ancient World Studies, Sapienza University of Rome, Piazzale Aldo Moro 5, 00185 Rome, Italy*
[l] *Centro Studi sul Quaternario ODV, via Nuova dell'Ammazzatoio, 7, Sansepolcro, Arezzo, Italy*
[m] *Istituto Italiano di Paleontologia Umana, Piazza Ruggero Bonghi, 2, 03012 Anagni, Italy*

A R T I C L E I N F O

Handling Editor. Dr Mira Matthews

Keywords:
Palynology
Homo neanderthalensis
Homo sapiens
Mousterian
Uluzzian
Middle-Upper Palaeolithic
Tephra
Italy

A B S T R A C T

The southern Italian Peninsula plays a crucial role as a biogeographical hotspot in Southern Europe, influenced significantly by the Mediterranean climate. This environment acted as a glacial refuge for diverse flora and fauna, humans included. This study employs pollen analysis on Mousterian and Uluzzian sediments from Grotta-Riparo di Uluzzo C in the Salento Peninsula (southern Italy) to reconstruct the vegetation landscapes encountered by the late Italian Neanderthals (thus far associated with the Mousterian) and early modern humans (linked to the Uluzzian) during the mid Marine Isotope Stage (MIS) 3. Our palynological analyses reveal a distinctive and diverse environment within the Mediterranean landscape. Tephrochronological and OSL constraints and paleoenvironmental variability consistently allow us to date the investigated interval between ~46.6 ka and 43.4 ka, encompassing the second part of the long Greenland interstadial 12 (GI-12) and the onset of the GI-11. Over these three millennia, the environment in the area of Uluzzo C is characterized by a rich flora mainly composed of evergreen elements. Additionally, heliophytes such as Amaranthaceae, *Artemisia*, and Poaceae are observed. The consistent presence of pollen taxa such as *Juglans*, and *Pinus halepensis/pinea*, among others, highlights the importance of this coastal area of Apulia for the long-term persistence of Mediterranean species during the Late Pleistocene. These taxa could be supported by a generally mild climate, as suggested by the occurrence of *Olea*, *Myrtus*, and *Cistus*. These diverse environments would undeniably have offered various opportunities for the survival of Neanderthals and early Upper Palaeolithic hominins, especially during the warm phases and, critically, the cold events of the Late Pleistocene. Our integrated approach underscores the importance of Grotta-Riparo di Uluzzo C as a MIS 3 archive, contributing to the ongoing debate on the spatial extent of glacial refugia. Our data from Uluzzo C corroborate the previous idea that the climatic and environmental setting were not the main reason for Neanderthals' abandonment of Uluzzo Bay and potentially southern Italy around 45,000 years ago.

* Corresponding author. Department of Environmental Biology, Sapienza University of Rome, Piazzale Aldo Moro 5, 00185 Rome, Italy.
E-mail address: juan.ochando@unisi.it (J. Ochando).

https://doi.org/10.1016/j.quascirev.2026.109830
Received 7 October 2025; Received in revised form 19 January 2026; Accepted 20 January 2026
Available online 23 January 2026

1. Introduction

The biodiversity and structure of palaeoecosystems, directly reconstructed from archaeological successions, have been insufficiently considered in research on the survival and disappearance of the Last Neanderthals and the arrival of modern human populations. Consequently, a broad investigation into the relationships between *Homo* evolution and Pleistocene palaeofloras in Europe and the Near East is required. The Italian Peninsula has been a region of confirmed *Homo* evolutionary activity and served as a significant enclave in terms of both human population survival and plant and animal biodiversity hotspot (Benazzi et al., 2011; Higham et al., 2011, 2024; Magri et al., 2017; Moroni et al., 2018; Badino et al., 2020, 2023; Romandini et al., 2020; Ermolli et al., 2022).

Grotta-Riparo di Uluzzo C (hereinafter called Uluzzo C; Figs. 1 and 2), is currently formed by a narrow central hall and a residual external deposit leaning against the rock wall and sloping towards the sea (Seghi et al., 2024). This evidence is what remains of a larger cavity whose vault finished collapsing during the Mousterian occupation (Borzatti von Löwenstern, 1965, 1966, 1969). It contains a key continental deposit (the top of which is located 14–15 m above the present sea level), including (from top to bottom): a reworked layer with Romanellian materials (layer A), a Uluzzian occupation (layers C and D), capped by a tephra deposit (layer B), and a thick Middle Palaeolithic sequence (layers E, F, G, and H), lying on a marine deposit attributed to the Tyrrhenian sea ingression (Fig. 3). This succession can be partly correlated with that brought to light in the nearby Grotta del Cavallo and Grotta di Uluzzo B (Figs. 1 and 2). Uluzzo C, also known as Grotta Cosma, was first visited in the 1960s by Carlo Cosma, a member of the Gruppo Speleologico di Maglie, who collected numerous Mousterian artefacts at the top of the external deposit together with a set of Neanderthal teeth (Seghi et al., 2024). Subsequently, in 1963, stratigraphic excavations were begun by the Istituto Italiano di Preistoria e Protostoria (IIPP) under the scientific direction of E. Borzatti von Löwenstern, who gave the site its current name, and went on until 1968 (Borzatti von Löwenstern, 1963, 1964, 1965, 1966; Borzatti von Löwenstern and Magaldi, 1969; Palma di Cesnola and Borzatti von Löwenstern, 1964). In 1963, a small test pit was opened, later enlarged in 1964 to 2.6 × 1.5-m x 2.5 m deep (corresponding to spit 5 of layer G, see Fig. 3). In 1967 and 1968, two other excavation seasons were conducted at Uluzzo C (Borzatti von Löwenstern, 1969). On this occasion, the trench was widened by approximately 1 m towards the outside, an area in which a marked decrease in lithic and faunal remains was noted, while the sedimentological characteristics remained unchanged. The sequence was completely re-excavated, reaching the Tyrrhenian marine deposit. This made it possible to establish that the bed rock was located ca. 5 m above the present sea level (Borzatti von Löwenstern, 1969, p. 16). Since 2015, multidisciplinary investigations encompassing new excavations (dating, sedimentological analysis, micromorphology, and the study of lithic artefacts and faunal remains) were carried out at Uluzzo C (Fiorini et al., 2019; Spinapolice et al., 2022; Seghi et al., 2024; Silvestrini et al., 2022a, 2022b, 2024). During these recent excavations, which are still ongoing by the University of Bologna with the collaboration of the Gruppo Speleologico Neretino, a 1 × 1 m grid was built, including the area investigated in the 1960s, and the site was divided into three sectors: A, B, and C. Sectors A and B are situated very close to the residual cave and correspond to the surface of the existing deposit and to the area occupied by Borzatti's trench (see Fig. 3a–b) respectively. Sector C includes the external deposit (Fiorini et al., 2019).

The new investigations only focused on the sequence down to layer F, overall confirming the cultural sequence originally proposed by Borzatti, consisting in seven main stratigraphic layers (Spinapolice et al., 2022).

Based on the faunal data from Sector B of the cave, published by Borzatti in the 1960s (Borzatti von Löwenstern, 1965; Borzatti von Löwenstern and Magaldi, 1966), and on the results of the more recent excavations and archaeozoological and ZooMS analyses from Sector A (Silvestrini et al., 2022a, 2022b), it is possible to reconstruct a

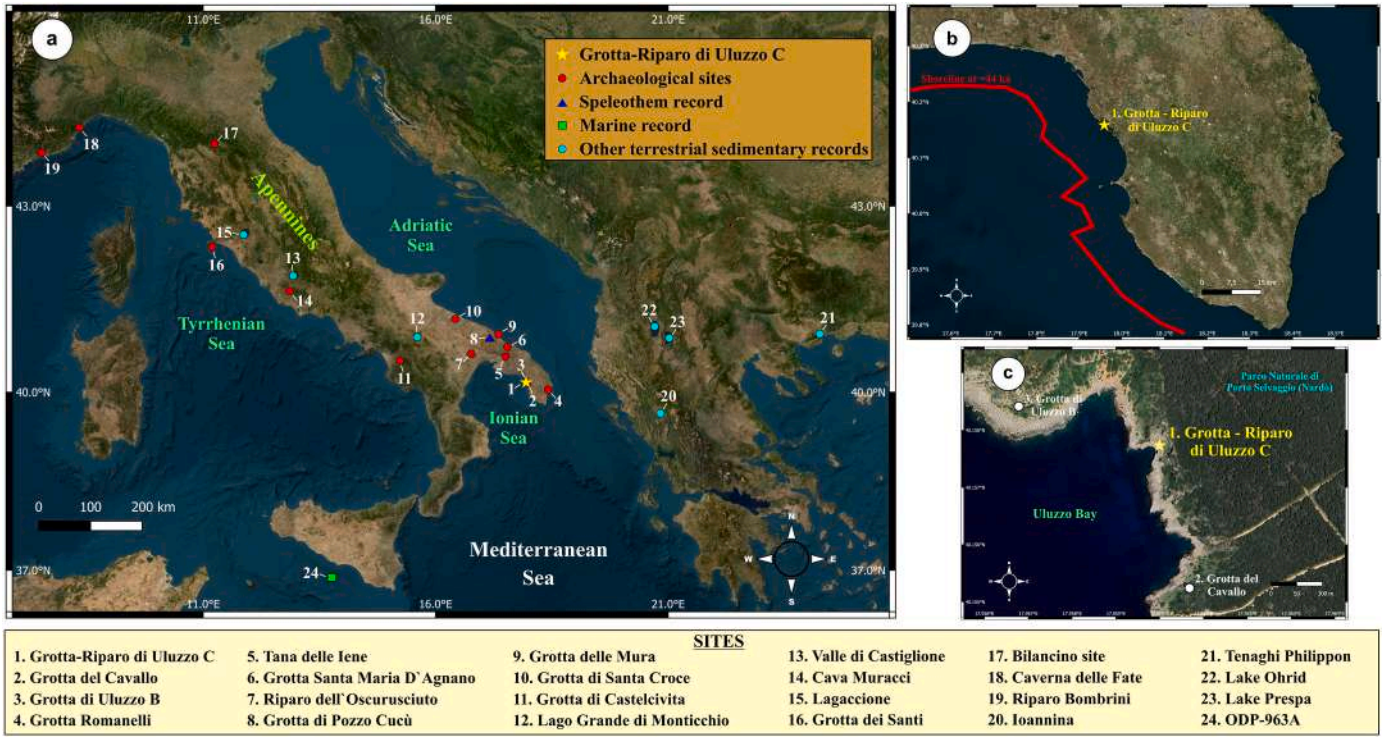

Fig. 1. a) Grotta-Riparo di Uluzzo C and Late Pleistocene sites from the Italian and Balkan Peninsula mentioned in the text, b) Position of the shoreline at ~44 ka relative to the western coast of the Salento Peninsula (Apulia, southern Italy), c) Location of the Uluzzo C, Grotta del Cavallo, and Grotta di Uluzzo B in the Uluzzo Bay.

comprehensive and coherent picture of the faunal assemblage and paleoenvironmental conditions. Despite differences in excavation areas and methodologies, the comparison of these datasets highlights consistent trends in species representation and habitat dynamics over time.

Excluding Unit G, which is currently undergoing a stratigraphic revision and detailed faunal reanalyses, the MIS3 faunal spectrum is dominated by ungulates, with cervids (*Cervus elaphus*, *Dama dama*, and *Capreolus capreolus*) and equids (*Equus ferus*, *Equus hydruntinus*) as the main taxa, while large bovids (*Bos primigenius*) and *Sus scrofa* occur in lower frequencies. Among carnivores, *Vulpes vulpes* is the most common taxon, followed by *Canis lupus*, with sporadic occurrences of *Mustela nivalis*, *Martes* sp., *Meles meles* and a single *Crocuta spelaea* tooth recovered from the Mousterian layer (SU 23). Although hyena remains are rare, their presence is supported by ancient sedimentary DNA and by indirect taphonomic evidence, such as bone corrosion and rounding due to carnivore digestion (Silvestrini et al., 2022a). The presence of *Lepus europaeus*, birds and *Testudo hermanni* is consistent throughout much of the stratigraphic sequence, enriching the paleoenvironmental picture.

Several attempts at radiocarbon dating were carried out on animal bones, but no reliable results were obtained. The collagen preserved in the bones proved to be insufficient in quality and/or quantity for robust radiocarbon determinations. Likewise, the charcoal fragments recovered are too small (millimetric in size) and structurally degraded to be suitable for the same type of analysis. For these reasons, the conventional Optically Stimulated Luminescence of quartz (OSL) was used in dating the sediment of Uluzzo C. Three OSL samples were conducted in Sector A between layers F and C (samples ULOC 5, 4, and 3) (Fig. 3c; Spinapolice et al., 2022). Sample ULOC 1 was taken in the uppermost part of the Mousterian layer G and returned an age of 46 ± 4.0 ka, the oldest chronology available so far for Uluzzo C. With an OSL date of 41.6 ± 2.7 ka at the very top of F (sample ULOC 5), which does not match the date of the overlying tephra Y-6 (ca. 45.0–44.9 ka), this layer would be in the mid-MIS3 at the conclusion of the Mousterian cycle, just like layer F of Grotta del Cavallo. For the Uluzzian layers D and C (samples ULOC 4 and 3), the resulting optical ages (grand weighted mean 40.6 ± 1.4 ka) range from 42.7 ± 2.6 to 38.1 ± 2.2 ka. These ages imply that Uluzzian occupation of the site has most probably to be constrained between 42 and 39 ka (Fig. 3c).

Pollen analysis has proven to be a valuable method in reconstructing past ecosystems in hominin evolutionary contexts (García-Antón and Sáinz-Ollero, 1991; Carrión et al., 2019a, 2019b, 2019c; Burjachs, 2001; Finlayson and Carrión, 2007; Bonnefille et al., 2004; Messager et al., 2011; Langgut et al., 2018; Ochando et al., 2020a, 2020b, 2020c, 2020d, 2022a). In the Italian Peninsula, a number of Late Pleistocene caves, including Grotta dei Santi in Tuscany (Ochando et al., 2025), Cava Muracci in Lazio (Gatta et al., 2016), Tana delle Iene in Apulia (Gatta et al., 2016), and Caverna delle Fate in Liguria (Karatsori et al., 2005), have provided palaeoenvironmental reconstructions from pollen in coprolites that demonstrate the dynamism of the landscape mainly on a regional scale, butalso in the close vicinity of the sites.In particular, the

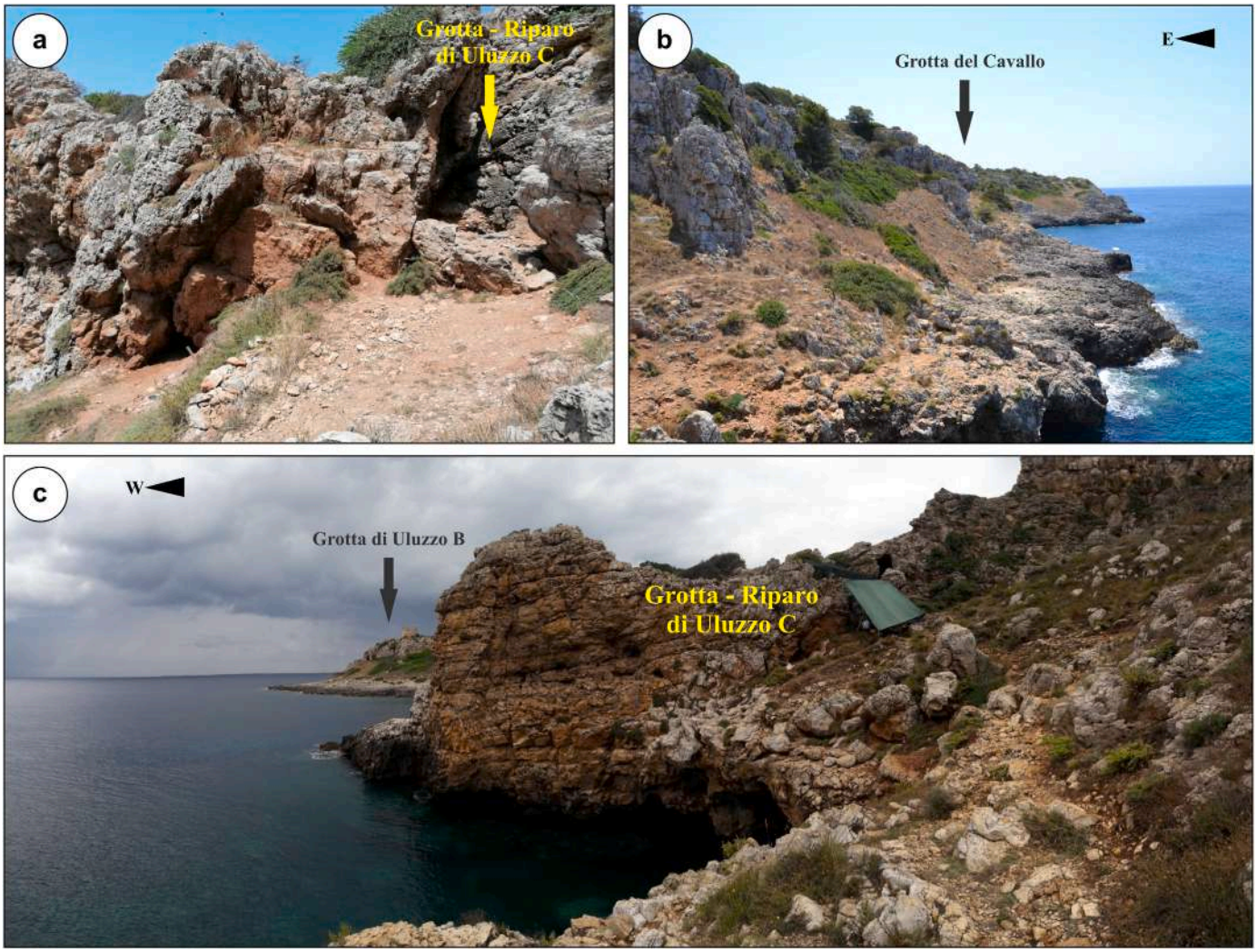

Fig. 2. Grotta-Riparo di Uluzzo C. a) site entrance, b) area of access to the site (Uluzzo Bay), c) Panoramic view of Uluzzo C in the Uluzzo Bay.

Apulia-Basilicata region offers a wealth of palaeobotanical and paleoclimatic data that allow combined and detailed reconstructions of the events between the demise of Neanderthals and the arrival of early modern humans, as the palynological and tephrostratigraphic investigation of Grotta del Cavallo (Zanchetta et al., 2018; Ricciardi, 2020), the pollen record from Lago Grande di Monticchio (Watts et al., 1996; Allen et al., 2000), the paleoenvironmental research from Riparo l'Oscurusciuto (Albert et al., 2025), and the speleothem record from Pozzo Cucù Cave in Apulia (Columbu et al., 2020), suggesting a pattern of alternating landscapes with stable paleoclimatic conditions during MIS 3.

