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DOI:10.1016/j.revpalbo.2021.104577

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Journal Pre-proof

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PII: S0034-6667(21)00201-3

DOI: https://doi.org/10.1016/j.revpalbo.2021.104577

Reference: PALBO 104577

To appear in: *Review of Palaeobotany and Palynology*

Received date: 9 August 2021

Revised date: 24 November 2021

Accepted date: 27 November 2021

Please cite this article as: E.R. Ermolli, A. Masi, C. Vignola, et al., The pollen record from Grotta Romanelli (Apulia, Italy): New insight for the Late Pleistocene Mediterranean vegetation and plant use, *Review of Palaeobotany and Palynology* (2021), https://doi.org/10.1016/j.revpalbo.2021.104577

The pollen record from Grotta Romanelli (Apulia, Italy): new insight for the Late Pleistocene Mediterranean vegetation and plant use

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Abstract

Pollen analyses have been carried out on the infilling deposits of Grotta Romanelli (Apulia, Italy), a reference site for the Middle and Upper Palaeolithic of Italy. The analysis focused on *Terre rosse*, a fine unit till now ascribed to an interstadial phase following the Würm acme, and on the uppermost unit (*Terre brune)*, recently dated to the latest Late Pleistocene-Early Holocene. Despite the diffuse barrenness and low pollen concentration of many levels, pollen data from Grotta Romanelli gives insights into the palaeoenvironmental setting of the deposits and their chronological attribution. The presence of *Olea* in all levels of *Terre rosse* strongly suggests their attribution to the Last Interglacial (Eemian), during which this plant was diffused in the Mediterranean area. The *Terre brune* deposition occurred when the environment was open, with rare trees and shrubs and prevailing steppe elements. This association reflects the climatic conditions of the Lateglacial, with evidence of both the warm interstadial Bølling/Allerød and the cold stadial Younger Dryas. Mediterranean, mesophilous and riparian arboreal elements are present, especially in the Early Holocene levels. Comparison with modern pollen material allowed some fossil grains, found in high amounts and in clusters, to be tentatively ascribed to the species *Crithmum maritimum* (Apiaceae), *Muscari comosum* and to *Asparagus maritimus*/*Ornithogalum* (Asparagaceae). The significant occurrence of such entomophilous plants reveals differential transportation inside the cave and, since most of them are edible and/or have medicinal properties, suggests an intentional introduction and possible use during time, by both Neanderthals and modern humans.

Keywords

Eemian; Lateglacial; *Olea*; edible plants; Neanderthals; *Homo sapiens*

1. Introduction

The Italian Peninsula occupies a strategic position in the heart of the Mediterranean area, playing a pivotal role in the study of paleoenvironmental dynamics during the Quaternary (e.g. Suc et al., 1995, Sadori et al., 2013, Sardella et al., 2018). The wide latitudinal extension of this territory (47°-35°N), and the presence of a mountain chain (Apennines) all along this axis, causes a strong climatic gradient and marked regional differences. This variety of environmental conditions strongly impacted faunal and floral assemblages during the last 2.6 Ma, a period that experienced major climatic oscillations and a general drop in temperatures and humidity (e.g. Suc et al., 1995, Sardella et al., 1998, Sala and Masini, 2007, Bertini, 2010, Kustatscher et al., 2014, Combourieu-Nebout et al., 2015). In this context, the Apulia region represents a kind of "peninsula in the peninsula", spanning for more than 350 km in the NW-SE direction and only 30 km along the SW-NE axis (Fig. 1a). The remarkable number of Middle Pleistocene to Holocene deposits makes this region a key territory for the study of the Quaternary terrestrial ecosystems in the Mediterranean area, especially concerning faunal assemblages.

The earliest archaeological research in Apulia took place in the late 1800s, with the discovery of a number of coastal caves, which yielded a rich paleontological record, including human fossils. Grotta Romanelli (GR) was discovered by Ulderigo Botti in 1874. The cave was inaccessible because it was completely filled by sediments, and therefore Botti focused his study on the breccia cropping out outside the cave (Botti, 1874). The first excavation campaigns were conducted by Paolo Emilio Stasi in the early 1900s and directed by Gian Alberto Blanc since 1914. These activities immediately had a great resonance in the international scientific community, bearing the first evidence of the Upper Palaeolithic in

Italy. Grotta Romanelli was the first site where the systematic palaeontological/archaeological and stratigraphical approach was applied by using a scientific method, still adopted today (Blanc, 1920, 1928, Sardella et al., 2018, 2019, Tarantini, 2018; Forti et al., 2020). The fieldwork activities continued until the early 1970s, directed by Istituto Italiano di Paleontologia Umana (Italian Institute of Human Paleontology), coordinated by Luigi Cardini.

In 2015, new multidisciplinary research started, coordinated by Sapienza, University of Rome, with the support of other research institutions and with the authorization of Soprintendenza Archeologia Belle Arti e Paesaggio, Brindisi e Lecce. The aim of this project is to update and redefine the stratigraphical and chronological context as well as to revise fossil remains (including *Homo*), artefacts, and cave and mobiliary art.

In the framework of this last research project, the first palynological analyses were carried out on the infilling deposits of the cave in order to give further constraints to the palaeoenvironmental context and its chronological implications. Due to the detritic nature of the deposits covering the Middle and Late Pleistocene, no continuous pollen sequence is available in Apulia, where only Holocene records were analysed (Caroli and Caldara, 2007, Di Rita and Magri, 2009). This makes the new data from GR particularly important in contributing to defining the palaeoenvironments of the Middle and Upper Palaeolithic.

FIGURE 1

2. Study site

Grotta Romanelli (40°00’58" N, 18°26’01" E) is a cave located on the Ionian side of the Salento peninsula (southernmost part of Apulia, Italy), in the municipality of Castro (Lecce) (Fig. 1a). The Salento peninsula is part of the Apulia Carbonate Platform, and is composed of Jurassic-Cretaceous limestone and dolostone capped by Neogene to Quaternary sediments stretching between the Adriatic and Ionian Seas (Fig. 1b). Karstic landforms characterize this territory, as testified by many coastal caves, sinkholes and karst fissures. The Ionian coast, between Otranto and Leuca, is characterised by steep sea-cliffs 50 to 100 metre high. In this area, many caves open into the steep coastline (e.g. Grotta Romanelli, Grotta Zinzulusa, Grotta delle Striare) or are submerged beneath the present sea level (e.g. Grotta Azzurra, Grotta Palombara). Grotta Romanelli opens at 7.3 m a.s.l into the Ciolo limestone Formation, a bioclastic calcarenite-calcirudite of the Upper Cretaceous, which is overlapped by the Castro limestone Formation, a fringing reef of the Oligocene (Pomar et al., 2014) (Fig. 1c).