Despite the extensive multidisciplinary evidence available, additional research is necessary to contextualize the decline of the Neanderthal population within a paleoenvironmental framework. A reliable chronology is crucially needed for framing the local palaeoecological information in the wider regional and extra-regional context of the Pleistocene climate variability. For the late Mousterian-Early Upper Paleolithic time windows, the ^{14}C method can be still successfully

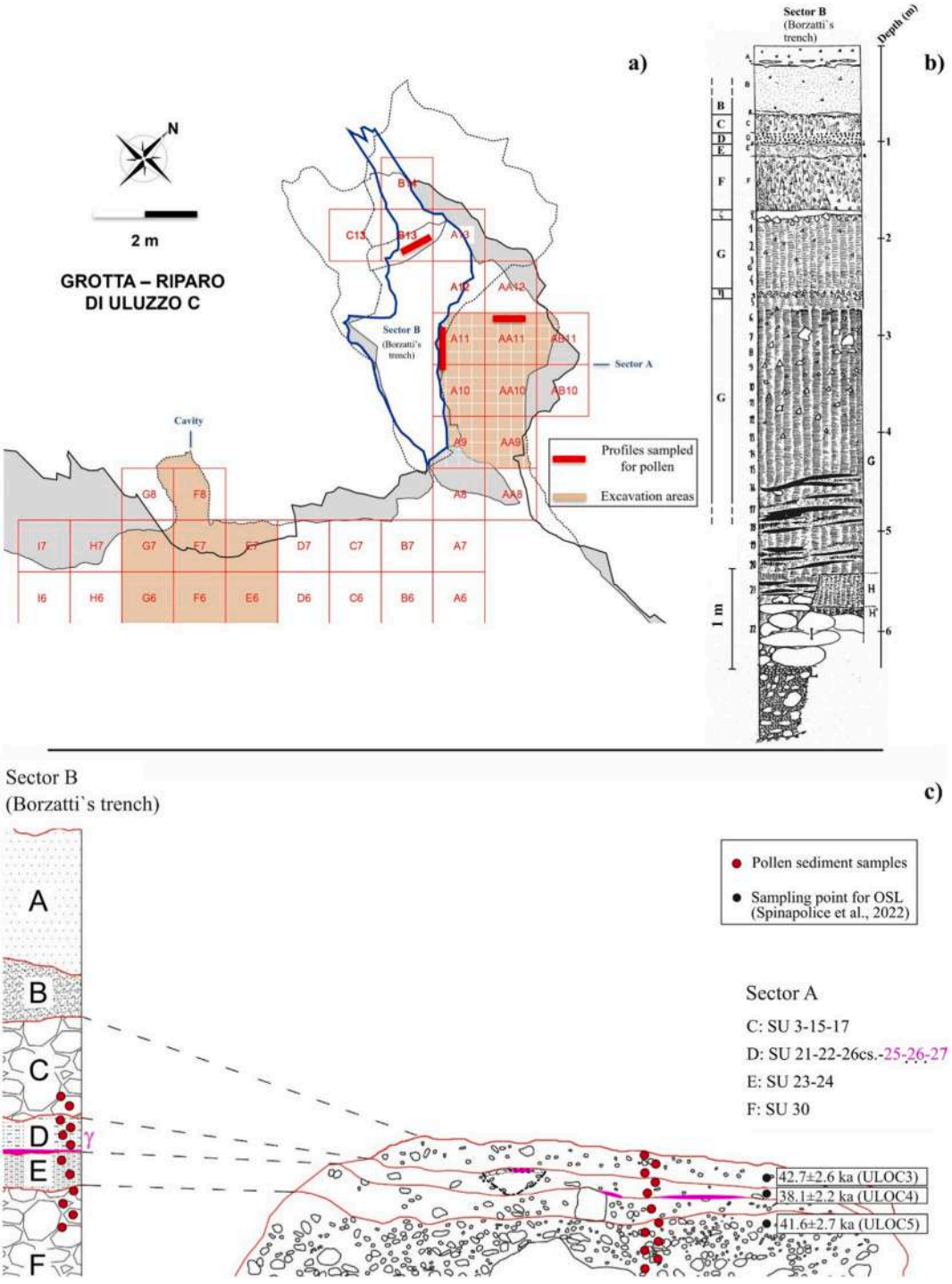

Fig. 3. a) Stratigraphy and profiles sampled for pollen analysis at Uluzzo C, b) Stratigraphic sequence of Uluzzo C, Sector B (Borzatti's trench) (modified after Borzatti von Löwenstern, 1965; Borzatti von Löwerstern, 1966), c) Stratigraphy with the position of pollen sediment samples in Sector A and Sector B (Borzatti's trench) of Uluzzo C, and geochronological data (further details in Table 1) (Borzatti von Löwenstern, 1965), as well as of the primary ash layer γ, described by Borzatti von Löwenstern (1969).

applied (e.g., Higham et al., 2008, 2011, 2014) but with increasing uncertainties, due to the very low radiocarbon activity ratio for such ancient samples. In the central Mediterranean area, tephrochronology has been proven to be a powerful tool method for investigating the Middle-Upper Paleolithic transition, not only for dating but also for synchronizing archaeological successions with paleoclimatic records (e.g., Giaccio et al., 2017a; Zanchetta et al., 2018; Spagnolo et al., 2024).

Besides, on-site palynological research can be used to decipher the palaeoenvironmental conditions across time and their likely impact on human population activities during site occupation. While off-site records reconstruct high-resolution regional vegetation dynamics (Genet et al., 2021; Badino et al., 2023), on-site palynological studies provide detailed information on past flora and vegetation and on the local/regional environment (Mercuri, 2014; Ochando et al., 2022b, 2024a, 2024b).

This paper presents a palynological study performed on MIS 3 sediment layers from Uluzzo C, with the aim of increasing our knowledge on the vegetation landscape occupied by Late Neanderthals and early modern human populations in southern Italy at both local and regional level. The study is supported by new tephrochronological data which are added to the set of OSL dates already published (Spinapolice et al., 2022), and to cultural information (Silvestrini et al., 2022a; Borzatti von Löwenstern, 1963, 1965, 1966, 1969) in order to provide the most accurate chronology of the palaeoenvironmental and cultural events that occurred in the time span between the Late Mousterian and Uluzzian occupations.

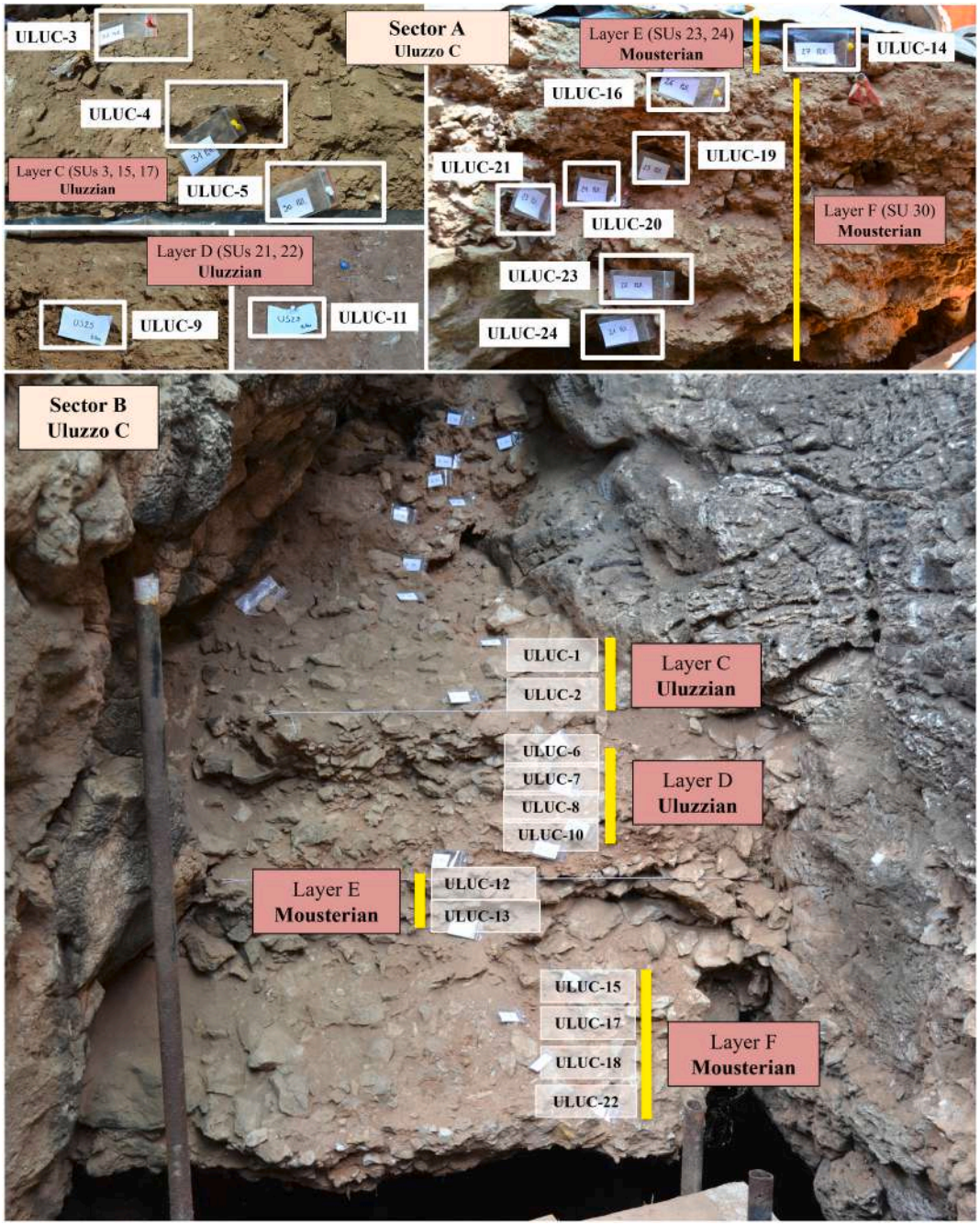

Fig. 4. Stratigraphic layers and profiles sampled for pollen analysis in Uluzzo C with the position of pollen sediment samples (Sectors A and B) (further details in Table 1).

2. The site

2.1. Physical setting, modern climate, vegetation and stratigraphic context

The Salento Peninsula, which extends between the Adriatic and Ionian Seas with coastlines spanning >350 km, is entirely isolated from the Apennine chain. Elevated areas (>500 m asl) in the region are located >150 km distance from Uluzzo C (Biondi et al., 2004). Salento is composed of Jurassic-Cretaceous limestone and dolostone that have been capped by Neogene to Quaternary sediments, as a part of the Apulia Carbonate Platform (Mastrogiacomo et al., 2012, Fig. 2). This region is characterized by karstic landforms, as evidenced by the numerous coastal caves with archaeological remains (Blanc, 1958–1961; Borzatti von Löwerstern, 1966, 1970, 1971; Borzatti von Löwenstern and Magaldi, 1967; Spinapolice, 2008, 2009, 2012, 2018, 2022; Moroni et al., 2018; Fiorini et al., 2019; Boschin et al., 2022; Ermolli et al., 2022; Pieruccini et al., 2022, 2024).

Global eustatic reconstructions based on benthic foraminiferal $\delta^{18}O$ records indicate that sea level during MIS 3 remained significantly lower than present, generally between −40 and −70 m (Waelbroeck et al., 2002; Grant et al., 2014; Rohling et al., 2014, 2022). Recent observational and modelling data from the central Mediterranean, corrected for tectonic uplift and glacial isostatic adjustment, further constrain MIS 3 sea-level highstands to approximately −30 to −50 m (Antonioli et al., 2021). On the low-gradient Apulian shelf, this sea-level lowering likely displaced the shoreline at Uluzzo Bay several kilometres seaward of the present coastline, probably on the order of ~10 km or more (Fig. 1b).

The Mediterranean climate in the vicinity of Uluzzo C is characterised by warm and dry summers, with rain mainly concentrated in winter and autumn (Polemio and Lonigro, 2013). The nearby meteorological station in Nardò shows an annual average temperature of 17.7 °C (10.1 °C in the coldest month, 26.9 °C in the warmest month), which can reach maxima above 31 °C in summer, and annual average precipitation of 659 mm (https://en.climate-data.org/europe/italy/apulia/nardo-14065/).

The local vegetation in the Parco Naturale Regionale di Porto Selvaggio (established in 1980) is characterised by Mediterranean open forest growing on limestone substrates in the upper dry (ombrotype horizon) and upper thermomediterranean (thermotype horizon) bioclimatic belts (Rivas-Martinez et al., 2001; Biondi et al., 2004, 2006). Several authors have examined the flora and the characteristics, distribution, and ecology of the coastal vegetation in Apulia (Corbetta et al., 1992–1989; Biondi et al., 2004, 2006; Biondi and Casavecchia, 2010). In limestone cliffs, seawater creates corrosion basins, which provide conditions for the growth of the *Crithmo maritimi-Inuletum crithmoidis* association (characteristic species of the association are *Inula crithmoides* L. and *Crithmum maritimum* L.), while in the parts of the sheer cliffs over the sea, the cracks in the rocks are colonised by the *Limonietum japigyci* association (charact. species of the association is *Limonium japygicum* (Groves) Pign.) (Biondi et al., 2006). Inland, the Mediterranean open forest is primarily dominated by holm oaks (*Quercus ilex* L.) and kermes oaks (*Q. coccifera* L.), which are frequently mixed with downy oaks (*Q. pubescens* Willdenow), while local formations of the Macedonian oak (*Q. trojana* Webb) and Valonia oak (*Q. ithaburensis* subsp. *macrolepis*) are also common in the region. It is noteworthy that Aleppo pine (*Pinus halepensis* Mill.) is present as a natural species (Chambel et al., 2013). Commonly associated trees and shrubs are: *Juniperus phoenicea* L., *Ceratonia siliqua* L., *Arbutus unedo* L., *Olea europaea* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Rhamnus alaternus* L., *Myrtus communis* L., *Cistus* spp., *Salvia rosmarinus* Spenn., *Erica manipuliflora* Salisb., *Laurus nobilis* L., *Fraxinus ornus* L., *Paliurus spina-christi* Miller, *Prunus spinosa* L., *Pyrus amygdaliformis* Villars (Macchia et al., 2000; Biondi et al., 2004). Among the most common herbaceous species it is worth mentioning *Asphodelus ramosus* L., known in the Salento dialect as "uluzzu", which inspired the name Uluzzo for the bay. Every spring, as the blossoming bursts, it invades the sunny and rocky areas.

Uluzzo C is situated at 40°9′27.84″ N, 17°57′35.34″E on the western side of the Ionian coast of Salento (the heel of the Italian boot), the easternmost region in southern Italy (Fig. 1). It is located in the Parco Naturale di Porto Selvaggio e Palude del Capitano (Nardò), in the middle of the Uluzzo Bay, <300 m from Grotta di Uluzzo and Grotta del Cavallo (originally named Uluzzo B and Uluzzo A, respectively).

During the 1963-64 fieldwork seasons at Uluzzo C, the following layers (labelled with capital letters, from A to G) intercalated by thin volcanic layers (designated with Greek letters: α, β and γ) were identified and described (Borzatti von Löwenstern, 1965):

A (0–17 cm) reworked topsoil with blue-coloured volcanic pumiceous sand lenticels (**α**). Romanellian industry.

B (17–62 cm) volcanic pumiceous sand mixed with red detrital quartz sand. At the base a thin layer of silvery-grey pumiceous sand (**β**). Archaeologically sterile.

C (62–80 cm) strongly cemented red sediment with debris. Uluzzian. Layer C corresponds to SUs 3, 15, and 17 of the new excavation.

D (80–90 cm). Red sandy sediment with fine debris. At the base lenses of greenish pumice sand (γ = SUs 25 and 27). Uluzzian layer D corresponds to SUs 21, 22, and 26cs. (combustion structure) of the new excavation. At the top and within the body of the structure (26cs), a lens of pumice and sand mixed with stones fine sediment, yellowish to olive-green in colour and bright in the light, was identified and recorded as SU26 in recent excavations, 2015–2022 (Fig. 3).

E (90–100 cm). Cemented red sandy-silty sediment with few debris. Above a thin violaceous clay layer (**δ**). Mousterian lithics associated with a few Uluzzian materials infiltrated from layer D. Layer E corresponds to SUs 23 and 24 of the new excavation.

F (100–150 cm). Strongly cemented red sediment with debris capped by a thin sandy-clayey yellowish layer (ε). Between G and F there is a 15–20 cm gap (ζ) formed by a hollow zone. Scarce Mousterian lithics. Layer F corresponds to SU 30 of the new excavation.

A major environmental change at Uluzzo C is marked by the collapse of the cave roof towards the top of layer G, after which event sedimentation patterns indicate open-air conditions increasingly influenced by surface runoff, as evidenced by secondary calcite formations and sediment thinning.

G (165–250 cm = spits 1–5) dark brown loose sandy-clayey sediment with few debris sealed by a horizon rich in large and small stones, slightly cemented. Between spits 4 and 5 there is a layer (**η**) made of often broken and corroded stones and pebbles generally covered with thick patinas of manganese and iron oxides. Layer G is rich in lithic artefacts and very fragmented faunal remains. Both lithics and fauna often show traces of burning.

During the 1965 excavation campaign, the trench was further deepened in layer G (spits 6–21, each one about 10–15 cm thick) and beyond (layer I spit 22 and layer L) to a total depth of 6.40 m. The deposit of layer G below η, slightly inclined towards the left wall of the cave (i.e., towards the south), was divided into two horizons (Borzatti von Löwenstern, 1966): spits 5–15 and spits 16–21, due to the appearance of a series of hearths in the latter horizon, which were distributed over a thickness of about 1.20 m. These hearths were formed by layers of slightly hardened reddish sand over hardened whitish ashes. From a sedimentological point of view, layer G below η is uniformly described as a coarse sandy-silty sediment with few debris and rare larger stones, many of which were decalcified and corroded, becoming fewer and fewer downwards.

H In lateral contact with spit 21 of layer G is a deposit of strongly cemented red ochraceous clayey sandy sediment called layer H, with rare Mousterian artefacts, which lies on a dark, loose, fine sand layer

(H′). According to the sedimentological study carried out by D. Magaldi (1969 p. 6), layer H is interpreted as a possible remnant of an older, partially eroded sediment.

The Middle Palaeolithic succession rests directly on:

I a series of large calcareous rock blocks up to 1 m long exhibiting signs of bioerosion (lithodomes) (layer I = spit 22), which, in turn, lie on layer L.

L conglomerate of much smaller, more or less rounded blocks, contained in a coarse white predominantly calcareous sand tenaciously cemented and travertinised, with many marine fossils, currently lying 7.5–8 m asl. The marine event represented by layers I and L was attributed by Borzatti to MIS5e.

2.2. The lithic industry

2.2.1. *The Mousterian* (layers G, F, E and SUs 23, 24, 30)

According to Borzatti (1963; 1965, 1966, 1969) the abundant lithic industry from layer G is mostly composed of scrapers (side, transverse and side-transverse; Supplementary Material 1, Figs. S1–S6). Points, mainly characterized by specimens with wide bases, denticulates and a few *limaces* are also documented. Thinned ventral faces, carenoid and ipercarenoid (named planes) implements with stepped or demi-stepped retouch and artefacts with dihedral ventral face of the Quinson type are common. The occurrence of bifacial artefacts on limestone, among which an handaxe (Borzatti von Löwenstern, 1965) from the upper spits of layer G (above η), is recorded. Rare side-scrapers on pebbles are also present.

In addition, it is worth noting the presence of some retouched tools on *Callista chione* and *Glicymeris* from spit 1 (Borzatti von Löwerstern, 1965, p. 14; Dantoni, 1980; Sarti and Martini, 2020 p. 543) and of a *talus* of *Bos primigenius* (Borzatti, 1969 Fig. 6 p. 16) bearing on the distal articular face deeply incised signs, from the middle of layer G. These signs are very similar to those occurring on lithic pebbles found at Grotta Torre dell'Alto layer C (Borzatti von Löwenstern and Magaldi, 1967, Fig. 1), Grotta Marcello Zei layer A spit 3 (Dantoni and Nardi, 1980) and Grotta del Cavallo layer F (Sarti and Martini, 2020).

The lithic assemblage from layer G is attributed by Borzatti (1965, 1969) to the Quina-type Charentian, without going into chronological detail, but specifying that, although more recent, it is in the same cultural tradition as that of the nearby Grotta Torre dell'Alto. In more recent works (Palma di Cesnola 2001; Sarti and Martini, 2020) spits 5–21 of layer G are culturally reconnected with layer M of Grotta del Cavallo, while the following Mousterian phase (spits 1–4 of level G) is assimilated to that of layer L of the same cave.

The lithic industry of layer F (SU 30 of the new excavation) is represented by a few dozen pieces made of the same raw material as that of layer G (Supplementary Fig. 1). Butts are mainly flat. Retouched tools (n. 9) include scrapers, denticulates and a point with facetted butt (Borzatti von Löwenstern, 1965 Fig. 8 n. 8). Thick artefacts with typical stepped retouching are missing.

The assemblage of layer E comprises 70 and 23 artefacts coming from Borzatti's 1964 and 1967-68 excavations respectively, and 152 coming from the new excavation (SUs 23 and 24) (Borzatti von Löwenstern, 1965, 1969). This layer is primarily characterised by Mousterian elements, including side-scrapers, points, and a *limace* (Borzatti von Löwenstern, 1965, Fig. 9, nos. 7, 8; Silvestrini et al., 2022a). However, some pieces (e.g., a lunate) clearly indicate an infiltration from the overlying Uluzzian layer D (Borzatti von Löwenstern, 1965, Fig. 9, no. 11).

2.2.2. *The Uluzzian* (layers D-C and SUs 25, 21, 22, 26, 27, 3, 15, 17)

During Borzatti's excavations (Borzatti von Löwenstern, 1965), 75 artefacts were recovered from both layers (45 from D and 30 from C) among which 2 side-scrapers and 8 denticulates on flake from D, and a burin, a lunate, a truncation, 2 side-scrapers, 3 denticulates on flake and a bipolar core from C. The recent excavation yielded 471 artefacts from layer C and 177 from layer D. The following description, which is the fruit of a recent revision of the whole Uluzzian lithic assemblage from Uluzzo C, takes into account both the Borzatti's and the recent excavation data and provides an integrated overview of the two layers.

The target products—flakes and bladelets—were obtained through two main strategies: (i) unidirectional debitage using the bipolar

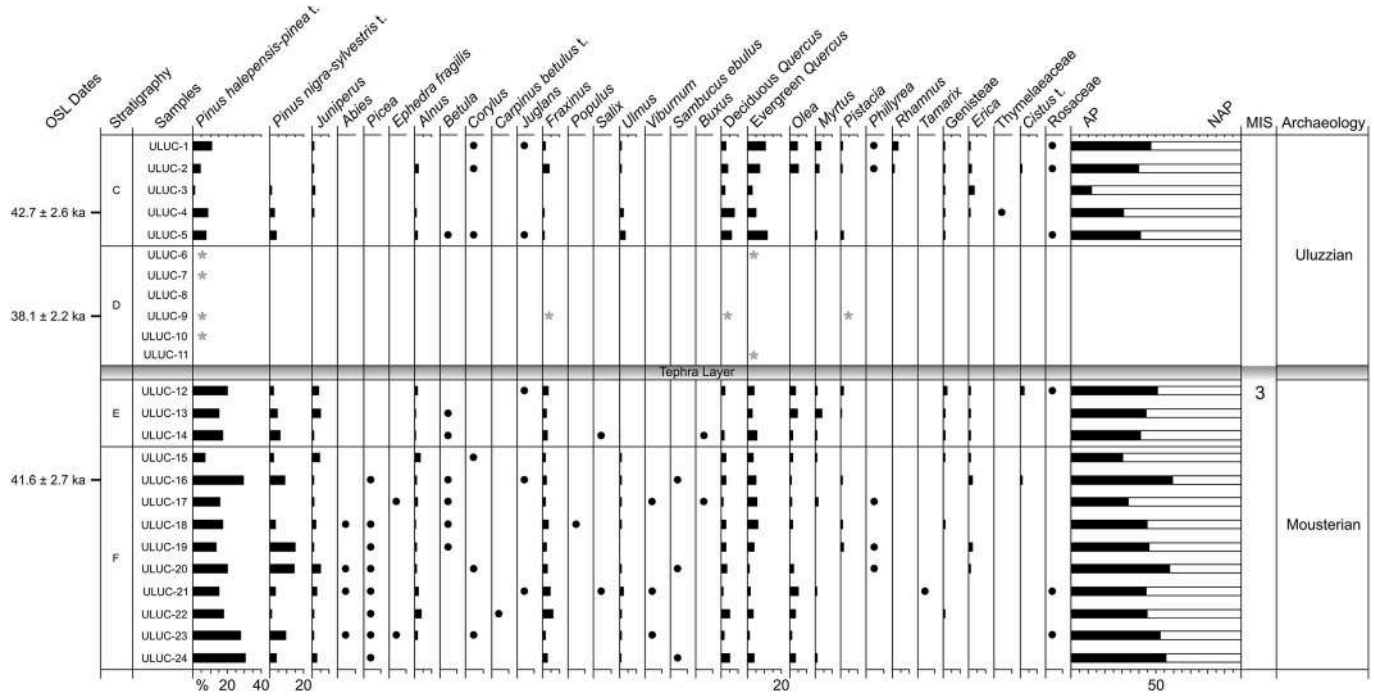

Fig. 5. Percentage pollen diagram of the woody component from sediment samples of Uluzzo C. Black dots for percentages <3 %. Grey asterisks represent occurrences in poorly counted samples. Black horizontal lines indicate divisions between layers.

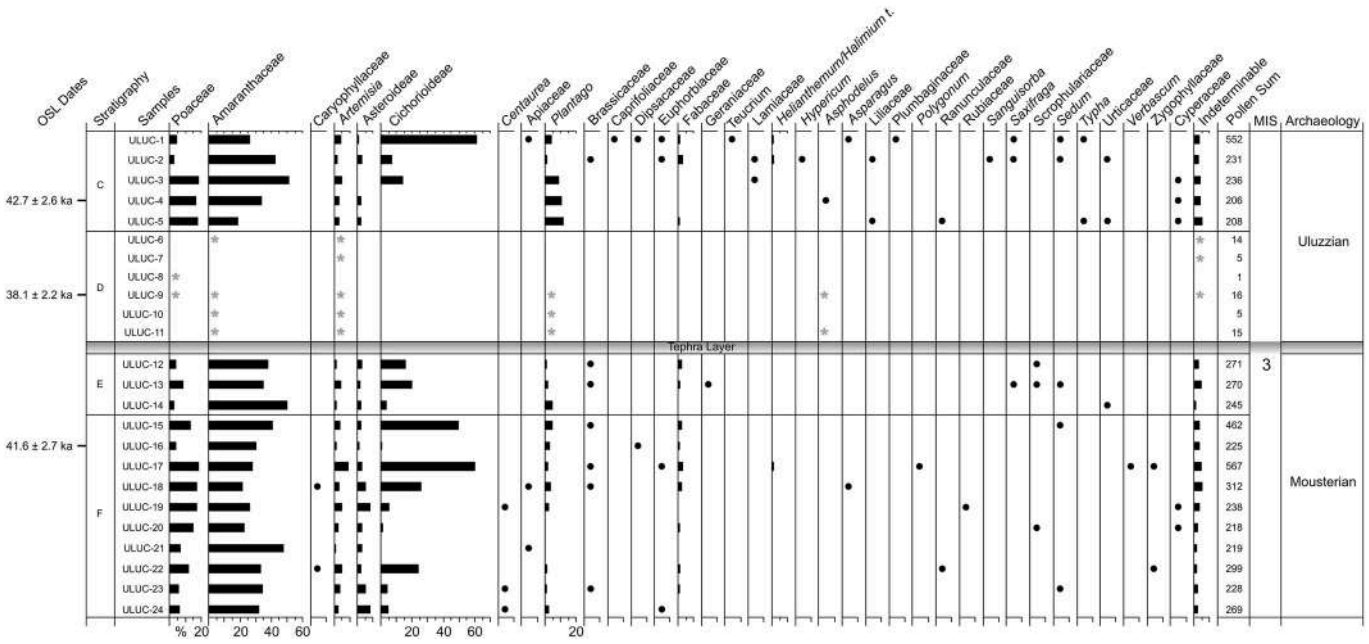

Fig. 6. Percentage pollen diagram of the non-arboreal elements from sediment samples of Uluzzo C. Black dots for percentages <3 %. Grey asterisks represent occurrences in poorly counted samples. Black horizontal lines indicate divisions between layers.

technique on an anvil, characterised by unprepared striking platforms and minimal or no management of core convexities; and (ii) lamellar production involving parallel unidirectional reduction by direct percussion, with deliberate management of lateral and distal convexities to facilitate bladelet production. The absence of Levallois further supports the attribution of the assemblage to the Uluzzian techno-complex (Silvestrini et al., 2022a).

Retouched tools are mostly found on flakes and fragments. Side-scrapers are the most frequent, followed by transverse scrapers, an end-scraper, and a few retouched bladelets. Notably, the presence of two lunates is particularly significant, as these are considered diagnostic elements of the Uluzzian techno-complex. The characteristics of Uluzzian assemblage from layers C and D mainly resemble those of layer D found at Grotta del Cavallo.

3. Materials and methods

3.1. Tephra sampling and analyses

Three samples for tephra analyses were collected in layer γ between layer D and E (UC27, UC26, and UC25) during the excavation of Sector A (Fig. 3c). After mounting on slides and polishing, the glass shards and (micro-) pumice fragments were analysed by single shard major element chemical analysis using the electron probe microanalyser (EPMA). Analyses were carried out at the Dipartimento di Scienze della Terra, Università degli Studi di Firenze (Florence, Italy), with a Jeol Superprobe JXA-8230 equipped with five-WDS spectrometers. Operating conditions were set to 15 kV accelerating voltage, 10 nA beam current and 10 μm defocused beam diameter to limit Na mobilisation. Element counting times were 15 s for all elements except for Na (10s), F (20s), S (30s), Mn, P and Cl (40s). Albite (Si and Na), ilmenite (Ti and Fe), plagioclase (Al), bustamite (Mn), olivine (Mg), diopside (Ca), sanidine (K), apatite (P), fluorite (F), tugtupite (Cl) and celestine (S) were used as internal standards. The accuracy of the measurements was assessed using the glass secondary standards GOR128-G, ATHO-G and StHs6/80-G (Jochum et al., 2006).

3.2. Pollen sampling and preparation

The sampling of the sediment for pollen analysis was conducted on vertical stratigraphic profiles, as it is proposed for archaeological deposits (Girard, 1975), during the 2022 fieldwork campaign. Twelve samples were taken from two archaeological profiles (samples ID ULUC-1 to ULUC-12) in Sector A, in layers C, D, E, and F (squares A-AA11, A-A10, A-A11 of the excavation grid; Figs. 3 and 4; Table 1), and additional twelve samples were taken from one archaeological profile in Sector B, in layers C, D, E, and F (square B13 of the excavation grid; Figs. 3 and 4; Table 1). In Sector A, samples were not collected in the basal part of layer F because of the accumulation of fallen rocks caused by a roof collapse (Figs. 3 and 4). Exposed sediment surface was cleaned back and discarded to a depth of 10–15 cm, to avoid potential sources of contamination and/or recent bioturbation.

In the laboratory, after the samples were weighed (Table 1), the "Classic Chemical Method" was followed for the extraction of palynomorphs (Erdtman, 1969; Dimbleby, 1985), with the modifications proposed by Girard and Renault-Miskovsky (1969):

- Approx. 40 mL of Hydrochloric Acid (HCl) were added to each sample, together with tablets with a known number of *Lycopodium* spores, in order to estimate the pollen concentration.
- After centrifugation for 6 min at 3600 RPM and elimination of the supernatant liquid, Hydrofluoric Acid (HF) was added and left two days under the fume cupboard for the reactions.
- Approx. 25 mL NaOH (10 %) was added and left in a water bath for 10 min.
- Zinc chloride ($ZnCl_2$) was then used, to separate sediments at the bottom of the tube from the palynomorphs at the top, which were poured out into another tube.
- A few drops of Glycerol ($C_3H_8O_3$) were added to each sample before storage in collection tubes.

After the chemical treatment, the samples were mounted on slides with the use of liquid paraffin. The palynological identification was made by conventional microscopy (400x to 1000x) using an optical microscope, with the use of oil immersion objective (1000x) We used the pollen reference collection of the Department of Environmental Biology

Table 1
Summary of palynological features at the Uluzzo C sequence.

Sample	Layer	Square	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	[a]Pollen sum	Number of taxa (Pollen)	Spores sum
ULUC-1	C	B13, W	29.20	19.30	15,043	3.33	552	211	34	21
ULUC-2	C	B13, W	28.30	16.20	66,249	2.89	231	209	34	19
ULUC-3	C	A-AA11, NE	122.62	69.88	259	3.94	236	203	14	484
ULUC-4	C	A-AA11, NE	35.74	20.35	995	3.96	206	202	18	162
ULUC-5	C	A-AA11, NE	28.34	16.13	3764	4.90	208	204	25	238
ULUC-6	D	B13, W	10.46	10.46	477	14.28	14	14	4	0
ULUC-7	D	B13, W	10.79	10.79	645	20.00	5	5	2	0
ULUC-8	D	B13, W	18.43	18.43	377	0.00	1	1	1	0
ULUC-9	D	A-AA11, NE	28.91	16.47	361	10.00	16	15	9	0
ULUC-10	D	B13, W	13.96	13.96	498	0.00	5	5	4	0
ULUC-11	D	A-AA11, NE	102.42	58.36	179	0.00	15	15	5	9
ULUC-12	E	B13, W	10.70	10.70	7340	2.75	271	221	24	19
ULUC-13	E	B13, W	10.67	10.67	2794	4.76	270	211	24	15
ULUC-14	E	A-A10, NW	367.83	71.43	2897	1.30	245	231	22	49
ULUC-15	F	B13, W	15.26	15.26	46,795	3.65	462	223	22	70
ULUC-16	F	A-A11, NW	220.50	59.61	1536	3.62	225	222	24	44
ULUC-17	F	B13, W	22.23	22.23	7549	4.32	567	210	27	166
ULUC-18	F	B13, W	20.13	20.13	1051	5.28	312	217	26	40
ULUC-19	F	A-A11, NW	77.81	44.34	268	3.43	238	205	21	66
ULUC-20	F	A-A11, NW	9.87	9.87	185	2.40	218	209	23	12
ULUC-21	F	A-A11, NW	9.12	9.12	1704	1.42	219	213	22	8
ULUC-22	F	B13, W	19.05	19.05	31,191	1.84	299	220	22	13
ULUC-23	F	A-A11, NW	7.28	7.28	445	2.44	228	207	25	8
ULUC-24	F	A-A11, NW	8.34	8.34	1485	2.16	269	233	19	6
							TOTAL 5312	3906		1449

[a] Asteroideae, Cichorioideae, and *Centaurea* excluded.

(Sapienza University of Rome) and of the Department of Plant Biology (University of Murcia).

A pollen grain count of 150–300 grains per sample is necessary to be considered statistically significant and adequate for paleoenvironmental interpretations (Erdtman, 1931; Barkley, 1934; Sánchez-Goñi, 1993; Lytle and Wahl, 2005; Lau et al., 2018; Djamali and Cilleros, 2020; Weng and Hooghiemstra, 2024). A minimum count of 200 grains was attained for all samples, except layer D, where <20 grains per sample were counted. Along with spores and NPPs (Non-Pollen Palynomorphs), we excluded from the total pollen sum the counts of Asteroideae, Cichorioideae, and *Centaurea*, assuming they might be overrepresented due to taphonomic and preservation processes (Havinga, 1984). The pollen count data was treated with the Tilia Graph 1.7.16 program in order to plot the pollen diagrams.

Pine pollen grains with corpus >60 μ m were included within the *Pinus halepensis - pinea* type (Desprat et al., 2015) and pine pollen grains with corpus <60 μ m were included in the *Pinus nigra – sylvestris* type.

3.3. Composite pollen profile (sectors A-B)

The pollen sequences from Sector A and Sector B have been directly correlated with each other (Fig. 3), supported by the stratigraphy by Borzatti von Löwenstern and Magaldi (1969) and Spinapolice et al. (2022). Based on their stratigraphic position and on a precise repositioning of the samples (exhaustive coordinate), 12 samples from Sector A belonging to layers F, E, D, and C, and 12 samples from Sector B belonging to layers F, E, D, and C, were combined to create a composite pollen profile (Figs. 5 and 6).

A synthetic pollen profile is represented in Fig. 7, including the following ecological groups: warm temperate forest (evergreen *Quercus*, *Buxus*, *Olea*, *Pistacia*, *Phillyrea*, *Cistus*, *Myrtus*, *Fraxinus*, *Juglans*, *Rhamnus*, *Tamarix*, Thymelaeaceae, and *Erica*), temperate forest (deciduous *Quercus*, *Alnus*, *Corylus*, *Carpinus betulus*, *Fraxinus*, *Populus*, *Ulmus*, *Salix*, *Viburnum*, *Sambucus ebulus*, and Rosaceae), Cool temperate forest (*Picea*, *Abies*, and *Betula*), Eurythermic conifers (*Pinus* and *Juniperus*), Grassland and dry shrubland (Poaceae, Cyperaceae, Genisteae, *Asphodelus*, Liliaceae, Lamiaceae, and *Teucrium*), and Xerophytic steppe (*Artemisia*, Amaranthaceae, and *Ephedra fragilis*).

4. Results

4.1. Tephra lithology and composition

The three samples present as a mixture of detrital sediment and

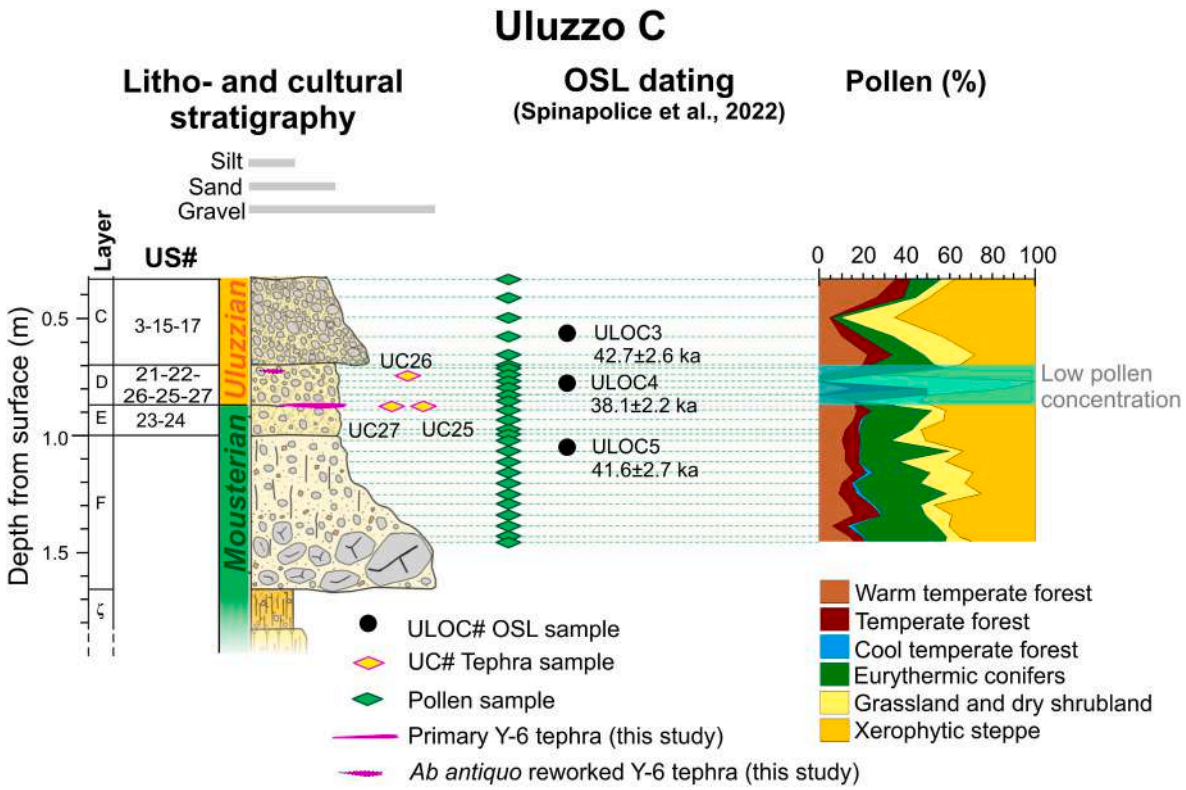

Fig. 7. Composite pollen profile (Sector A and Sector B) correlated with stratigraphic section from Uluzzo C. The position of the tephra samples UC27, UC26 and UC25, analysed in this study, as well as of the primary ash layer γ, described by Borzatti von Löwenstern (1969), are also shown.

volcanic material with variable amounts of the clastic and volcanic components. Sample UC27 is a lenticular level with the highest concentration of the volcanic component, being almost completely made of purely glass shards, while the stratigraphically equivalent samples UC25 and UC26 comprise relatively large amounts of detrital particles. In all samples, the volcanic fraction is made by high-vesicular, green micropumices and glass shards often represented by elongated to convolute thin fragments of bubble-walls or stocky particles with spherical bubbles and thick septa (Fig. 8a). The micro-pumice and glass shards are well-preserved in sample UC27, while in samples UC26 and UC25 they show some degree of physical alteration and chemical weathering. The glass major element composition of all three samples is peralkaline (Na2O + K2O > Al2O3) rhyolitic, which makes them classifiable as Pantellerites (Fig. 8b).