The climate of Apulia is characterised by warm-dry summers and more humid conditions in autumn and winter, with isotherm gradients from North to South. Mean annual temperature and precipitation are typically Mediterranean (18°C and 675 mm respectively; Polemio and Lonigro, 2013) while climatic parameters vary in the hills and mountains of the Apennines, lying in the northern part of the region, where colder (and snowy) winters and cooler summers are attested. The local vegetation is characterised by the Mediterranean open forest growing on limestone substrates in the lower mesomediterranean bioclimatic belt (Biondi et al., 2004). Oak woods dominate and are mainly formed by holm oaks (*Quercus ilex* L.) and kermes oaks (*Q. coccifera* L.) often mixed with downy oaks (*Q. pubescens* Willdenow), even if local formations of the Macedonian oak (*Q. trojana* Webb) are also frequent in the central part of the region. Evergreen sclerophyllous elements are abundant, such as strawberry tree (*Arbutus unedo* L.), olive tree (*Olea europaea* L.), green olive tree (*Phillyrea latifolia* L.), lentisk (*Pistacia lentiscus* L.), Italian buckthorn (*Rhamnus alaternus* L.), myrtle (*Myrtus communis* L.), often mixed with mesophilous trees like manna ash (*Fraxinus ornus* L.), Christ's thorn (*Paliurus spina-christi* Miller), blackthorn (*Prunus spinosa* L.), almond-leaved pear (*Pyrus amygdaliformis* Villars) (Macchia et al., 2000). In the Salento peninsula kermes oaks and holm oaks form the main arboreal component of woods with shrubs such as lentisk, Italian buckthorn, strawberry tree and myrtle. Worth of mention is the presence of Aleppo pine (*Pinus halepensis* Mill.) along the Salento Adriatic coast (Fady et al. 2003).

2.1. The deposits infilling the cave

The sedimentary succession of GR was firstly described by Stasi and Regalia (1904), who identified the main complexes infilling the cave. The stratigraphic scheme was implemented by Blanc (1920, 1928) and later enriched by radiometric dates in the 1950s and 1960s. Blanc reported a basal marine conglomerate (level K) directly covering the Upper Cretaceous carbonatic bedrock (level L, Fig. 2) and testifying to the submersion of the cave during the Last Interglacial period (Riss-Würm). On top of level K, Blanc (1928) reported traces of a fireplace and fossil bones of warm faunas including hippo, elephas and rhino. The thick level of calcareous breccia (level I) covering the beach (level K) was interpreted as the result of rock falls occurring within the cave during the same warm period, as testified by the presence of the same fauna, traces of fire and a few limestone tools (Blanc, 1928). A speleothem of ca. 20 cm (level H), sealing levels K and I, was considered the first evidence of a profound hydroclimatic change linked to the Würm glaciation (Blanc, 1928). Speleothem H is covered by the fine complex of *Terre rosse* (level G). This deposit was attributed to a warm and dry interstadial phase, following the Würm acme (*sensu* Blanc, 1928). Due to its aeolic origin and the diffuse occurrence of pachyderms, level G was associated with the existence of a wide coastal plain drained by rivers, formed in front of GR thanks to a marine regression. The chronological attribution proposed by Blanc (1928) was considered too young by several authors (e.g. Piperno, 1974, Masini et al., 1990, Sala et al., 1992, Sardella et al., 2014, 2018) who ascribed a more archaic character to both the faunal assemblages and lithic industries. The thin speleothem F, discontinuously covering the *Terre rosse* (Fig. 2), was as well ascribed to a period of enhanced precipitation associated at that time (Blanc, 1928) with the last advance of the Würm glaciation. Thanks to the U/Th dating of speleothems H and F (Fig. 2, Table 1), the *Terre rosse* deposition was successively constrained to a period between <69,000 and ca. 40,000 yrs BP (Fornaca-Rinaldi and Radmilli, 1968), at present encompassing part of Marine Isotope Stage (MIS) 4 and MIS 3. These radiometric data confirmed the chronology of the lower part of the deposit previously proposed by Blanc.

Speleothem F marks the transition between the *Terre rosse* and the overlying *Terre brune* (levels A-E). The latter, ascribed to aeolian deposition during a cold and arid period (Blanc, 1928), was characterised by a rich fossil fauna with horses and birds, among others, typical of steppic environments, and ascribed to the last phases of the Würm glaciation. The successive radiocarbon dating of several samples from levels A to E (Table 1; Bella et al., 1958, Vogel and Waterbolk, 1963, Alessio et al., 1965) constrained the deposition of *Terre brune* to a period between ca. 11,000 and ca. 9000 yr BP, now corresponding to the Early Holocene.

FIGURE 2 - TABLE 1

The results of more recent AMS ^{14}C dating, obtained by teeth and postcranial elements of mammal fossils collected from *Terre brune* (Table 1; Calcagnile et al., 2019, Sigari et al., 2021), expand and refine the previous chronology, with lower levels (level E *sensu* Blanc, 1920; Fig. 2) encompassing the Late Pleistocene-Holocene boundary and extending the chronology of the upper levels (level B *sensu* Blanc, 1920; Fig. 2) to the earliest Early Holocene.

Since the first discovery of modern human bones in *Terre brune* (Stasi and Regalia, 1904), fragmentary remains of at least six adults and six children were studied by Fabbri (1987) and compared to the Upper Palaeolithic populations of Italy and Europe. Very abundant lithic tools (more than 10,000), artifacts, and bone industry, attributed to the final Epigravettian, the so-called Romanellian (Mussi, 2002, Bietti, 2003), were recovered in *Terre brune*, demonstrating occupation by modern humans in different stratigraphic levels. No bone artifact was recovered from the *Terre rosse* but the over 1000 limestone tools found in its basal levels and referred to the Middle Palaeolithic (Mousterian: Piperno, 1974, Spinapolice, 2008, 2018) indicate occupation by Neanderthals. The first evidence of their presence in the cave is provided by remains of fireplaces discovered below *Terre rosse*, associated with some limestone, flint, and quartzite tools (Blanc, 1928, Piperno, 1974).

3. Palaeoenvironmental and paleoclimatic data based on faunal assemblages

Preliminary palaeoenvironmental and paleoclimatic reconstruction of GR was performed by Blanc (1920, 1928), who interpreted *Terre rosse* on the basis of faunal finds as typical of warm and arid climatic conditions and *Terre brune* of cold climatic conditions.

The fossils from *Terre rosse,* never formally described or figured, were included in a faunal list more than one hundred years ago by Blanc (1920) (Table 2). A large revision is in progress to update the taxonomical attribution, as well as to investigate morphological and biometric adaptations in response to climate changes, and to get taphonomic data in relation to a possible human exploitation.

TABLE 2

In the last decade, the canid remains from *Terre rosse* were attributed to *Canis lupus* by Sardella et al. (2014), whereas the rhino sample from the same level was referred to *Stephanorhinus hemitoechus* (Falconer, 1868) by Pandolfi et al. (2017). Recently, the occurrence of *Lutra lutra* from *Terre rosse* was also confirmed by Mecozzi et al. (2021). The presence of this carnivoran is of considerable interest for paleoenvironmental reconstruction, since its ecological profile indicates a strong relation to large freshwater bodies (rivers or lakes). These kinds of habitats are no longer present in the southern part of Apulia, suggesting important landscape and hydrological changes during the late Quaternary. Moreover, 109 different bird species were identified, based on ca. 32,000 fossil remains from

Terre brune that currently represents the largest osteological Italian sample (Cassoli and Tagliacozzo, 1997). The species identified were prevalently adapted to cold-temperate climates (75% of the remains), referable to steppe and grassland environments. One of the most important climatic indicators for *Terre brune* is the great auk *Pinguinus impennis* (Linnaeus, 1758) (=*Alca impennis*), a North Atlantic and Subarctic marine species (Blanc, 1927, Cassoli and Tagliacozzo, 1997). The mammal fauna of *Terre brune* is dominated by *Cervus elaphus* (25.7%) and red fox, *Vulpes vulpes* (Linnaeus, 1758) (25.1%), followed by Regàlia ass *Equus hydruntinus* Regàlia, 1906 (21.7%) and *Bos primigenius* (19%). Other species are instead sporadic (Table 2). Of considerable interest is the presence of the Alpine marmot *Marmota marmota* (Linnaeus, 1758). Nowadays, this species inhabits alpine meadows and high-altitude pastures, typically on south-facing slopes from 1200-3000 m. Its findings in GR attests to the occurrence of open environments and cold climatic conditions, also supported by abundant remains of *E. hydruntinus* and *B. primigenius*. However, the rich sample of *C. elaphus* also suggests the presence of forests.