4.2. Pollen

All the analysed sediment samples contained pollen grains (Figs. 5 and 6; Supplementary Material 1, Figs. S7–S10). A total of 5312 pollen grains and 1449 spores (Supplementary Material 1, Figs. S11–S12) were identified. The percentage of indeterminable grains is lower than 10 % (Table 1), except for samples ULUC-6 (>14 %) and ULUC-7 (20 %), and the preservation is generally good. The mean number of pollen types per sample is 24 (66 identified taxa), excluding layer D that was very poor. The pollen concentration varies between 179 and 66,249 grains/g (Table 1).

Layer F: this layer includes samples ULUC-24 to ULUC-15 (Figs. 5 and 6). AP is found across all samples between 60 and 30 %. *Pinus halepensis/pinea* (7–31 %) and *Pinus nigra/sylvestris* (1–15 %) show high percentages. Deciduous and evergreen *Quercus*, *Juniperus*, *Fraxinus*, and *Olea* do not exceed 7 %. Accompanying AP are *Abies*, *Picea*, *Alnus*, *Ulmus*, and *Erica*. *Betula*, *Corylus*, *Carpinus betulus*, *Juglans*, *Salix*, *Populus*, *Viburnum*, *Sambucus ebulus*, *Buxus*, *Myrtus*, *Pistacia*, *Phillyrea*, *Tamarix*, *Ephedra fragilis*, *Cistus*, Genisteae, and Rosaceae show occasional appearances. In NAP,

Amaranthaceae (22–47 %), Poaceae (4–19 %), and *Artemisia* (1–9 %) are dominant, while *Plantago* does not exceed 5 %. NAP also include Asteroideae, Cichorioideae, Apiaceae, Brassicaceae, and Fabaceae, as well as a limited presence (<1 %) of *Centaurea*, Caryophyllaceae, Dipsacaceae, Euphorbiaceae, *Helianthemum/Halimium*, *Asparagus*, *Polygonum*, Ranunculaceae, Rubiaceae, Scrophulariaceae, *Sedum*, *Verbascum*, Zygophyllaceae, and Cyperaceae.

Layer E: this layer includes sample ULUC-14 to ULUC-12 (Figs. 5 and 6). NAP is dominant in samples ULUC-14 (>59 %) and ULUC-13 (>55 %), while AP is dominant in sample ULUC-12 (>51 %). In NAP, Amaranthaceae (35–50 %), Poaceae (3–9 %), and *Artemisia* (1–4 %) are abundant, while *Plantago* does not exceed 4 %. NAP also includes Asteroideae, Cichorioideae, *Plantago*, and Fabaceae, as well as limited presence of Brassicaceae, Geraniaceae, *Saxifraga*, Scrophulariaceae, Urticaceae, and *Sedum*. Within AP, *Pinus halepensis/pinea* (15–20 %), evergreen *Quercus* (3–6 %) *Pinus nigra/sylvestris* (2–6 %), *Olea* (2–5 %), *Juniperus* (1–5 %), and *Myrtus* (1–4 %) are dominant. *Alnus*, *Fraxinus*, *Pistacia*, Genisteae, and *Erica* are very well represented throughout the layer, while deciduous *Quercus*, *Betula*, *Juglans*, *Salix*, *Ulmus*, *Buxus*, *Cistus*, and Rosaceae show sporadic occurrences.

Layer D: this layer includes samples ULUC-11 to ULUC-6 (SUs 23, 25) (Figs. 5 and 6). The lowest pollen richness and concentration were recorded (Table 1). Pollen counts were too low to calculate the percentages. Because of this, taxa that have been identified are only shown in the diagrams with asterisks indicating their occurrence (Figs. 5 and 6). NAP include *Artemisia*, Amaranthaceae, and Poaceae, accompanied by *Plantago* and *Asphodelus*. In the AP it is important to emphasise the presence of *Pinus halepensis/pinea*, deciduous *Quercus*, *Fraxinus*, evergreen *Quercus*, and *Pistacia*.

Layer C: this layer includes pollen samples ULUC-5 to ULUC-1 (SUs 17, 15, 3) (Figs. 5 and 6). NAP is dominant with total values of 53–88 %, being characterised by high percentages of Amaranthaceae (19–51 %), Poaceae (3–18 %), *Plantago* (1–12 %), and *Artemisia* (2–5 %).

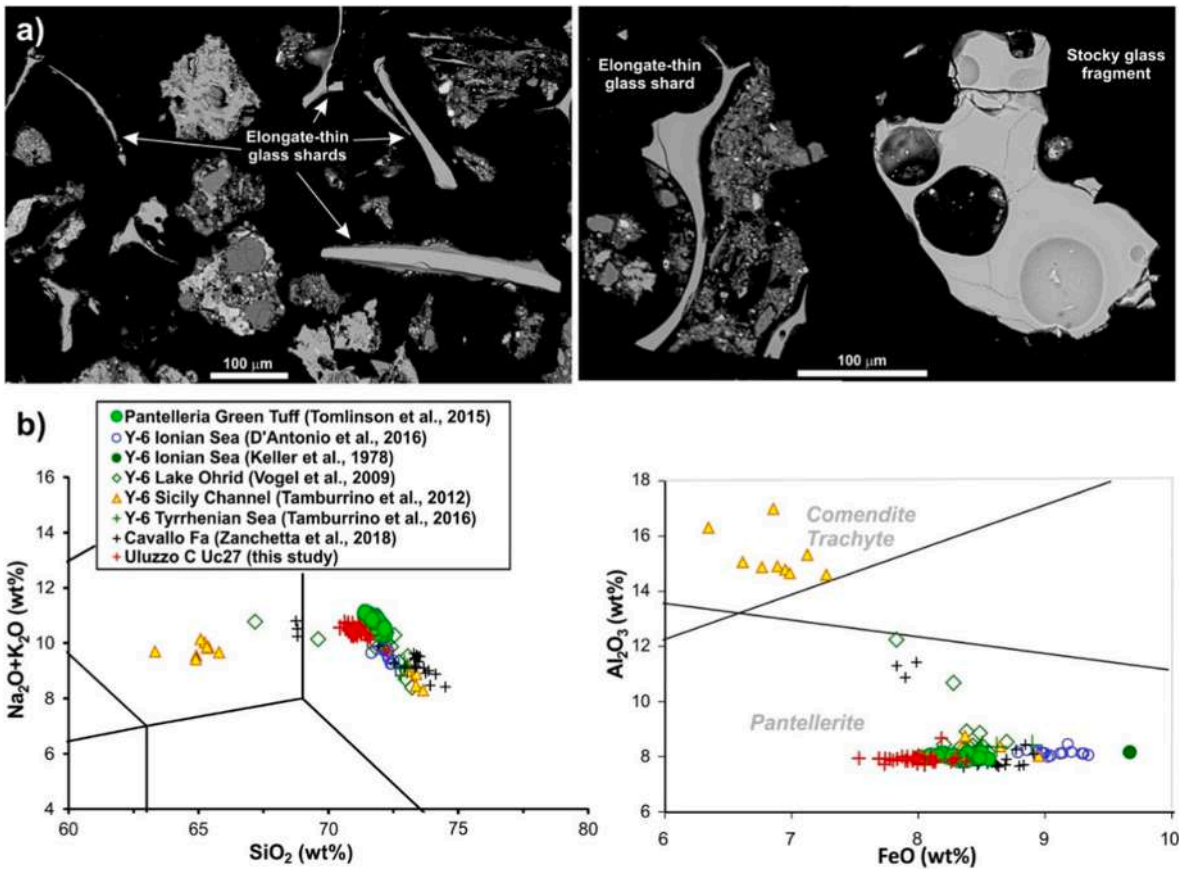

Fig. 8. Textural and geochemical features of Uluzzo C UC27 tephra. **a)** Backscatterd images showing the morphology of the glass shards, including both thin-elongated and stocky particles. **b)** Total alkali versus silica classification diagram (TAS, Le Bas et al., 1986; Macdonald, 1974) classification scheme for peralkaline silicic rocks for the Uluzzo C UC27 tephra compared with the proximal Pantelleria Green Tuff and its equivalent marine-lacustrine Y-6 tephra and Cavallo Fa layer.

Asteroideae, Cichorioideae, Apiaceae, Brassicaceae, Caprifoliaceae, Dipsacaceae, Euphorbiaceae, Fabaceae, *Helianthemum/Halimium*, Lamiaceae, *Asphodelus*, Liliaceae, Ranunculaceae, Plumbaginaceae, *Saxifraga*, *Sedum*, *Typha*, Urticaceae, and Cyperaceae are also present. In AP, evergreen *Quercus* (3–12 %), *Pinus halepensis/pinea* (1–11 %), deciduous *Quercus* (2–7 %), *Olea* (1–5 %), *Fraxinus* (1–4 %), and *Rhamnus* (1–4 %) are well represented. AP also include *Pinus nigra/sylvestris*, *Juniperus*, *Alnus*, *Betula*, *Corylus*, *Juglans*, *Ulmus*, *Myrtus*, *Pistacia*, *Phillyrea*, Genisteae, *Erica*, *Cistus*, Thymelaeaceae, and Rosaceae.

5. Discussion

5.1. Tephra: nature, correlation and age

The glass from the stratigraphically closed samples UC27, UC26 and UC25 show very similar lithological features and peralkaline rhyolitic composition, which allow interpreting them as deriving from the same eruption. The overall lithological features of the better preserved UC27, high concentrated volcanic glass shards, allow this lenticular level to be interpreted as the first tephra sedimentary input recognizable in Uluzzo C, while the stratigraphically equivalent UC26 and UC25, with less abundant and less-preserved glass shards, as slightly displaced material deriving from the reworking of the sub-primary UC27 level. Considering the stratigraphic position of UC27 and UC25 and their lithological features, these lenticular levels can be correlated with the lens of "greenish volcanic ash" occurring between layers E and D, as described by Borzatti von Löwenstern (1969). The possible occurrence of remnants of volcanic sediments in the lower part of D from recent excavations (UC25) should be interpreted as material reworked from the lower ash horizon γ found at the base of layer D, as also demonstrated by the characteristics of the lithic industry. Therefore, the primary tephra deposition, and consequently the related isochrone, can be placed in correspondence with the layer γ described by Borzatti von Löwenstern (1969).

As for as the origin of the UC27-26 volcanic glass, and thus of the primary γ tephra laying at base of layer D, its peralkaline rhyolitic composition, which is really peculiar in the framework of the central Mediterranean tephrostratigraphy (e.g., Branca et al., 2023), allows identifying the island of Pantelleria as the volcanic source. Based also on its stratigraphic position and the available OSL chronology, between ca. 48 ka and 34 ka (whole chronological range at 2-sigma uncertainties; Fig. 7), γ/UC27 can be reliably correlated to the Pantelleria Green Tuff (PGT), dated by the $^{40}Ar/^{39}Ar$ method at 45.5 ± 1.0 ka (2σ; Scaillet et al., 2013; recalculated age as reported in Zanchetta et al., 2018) and its marine equivalent Y-6 layer (Paterne et al., 2008). A comparison with glass composition of the PGT proximal deposit and its distal equivalent Y-6 tephra, shows a good geochemical matching (Fig. 8). This attribution is further supported by the identification of the PGT/Y-6 in the same archeostratigraphic position, i.e., in between the Mousterian and Uluzzian layers, in the succession of Grotta del Cavallo (Zanchetta et al., 2018), which alongside Uluzzo C and other caves and rock shelters form the cluster of Paleolithic sites of the Uluzzo Bay (Fig. 1).

5.2. Tephra synchronization and paleoclimatic alignment of the Uluzzo C pollen record

The PGT/Y-6 is a widespread tephra marker covering the area between the Sicily Channel and the southern Balkan Peninsula and occurring in a number of marine and terrestrial paleoclimatic records

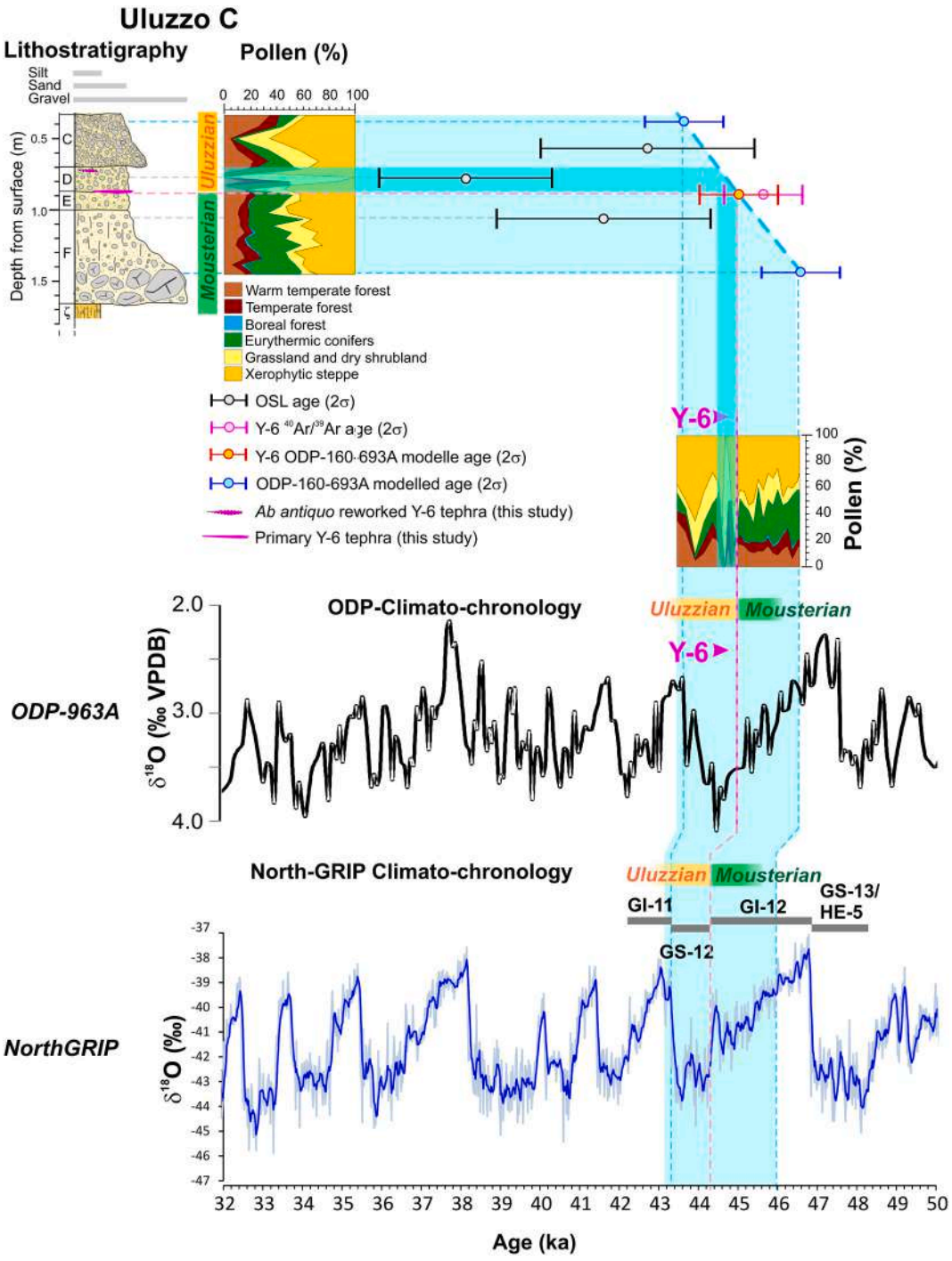

Fig. 9. Tephra synchronization and paleoclimatic alignment of the Uluzzo C pollen record with the marine record of the Sicily Channel ODP-963A (Sprovieri et al., 2012) and the North-GRIP GICC05 timescales (Rasmussen et al., 2014).

(Zanchetta et., 2018 and reference therein), so offering the opportunity of a direct synchronization with the Uluzzo C composite pollen record (Fig. 7). Specifically, the high-resolution planktic record of the Sicily Channel ODP-963A (Sprovieri et al., 2012, Figs. 8 and 9) allows evaluating the climatostratigraphic position of the Y-6 tephra within the framework of the MIS 3 millennial scale climatic variability. According to this record, the Y-6 occurs at the very end of a relatively long and pronounced interstadial correlated to Greenland interstadial 12 (GI-12) or the very beginning of a stadial, corresponding to the Greenland stadial 12 (GS-12) (Fig. 9) (Tamburrino et al., 2012).

Similarly, in the Uluzzo C composite pollen record, the tephra UC27/ Y-6 falls during a phase of open landscape including warm temperate elements (evergreen *Quercus*, *Olea*, *Myrtus*, *Pistacia*, and *Phillyrea*) and mediterranean pines, which may correspond to the end of the relatively mild interstadial GI-12 (Fig. 9). In the interval following the Y-6 deposition, the Uluzzo C pollen percentages are uncertain because of the very low pollen concentration found in layer D, in both Sectors A and B. The low pollen preservation of this layer may be indicative of oxidation, a condition occurring in dry climates where the depositional layers are exposed to atmospheric agents for an extended period of time and there is no buildup of organic materials from the plants. In layer C, the warm temperate woodland shows two expansions, culminating at the top of

the sequence with the maximum percentage of ca. 35 % (Fig. 9). Such sequence of events by and large corresponds to that observed in the Sicily Channel marine record ODP-963A (Sprovieri et al., 2012), where the Y-6 tephra is followed by a stadial, correlated to GS-12, and then by GI-11 (Fig. 9). Accordingly, layer D with low pollen concentration might correspond to GS-12 and the peak in warm temperate arboreal taxa of layer C to GI-11 (Fig. 9). The ODP-963A age can be tentatively applied to the Uluzzo C record by aligning the two sequences (Fig. 9). According to the Bayesian modelled ages of the ODP-963A, based on a detailed tuning with the Greenland isotope record (Sprovieri et al., 2012), the age of the beginning of the GI-11 is ~43.4 ± 1.0 ka, while that of the Y-6 is 45.0 ± 1.0 ka. A further point of alignment of Uluzzo C with the ODP-963A can be made assuming that the relatively sharp drop in arboreal pollen at ca. 1.4 m corresponds with the isotopic fluctuation that in ODP-963A marks the end of the more pronounced interstadial condition of the GI-12 (Fig. 9). Finally, by linearly extrapolating the intercepts between these three tie points (one tephra-synchronizing point and two paleoclimatic-aligment points), we obtain a rough age-model for the whole pollen succession (Fig. 9). According to this simple age-depth curve, the investigated succession would span the very short interval of 3.2 kyr, between 46.6 and 43.4 ka, using the ODP-963A chronology, or 46.0 and 43.2 ka, according to the North-GRIP GICC05 timescale

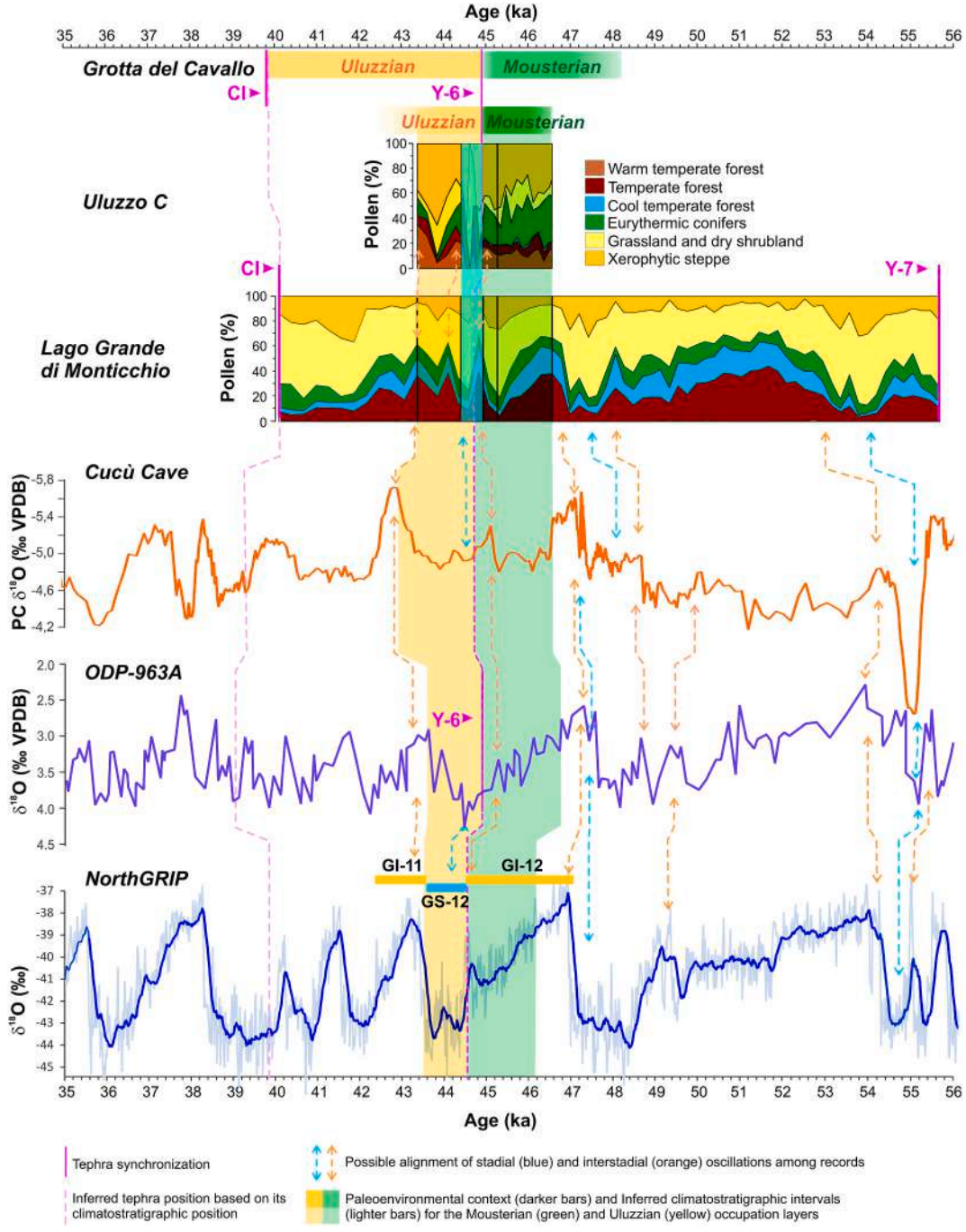

Fig. 10. Positive correlation of the pollen sequence of Uluzzo C with chronologies align with those inferred from the nearby Grotta del Cavallo (Zanchetta et al., 2018), the Lago Grande di Monticchio record (Watts et al., 1996; Allen et al., 2000), the speleothem record from Pozzo Cucù Cave in Apulia (Columbu et al., 2020), the ODP-963A climato-chronology record (Sprovieri et al., 2012), the North-GRIP GICC05 climato-chronology record (Rasmussen et al., 2014), interpreted as belonging to warm events (GI-12 and GI-11) and cold event (GS-12).

(Rasmussen et al., 2014, Figs. 9 and 10). Overall, the ODP-963A-based chronology of Uluzzo C composite pollen is in good agreement with the $^{40}Ar/^{39}Ar$ age of the PGT/Y-6 and is well within the uncertainties of two (ULOC1 and ULOC3) out of three of the available OSL dates, which likely underestimate the sediment age (Fig. 9).

The Apulia-Basilicata region offers a wealth of well-dated archaeological, palaeobotanical, paleontological and paleoclimatic data that allow combined and detailed reconstructions of the events between the demise of Neanderthals and the arrival of early modern humans. In particular, the paleoenvironmental record of Uluzzo C can be correlated with the nearby Grotta del Cavallo (Zanchetta et al., 2018; Ricciardi, 2020), the pollen record from Lago Grande di Monticchio (Watts et al., 1996; Allen et al., 2000), and the speleothem record from Pozzo Cucù Cave in Apulia (Columbu et al., 2020), based on their respective chronologies (Fig. 10).

The Lago Grande di Monticchio record, reaching back 132 ka BP, reveals the vegetation and climate variability in the southern Italian Peninsula (Watts et al., 1996; Allen et al., 2000). The chronology of the record was based on counts of annually laminated sediments, radiocarbon and radioisotopic dates, and tephrachronology (Allen et al., 1999). Successive developments in tephrachronology led to revised chronological settings (Brauer et al., 2007; Wutke et al., 2015). We further reconsidered the chronology of the Monticchio record, by taking advantage of the abundance of tephra layers found in its lacustrine archive (Narcisi, 1996; Wulf et al., 2004; Wutke et al., 2015). More specifically, we re-dated the pollen data retrieved from the Neotoma Paleoecology Database (core LGM90D, ID 26608; Watts et al., 1996; Allen et al., 2000) between 56 ka and 40 ka, based on the linear interpolation between the two marker tephra; i.e., the TM-19, correlated to the Monte Epomeo Green Tuff, from Ischia, and T_18, correlated to the Campanian Ignimbrite, from Campi Flegrei (CI), dated at 56.1 ± 1.0 ka (Giaccio et al., 2017b) and 40.0 ± 0.1 ka (Giaccio et al., 2017a), respectively, and precisely located at the original depths reported by Zolitschka and Negendank (1996) (Fig. 10). At present, compared to the Salento Peninsula that is characterized by Mediterranean plant taxa, the volcanic area of Lago Grande di Monticchio, located at >650 m asl, shows a dominance of temperate deciduous forest. A similar difference can be noted when the pollen records of Uluzzo C and Monticchio from GI-12 to GI-11 are compared (Fig. 10). Even so, a general correspondence is clear.

Some details about the taphonomic processes that pollen grains go through in on-site records must be mentioned. The composition of the palynological record is impacted by processes that are unique to each pollen taxon, including production, transport, deposition, and taphonomic alterations (Hevly, 1981; Coles et al., 1989; Coles and Gilbertson, 1994; Campbell, 1999; Hunt and Fiacconi, 2018). The morpho-geological features, the distance of the archaeological profiles from the entrance of the cave, the presence of roof fissures that may allow water and other particles to seep in, the type and orientation of each site's opening or openings, and the depth of each deposit will all have a significant impact on the entry mode, dispersion, and deposition of palynomorphs through the various dispersion vectors (anemophilous or entomophilous pollen grains, for instance). These taphonomic processes, which are widespread in archaeological deposits, affect the original pollen rain and influence the fossil pollen spectra (Lebreton et al., 2010). In this sense, on-site records can show a “differential preservation of palynomorphs', where the percentage of taxa can differ between sediment samples within the same stratigraphic and/or cultural context. However, studies conducted in recent years have demonstrated a consistent palaeoecological reconstruction of the vegetation and climate context when the pollen assemblage from a set of samples with different origins come from the same archaeological layer (Val-Peón et al., 2019; Ochando et al., 2024b).

The pollen record of layers F and E (both Mousterian) may reflect the last part of the GI-12 (Fig. 10). As regards layer F, there is a spread of conifers and cool temperate forest with *Pinus halepensis/pinea*, *Pinus nigra/sylvestris*, *Juniperus*, *Abies*, and *Picea*, as well as a wide diversity of temperate and warm temperate taxa, as with the increase of steppes with Amaranthaceae at the end of the layer (Fig. 10). These data show a general correspondence with the dynamics of GI-12 in Monticchio sequence (ca. 46.7–45.6 ka), which shows high percentages of temperate forest (deciduous *Quercus*, *Ulmus*, *Carpinus betulus*, and *Fraxinus*), cool temperate forest (*Abies*, *Fagus*, *Betula*), and eurythermic forest (*Pinus* and *Juniperus*) at the beginning of GI-12, with an increase in grassland and dry shrubland (Poaceae and Cyperaceae) and xerophytic steppes (*Artemisia* and Amaranthaceae) toward the end of the phase (Watts et al., 1996; Allen et al., 2000, Fig. 10). Anthracological evidence at Grotta delle Mura (Fiorentino and Parra, 2015) and Grotta S. Maria D'Agnano (Fiorentino, 2012) support the prevalence of *Pinus* cf. *halepensis* during the Late Pleistocene in the Apulia region.

As regards layer E, Monticchio and Uluzzo C sequences show an opposite pattern of development of forest (Fig. 10). In Monticchio sequence (ca. 45.6–45.1 ka), there was a greater openness of the landscapes with an increase in grasslands and xerophytic steppes, mainly formed by *Artemisia*, Poaceae and Amaranthaceae (Fig. 10), while Uluzzo C shows the increase of eurythermic conifers (*Pinus* and *Juniperus*), warm temperate forest (evergreen *Quercus*, *Fraxinus*, *Olea*, and *Myrtus*), and temperate forest (deciduous *Quercus* and *Alnus*).

In Uluzzo C (layers F and E), a diverse landscape can be inferred, with patches of pine, oak, and juniper, steppe-like saltmarshes, Poaceae-*Artemisia* steppes, riverine forest patches, *Quercus*-Poaceae parklands, shrubby grasslands with patches of conifers and mesophytes, rocky scrub with chamaephytes and hemicryptophytes, grasslands with heaths, heliophytic shrublands, and litoral vegetation (Fig. 5). Interestingly, the pollen spectra of Sector A and B for layers F and E shows a considerable consistency, with all ecological groups and the main pollen contributors presenting similar percentages in both sequences (Supplementary Material 1, Fig. S13). Pollen assemblages display a general landscape stability, showing abundant Amaranthaceae, Poaceae, *Pinus halepensis/pinea*, *Pinus nigra/sylvestris*, *Juniperus*, *Alnus*, *Fraxinus*, evergreen and deciduous *Quercus*, *Olea*, *Artemisia*, Cichorioideae, and *Plantago* (Supplementary Material 1, Fig. S13). In addition, it should be noted the appearance of exclusive taxa for layer F, such as *Abies*, *Picea*, *Carpinus betulus*, *Populus*, *Sambucus ebulus*, *Ephedra fragilis*, *Polygonum*, and Rubiaceae. *Abies* (<3 %) is currently absent from the Apulia region, but it lives in Calabria at ca. 140 km from Uluzzo Bay and might have been more abundant during MIS 3. *Picea* (<1 %) was probably of distant origin, as it currently lives far away from the northern Apennines, the Alps, and in the Balkan Peninsula.

The frequencies of *Myrtus* throughout the Uluzzo C pollen sequence are remarkable, especially because Mediterranean myrtle (*Myrtus communis* L.) pollen is poorly dispersed (mainly entomophily) and consequently is underrepresented (Knight et al., 2005; González-Varo et al., 2009), suggesting a wider presence in the immediate vicinity of Uluzzo C throughout the GI-12 and the GI-11.

The pollen results from Uluzzo C of layer D and layer C (both Uluzzian) are defined in Sectors A and B by the sediment samples. In layer D, the majority of taxa are absent, and pollen preservation is poor. The existence at Uluzzo C of the Y-6 tephra that was discovered at the base of layer D (ca. 45.0–44.9 ka) is noteworthy (Figs. 7, 9 and 10). The preservation of pollen grains may have been impacted by an erosive phase during the first part of the GS-12. This effect appears to have persisted during the sedimentation of layer D until the recovery of the majority of the taxa in layer C that were previously found in layer E. However, several taxa persisted in layer D, such as *Pinus halepensis/pinea*, deciduous *Quercus*, *Fraxinus*, evergreen *Quercus*, *Pistacia*, *Artemisia*, Poaceae, Amaranthaceae, *Plantago*, and *Asphodelus* (Supplementary Material 1, Fig. S13), although these may also reflect reworked material. There is also an issue with the sedimentation in the Monticchio record at this time (ca. 45.1–44.7 ka), since the sequence is interrupted by an event as evidenced by slump structures (Zolitschka and Negendank, 1996). This may have affected the normal lacustrine sedimentation, and

consequently the deposition and subsequent interpretation of the pollen records derived from that level, as evidenced by the unusual increases in temperate and cool temperate taxa, including deciduous *Quercus*, *Ulmus*, *Fagus*, and *Betula* (Fig. 10).

The pollen record from Uluzzo C of layer C may reflect the last part of the GS-12 and the beginning of the GI-11 (ca. 44.6–43.4 ka) and reveals a dynamic of the alternate landscapes that is comparable to that of the Monticchio record (ca. 44.7–43.4 ka) (Fig. 10). In both sequences, there are two events of tree taxa expansion, represented by the ecological groups of warm temperate forest, temperate forest, and eurythermic conifers in Uluzzo C, and by the ecological groups of temperate forest, cool temperate forest, and eurythermic conifers in Monticchio, with an intermediate event of xerophyte, grassland, and dry shrubland expansion (Fig. 9). Overall, at Uluzzo C, there was an openness of the landscapes with an increase in steppes, mainly formed by xerophytic elements such as Amaranthaceae, Poaceae, *Artemisia*, *Asphodelus*, and Lamiaceae. A wide diversity of secondary landscapes in the vicinity of the site persisted, with shrubby grasslands with conifers, *Quercus*-Poaceae parklands, mesophytes patches and heliophytic shrublands (Supplementary Material 1, Fig. S13).

In Lago Grande di Monticchio, as well as in Ioannina (470 m asl), Lake Ohrid (693 m asl), and Lake Prespa (849 m asl), an altitudinal pattern can be seen, with larger populations of temperate trees reflecting warmth and high humidity growing close to mid-altitude sites (Watts et al., 1996; Allen et al., 2000; Tzedakis et al., 2002; Panagiotopoulos et al., 2014; Donders et al., 2021), while small pockets of warm temperate woodland featuring Mediterranean taxa reflecting summer warmth and dryness are only found at sites at lower altitudes (<400 m asl, e.g. Valle di Castiglione, Lagaccione, and Tenaghi Philippon) during specific D–O cycles (Follieri et al., 1988, 1998; Magri, 1999; Fletcher et al., 2010; Wulf et al., 2018). The pollen record from Uluzzo C reveals a composition of the landscapes that is comparable to those of sites at lower altitudes in regard to the principal warm temperate elements, with some differences in the dynamics and frequencies, including *Quercus*, *Olea*, *Pistacia*, *Myrtus*, and *Fraxinus*. According to this pattern, the Mediterranean's interstadial vegetation may have zonated in response to altitudinal climatic contrasts similar to the currently recognized bioclimatic stages (Quézel and Médail, 2003; Tzedakis et al., 2013).

The pollen results from Uluzzo C are supported by the faunal remains. Layer F documents a short-lived return to drier conditions, characterized by an increased frequency of equids, a renewed presence of wolves, and a marked decline in aurochs, a taxon typically associated with humid environments. Layer E, in contrast, reflects a return to humid conditions, dominated by cervids, bovids, wild boars, and wolves, consistent with a mixed environment of forests and wet grasslands under cool climatic conditions.

The Uluzzian layers (layer D – SUs 21, 22, 25, 26, 27 and C - SUs 3, 15, 17) reflect a progressive environmental shift from more wooded and humid conditions to increasingly open and fragmented landscapes. Layer D is characterized by a faunal assemblage dominated by cervids with a relatively low frequency of equids, large bovids and *Sus scrofa*, suggesting forested or mixed environments with humid conditions.

In contrast, layer C shows a clear faunal shift, marked by a significant increase in equids, large bovids, and *Sus scrofa*, along with the exclusive presence of *Rupicapra* sp. (Silvestrini et al., 2022a), which is generally associated with rocky, open, and colder environments. The presence of *Mustela nivalis*, together with *Rupicapra*, may further support the inference of more open and possibly cooler conditions compared to the preceding unit. The persistence of cervids, however, suggests that Mediterranean evergreen woodland patches still persisted in the surrounding landscape. These faunal trends are corroborated by micromammal and avian studies, which point to a mosaic landscape of open forests, grasslands, and steppe-like environments, closely matching the macrofaunal evidence (Silvestrini et al., 2022a).

This trend closely parallels the ungulate assemblage from the Uluzzian layer EIII5 at Grotta del Cavallo, where aurochs dominate alongside red deer and equid, while fallow deer, indicative of denser woodland, disappears. The sporadic presence of *Equus hydruntinus* and wild boar in EIII5 further supports the interpretation of a mixed but increasingly open landscape (Boscato and Crezzini, 2012). Taken together, these pollen and faunal records of Uluzzo C and Cavallo highlight a coherent regional environmental shift during the Uluzzian, marked by alternating warm-temperate woodland phases and open woodlandphases, likely linked to the climatic oscillations of GS-12 and GI-11.

Based on their respective chronologies, the paleoenvironmental record of Uluzzo C can be directly compared with the stalagmite of Pozzo Cucù Cave in Apulia, where 27 stratigraphically aligned U-Th dates were utilized to create an age-depth model (Columbu et al., 2020). The uninterrupted growth of the stalagmite from Pozzo Cucù Cave expanded continuously from 106.0 + 2.8/-2.7 to 26.6 + 0.8/-0.9 ka, covering MIS 5-3 (Fig. 10). Given that continuous speleothem deposition is only possible if rainfall recharged the karst reservoir and soil bioactivity builds up high quantities of CO_2 into infiltrating water, the Apulia's glacial climate may have been milder than other regions in the western and central Mediterranean. More negative (positive) $\delta^{18}O$ readings in Pozzo Cucù Cave indicate more (lower) rainfall during interstadials (stadials), which correspond to the rainfall oscillations in Apulia over DO cycles (Drysdale et al., 2009; Columbu et al., 2020). The generally low $\delta^{13}C$ values and the lack of growth pauses in Pozzo Cucú Cave provide compelling evidence for a continuously vegetated catchment of the cave's drip water, with trees growing sparser during GSs and forests expanding during GIs, which shows a general correspondence with the dynamics of vegetation development in Uluzzo C (Fig. 10).