Iannucci et al. (2020) studied a large sample of *Sus scrofa* from the Quaternary record of Apulia, including the record from *Terre brune*. The results indicate that *S. scrofa* from GR had a smaller size, similar to the fossil record from the cooler stages of the Late Pleistocene in Apulia, significantly different from the Last Interglacial record of this region.

4. Materials and methods

The palaeobotanical samples analysed in this work were collected from four different sections of the cave: one located in the western sector (SS1), two located in the northern sector (SS2 and SS3), and one located in the southern sector (SS4) (Fig. 3). Details concerning thickness and chronology of the sampled sections can be found in Fig. 4.

FIGURES 3, 4

Pollen analysis was carried out on 49 sediment samples (Fig. 4), 17 of which from *Terre rosse* (SS2 and SS4), and 32 from *Terre brune* (SS1, SS2, SS3, and SS4).

The amount of processed dry sediment varies from 2 to 5 grams. Samples were treated with standard laboratory procedures for the extraction of fossil pollen grains (e.g. HCl 37%, HF 40%, NaOH 10%) following Fægri and Iversen (1989). In addition to the above-mentioned procedures, ultrasonic sieving (11 µm) and floating with $ZnCl_2$ were carried out for increasing pollen concentration in all samples of *Terre rosse*. Pollen concentration was calculated by adding *Lycopodium* spores to the known amount of sediment (Stockmarr, 1971). The identification of pollen grains was based on atlases (Reille, 1992, 1995, 1998) and reference collections. Following Smit (1973), *Quercus robur* type groups pollen of deciduous oaks and *Quercus cerris* type those of semi-evergreen oaks plus *Q. suber*; *Q. ilex* and *Q. coccifera* are included in the *Quercus ilex* type. We used the tribe name Cichorieae for fenestrate pollen grains as this is the only European tribe of Asteraceae Cichorioideae with this feature (Florenzano et al., 2015).

In some levels, Apiaceae and monocolpate, ornamented pollen grains of monocot families (whose systematic was recently deeply revised, see Stevens, 2001 onwards) were recognised in significant amounts and in clusters. In order to possibly identify single species and discuss their significance in our pollen record, a comparison between fossil and modern pollen grains was attempted. The modern species were selected on the basis of their morphological pollen features and geographical distribution (coastal areas of the Mediterranean). In particular, the small (longest axis 20-25 µm) fossil grains of Apiaceae were compared with modern samples of the species *Ammi visnaga* (L.) Lam. (syn. *Visnaga daucoides* Gaertn.) (Plate I, 1-2), *Crithmum maritimum* L. (Plate I, 3-4), and *Trinia glauca* (L.) Dumort. (Plate I, 5-6). Concerning the reticulate/perforate monocot fossil pollen grains, they were compared with different Asparagaceae (*sensu* Stevens, 2001 onwards) species selected on the basis of their pollen morphology, ecology and distribution (Pignatti, 1982): *Asparagus acutifolius* L. (Plate II, 1), *A. aphyllus* L. (Plate II, 2), *A. maritimus* (L.) Mill. (syn. *A. scaber*) (Plate II, 3), *Loncomelos pyrenaicus* (L.) L.D. Hrouda (syn. *Ornithogalum pyrenaicum L.*) (Plate II, 4), *Muscari comosum* (L.) Mill. (Plate II, 5), *Ornithogalum exscapum* Ten. (Plate II, 6), and *O. umbellatum* L. (Plate II, 7). The modern material, provided by the *Herbarium Sapienza* (Rome, Italy) and recovered in the proximity of the cave, was treated with acetolysis in order to remove the cytoplasm content and highlight the pollen wall morphology.

5. Results

Terre rosse are almost depleted in pollen while *Terre brune* have quite variable counts and concentration, whose values range from 67 pollen grains/g in sample B311 (SS1) to ca. 21,000 grains/g in sample B328 (SS4). Concentration values in *Terre rosse* are even lower, ranging from 0 in barren levels to 1390 grains/g in the richest sample (B317, SS4).

Due to the variable pollen content and the high values of Asteroideae and Cichorieae, raw data are presented in tables (Table 3 for *Terre rosse* and Tables 4, 5, 6 for *Terre brune*) instead of percentage diagrams. The bad preservation and resulting over-representation of Asteraceae (Cichorieae and Asteroideae), the low diversity and the very low pollen concentration are expected in cave records (Carrión et al., 1999, Navarro Camacho et al., 2000, Lebreton et al., 2010, Hunt and Fiacconi, 2018), and we are aware of the fact that different taphonomic biases occurred at GR, favouring the selective preservation of pollen grains in some levels. Nonetheless, the different pollen assemblages from *Terre rosse* and *Terre brune* samples seem to confirm that our pollen spectra represent source vegetation at both local and regional scales.

TABLES 3-6

As a general remark, the basal part of *Terre rosse* (SS2 and SS4) provided samples richer than the upper part, which is almost barren in pollen (Table 3). The ubiquitous and main element in all samples is *Olea*, accompanied by a few other trees (e.g. *Quercus ilex* type, *Q. robur* and *Q. cerris* types, *Pinus*) and some frequent herb taxa (e.g. Asteroideae, Cichorieae, Asparagaceae, Brassicaceae, Caryophyllaceae, Poaceae, Apiaceae). A sporadic presence of *Abies* and *Fagus* is notable. It is worth mentioning the occurrence of considerable amounts of Asparagaceae pollen in two levels from section SS4 (B317 and B314) and a single occurrence in one level from SS2 (B331). The pollen grains of all Asparagaceae from *Terre rosse* show a high similarity with those of *Muscari comosum* (Plate II, 11-13). Comparison of the numerous grains of Apiaceae (often in clusters) found in the basal level of *Terre rosse* (B314, SS4) with modern pollen of selected taxa suggests similarities with the species *Trinia glauca* (L.) Dumort and *Crithmum maritimum* L. (Plate I, 9, 10, 12). The latter, currently present near the cave, shows a greater resemblance to our fossil grains.

Most of the pollen record from *Terre brune* is characterised by the overwhelming presence of Cichorieae, accompanied by other herb taxa (e.g. Asteroideae, Brassicaceae, Amaranthaceae, Poaceae, Ranunculaceae, Asparagaceae). Tree taxa are represented by sporadic elements of the mesophilous (e.g. *Q. robur* and *Q. cerris* types, *Ulmus*) and Mediterranean (e.g. *Q. ilex* type, *Juniperus*, *Olea*, *Cistus*, *Pistacia*) vegetation (Tables 4, 5, 6). Riparian trees are also present (e.g. *Tamarix*, *Alnus*, *Salix*, *Populus*). The basal part of *Terre brune* from SS1 shows a quite high pollen variability with respect to the upper part: at the bottom herb pollen prevails, whereas toward the top, in samples with very low pollen concentrations and counts, tree pollen dominates and even the well-resistant pollen grains of the Asteraceae family (Asteroideae, Cichorieae) are absent.

The pollen amount in *Terre brune* from SS4 is notable. Both the lower and upper levels show a selective preservation highlighted by the high amounts of Cichorieae, while peaks of single taxa appear in the other samples. In level B326, the dominant taxon is *Juniperus*, accompanied by a few herbs (*Artemisia*, Ranunculaceae, Poaceae). On the other hand, level B328, which is the richest in pollen, displays very high amounts of Apiaceae and Asparagaceae together with Fabaceae, Ranunculaceae and Poaceae.

Also the pollen grains of Apiaceae from *Terre brune* are more similar to *Crithmum maritimum* (Plate I, 7, 8, 11), a Mediterranean species of the carrot family. Concerning the Asparagaceae, a convincing similarity is found between the fossil grains from *Terre brune* and the species *Asparagus maritimus* and *Ornithogalum* (Plate II, 8-10).

PLATES I-II

6. Discussion

Carbonate rich cave sediments are characterised by the scarcity of pollen due to a number of limiting factors. The absence of waterlogged conditions and consequent chemical degradation (i.e. oxidation) can lead to differential preservation with possible over-representation of pollen grains more resistant to oxidation (e.g. Asteraceae; see also Carrión et al., 1999). Moreover, sedimentation is generally discontinuous, with events of erosion and redeposition (Hunt and Fiacconi, 2018, Spinapolice et al., 2021) and pollen can be transported either by water through the soil or by wind into the cave itself (Cremaschi et al., 2014), making uncertain the time lapse between pollen production and sedimentation. The role of humans and animals in pollen transportation is a further complication (Mercuri, 2008a, b) but can provide interesting knowledge on the cave occupation. The contribution of entomophilous and zoophilous pollen from local vegetation to cave records is attested through several vectors (Burney and Burney, 1993). In addition, the pollen counts and the number of taxa are generally so low that they do not allow a statistical representation. Despite these taphonomic biases, fossil pollen sequences from caves have been used to reconstruct past landscape in the

Mediterranean environments where lacustrine deposits are not common (e.g. Renault-Miskovsky, 1972, Gale et al., 1993, Carrión et al., 1999, Mancini et al., 2002, Kaniewski et al., 2004, 2005a-c, Karatsori et al., 2005, Polk et al., 2007, de Porras et al., 2011, Peretto et al., 2020), as in the case of Apulia. As a matter of fact, pollen data from GR provides new insights into the palaeoenvironmental setting of the deposits, with implications on their chronological attribution, and into the possible plant use by humans.

6.1. Pollen evidence of changing climates and environments

Despite the general scarcity of pollen in all samples from *Terre rosse*, it is noteworthy that *Olea* is the only taxon which is always represented with the highest number of grains (Table 3). The wild olive is a thermophilous plant, typical of the Mediterranean vegetation, which colonizes the coastal areas, including rocky ones, of the Mediterranean basin (Pignatti, 1982). Its presence in all samples is clear evidence that the sedimentation of *Terre rosse* occurred during a warm and probably arid period.

The high amount of *Olea* pollen in the *Terre rosse* samples stimulated us to carry out a comparison with the nearest continuous pollen records covering the last climatic cycles. In particular, at Valle di Castiglione, near Rome, *Olea* is sporadic all along the sequence (MIsS 9a to MIS 1; Follieri et al., 1988) with the exception of MIsS 5e, where it shows a significant peak reaching 10% (Fig. 5). The same behaviour can be noticed in the pollen records of Ioannina (Tzedakis and Bennett, 1995) and Tenaghi Philippon (Fletcher et al., 2013, Milner et al., 2016), in Greece, where the only significant peak of *Olea* is recorded during MIsS 5e, being almost absent during the other intercepted interglacial stages (Fig. 5). At Monticchio (southern Italy), *Olea* has a peak during MIsS 5e (Allen et al., 2000, Allen and Huntley, 2009) but the record ends at MIS 6, so it is not possible to say if it was present during older interglacial phases. In the Massif Central (Velay, France) the *Olea* record is more variable and probably represents long-distance pollen transport, but clearly shows higher values during MIsS 5e (Tzedakis et al., 2001). No separate curve for *Olea* is provided for the long pollen record of Carrizar de Villarquemado, in Spain (González-Sampériz et al., 2020)

All considered data suggest constraining *Terre rosse* to the Eemian (MIsS 5e), confuting the stratigraphical attribution of Blanc (1920) that had ascribed this deposit to a warm and dry phase following the Würm acme, later ascribed to MIS3 by the U/Th dating (Fig. 2, Table 1; Fornaca-Rinaldi and Radmilli, 1968). From a paleontological viewpoint, the fossil assemblage from *Terre rosse* assumed an important role for the evolution of mammal palaeocommunities (e.g. Di Stefano et al., 1992, Mazza, 1995, Palombo et al., 2001). Considering the old U/Th age (Table 1), the record from *Terre rosse* was long deemed as the latest occurrence of *P. antiquus* and *H. amphibius*. Instead, an attribution of the *Terre rosse* mammal assemblage to MIsS 5e is in agreement with the wide diffusion of these two large herbivores all along the Italian Peninsula during this stage, also confirming that their extinction could have occurred at the end of the Last Interglacial. A MISs 5e age for *Terre rosse* is also consistent with the presence of *L. lutra*, a carnivoran with an ecological profile indicating a strong relation to large freshwater bodies (rivers or lakes), habitats that are no longer present in the southern part of Apulia.

Very few cave records in the Mediterranean region provide evidence of the Last Interglacial period (Carrión et al., 1998, Ochando et al., 2020). In particular, the pollen sequence at Cueva de la Carihuela (Granada, southern Spain) covers most of the last glaciation starting at the end of the Last Interglacial, which is characterised by both a *Quercus-Olea* association and noteworthy pollen diversity of meso-thermophilous species (Carrión et al., 1998). In those basal levels of the cave deposits, *Olea* shows very high values, reaching 40%, before suddenly dropping until disappearing during the last glacial period.

The abundance of *Olea* recorded during MIsS 5e all around the Mediterranean suggests that this warm phase was drier with respect to other interglacials. In southern Italy, the Last Interglacial was marked by the expansion of Mediterranean communities at low altitudes and even at middle altitudes, especially south of 43°N (Combourieu-Nebout et al., 2015). Pollen-based climate reconstructions for southern Italian sites show that Mean Temperature of the Coldest Month during MIsS 5e was nearly as warm as during the Early Pleistocene interglacials. Nevertheless, annual precipitation remained low compared to the earlier interglacials (Combourieu-Nebout et al., 2015). The available quantitative estimates of climate and bioclimate parameters in western Balkans (Sinopoli et al., 2018, 2019) show that mean annual temperatures were rather high during MIsS 5e, while mean annual precipitation resulted as a whole slightly lower with respect to the following interstadials of MIS 5 (MIsS 5a and 5c).