Similarly, and connected to the previous point, the question of glacial refuges for woody taxa during the Pleistocene is crucial. Combined studies in paleoecology and phylogeography have brought to light the effects of plant species refuges on the pattern of biodiversity in mid- and high latitudes (Huntley and Birks, 1983; Bennett et al., 1991; Willis and Whittaker, 2000; Bhagwat and Willis, 2008; Provan and Bennett, 2008), on species diversity and endemism levels (Tzedakis et al., 2002; Jansson, 2003), and on the persistence of glacial traces left by past glacial patterns that partially explain the distribution and richness of forest formations in North America and Europe (Svenning and Skov, 2007). In particular, the Apulia region includes a significant number of endemic vascular plants, indicating its distinctive phytogeographical character with respect to other southern Italian peninsular regions and proving its long-term refugee status (Peruzzi et al., 2014). Therefore, from a palaeoecological perspective, Uluzzo C appears as a unique palaeofloristic record in southern Italy, in relation to the palaeoenvironment of last Neanderthals and early modern humans, highlighted by a high plant diversity, typical of the glacial refugia in the southern European regions (Follieri et al., 1998; Magri, 1999; Magri and Sadori, 1999; Giardini, 2007; Pini et al., 2010).

The Neanderthal and modern human groups that inhabited Uluzzo C were undoubtedly experts in diverse ecosystems, along with wooded ravines, in areas that combined the coastal platforms, the rocky cliffs, and the inland plains of the Salento Peninsula, as demonstrated by integrating faunal, chronological and paleoclimatic data from other sites (e.g.: Grotta di Santa Croce, Grotta del Cavallo, Riparo L'Oscurusciuto, and Pozzo Cucù Cave - Boschin et al., 2022). Likewise, the use of plant-based resources for food and technology cannot be disregarded (Ward et al., 2012a, 2012b; Hardy, 2018; Zilhão et al., 2020). In the specific case of Middle Paleolithic populations, Salazar-García et al. (2013) suggest that Neanderthals consumed a wide variety of plant resources, and analyses of dental calculus have highlighted instances of Neanderthals using plant resources for medicinal purposes or as part of their diet (Buck and Stringer, 2014; Fiorenza et al., 2011; Henry et al., 2014; Weyrich et al., 2017). Besides, several recent studies have demonstrated the importance of plants to the diet of hominids (Barton et al., 1999; Carrión et al., 2008, 2018; Hardy et al., 2012; De Vynck et al., 2016; Ochando et al., 2019, 2020a, b, c, 2024b), as attested by the oldest Italian evidence of flour processing by Neanderthals and *Homo*

sapiens in two sites, Riparo Bombrini and Grotta di Castelcivita, where there is the first direct evidence of starch grains in association with use wear traces (Mariotti Lippi et al., 2023). This technology is documented also during the Italian Gravettian at the Bilancino open-air site (Tuscany), and Grotta Paglicci (Gargano, Apulia) (Aranguren et al., 2007; Aranguren and Revedin, 2008; Mariotti Lippi et al., 2015), where grinding tools preserved starch grains on their surfaces that were primarily similar to cattail (*Typha* sp.) rhizomes and grass caryopses (Poaceae) (Bilancino), and oats and acorns (Paglicci).

According to Henry et al. (2014), the available archaeological data from Middle Stone Age Africa and Middle and Upper Paleolithic Eurasia indicates that Neanderthals were as reliant as early humans on plant foods. In this sense, the recent study carried out by Florin and Ramsey (2025) proposed a new Broad Spectrum Species hypothesis based on the archaeobotanical evidence for the early use and processing of plant foods since at least the Middle Paleolithic. Thus, we anticipate that both Neanderthals and modern humans used a broad range of plant foods, adapting their diet to the available resources, even in the most severe conditions. Thereby, we can add to the human diet the possibility of a broad spectrum of edible plants that likely grew in the proximity of Uluzzo C, such as hazelnut (*Corylus avellana*), walnut (*Juglans regia*), dwarf elderberry (*Sambucus nigra*), olive (*Olea europaea*), cattail (*Typha* sp.), tubers of asphodels (*Asphodelus* sp.), asparagus (*Asparagus* sp.), Poaceae (wild cereals), and probably wild Rosaceae.

As a final remark we need to underline that the paleoenvironmental data from Uluzzo C support the idea that the climatic-environmental changes in southern Italy from the Neanderthals to modern human populations were relatively minor on a millennial timeframe (e.g., D/O cycles), as indicated by the work on Pozzo Cucù Cave (Columbu et al., 2020). According to Boschin et al. (2022), the Apulia region offered resources and suitable stable climatic conditions for both late Neanderthal persistence and the early settling of modern human populations. In this scenario, the well-dated Palaeolithic sequences found in central and southern Italy allow for a comprehensive reconstruction of events between the demise of the Neanderthal population and the arrival of the first modern humans (Supplementary Material 1, Tables S1–S4). Examples of this include Grotta dei Santi and Grotta La Fabbrica in Tuscany (Ochando et al., 2025), Grotta del Cavallo (Sarti and Martini, 2020; Moroni et al., 2018; Zanchetta et al., 2018; Higham et al., 2024), Riparo dell'Oscurusciuto in Apulia (Higham et al., 2024), Grotta di Castelcivita and Grotta della Cala in Campania (Higham et al., 2024). As several authors have previously reported (e.g. Moroni et al., 2018; Arrighi et al., 2020; Marciani et al., 2020, 2025), a clear behavioural gap exists at these sites in the techno-typological setting of lithic industries and other significant aspects of material culture between the Mousterian and Uluzzian technocomplexes, ascribed to Neanderthals and *Homo sapiens*, respectively, also basing on the human remains found at Grotta del Cavallo (Benazzi et al., 2011; Sarti and Martini, 2020), which consist of four Neanderthal teeth from the Mousterian series (Fabbri and Vincenti, 2020) and two modern teeth from the Uluzzian layer EIII (Benazzi et al., 2011). Significant differences have also been highlighted in the exploitation of animal resources at Grotta del Cavallo (Boscato and Crezzini, 2012), despite the shared macrofaunal context. All this evidence is corroborated by stratigraphic and chronological data (Higham et al., 2024; Villa et al., 2018), which indicates a gap of a few thousand years (2000–4000) between the Mousterian and Uluzzian occupations in both central and southern Italy.

6. Conclusions

The Apulia-Basilicata region enables comprehensive and in-depth reconstructions of the events that elapsed between the demise of Neanderthals and the arrival of early modern humans in the Italian Peninsula, based on well-dated archaeological, palaeobotanical, paleontological and paleoclimatic data.

As evidenced by the identification of the tephra PGT/Y-6 (ca. 45.0–44.9 ka) between the Mousterian layer E and the Uluzzian layer D, and by other tephrochronological constraints, paleoenvironmental variability can be consistently dated between ca. 46.6 ka and 43.4 ka, offering the opportunity of a direct synchronization of the Uluzzo C composite record with nearby marine and terrestrial paleoclimatic records.

The sediment pollen record from Uluzzo C provides an additional and unique opportunity to reconstruct the palaeoenvironment encountered by the Late Italian Neanderthals and early modern humans during a relatively short interval of the Late Pleistocene, precisely constrained between the second part of the Greenland interstadial 12 (GI-12) and the onset of the GI-11.

Archaeological sites like Uluzzo C, located in physiographically distinct scenarios from lake and mire sites, can provide important insights into the location of glacial reservoirs of specific plant species and the palaeovegetation along the coast. The pollen assemblages described here (i) indicate the presence of vegetation with a higher plant diversity and a more humid environment than today, which emerges as an optimal mesothermic refuge for the Late Pleistocene, even if it is impossible to verify the continuing local presence of tree populations across GS-12 due to the almost complete lack of pollen from Layer D; (ii) stand out as a unique coastal palaeofloristic record in southern Italy, distinguished by a mixed oak-pine habitat throughout the GI-12 (layers F and E), and the GS-12 - GI-11 (layer C); and (iii) satisfactorily correlate with lacustrine pollen records, with rainfall oscillations (PC $\delta^{18}O$) in Apulia during D-O cycles, and with the faunal remains.

The data produced by our study propose substantially unchanged palaeoecological conditions during the shift from Middle to Upper Palaeolithic, despite the clear shifts in populations and industries. It follows that paleoenvironmental factors were not the main reason why Neanderthals abandoned the Uluzzo Bay and, possibly, southern Italy, around 45,000 years ago.

Author contributions

Juan Ochando: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Donatella Magri:** Conceptualization; Formal analysis; Investigation; Methodology; Resources; Supervision; Validation; Writing – original draft; Writing – review and editing. **Biagio Giaccio:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Giovanni Zanchetta:** Methodology; Supervision; Validation; Writing – original draft. **Antonino Vazzana:** Supervision; Validation. **Omry Barzilai:** Supervision; Validation; Writing – original draft; Project administration. **Francesco Berna:** Supervision; Validation; Writing – original draft; Project administration. **Gruppo Speleologico Neretino:** Supervision; Validation. **Giulia Marciani:** Data curation; Formal analysis; Investigation; Methodology; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Andrea Zerboni:** Supervision; Validation. **Sara Silvestrini:** Supervision; Validation; Writing – original draft. **Enza E. Spinapolice:** Resources; Supervision; Validation; Writing – original draft; Project administration. **Adriana Moroni:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Gabriele Terlato:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Matteo Romandini:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review and editing. **Stefano Benazzi:** Funding acquisition; Project administration; Resources; Supervision; Validation; Investigation; Writing – original draft; Writing – review and editing.

Acknowledgements

The archaeological excavations at Uluzzo C were supported by the European Union - Next Generation EU PRIN 2022 TRACE project (PIs: S. Benazzi and A. Moroni) and by ERC SyG n. 101118565 – LAST NEANDERTHALS (PIs: S. Benazzi, O. Barzilai and F. Berna). Indeed, this work was supported by the projects: i) HOMEDSCAPE PID2022-136832NB-I00, funded by FEDER/Ministry of Science and Innovation–Agencia Estatal de Investigación. Tephra investigation was supported by the projects COMET (MUR, PRIN 2022; grant 2022MS9KWR, B. Giaccio coordinator) and FUTURE (MUR, PRIN 2017; grant 20177TKBXZ_003, G. Zanchetta coordinator) financed by the Italian Research Ministry. The work of JO was funded by the European Union – NextGenerationEU (Margarita Salas postdoctoral grant, Ministerio de Universidades of the Government of Spain). The authors are grateful to MiC that released the permits to excavate the site and analyse the sediment (Decr nm,eto del Direttore Generale rep. n. 259 del March 18, 2022), to JS Carrión for making the palynology facility of the ECCE HOMO research group available for the processing of some pollen samples, as well as to the Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Brindisi e Lecce. Giulia Marciani and Sara Silvestrini are funded by European Research Council ERC-AdG-101019659 “FIRSTSTEPS” awarded to Katerina Harvati. Gabriele Terlato is supported by PRIN 2022 “TRACE”.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2026.109830.

Data availability

All data and/or code is contained within the submission.

References

Albert, R.M., Ochando, J., Martini, I., Rivera-Rondón, C.A., Crezzini, J., Dominici, C., Spagnolo, V., Boscato, P., Ronchitelli, A., Boschin, F., Berna, F., 2025. The palaeoenvironmental context of MIS 3 and the use of plants by Neanderthal groups in southern Italy: results from the Riparo l'oscurusciuto site. J. Archaeol. Sci. Reports 67, 105399.

Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhänsli, H., Watts, W.A., Wulf, S., Zolitschka, B., 1999. Evidence of rapid last glacial environmental fluctuations from southern Europe. Nature 400, 740–743.

Allen, J.R., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. Quat. Int. 73, 91–110.

Antonioli, F., Calcagnile, L., Ferranti, L., Mastronuzzi, G., Monaco, C., Orrù, P., Quarta, G., Pepe, F., Scardino, G., Scicchitano, G., Stocchi, P., Taviani, M., 2021. New evidence of mis 3 relative sea level changes from the Messina strait, Calabria (Italy). Water 13, 2647.

Aranguren, B., Revedin, A. (Eds.), 2008. Un Accampamento Di 30.000 Anni Fa a Bilancino (Mugello, Firenze). Origines. IIPP, Firenze.

Aranguren, B., Becattini, R., Mariotti Lippi, M., Revedin, A., 2007. Grinding flour in upper palaeolithic Europe (25000 years bp). Antiquity 81, 845–855.

Arrighi, S., Moroni, A., Tassoni, L., Boschin, F., Badino, F., Bortolini, E., Boscato, P., Crezzini, J., Figus, C., Forte, M., Lugli, F., Marciani, G., Oxilia, G., Negrino, F., Riel-Salvatore, J., Romandini, M., Peresani, M., Spinapolice, E.E., Ronchitelli, A., Benazzi, S., 2020. Bone tools, ornaments and other unusual objects during the Middle to upper Palaeolithic transition in Italy. Quat. Int. 551, 169–187.

Badino, F., Pini, R., Ravazzi, C., Margaritora, D., Arrighi, S., Bortolini, E., Figus, C., Giaccio, B., Lugli, F., Marciani, G., Monegato, G., Moroni, A., Negrino, F., Oxilia, G., Peresani, M., Romandini, M., Ronchitelli, A., Spinapolice, E.E., Zerboni, A., Benazzi, S., 2020. An overview of Alpine and Mediterranean palaeogeography, terrestrial ecosystems and climate history during MIS 3 with focus on the middle to upper Palaeolithic transition. Quat. Int. 551, 7–28.

Badino, F., Pini, R., Ravazzi, C., Chytrý, M., Bertuletti, P., Bortolini, E., Dudová, L., Peresani, M., Romandini, M., Benazzi, S., 2023. High-resolution ecosystem changes pacing the millennial climate variability at the middle to upper Palaeolithic transition in NE-Italy. Sci. Rep. 13, 12478.

Barkley, F.A., 1934. The statistical theory of pollen analysis. Ecology 15, 283–289.

Barton, R.N.E., Currant, A.P., Fernandez-Jalvo, Y., Finlayson, J.C., Goldberg, P., Macphail, R., Pettitt, P.B., Stringer, C.B., 1999. Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex caves. Antiquity 73, 13–23.

Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. Nature 479, 525–528.

Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of north European trees. J. Biogeogr. 18, 103–115.

Bhagwat, S.A., Willis, K.J., 2008. Species persistence in Northerly glacial refugia of Europe: a matter of chance or biogeographical traits? J. Biogeogr. 35, 464–482.

Biondi, E., Casavecchia, S., 2010. The halophilous retro-dune grasslands of the Italian Adriatic coastline. Braun-Blanquetia 46, 11–127.

Biondi, E., Casavecchia, S., Guerra, V., Medagli, P., Beccarisi, L., Zuccarello, V., 2004. A contribution towards the knowledge of semideciduous and evergreen woods of Apulia (south-eastern Italy). Fitosociologia 41, 3–28.

Biondi, E., Casavecchia, S., Guerra, V., 2006. Analysis of vegetation diversity in relation to the geomorphogical characteristics in the Salento coasts (Apulia-Italy). Fitosociologia 43, 25–38.

Blanc, A.C., 1958. La Grotta dei Giganti. Quaternaria V, 308–310.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proc. Natl. Acad. Sci. USA 101, 12125–12129.

Borzatti von Löwenstern, E., 1963. La Grotta di Uluzzo: campagna di scavi 1963. Rivista di Scienze Preistoriche 18, 75–89.

Borzatti von Löwenstern, E., 1964. La Grotta di Uluzzo: campagna di scavi 1964. Rivista di Scienze Preistoriche 19, 41–52.

Borzatti von Löwerstern, E., 1965. La Grotta- riparo di Uluzzo C. Rivista di Scienze Preistoriche XX, 1–31.

Borzatti von Löwerstern, E., 1966. Alcuni aspetti del Musteriano del Salento. Rivista di Scienze Preistoriche 21.

Borzatti von Löwerstern, E., 1970. Prima campagna scavi nella Grotta Mario Bernardini (Nardò-Lecce). Rivista di Scienze Preistoriche 25, 89–125.

Borzatti von Löwerstern, E., 1971. Seconda campagna scavi nella Grotta Mario Bernardini (Nardò-Lecce). Rivista di Scienze Preistoriche 26, 31–62.

Borzatti von Löwerstern, E., Magaldi, D., 1966. Risultati conclusivi dello studio paletnologico e sedimentologico della Grotta di Uluzzo C (Nardò- Lecce). Rivista di Scienze Preistoriche 21, 16–64.

Borzatti von Löwerstern, E., Magaldi, D., 1967. Ultime ricerche nella Grotta dell'Alto (S. Caterina, Lecce). Rivista di Scienze Preistoriche 22, 205–250.

Boscato, P., Crezzini, J., 2012. Middle-Upper Palaeolithic transition in Southern Italy: uluzzian macromammals from Grotta del Cavallo (Apulia). Quat. Int. 252, 90–98.

Boschin, F., Columbu, A., Spagnolo, V., Crezzini, J., Bahain, J.J., Falguères, C., Benazzi, S., Boscato, P., Ronchitelli, A., Moroni, A., Martini, I., 2022. Human occupation continuity in southern Italy towards the end of the middle Palaeolithic: a palaeoenvironmental perspective from Apulia. J. Quat. Sci. 37, 204–216.

Branca, S., Cinquegrani, A., Cioni, R., Conte, A.M., Conticelli, S., De Astis, G., de Vita, S., De Rosa, R., Di Vito, M.A., Donato, P., Forni, F., Francalanci, L., Gaeta, M., Giaccio, B., Giordano, G., Giuffrida, M., Isaia, R., Lucchi, F., Marra, F., Massaro, S., Nicotra, E., Palladino, D.M., Perinelli, C., Petrosino, P., Pistolesi, M., Sepulveda-Birke, J.P., Sottili, G., Romagnoli, C., Rotolo, S., Sulpizio, R., Tranne, C.A., Viccaro, M., 2023. The Italian quaternary volcanism. Alpine and Mediterranean. Quaternary 36, 221–284.

Brauer, A., Allen, J.R.M., Mingram, J., Dulski, P., Wulf, S., Huntley, B., 2007. Evidence for last interglacial chronology and environmental change from Southern Europe. Proc. Natl. Acad. Sci. USA 104, 450–455.

Buck, L.T., Stringer, C.B., 2014. Having the stomach for it: a contribution to Neanderthal diets? Quat. Sci. Rev. 96, 161–167.

Burjachs, F., 2001. Paleoecología del *Homo antecesor*: palinología de las unidades TD5, 6 y 7 de la Gran Dolina de Atapuerca (Burgos, Spain). XXII Jornadas de la Sociedad Española de Paleontología 365–372.

Campbell, I.D., 1999. Quaternary pollen taphonomy: examples of differential redeposition and differential preservation. Palaeogeogr. Palaeocl. 149, 245–256.

Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135.

Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. Review of Palaeobotany and Palynology, Special Issue. In: Carrión, J.S., deMenocal, P., Scott, L. (Eds.), Human Evolution and Palaeofloras: the Contribution and Potential of Palaeobotany in the Environmental Reconstruction of hominin-bearing Sites. Review of Palaeobotany and Palynology, 259, pp. 63–80.

Carrión, J.S., Scott, L., deMenocal, P. (Eds.), 2019a. Paleofloras, Paleovegetation and Human Evolution. Review of Palaeobotany and Palynology, pp. 32–38. Special Issue 267.

Carrión, J.S., Lalueza-Fox, C., Stewart, J., 2019b. Neanderthals: ecology and evolution. Quat. Sci. Rev. 217, 1–6.

Carrión, J.S., Fernández, S., Jiménez, J., Munuera Giner, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch, Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019c. The sequence at Carihuela cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. Quat. Sci. Rev. 217, 194–216.

Chambel, M.R., Climent, J., Pichot, C., Ducci, F., 2013. Mediterranean Pines (Pinus halepensis Mill. and Brutia Ten.). Forest Tree Breeding in Europe: Current state-of-the-art and Perspectives, pp. 229–265.

Coles, G.M., Gilbertson, D.D., 1994. The airfall-pollen budget of archaeologically important Caves: Creswell Crags, England. J. Archaeol. Sci. 21, 735–755.
Coles, G.M., Gilbertson, D.D., Hunt, C.O., Jenkinson, R.D.S., 1989. Taphonomy and the palynology of cave sediments. Cave Sci. 16, 83–89.
Columbu, A., Chiarini, V., Spötl, C., Benazzi, S., Hellstrom, J., Cheng, H., De Waele, J., 2020. Speleothem record attests to stable environmental conditions during neanderthal–modern human turnover in southern Italy. Nat. Ecol. Evol. 4, 1188–1195.
Corbetta, F., Gratani, L., Moriconi, M., Pirone, G., 1992. Lineamenti vegetazionali e caratterizzazione ecologica delle spiagge dell'Arco Jonico da Taranto alla Foce del Sinni [Vegetation outlines and ecological characterization of the "Arco Jonico" beaches from Taranto to the mouth of Sinni]. Colloq. Phytosociol. 19, 461–521.
Dantoni, G., 1980. I livelli musteriani con strumenti su valva di Callista (Callista) chione (L.) nel Salento. Studi Ecol.l Quaternario 2, 67–76.
Dantoni, G., Nardi, N., 1980. La Grotta Riparo Marcello Zei. Santa Caterina, Nardò) Studi per l'Ecologia del Quaternario 2, 97–120.
Desprat, S., Díaz Fernández, P.M., Coulon, T., Ezzat, L., Pessarossi-Langlois, J., Gil, L., Morales-Molino, C., Sánchez Goñi, M.F., 2015. *Pinus nigra* (European black pine) as the dominant species of the last glacial pinewoods in south-western to central Iberia: a morphological study of modern and fossil pollen. J. Biogeogr. 42, 1998–2009.
De Vynck, J.C., Cowling, R.M., Potts, A.J., Marean, C.W., 2016. Seasonal availability of edible underground and aboveground carbohydrate resources to human foragers on the Cape south coast, South Africa. PeerJ 4, e1679.
Dimbleby, G.W., 1985. The Palynology of Archaeological Sites. Academic Press, London.
Djamali, M., Cilleros, K., 2020. Statistically significant minimum pollen count in Quaternary pollen analysis; the case of pollen-rich lake sediments. Rev. Palaeobot. Palynol. 275, 104156.
Donders, T., Panagiotopoulos, K., Koutsodendris, A., Bertini, A., Mercuri, A.M., Masi, A., Combourieu-Nebout, N., Joannin, S., Kouli, K., Kousis, I., Peyron, O., Torri, P., Florenzano, A., Francke, A., Wagner, B., Sadori, L., 2021. 1.36 million years of Mediterranean forest refugium dynamics in response to glacial-interglacial cycle strength. Proc. Natl. Acad. Sci. USA 118, e2026111118.
Erdtman, G., 1931. Pollen-statistics: a new research method in paleoecology. Science 73, 399–401.
Erdtman, G., 1969. Handbook of Palynology. Hafner Publishing Company, Nueva York.
Ermolli, E.R., Masi, A., Vignola, C., Di Lorenzo, H., Masci, L., Bona, F., Forti, L., Lembo, G., Mazzini, I., Mecozzi, B., Muttillo, B., Pieruccini, P., Sardella, R., Sadori, L., 2022. The pollen record from Grotta Romanelli (Apulia, Italy): new insight for the late Pleistocene Mediterranean vegetation and plant use. Rev. Palaeobot. Palynol. 297, 104577.
Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol. Evol. 22, 213–222.
Fiorentino, G., 2012. L'analisi antracologica della sepoltura Ostuni 1 di S.Maria di Agnano: considerazioni paleoambientali e paletnologiche. In: Coppola, D. (Ed.), Il Riparo Di Agnano Nel Paleolitico Superiore. La Sepoltura Ostuni 1 Ed i Suoi Simboli. Università di Tor Vergata Editor, Roma, pp. 11–15.
Fiorentino, G., Parra, I., 2015. "Lost" postglacial littoral environments in SE Italy: anthracological evidence at Grotta delle Mura. Rev. Palaeobot. Palynol. 218, 198–203.
Fiorenza, L., Benazzi, S., Tausch, J., Kullmer, O., Bromage, T.G., Schrenk, F., 2011. Molar macrowear reveals Neanderthal eco-geographic dietary variation. PLoS One 6, e14769.
Fiorini, A., Curci, A., Spinapolice, E.E., Benazzi, S., 2019. Grotta di Uluzzo C (Nardò-Lecce): risultati preliminari, strumenti e metodi dell'indagine archeologica. FOLD&R. ISSN: 1828-3179.
Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R., Cheddadi, R., Combourieu-Nebout, N., Huntley, B., Lawson, I., Londeix, L., Magri, D., Margari, V., Müller, U.C., Naughton, F., Novenko, E., Roucoux, K., Tzedakis, P.C., 2010. Millennial-scale variability during the last glacial in vegetation records from Europe. Quat. Sci. Rev. 29, 2839–2864.
Florin, S.A., Ramsey, M.N., 2025. The broad spectrum species: plant use and processing as deep time adaptations. J. Archaeol. Res. 1–52.
Follieri, M., Magri, D., Sadori, L., 1988. 250,000 year pollen record from Valle di Castiglione (Roma). Pollen Spores 30, 329–356.
Follieri, M., Giardini, M., Magri, D., Sadori, L., 1998. Palynostratigraphy of the last glacial period in the volcanic region of central Italy. Quat. Int. 47–48, 3–20.
García-Antón, M., Sainz-Ollero, H., 1991. Pollen records from the middle Pleistocene Atapuerca site (Burgos, Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 85, 199–206.
Gatta, M., Sinopoli, G., Giardini, M., Giaccio, B., Hajdas, I., Pandolfi, L., Bailey, G., Spikins, P., Rolfo, M.F., Sadori, L., 2016. Pollen from late Pleistocene hyena (*Crocuta crocuta spelaea*) coprolites: an interdisciplinary approach from two Italian sites. Rev. Palaeobot. Palynol. 233, 56–66.
Genet, M., Daniau, A.L., Mouillot, F., Hanquiez, V., Schmidt, S., David, V., Georget, M., Abrantes, F., Anschutz, P., Bassinot, F., Bonnin, J., Dennielou, B., Eynaud, F., Hodell, D.A., Mulder, T., Naughton, F., Rossignol, L., Tzedakis, P., Sánchez-Goñi, M. F., 2021. Modern relationships between microscopic charcoal in marine sediments and fire regimes on adjacent landmasses to refine the interpretation of marine paleofire records: an Iberian case study. Quat. Sci. Rev. 270, 107148.
Giaccio, B., Hajdas, I., Isaia, R., Deino, A., Nomade, S., 2017a. High-precision ^{14}C and $^{40}Ar/^{39}Ar$ dating of the Campanian Ignimbrite (Y-5) reconciles the time-scales of climatic-cultural processes at 40 ka. Sci. Rep. 7, 45940.
Giaccio, B., Niespolo, E.M., Pereira, A., Nomade, S., Renne, P.R., Albert, P.G., Arienzo, I., Regattieri, E., Wagner, B., Zanchetta, G., Gaeta, M., Galli, P., Mannella, G., Peronace, E., Sottili, G., Florindo, F., Leicher, N., Marra, F., Tomlinson, E.T., 2017b. First integrated tephrochronological record for the last ~190 kyr from the Fucino Quaternary lacustrine succession, central Italy. Quat. Sci. Rev. 158, 211–234.
Giardini, M., 2007. Late quaternary vegetation history at stracciacappa (Rome, central Italy). Veg. Hist. Archaeobotany 16, 301–316.
Girard, M., 1975. Prévèlement d'échantillons en grotte et station de terrain sec en vue de l'analyse pollinique. Bull. Soc. Prehist. Fr. 72, 158–160.
Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de preparation en palynologie appliques a trois sediments du Quaternaire final de l'Abri Corneille (Istres-Bouches-du-Rhone). Bulletin de l'Association Francaise pour l'Etude du Quaternaire 4, 275–284.
González-Varo, J.P., Arroyo, J., Aparicio, A., 2009. Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (Myrtus communis). Biol. Conserv. 142, 1058–1065.
Grant, K.M., Rohling, E.J., Ramsey, C.B., Cheng, H., Edwards, R.L., Florindo, F., Heslop, D., Marra, F., Roberts, A.P., Tamisiea, M.E., Williams, F., 2014. Sea-level variability over five glacial cycles. Nat. Commun. 5, 5076.
Hardy, K., 2018. Plant use in the Lower and Middle Palaeolithic: food, medicine and raw materials. Quat. Sci. Rev. 191, 393–405.
Hardy, K., Buckley, S., Collins, M.J., Estalrrich, A., Brothwell, D., Copeland, L., GarcíaTabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Fernandez Cortes, A., Rosas, A., 2012. Neanderthalmedics? Evidence for food, cooking, andmedicinal plants entrapped in dental calculus. Naturwissenschaften 99, 617–626.
Havinga, A.J., 1984. A 20-year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. Pollen Spores 26, 541–558.
Henry, A.G., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. J. Hum. Evol. 69, 44–54.
Hevly, R.H., 1981. Pollen production, transport and preservation: potentials and limitations in archaeological palynology. J. Ethnobiol. 1, 39–54.
Higham, T.F.G., Barton, H., Turney, C.M.T., Barker, G., Bronk, C., Ramsey Brock, F., 2008. Radiocarbon dating of charcoal from tropical sequences: results from the Niah Great Cave, Sarawak and their broader implications. J. Quat. Sci. 24, 189–197.
Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., Chandler, B., Gröning, F., Collins, C., Hillson, S., O'Higgins, P., FitzGerald, C., Fagan, M., 2011. The earliest evidence for anatomically modern humans in northwestern Europe. Nature 479, 521–524.
Higham, T., Douka, K., Wood, R., Bronk Ramsey, C., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruíz, C., Bergman, C., Boitard, C., Boscato, P., Caparrós, M., Conard, N.J., Draily, C., Froment, A., Galván, B., Gambassini, P., García-Moreno, A., Grimaldi, S., Haesaerts, P., Holt, B., Iriarte-Chiapusso, M.J., Jelinek, A., Jordá Pardo, J.F., Maíllo-Fernández, J.-M., Marom, A., Maroto, J., Menéndez, M., Metz, L., Morin, E., Moroni, A., Negrino, F., Panagopoulou, E., Peresani, M., Pirson, S., de la Rasilla, M., Riel-Salvatore, J., Ronchitelli, A., Santamaria, D., Semal, P., Slimak, L., Soler, J., Soler, N., Villaluenga, A., Pinhasi, R., Jacobi, R., 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512, 306–309.
Higham, T., Frouin, M., Douka, K., Ronchitelli, A., Boscato, P., Benazzi, S., Crezzini, J., Spagnolo, V., McCarty, M., Marciani, G., Falcucci, A., Rossini, M., Arrighi, S., Dominici, C., Devièse, T., Schwenninger, J.-C., Martini, I., Moroni, A., Boschin, F., 2024. Chronometric data and stratigraphic evidence support discontinuity between Neanderthals and early Homo sapiens in the Italian Peninsula. Nat. Commun. 15, 8016.
Hunt, C.O., Fiacconi, M., 2018. Pollen taphonomy of cave sediments: what does the pollen record in caves tell us about external environments and how do we assess its reliability? Quartern. Int 485, 68–75.
Huntley, B., Birks, H.J.B., 1983. An Atlas of past and Present Pollen Maps of Europe: 0–13,000 Years ago. Cambridge Uni versity Press, Cambridge.
Jansson, R., 2003. Global patterns in endemism explained by past climatic changes. Proc. Biol. Sci. 270, 583–590.
Jochum, K.P., Stoll, B., Herwig, K., Willbold, M., Hofmann, A.W., Amini, M., Aarburg, S., Abouchami, W., Hellebrand, E., Mocek, B., Raczek, I., Stracke, A., Alard, O., Bouman, C., Becker, S., Dücking, M., Brätz, H., Klemd, R., De Bruin, D., Canil, D., Cornell, D., de Hoog, C.-J., Dalpé, C., Danyushevsky, L., Eisenhauer, A., Gao, Y., Snow, J.E., Groschopf, N., Günther, D., Latkoczy, C., Guillong, M., Hauri, E.H., Höfer, H.E., Lahaye, Y., Horz, K., Jacob, D.E., Kasemann, S.A., Kent, A.J.R., Ludwig, T., Zack, T., Mason, P.R.D., Meixner, A., Rosner, M., Misawa, K., Nash, B.P., Pfänder, J., Premo, W.R., Sun, W.D., Tiepolo, M., Vannucci, R., Vennemann, T., Wayne, D., Woodhead, J.D., 2006. MPI-DING reference glasses for in situ microanalysis: new reference values for element concentrations and isotope ratios. G-cubed 7.
Karatsori, E., Renault-Miskovsky, J., de Lumley, H., Lebreton, V., 2005. Environnement de l'Homme de Néandertal en Ligurie au Pléistocène supérieur. Analyse pollinique de la Caverna delle Fate (Finale Ligure, Italie). C. R. Palevol 4, 395–404.
Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M. R., Johnston, M.O., Mitchell, R.J., Ashman, T.-L., 2005. Pollen limitation of plant reproduction: pattern and process. Annu. Rev. Ecol. Systemat. 36, 467–497.
Langgut, D., Almogi-Labin, A., Bar-Matthews, M., Pickarski, N., Weinstein-Evron, M., 2018. Evidence for a humid interval at ~56–44 ka in the Levant and its potential link to modern human dispersal out of Africa. J. Hum. Evol. 124, 75–90.
Lau, P., Bryant, V., Rangel, J., 2018. Determining the minimum number of pollen grains needed for accurate honey bee (Apis mellifera) colony pollen pellet analysis. Rev. Palaeobot. Palynol. 42, 36–42.
Le Bas, M., Maitre, R.L., Streckeisen, A., Zanettin, B., IUGS Subcommission on the Systematics of Igneous Rocks, 1986. A chemical classification of volcanic rocks based on the total alkali-silica diagram. J. Petrol. 27, 745–750.