FIGURE 5

Radiocarbon dates circumscribe most of *Terre brune* to the Lateglacial period and some levels to the beginning of the Holocene (see the chronostratigraphical scheme for NW Europe by Cohen and Gibbard, 2019). On the whole, the Lateglacial levels from the dated investigated sections can be correlated to both the interstadial Bølling/Allerød and to the stadial Younger Dryas. In fact, minor differences in pollen data seem to confirm the different environments, with arboreal pollen of mesophilous and Mediterranean trees prevailing on non-arboreal pollen of steppe taxa in the interstadial levels. In this respect, worth of mention is the quite ubiquitous presence of *Olea* in the northern sector (SS2 and SS3), with a peak in level B351 from SS3 (Table 5). Its occurrence clearly testifies to the expansion of thermophilous vegetation during the Bølling/Allerød interstadial. On the other hand the samples from SS4, for which radiocarbon dates are not available, suggest colder and dryer climatic conditions, with presence of *Artemisia* in the three lowermost levels (Table 6). The most recent of them shows the remarkable abundance of the pioneer *Juniperus* (151 pollen grains out of 198). It is also interesting the presence of other arboreal plants such as *Tamarix* and *Quercus*. The upper levels of SS4 show an increase of trees. The plant environment is consistent with the changes that occurred at the end of the last glacial/start of the present interglacial in the Adriatic region and in the close Balkan area (Lowe et al., 1996, Combourieu-Nebout et al., 2013, Masi et al., 2018). The most interesting sample is B328 (Table 6): it represents an anomaly for the high pollen count (574 pollen grains), number of pollen types (19), and concentration (more than 21,000 pollen grains/g). The most striking features are the presence of entomophilous pollen in clusters (cf. *Crithmum maritimum*, *Asparagus maritimus/Ornithogalum*, Fabaceae) and the complete absence of Asteraceae, both Asteroideae and Cichorieae. Another peculiarity is the presence of pollen from riparian trees such as *Alnus*, *Tamarix* and *Salix*. The good state of preservation and the presence of pollen clumps should be related to faeces, possibly indicating frequentation of the cave at the beginning of the Holocene. The uppermost samples see the overwhelming presence of Cichorieae.

In most of *Terre brune* Asteraceae prevail, accompanied by other herbs. Even if oxidation processes have been already postulated for the over-representation of Asteraceae (Carrión et al., 1999), other taphonomic issues (such as pollen transport by animals and/or humans into the cave) should be taken into account (Lebreton et al., 2010). As a matter of fact, the overwhelming presence of these herbs in *Terre brune* can be associated with the Lateglacial landscape (see the MD90917 Adriatic core, Combourieu-Nebout et al., 2013), as clearly testified by their disappearance in the SS1 levels dated to the early Holocene (Table 4). The identification of alpine marmot (*M. marmota*) from the same deposits confirms the spread of dry pastures in the region. At GR the *quasi* ubiquitous presence of riverine tree pollen (*Alnus*, *Salix*, *Tamarix*) refers to freshwater environments and might be fostered by the preferential transport of pollen through karstic canals.

Samples dated to the Holocene (B311, B312, B313 from SS1; Fig. 4a, Table 4) are almost depleted in pollen, with minor presence of herbs and a major component of trees. Mediterranean trees (e.g. *Q. ilex*) and pioneer plants such as *Juniperus* and Rosaceae (for the latter a possible use as fruit trees could be advanced) prevailed and preceded the following expansion of Holocene vegetation.

6.2. Human-environment interactions in Middle and Upper Palaeolithic

In the lower pollen samples of *Terre rosse* from both SS2 and SS4, we emphasize the presence (more abundant in SS4) of cf. *Muscari comosum* (grape hyacinth), a species of Asparagaceae family which is absent in the higher levels (Plate II, 11-13). This herb, typical of the Mediterranean coastal areas, grows in the olive zone and prefers limestone soils; its bulb (locally named "lampascione") is consumed as a traditional food in Italy, and especially in Apulia. In the lowermost sample of SS4, noteworthy is also the presence of numerous single grains and clusters very similar to *Crithmum maritimum* (rock samphire/sea fennel), an edible wild plant typical of rocky marine coasts, with a wide latitudinal distribution, ranging from Great Britain and Ireland to North Africa and Canary Islands (Plate I, 12). Sea fennel is still part of the traditional food of Mediterranean countries either gathered from rocky shelters or cultivated and served as a vegetable with fish dishes. It was also used by sailors for its high content of C vitamin.

Grape hyacinth and sea fennel are both entomophilous herbs producing rather low pollen amounts, mostly dispersed by insects and not by wind. The high amount of their pollen grains found at the base of *Terre rosse* suggests transportation inside the cave by animals or humans. Clumps of pollen may in fact be a marker of faeces, suggesting the ingestion of flowers (Mercuri 2008a) by animals and/or humans. It is worth stressing that, apart from the occurrence of cf. *Muscari comosum* and cf. *Crithmum maritimum*, pollen in *Terre rosse* is slightly more abundant in the lower samples (Table 3, from B331 to B317). In the same levels, new fossils and lithic tools, found during 2016-2019 excavations and currently under study, are added to those already collected during historical excavations (e.g. Stasi and Regalia, 1904, Blanc, 1920, 1928, Piperno, 1974). The majority of these materials, among which a rich sample of limestone artefacts referred to the Mousterian (Middle Palaeolithic), clearly indicates the occupation of the cave by Neanderthals (Piperno, 1974, Spinapolice, 2018). According to Blanc (1920), many fossils of large mammals display traces of exploitation, which strongly suggests that those animals had been hunted and consumed by Neanderthals. This aspect, however, will be clarified thanks to the new data obtained during the last excavations. By contrast, the upper levels of *Terre rosse* are depleted (or completely barren) in artefacts or bones. The scarcity of archaeological evidence from these levels was noted by Piperno (1974), who described 997 artefacts from the lower levels, out of 1105 recovered from the entire unit. The upper levels of *Terre rosse* are also very poor or completely barren in pollen (Table 3). This coincidence allows us to postulate that the relatively higher presence of pollen in the lower levels may be related to intentional transport by humans, probably for food or other purposes. Transport by animals on their furs cannot be ruled out. Despite Neanderthals are most often viewed as carnivores who derived the vast majority of their diet from meat, studies of Neanderthal tools and teeth from Eastern and Western European sites have shown that they were using several kinds of plants in their diets and, perhaps more importantly, in their medicinal and ritual traditions (Hardy et al., 2012, Salazar-Garcìa et al., 2013, Shipley and Kindscher, 2016, Power et al., 2016, 2018, Miras et al., 2020). Particularly interesting is the finding, among others, of *Muscari* remains in the

Shanidar grave (northern Iraq), in which a Neanderthal was buried with several plants recognized as having medicinal properties (Solecki, 1975).

As already stressed for *Terre rosse,* we found high amounts and clusters of cf. *Crithmum maritimum* (Plate I, 11) even in *Terre brune,* in addition to a great number of pollen grains (176 pollen grains in sample B328 of SS4) of *Asparagus maritimus*/*Ornithogalum* (Plate II, 8-10). As discussed for *Muscari*, since the pollination of Asparagaceae is entomophilous and pollen grains are big, the occurrence of these pollen grains could mean a preferential transportation inside the cave by animals and/or humans. On the other hand, the contribution to the human diet from plants of the local vegetation, having underground storage organs rich in starch and, therefore, being processed as a source of carbohydrates and energy, is documented since the earliest phase of the Upper Palaeolithic (Revedin et al., 2010). In contrast to the grape hyacinth found in *Terre rosse*, which has an edible bulb, a number of toxic species belong to the genus *Ornithogalum*. Nonetheless, if the bulbs are boiled, they can be consumed and the same is true for the flower stems, edible if cooked like the more common *Asparagus*. The use of such stems, which could be served as human food, was postulated for the Upper Palaeolithic of Europe (e.g. Jones, 2009). For all this evidence, we can assume that the consumption of these plants probably contributed to the essentially carnivore diet of the modern humans frequenting GR, also demonstrated by the abundant bone remains, mostly of birds, found throughout *Terre brune*. As a matter of fact, the archaeozoological analysis of mammal remains revealed that most of the fossils were hunted by humans, even if the presence of coprolites and bite marks also supports the frequentation of the cave by carnivorans for short times (Tagliacozzo, 2003). Similar results were reported by the analysis of bird bones from the same levels of *Terre brune*, with evident signs of butchering (i.e. cut marks and burning: Cassoli and Tagliacozzo, 1997, Cassoli et al., 2003). Moreover, the long-lasting occupation of the cave by *Homo sapiens* during the Upper

Palaeolithic is documented by a diversified record, which includes not only human fossils and lithic artefacts as already reported, but also hearts, mobiliary and parietal art (Blanc, 1928, Sardella et al., 2018, Sigari et al., 2021).

Although differential preservation of Asteraceae pollen could have occurred, the relative abundance of both Cichorieae and Asteroideae pollen in *Terre brune* (and their *quasi* absence in *Terre rosse*) is incontestable. It could have been tied to animal introduction (e.g. faeces) or to intentional transport as food, medicine, and/or ritual plants, since such herbs have leaves and seeds that may have been gathered by modern humans (e.g. Riehl et al., 2015, Martkoplishvili and Kvavadze, 2015).

Other pollen taxa found at GR, including possible edible plants, are Amaranthaceae, Fabaceae and Poaceae, whose contribution to the diet of our ancestors is becoming well-known thanks to the study of plant microfossils from a variety of archaeological deposits (e.g. Piperno et al., 2004, Aura et al., 2005, Pryor et al., 2013, Power and Williams, 2018). In particular, the first-documented preference for Poaceae caryopses, as opposed to underground organs, in processing plant food with high nutritional value (i.e. flour), comes from Grotta Paglicci in northern Apulia, where oat starch grains from grinding tools of the early Upper Palaeolithic levels (ca. 32 600 years BP) have been studied (Mariotti Lippi et al., 2015).

Conclusions

Notwithstanding the possible biases affecting pollen studies in caves (e.g. low pollen concentration and taphonomical issues), we have highlighted the different environments in which *Terre rosse* and *Terre brune* deposited. The attribution of *Terre rosse* to the Eemian is the main novelty of this study and was based on the presence, in the pollen spectra, of consistent amounts of olive tree, whose expansion is recorded all around the Mediterranean area during MIsS 5e. This new chronological attribution opens up interesting implications on the stratigraphical significance of the beach (level K) identified by Blanc (1920, 1928) below *Terre rosse* (level G), and ascribed to the Last Interglacial period (Riss-Würm). The cold character of the interposed speleothem (level H) suggests possibly assigning that marine highstand (beach, level K) to a previous interglacial phase. New U/Th dating of speleothems H and F, which is in progress, will help clarify the question.

The *Terre brune* deposition occurred when the environment was relatively open, with rare trees and shrubs and prevailing herbs. Mediterranean, mesophilous and riparian arboreal elements are present, with changes among sections and single samples.

The use of plants is not easily detectable through pollen in cave sites, where during most of Prehistory humans exploited wild plants. No particular evidence of accumulation of plants is found at GR, apart from some clusters of Apiaceae pollen, probably belonging to marine fennel, a wild, edible Mediterranean herb. The presence of some monocot pollen grains belonging to Asparagaceae suggest the possible consumption of bulbs and young sprouts by both Neanderthals and *Homo sapiens*. The interpretation of the high percentages of Asteraceae, a family to which numerous edible, medicinal, and ornamental herbs belong, is still open. Asteraceae pollen grains are almost absent in *Terre rosse*, whose sedimentation occurred in the Last Interglacial.

Still ongoing excavations at GR will hopefully provide new evidence about human-plant interactions and the environment of the last interglacial/glacial cycle, till now only partially known in southern Italy.

Acknowledgements

Authors wish to thank Judy Allen and Chronis Tzedakis for sharing their raw pollen data from Monticchio and Ioannina. An acknowledgement to Mauro Iberite and Agnese Tilia for supporting in the selection of modern plant material, and to Maretta Colasante for her suggestions on Iridaceae pollen. Authors are also thankful to the Soprintendenza archeologia, belle arti e paesaggio delle province di Brindisi, Lecce e Taranto for the authorisation of the research and field activities (2015–2017 and 2018–2020, resp. R. Sardella) (Maria Piccarreta, Laura Masiello and Serena Strafella), as well as to Castro municipality, the Capitanerie di Porto di Castro e di Otranto, and Parco Naturale Regionale Costa Otranto S.M. di Leuca - Bosco di Tricase. Many colleagues helped during the fieldwork activities: Jacopo Conti, Alessio Iannucci, Dawid Adam Iurino, Dario Sigari and Flavia Strani. Ninì Ciccarese, Toto De Santis, Don Piero Frisullo, Luigi Fersini, Alberto Antonio Capraro, Michele Rizzo and Gruppo Speleologico Salentino for their continuous and precious logistic support. We thank Rosalia Gallotti, Biagio Giaccio, Filomena Ranaldo, Simona Rosselli and Enza Spinapolice for their useful suggestions and help.

Vincent Lebreton and two anonymous reviewers are deeply thanked for their fruitful comments on the original manuscript.

Funding sources

This work was supported by Sapienza University of Rome (resp. Raffaele Sardella) grants Grandi Scavi 2016 (ref. SA116154CD9592F3), Grandi Scavi 2017 (ref. SA11715C81468801), Grandi Scavi 2018 (ref. SA1181642D3B3C58), Grandi Scavi 2019 (ref. SA11916B513E7C4B), Grandi Scavi 2020 (ref. SA120172B2C05E68).

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Plate I. Grotta Romanelli (Apulia, Italy). Reference pollen material (from the *Herbarium Sapienza* and the actual vegetation of the cave area): *Amni visnaga* 1-2; *Crithmum maritimum* 3-4; *Trinia glauca* 5-6. Apiaceae pollen grains from *Terre brune* (7, 8, 11) and *Terre rosse* (9, 10, 12) samples. Bars stand for 20 micron.

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Table 1. Grotta Romanelli (Apulia, Italy). Chronology of the deposits: old and new dates. Ages are calibrated with OxCal v.4.4 (Bronk Ramsey, 2017) using the IntCal20 curve (Reimer et al., 2020). If not specified, the probability is above 90%. For samples labelled with P the collagen was extracted from bone fragments or from crushed bones and dated. Greek letters refer to dates reported in Fig. 4.