Lebreton, V., Messager, L., Marquer, L., Renault-Miskovsky, J., 2010. A neotaphonomic experiment in pollen oxidation and its implications for archaeopalynology. Rev. Palaeobot. Palyno. 162, 29–38.
Lytle, D.E., Wahl, E.R., 2005. Palaeoenvironmental reconstructions using the modern analogue technique: the effects of sample size and decision rules. Holocene 15, 554–566.
Macchia, F., Cavallaro, V., Forte, L., Terzi, M., 2000. Vegetazione e clima della Puglia. In: Marchiori, S., De Castro, F., Myrta, A. (Eds.), La Cooperazione italo-albanese per la Valorizzazione Della Biodiversità. CIHEAM, Bari, pp. 33–49.
Macdonald, R., 1974. Nomenclature and petrochemistry of the peralkaline oversaturated extrusive rocks. Bull. Volcanol. 38, 498–516.
Magri, D., 1999. Late Quaternary vegetation history at Lagaccione near Lago di Bolsena (central Italy). Rev. Palaeobot. Palynol. 106, 171–208.
Magri, D., Sadori, L., 1999. Late Pleistocene and Holocene pollen stratigraphy at lago di Vico, central Italy. Veg. Hist. Archaeobotany 8, 247–260.
Magri, D., Di Rita, F., Aranbarri, J., Fletcher, W., González-Sampériz, P., 2017. Quaternary disappearance of tree taxa from Southern Europe: timing and trends. Quat. Sci. Rev. 163, 23–55.
Marciani, G., Ronchitelli, A., Arrighi, S., Badino, F., Bortolini, E., Boscato, P., Boschin, F., Crezzini, J., Delpiano, D., Falcucci, A., Figus, C., Lugli, F., Oxilia, G., Romandini, M., Riel-Salvatore, J., Negrino, F., Peresani, M., Spinapolice, E.E., Moroni, A., Benazzi, S., 2020. Lithic techno-complexes in Italy from 50 to 39 thousand years BP: an overview of lithic technological changes across the middle-upper Palaeolithic boundary. Quat. Int. 551, 123–149.
Marciani, G., Carmignani, L., Djakovic, I., Roussel, M., Arrighi, S., Rossini, M., Boschin, F., Ronchitelli, A., Benazzi, S., Moroni, A., Soressi, M., 2025. The uluzzian and châtelperronian: no technological affinity in a shared chronological framework. Journal of Paleolithic Archaeology 8, 3.
Mariotti Lippi, M., Foggi, B., Aranguren, B., Ronchitelli, A., Revedin, A., 2015. Multistep food plant processing at Grotta Paglicci (Southern Italy) around 32,600 cal BP. Proc. Natl. Acad. Sci. USA 112, 12075–12080.
Mariotti Lippi, M., Aranguren, B., Arrighi, S., Attolini, D., Benazzi, S., Boschin, F., Florindi, S., Moroni, A., Negrino, F., Pallecchi, P., Pisaneschi, L., Riel-Salvatore, J., Ronchitelli, A., Revedin, A., 2023. New evidence of plant food processing in Italy before 40ka. Quat. Sci. Rev. 312, 108161.
Mastrogiacomo, G., Moretti, M., Owen, G., Spalluto, L., 2012. Tectonic triggering of slump sheets in the Upper Cretaceous carbonate succession of the Porto Selvaggio area (Salento peninsula, southern Italy): synsedimentary tectonics in the Apulian Carbonate platform. Sediment. Geol. 269, 15–27.
Mercuri, A.M., 2014. Genesis and evolution of the cultural landscape in central Mediterranean: the 'where, when and how' through the palynological approach. Landsc. Ecol. 29, 1799–1810.
Messager, E., Lebreton, V., Marquer, L., Russo-Ermolli, E., Orain, R., Renault Miskovsky, J., Lordkipanidze, D., Desprie, J., Peretto, C., Arzarello, M., 2011. Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: new palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. Quat. Sci. Rev. 30, 1439–1447.
Moroni, A., Ronchitelli, A., Arrighi, S., Aureli, D., Bailey, S.E., Boscato, P., Boschin, F., Capecchi, G., Crezzini, J., Douka, K., Marciani, G., Panetta, D., Ranaldo, F., Ricci, S., Scaramucci, S., Spagnolo, V., Benazzi, S., Gambassini, P., 2018. Grotta del cavallo (Apulia–Southern Italy). The uluzzian in the mirror. Journal of Anthropological Sciences 96, 125–160.
Narcisi, B., 1996. Tephrochronology of a late Quaternary lacustrine record from the Monticchio Maar (vulture volcano, southern Italy). Quat. Sci. Rev. 15, 155–165.
Ochando, J., Carrión, J.S., Blasco, R., Fernández, S., Amorós, G., Munuera, M., Sañudo, P., Fernández Peris, J., 2019. Silvicolous Neanderthals in the far west: the mid-Pleistocene palaeoecological sequence of Bolomor cave (Valencia, Spain). Quat. Sci. Rev. 217, 247–267.
Ochando, J., López-Sáez, J.A., Pérez-Díaz, S., Ramos-Fernández, J., Munuera, M., Fernández, S., Galacho-Jiménez, F.B., Luelmo-Lautenschlaeger, R., Carrión, J.S., 2020a. A new pollen sequence from southern Iberia suggesting coastal Pleistocene phytodiversity hotspot. Rev. Palaeobot. Palynol. 281, 104281.
Ochando, J., Carrión, J.S., Blasco, R., Rivals, F., Rufà, A., Amorós, G., Munuera, M., Fernández, S., Rosell, J., 2020b. The Late Quaternary pollen sequence of Toll cave, a palaeontological site with evidence of human activities in Northeastern Spain. Quat. Int. 554, 1–14.
Ochando, J., Carrión, J.S., Blasco, R., Rivals, F., Rufá, A., Demuro, M., Arnold, L.J., Amorós, G., Munuera, M., Fernández, S., Rosell, J., 2020c. Neanderthals in a highly diverse, Mediterranean-Eurosiberian forest ecotone: the Pleistocene pollen record of Teixoneres Cave, Northeastern Spain. Quat. Sci. Rev. 241, 106429.
Ochando, J., Carrión, J.S., Rodríguez-Vidal, J., Jiménez-Arenas, J.M., Fernández, S., Amorós, G., Munuera, M., Scott, L., Stewart, J.R., Knul, M.V., Toro-Moyano, I., Ponce de León, M., Zollikofer, C., 2020d. Palynology and chronology of hyaena coprolites from the Piñar karstic caves las Ventanas and Carihuela, southern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 552, 109771.
Ochando, J., Amorós, G., Carrión, J.S., Fernández, S., Munuera, M., Camuera, J., Jiménez-Moreno, G., González-Sampériz, P., Burjachs, F., Marín-Arroyo, A.B., Roksandic, M., Finlayson, C., 2022a. Iberian Neanderthals in forests and savannahs. J. Quat. Sci. 37, 335–362.
Ochando, J., Carrión, J.S., Daura, J., Sanz, M., Araújo, A.C., Costa, A.M., 2022b. Coprolite palynology from Abrigo do Lagar Velho (Portugal) and a revision of Gravettian vegetation in the Iberian Peninsula. Rev. Palaeobot. Palynol. 299, 104609.
Ochando, J., Jiménez-Espejo, F.J., Giles-Guzmán, F., Neto de Carvalho, C., Carrión, J.S., Muñiz, F., Rubiales, J.M., Cura, P., Belo, J., Finlayson, S., Martrat, B., van Drooge, B. L., Jiménez-Moreno, G., García-Alix, A., Lozano Rodríguez, J.A., Albert, R.M., Ohkouchi, N., Ogawa, N., Suga, H., Camuera, J., Martínez-Ruiz, F., Villanueva, J., Teruel, O., Davtian, N., Moreira, N., Belaústegui, Z., Rodríguez-Vidal, J., Munuera, M., Menez, A., Finlayson, G., Finlayson, C., 2024a. A Neanderthal's specialised burning structure compatible with tar obtention. Quat. Sci. Rev. 241, 106429.
Ochando, J., Carrión, J.S., Magri, D., Marín-Arroyo, A.B., Di Rita, F., Munuera, M., Michelangeli, F., Amorós, G., Milošević, S., Bogićević, K., Dimitrijević, V., Nenadić, D., Roksandic, M., Mihailović, D., 2024b. Balkan Neanderthals: the late Pleistocene palaeoecological sequence of Pešturina Cave (Niš, Serbia). Quat. Sci. Rev. 330, 108600.
Ochando, J., Di Rita, F., Magri, D., Crezzini, J., Burgassi, A., Marciani, G., Berna, F., Boschin, F., Moroni, A., Spagnolo, V., 2025. Environment and hunting territories for Late Neanderthals in central Italy: new palaeoecological data from Grotta dei Santi (Monte Argentario Tuscany, Italy). In: Val-Peón, C., Ochando, J., Fernández-García, M. (Eds.), Neanderthal Landscapes in Southern Europe. J. Archaeol. Sci. Rep, 66, 105319.
Palma di Cesnola, A., Borzatti von Löwenstern, E., 1964. Gli scavi dell'Istituto Italiano di Preistoria e Protostoria nel Salento. In: Atti Della VIII E IX Riunione Scientifica, Trieste 19-20 Ottobre 1963, Calabria 6-8 Aprile 1964, pp. 27–43.
Panagiotopoulos, K., Böhm, A., Leng, M.J., Wagner, B., Schäbitz, F., 2014. Climate variability over the last 92 ka in SW Balkans from analysis of sediments from Lake Prespa. Clim. Past 10, 643–660.
Paterne, M., Guichard, F., Duplessy, J.C., Siani, G., Sulpizio, R., Labeyrie, J., 2008. A 90,000–200,000 yrs marine tephra record of Italian volcanic activity in the Central Mediterranean Sea. J. Volcanol. Geoth. Res. 177, 187–196.
Peruzzi, L., Conti, F., Bartolucci, F., 2014. An inventory of vascular plants endemic to Italy. Phytotaxa 168, 1. https://doi.org/10.11646/phytotaxa.168.1.1.
Pieruccini, P., Forti, L., Mecozzi, B., Iannucci, A., Yu, T.L., Shen, C.C., Bona, F., Lembo, G., Muttillo, B., Sardella, R., Mazzini, I., 2022. Stratigraphic reassessment of Grotta Romanelli sheds light on middle-late Pleistocene palaeoenvironments and human settling in the Mediterranean. Sci. Rep. 12, 13530.
Pieruccini, P., Forti, L., Mecozzi, B., Iannucci, A., Yu, T.L., Shen, C.C., Bona, F., Lembo, G., Muttillo, B., Sardella, R., Mazzini, I., 2024. Author Correction: stratigraphic reassessment of Grotta Romanelli sheds light on middle-late Pleistocene palaeoenvironments and human settling in the Mediterranean. Sci. Rep. 14, 19923.
Pini, R., Ravazzi, C., Reimer, P.J., 2010. The vegetation and climate history of the last glacial cycle in a new pollen record from Lake Fimon (southern Alpine foreland, NItaly). Quat. Sci. Rev. 29, 3115–3137.
Polemio, M., Lonigro, T., 2013. Climate variability and landslide occurrence in Apulia (Southern Italy). In: Margottini, C., Canuti, P., Sassa, K. (Eds.), Landslide Science and Practice. Springer, Berlin, Heidelberg.
Provan, J., Bennett, K.D., 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol. Evol. 23, 564–571.
Quézel, P., Médail, F., 2003. Ecologie Et Biogéographie Des Forêts Du Bassin Méditerranéen, 572. Elsevier, Paris.
Rasmussen, S.O., Birks, H.H., Blockley, S.P., Brauer, A., Hajdas, I., Hoek, W.Z., Lowe, J., Moreno, A., Renssen, H., Roche, D., Svensson, A.M., Valdes, P., Walker, M.J.C., 2014. Dating, synthesis, and interpretation of palaeoclimatic records of the last glacial cycle and model-data integration: advances by the INTIMATE (INTegration of Ice-core, MArine and TErrestrial records) COST Action ES0907. Quat. Sci. Rev. 106, 1–13.
Ricciardi, S., 2020. Archeopalinologia della sequenza musteriana. In: Il Musteriano Di Grotta Del Cavallo Nel Salento (Scavi 1986-2005). Cultura E Ambienti. Museo e Istituto Fiorentino di Preistoria Paolo Graziosi, pp. 123–134.
Rivas-Martinez, S., Penas, A., Diaz, T.E., 2001. Biogeographic Map of Europe. Cartographic Service, University of Léon, Spain.
Rohling, E.J., Foster, G.L., Grant, K.M., Marino, G., Roberts, A.P., Tamisiea, M.E., Williams, F., 2014. Sea-level and deep-sea-temperature variability over the past 5.3 million years. Nature 508, 477–482.
Rohling, E.J., Foster, G.L., Gernon, T.M., Grant, K.M., Heslop, D., Hibbert, F.D., Roberts, A.P., Yu, J., 2022. Comparison and synthesis of sea-level and deep-sea temperature variations over the past 40 million years. Rev. Geophys. 60 e2022RG000775.
Romandini, M., Crezzini, J., Bortolini, E., Boscato, P., Boschin, F., Carrera, L., Nannini, N., Tagliacozzo, A., Terlato, G., Arrighi, S., Badino, F., Figus, C., Lugli, F., Marciani, G., Oxilia, G., Moroni, A., Negrino, F., Peresani, M., Riel-Salvatore, J., Ronchitelli, A., Benazzi, S., 2020. Macromammal and bird assemblages across the late middle to upper Palaeolithic transition in Italy: an extended zooarchaeological review. Quat. Int. 551, 188–223.
Salazar-García, D.C., Power, R.C., Sanchis Serra, A., Villaverde, V., Walker, M.J., Henry, A.G., 2013. Neanderthal diets in central and southeastern Mediterranean Iberia. Quat. Int. 318, 3–18.
Sánchez-Goñi, M.F., 1993. Criterios de base tafonómica para la interpretación de análisis palinológicos en cueva: el ejemplo de la región cantábrica. In: Fumanal, M.P., Bernabeu, J. (Eds.), Estudios Sobre Cuaternario, Medios Sedimentarios, Cambios Ambientales, Hábitat Humano. Universitat de València, València, pp. 117–130.
Il Musteriano di Grotta del Cavallo nel contesto pugliese (MIS 7-3). In: Sarti, L., Martini, F. (Eds.), 2020. Il Musteriano Di Grotta Del Cavallo Nel Salento (Scavi 1986-2005): Culture E Ambienti. Museo e istituto fiorentino di preistoria" Paolo Graziosi.
Scaillet, S., Vita-Scaillet, G., Rotolo, S.G., 2013. Millennial-scale phase relationships between ice-core and Mediterranean marine records: insights from high-precision 40Ar/39Ar dating of the Green Tuff of Pantelleria, Sicily Strait. Quat. Sci. Rev. 78, 141–154.
Seghi, F., Sorrentino, R., Bailey, S.E., Piccirilli, E., Vazzana, A., Bortolini, E., Higgins, O. A., Marciani, G., Orlando, M.A., Spinapolice, E.E., Moroni, A., Benazzi, S., 2024. Morphological and morphometric study of the hominin dental casts from Grotta-

Riparo di Uluzzo C (Apulia, southern Italy). American Journal of Biological Anthropology 185, e24998.
Silvestrini, S., Romandini, M., Marciani, G., Arrighi, S., Carrera, L., Fiorini, A., López-García, J.M., Lugli, F., Ranaldo, F., Slon, V., Tassoni, L., Higgins, O.A., Bortolini, E., Curci, A., Meyer, M., Meyer, M.C., Oxilia, G., Zerboni, A., Benazzi, S., Spinapolice, E. E., 2022a. Integrated multidisciplinary ecological analysis from the Uluzzian settlement at the Uluzzo C Rock Shelter, south-eastern Italy. J. Quat. Sci. 37, 235–256.
Silvestrini, S., Lugli, F., Romandini, M., Real, C., Sommella, E., Salviati, E., Arrighi, S., Bortolini, E., Figus, C., Higgins, O.A., Marciani, G., Oxilia, G., Delpiano, D., Vazzana, A., Piperno, M., Crescenzi, C., Campiglia, P., Collina, C., Peresani, M., Spinapolice, E.E., Benazzi, S., 2022b. Integrating ZooMS and zooarchaeology: new data from the Uluzzian levels of Uluzzo C Rock Shelter, Roccia San Sebastiano cave and Riparo del Broion. PLoS One 17, e0275614.
Silvestrini, S., Real, C., Lugli, F., Delpiano, D., Harvati, K., Collina, C., Peresani, M., Spinapolice, E.E., Romandini, M., Benazzi, S., 2024. Hunting game: new data on the subsistence strategies during the Uluzzian in Italy. J. Archaeol. Sci.: Reports 57, 104575.
Spagnolo, V., Crezzini, J., Falguères, C., Tombret, O., Garbe, L., Bahain, J.J., Giaccio, B., Arrighi, S., Aureli, D., Eckberg, I., Boscato, P., Ronchitelli, A., Boschin, F., 2024. Grotta Grande (southern Italy). Disentangling the Neandertal and carnivore interaction in a short-term palimpsest at the last glacial onset (116-109 ka). Quat. Sci. Rev. 331, 108628.
Spinapolice, E., 2008. Technologie Lithique Et Circulation Des Matières Premières Au Paléolithique Moyen Dans Le Salento (Pouilles, Italie Méridionale): Perspectives Comportementales. Università Di Roma “La Sapienza”. Université de Bordeaux, p. 485, 1.
Spinapolice, E., 2009. Lithic industries and raw material in southern Italy mousterian: an exemple from Grotta dei Giganti (Salento, Apulia). In: Sternke, F. (Ed.), Non-Flint Raw Material Use in Prehistory. BAR International Series, Oxford, pp. 177–186.
Spinapolice, E.E., 2012. Raw material economy in Salento (Apulia, Italy): new perspectives on Neanderthal mobility patterns. J. Archaeol. Sci. 39, 680–689.
Spinapolice, E.E., 2018. Neanderthal mobility pattern and technological organization in the Salento (Apulia, Italy). In: Palaeolithic Italy Advanced Studies on Early Human Adaptations in the Apennine Peninsula. Sidestone Press, Acadmics: Leiden, pp. 95–124.
Spinapolice, E.E., Zerboni, A., Meyer, M.C., Talamo, S., Mariani, G.S., Gliganic, L.A., Buti, L., Fusco, M., Maiorano, M.P., Silvestrini, S., Sorrentino, R., Vazzana, A., Romandini, M., Fiorini, A., Curci, A., Benazzi, S., 2022. Back to Uluzzo – archaeological, palaeoenvironmental and chronological context of the mid-upper palaeolithic sequence at Uluzzo C Rock Shelter (Apulia, southern Italy). J. Quat. Sci. 37, 217–234.
Sprovieri, M., Di Stefano, E., Incarbona, A., Manta, D.S., Pelosi, N., d'Alcalà, M.R., Sprovieri, R., 2012. Centennial-to millennial-scale climate oscillations in the Central-Eastern Mediterranean Sea between 20,000 and 70,000 years ago: evidence from a high-resolution geochemical and micropaleontological record. Quat. Sci. Rev. 46, 126–135.
Svenning, J.C., Skov, F., 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. Global Ecol. Biogeogr. 16, 234–245.
Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C., 2002. Buffered tree population changes in a Quaternary refugium: evolutionary implications. Science 297, 2044–2047.
Tzedakis, P.C., Emerson, B.C., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. Trends Ecol. Evol. 28, 696–704.
Val-Peón, C., Expósito, I., Soto, M., Burjachs, F., 2019. A taphonomic approach to the pollen assemblage from layer M of the Abric Romaní archaeological site (NE Iberian Peninsula). Rev. Palaeobot. Palynol. 270, 19e39.
Villa, P., Pollarolo, L., Conforti, J., Marra, F., Biagioni, C., Degano, I., Lucejko, C.T., Pennacchioni, M., Zanchetta, G., Nicosia, C., Martini, M., Sibilia, E., Panzeri, L., 2018. From neandertals to modern humans: new data on the Uluzzian. PLoS One 13, e0196786.
Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., Mcmanus, J.F., Lambeck, K., Balbon, E., Labracherie, M., 2002. Sea-level and deep water temperature changes derived from benthic Foraminifera isotopic records. Quat. Sci. Rev. 21, 295–305.
Ward, S., Gale, R., Carruthers, W., 2012a. Late Pleistocene vegetation reconstruction at Vanguard Cave. In: Barton, R.N.E., Stringer, C.B., Finlayson, C. (Eds.), Neanderthals in Context. A Report of the 1995–1998 Excavations at Gorham's and Vanguard Caves, Gibraltar. Institute of Archaeology. University of Oxford, Oxford, pp. 218–223.
Ward, S., Gale, R., Carruthers, W., 2012b. Late Pleistocene vegetation reconstruction at gorham's cave. In: Barton, R.N.E., Stringer, C.B., Finlayson, C. (Eds.), Neanderthals in Context: a Report of the 1995–1998 Excavations at Gorham's and Vanguard Caves, Gibraltar. Oxford University School of Archaeology. Institute of Archaeology, University of Oxford, Oxford, Oxford, pp. 89–101.
Watts, W.A., Allen, J.R., Huntley, B., 1996. Vegetation history and palaeoclimate of the last glacial period at Lago Grande di Monticchio, southern Italy. Quat. Sci. Rev. 15, 133–153.
Weng, Ch, Hooghiemstra, H., 2024. How many pollen grains should we count? – a basic statistical view. Rev. Palaeobot. Palynol. 330, 105126.
Weyrich, L.S., Duchene, S., Soubrier, J., Arriola, L., Llamas, B., Breen, J., Morris, A.G., Alt, K.W., Caramelli, D., Dresely, V., Farrell, M., Farrer, A.G., Francken, M., Gully, N., Haak, W., Hardy, K., Harvati, K., Held, P., Holmes, E.C., Kaidonis, J., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Semal, P., Soltysiak, A., Townsend, G., Usai, D., Wahl, J., Huson, D.H., Dobney, K., Cooper, A., 2017. Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. Nature 544, 357–361.
Willis, K.J., Whittaker, R.J., 2000. The refugial debate. Science 287, 1406–1407.
Wulf, S., Kraml, M., Brauer, A., Keller, J., Negendank, J.F.W., 2004. Tephrochronology of the 100 ka lacustrine sediment record of Lago Grande di Monticchio (southern Italy). Quat. Int. 122, 7–30.
Wulf, S., Hardiman, M.J., Staff, R.A., Koutsodendris, A., Appelt, O., Blockley, S.P.E., Lowe, J.J., Manning, C.J., Ottolini, L., Schmitt, A.K., Smith, V.C., Tomlinson, E.L., Vakhrameeva, P., Knipping, M., Kotthoff, U., Milner, A.M., Müller, U.C., Christanis, K., Kalaitzidis, S., Tzedakis, P.C., Schmiedl, G., Pross, J., 2018. The marine isotope stage 1e5 cryptotephra record of Tenaghi Philippon, Greece: towards a detailed tephrostratigraphic framework for the Eastern Mediterranean region. Quat. Sci. Rev. 186, 236–262.
Wutke, K., Wulf, S., Tomlinson, E.L., Hardiman, M., Dulski, P., Luterbacher, J., Brauer, A., 2015. Geochemical properties and environmental impacts of seven Campanian tephra layers deposited between 40 and 38 ka BP in the varved lake sediments of Lago Grande di Monticchio, southern Italy. Quat. Sci. Rev. 118, 67–83.
Zanchetta, G., Giaccio, B., Bini, M., Sarti, L., 2018. Tephrostratigraphy of Grotta del Cavallo, Southern Italy: insights on the chronology of Middle to Upper Palaeolithic transition in the Mediterranean. Quat. Sci. Rev. 182, 65–77.
Zilhão, J., Angelucci, D.E., Igreja, M.A., Arnold, L.J., Badal, E., Callapez, P., Cardoso, J. L., d'Errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S., Hoffmann, D.L., Legoinha, P., Matias, H., Monge Soares, A.M., Nabais, M., Portela, P., Queffelec, A., Rodrigues, F., Souto, P., 2020. Last interglacial iberian neandertals as fisher-hunter-gatherers. Science 367, 6485.
Zolitschka, B., Negendank, J.F.W., 1996. Sedimentology, dating and palaeoclimatic interpretation of a 76.3 ka record from Lago Grande di Monticchio, southern Italy. Quat. Sci. Rev. 15, 101–112.