Sample	Level	Material	Lab. Code	Radiometric age	^{14}C cal yr BP (2σ) IntCal20	References
			First dating set			
	A	Charcoal	GrN-2056	9880 ± 100	11745-11141	Vogel and Waterbolk, 1963
	A	Charcoal	GrN-2305	10320 ± 130	12623-11689	Vogel and Waterbolk, 1963
	A	Humic acid	R-54	9050 ± 100	10502-9804	Alessio et al., 1965
	A	Charcoal	R-58	11800 ± 600	15800-12681	Alessio et al., 1964
	B	Humic acid	R-56	11960 ± 320	15024-13237	reported in Alessio et al., 1964
	B	Humic acid	R-56	11930 ± 520	15595-12846	Bella et al., 1958
	C	Charcoal	GrN-2153	10390 ± 80	12497-11941	Vogel and Waterbolk, 1963
	C	Charcoal	GrN-2154	9790 ± 80	11402-11067	Vogel and Waterbolk, 1963
	D	Charcoal	GrN-2055	10640 ± 100	12770-12451	Vogel and Waterbolk, 1963
	F	Stalagmite		40000 ± 3250 (U/Th)		Fornaca-Rinaldi and Radmilli ,1968
	H	Stalagmite		<69000 (U/Th)		Fornaca-Rinaldi and Radmilli, 1968
			New dating set			
GR2016-206	B	Bone	LTL17293A	8048 ± 75	9135-8639	Calcagnile et al., 2019
GR2016-162	B	Bone	LTL 17303A	8397 ± 45	9499-9393	Calcagnile et al., 2019
RR529	B-C	Bone	SacA 61166	9925 ± 45	11408-11234 (79.8%) $^{\alpha}$	Sigari et al., 2021
RR529-P	B-C	Collagen	SacA 61170	9955 ± 45	11509-11245 (79.1%) $^{\alpha}$	
GR2017-464	C	Bone	LTL 17741A	9657 ± 65	11207-10770	Calcagnile et al., 2019
GR2016-	C	Bone	LTL	9822 ± 45	11319-11188 $^{\beta}$	Calcagnile et al., 2019

158			17299A			
GR2016-154	C	Bone	LTL 17295A	9774 ± 40	11622-11261 [γ]	Calcagnile et al., 2019
GR2016-105	C	Bone	LTL 17292A	11328 ± 60	13282-13110	Calcagnile et al., 2019
RR9	C	Tooth	SacA 61166	10880 ± 50	12895-12736 [δ]	Sigari et al., 2021
GR2016-159	C	Bone	LTL 17300A	10100 ± 80	11940-11388 [ε]	Calcagnile et al., 2019
GR2016-157	C	Bone	LTL 17298A	10277 ± 45	12192-11822 (81.9%)	Calcagnile et al., 2019
GR2016-465	C	Bone	LTL 17740A	10295 ± 75	12471-11820	Calcagnile et al., 2019
GR2016-153	D	Bone	LTL 17294A	10990 ±50	1307[illegible]-12816 (85.2%)	Calcagnile et al., 2019
GR2016-622	D	Bone	LTL 17737A	11409 ± 85	13457-13159 [ζ]	Calcagnile et al., 2019
GR2016-581	D	Bone	LTL 17736A	11685 ± 65	13666-13413 (88.1%) [ζ]	Calcagnile et al., 2019
GR2016-156	D	Bone	LTL 17297A	11892 ± 80	13886-13589 (78.8%) [η]	Calcagnile et al., 2019
GR2016-616	D	Bone	LTL 17738A	11858 ± 85	13870-13575 (81.7%) [θ]	Calcagnile et al., 2019
GR2016-522	D	Bone	SacA 61167	10730 ± 45	12757-12677 [ι]	Sigari et al., 2021
GR2016-522-P	D	Collagen	SacA 61169	10455 ± 45	12402-12166 (43.9%) [ι]	
GR2016-779	E	Bone	SacA 61171	11440 ± 50	13442-13227 (88.2%) [κ]	Sigari et al., 2021
GR2016-779-P	E	Collagen	SacA 61168	11120 ± 45	13117-12908 [κ]	

Table 2. Grotta Romanelli (Apulia, Italy). Faunal list from *Terre brune* (Tagliacozzo 2003) and *Terre rosse* (Blanc 1920).

Species	Common name	Revised taxon
Terre brune		
Bos primigenius Bojanus, 1827	aurochs	
Sus scrofa Linnaeus, 1758	wild boar	
Cervus elaphus Linnaeus, 1758	red deer	
Capreolus capreolus (Linnaeus, 1758)	roe deer	
Equus hydruntinus Regàlia, 1906	Regàlia ass	
Canis lupus Linnaeus, 1758	grey wolf	
Felis silvestris Schreber, 1777	wildcat	
Lynx sp. (Kerr, 1792)	lynx	
Meles meles (Linnaeus, 1758)	Eurasian badger	
Marmota marmota (Linnaeus, 1758)	alpine marmot	
Martes martes (Linnaeus, 1758)	European pine marten	
Lepus europaeus Pallas, 1778	European hare	
Erinaceus europaeus Linnaeus, 1758	European hedgehog	
Monachus monachus (Hermann, 1779)	Mediterranean monk seal	
Delphinus delphis Linnaeus, 1758	common dolphin	
Terre rosse		
Elephas antiquus (Falconer and Cautley, 1847) (=*Palaeoloxodon antiquus*)	Straight tusked elephant	
Rhinoceros merckii (Jäger, 1839) (=*Stephanorhinus kirchbergensis*)	Merck rhinoceros	*Stephanorhinus hemitoechus*, narrow-nosed rhinoceros (Pandolfi et al. 2017)
Hippopotamus amphibius Linnaeus, 1758 *Hippopotamus pentlandi* von Meyer, 1832	hippo	
Bos taurus var. *primigenius* Bojanus, 1827 (=*Bos primigenius*)	aurochs	
Cervus elaphus, Linnaeus, 1758 *Cervus elaphus* var. *corsicanus* Erxleben, 1777 (=*Cervus elaphus*)	red deer	

Dama dama (Linnaeus, 1758)	fallow deer	
Capreolus capreolus (Linnaeus, 1758)	roe deer	
Equus caballus Linnaeus, 1758 (= *Equus ferus* Boddaert, 1785)	wild horse	
Hyaena crocuta var. *spelaea* (Goldfuss, 1823) (=*Crocuta crocuta spelaea*)	cave hyaena	
Canis lupus Linnaeus, 1758 *Canis aureus* Linnaeus, 1758	grey wolf golden jackal	*Canis lupus*, grey wolf (Sardella et al. 2014)
Meles taxus (Linnaeus, 1758) (=*Meles meles*)	Eurasian badger	
Lutra lutra (Linnaeus, 1758)	Eurasian otter	*Lutra lutra*, Eurasian otter (Mecozzi et al. 2021)
Oryctolagus cuniculus (Linnaeus, 1758)	European rabbit	
Pelagius monachus (Hermann, 1779) (=*Monachus monachus*)	Mediterranean monk seal	

Table 3. Grotta Romanelli (Apulia, Italy). Number of pollen grains of *Terre rosse* samples from SS2 and SS4 (from left to right, bottom to top sample, see Fig. 4c, d). Samples B332, B335 from SS2 and B319, B322 from SS4 are barren.

Grotta Romanelli (Apulia, Italy)	***Terre rosse* - SS2**					***Terre rosse* - SS4**							
Taxa / Samples	**B331**	**B333**	**B334**	**B336**	**B337**	**B314**	**B315**	**B316**	**B317**	**B318**	**B320**	**B321**	**B323**
Abies			2						1				
Pinus	3	2	3	3		6	3		4				
Alnus									1				
Carpinus					1		1						
Corylus									1				
Fagus									1				
Hedera						2			1				
Ligustrum			2					1					
Olea	3	4	8	2	1	8	6		20		1		1
Myrtus	1												
Quercus ilex type	1			1					5				
Quercus robur and *Q. cerris* types	1	1	2		3	2	3		8				
Ulmus									1				
Amaranthaceae									2				
Apiaceae cf. *Crithmum maritimum*						36							
Artemisia						1							
Asparagaceae cf. *Muscari comosum*	1					4	1		16	1			
Asphodelus			1						1				
Asteroideae		2	1			1	1		1			1	
Brassicaceae	4	3				1			6				

Campanula							1						
Caryophyllaceae					1	4	1		3				
Cichorieae	2		2	1		1	1		6			1	
Convolvulaceae									1				
Hypericum			1					1					
Knautia									1				
Lamiaceae						3							
Plantago						1			1				
Poaceae						1			4				
Ranunculaceae									1				
Rosaceae									1				
Scrophulariaceae		3				1			1				
Symphytum									1				
Total Sum	**16**	**15**	**22**	**7**	**6**	**72**	**18**	**2**	**89**	**1**	**1**	**2**	**1**
Pollen taxa	**8**	**6**	**9**	**4**	**4**	**15**	**9**	**2**	**25**	**1**	**1**	**2**	**1**
Concentration (grains/g)	**213**	**150**	**169**	**86**	**95**	**1358**	**375**	**200**	**1390**	**19**	**20**	**37**	**13**

Table 4. Grotta Romanelli (Apulia, Italy). Number of pollen grains of *Terre brune* samples from SS1 (from left to right, bottom to top sample, see Fig. 4a).

Grotta Romanelli (Apulia, Italy)	***Terre brune* - SS1**													
Taxa / Samples	**B300**	**B301**	**B302**	**B303**	**B304**	**B305**	**B306**	**B307**	**B308**	**B309**	**B310**	**B311**	**B312**	**B313**
Juniperus			2	2			3	9		2		4		
Pinus		1 .5	5.5	1.5		4								2
Alnus												1		
Ericaceae											1			
Pistacia		2												
Populus				1										
Quercus ilex type		1	2		2	2		2			2	2		1
Quercus cerris type		2	2			2				2				
Quercus robur type			3	2			4	4	3					
Rosaceae								1			7		1	1
Tamarix		14	2		2	1	2						3	2
Ulmus										2				
Amaranthaceae		2		1	3	5					2	1	1	
Apiaceae										1				
Artemisia				1		2					1		1	
Asparagaceae *Asparagus maritimus/ Ornithogalum*		4					2			7				
Asteroideae	5	18	29	11	9	6	4	2	4	2				
Brassicaceae		2	4					3			8			
Caryophyllaceae				3										
Centaurea cf. *nigra*					2			2						

Cichorieae		55	163	79	92	76	84	77	94	83				
Cyperaceae				1										
Fabaceae		18	1					2			1		1	1
Geranium			1											
Lamiaceae			2							2				
Limonium gr.						1								
Papaver		4												
Plantago						3					1	3		
Poaceae	2	7	3	5	5			6			1			1
Ranunculaceae		8	8				6				4	1	2	1
Sanguisorba cf. *minor*								2						
Saxifraga													2	
Scabiosa			2											
Urtica											2			2
Total Sum	**7**	**138.5**	**229.5**	**107.5**	**115**	**102**	**105**	**110**	**101**	**101**	**30**	**12**	**11**	**11**
Pollen taxa	**2**	**14**	**15**	**11**	**7**	**10**	**7**	**11**	**3**	**8**	**11**	**6**	**7**	**8**
Concentration (grains/g)	**138**	**3179**	**12,735**	**4503**	**960**	**1018**	**1079**	**1075**	**1105**	**893**	**267**	**67**	**86**	**68**

Table 5. Grotta Romanelli (Apulia, Italy). Number of pollen grains of *Terre brune* samples from SS2 and SS3 (from left to right, bottom to top sample, see Fig. 4b, c).

Grotta Romanelli (Apulia, Italy)	***Terre brune* - SS2**					***Terre brune* - SS3**					
Taxa / Samples	**B338**	**B339**	**B340**	**B341**	**B342**	**B354**	**B353**	**B352**	**B351**	**B350**	**B349**
Juniperus	3	1			2	2				1	
Pinus					2			2			2
Alnus		1					2	2			
cf. *Ligustrum*		1									
Olea		4	3	1	4			2	16		3
Quercus ilex type	2				4			3	5	2	
Quercus cerris type									2		
Quercus robur type			3		4	1			2	4	2
Rosaceae					2						
Salix									2		
Tamarix							2				
Amaranthaceae	3	3	6	4		3	2		2		
Artemisia		6	8						2		
Asteroideae	2	1		2	6	8	16	6	6	8	
Brassicaceae	6	1			20	4		9	3	2	
Caryophyllaceae		3	6		6			2		2	
Centaurea cf. *nigra*								2			
Cichorieae	86	80	161	96	192	126	11	86	94	87	91
Fabaceae						1					
Liliaceae								1	5	4	
Linum									1		
Plantago		1								1	
Poaceae		4				3	2	3	2		8
Ranunculaceae							2	1	2		
Urtica									2		
Thalictrum					1						
Valerianaceae							3				

Total Sum	**102**	**106**	**187**	**103**	**243**	**148**	**40**	**119**	**146**	**111**	**106**
Pollen taxa	**6**	**12**	**6**	**4**	**10**	**8**	**8**	**12**	**15**	**9**	**5**
Concentration (grains/g)	**691**	**1787**	**3793**	**1292**	**9343**	**2655**	**1296**	**1140**	**1251**	**585**	**719**

Table 6. Grotta Romanelli (Apulia, Italy). Number of pollen grains of *Terre brune* samples from SS4 (from left to right, bottom to top sample, see Fig. 4d).

Grotta Romanelli (Apulia, Italy)	***Terre brune* - SS4**						
Taxa / Samples	**B324**	**B325**	**B326**	**B327**	**B328**	**B329**	**B330**
Juniperus		7	151	6	20		
Pinus	2	1				1	4
Alnus					2		
Cistus					3		
Olea	1						3
Phillyrea						1	
Quercus ilex type	2	1	3	2	8	4	
Quercus cerris type					8	3	
Quercus robur type	7						5
Rosaceae			1	4	3		
Salix					11	2	
Tamarix			7	7	7		
Ulmus							
Amaranthaceae			1	1	1		5
Apiaceae cf. *Crithmum maritimum*				1	103	1	
Artemisia	2	9	10				
Asparagaceae *Asparagus maritimus/ Ornithogalum*					178	9	
Asteroideae	4	1	3			5	10
Brassicaceae					7		10
Caryophyllaceae		1		2			3
Centaurea cf. *nigra*	1						
Cichorieae	83	1				82	157
Fabaceae				3	82		
Lamiaceae					4		
Plantago		2	1	3	4		3

Poaceae	1		7	2	29	1	
Ranunculaceae		1	11	13	80	2	3
Saxifraga					17		
Spergularia			1				
Urtica			2	1	5		
Total Sum	**103**	**24**	**198**	**41**	**572**	**111**	**203**
Pollen taxa	**9**	**9**	**12**	**12**	**19**	**11**	**10**
Concentration (grains/g)	**934**	**132**	**696**	**173**	**21,124**	**1281**	**4686**

Highlights

Pollen was preserved in Late Pleistocene/Early Holocene deposits of Grotta Romanelli

Olea pollen constraints the deposition of *Terre rosse* to the Eemian (MIsS 5e)

Steppe herbs and rare arboreal pollen in *Terre brune* mark the Lateglacial

Clusters/high amounts of entomophilous pollen may reveal the use of plants by humans

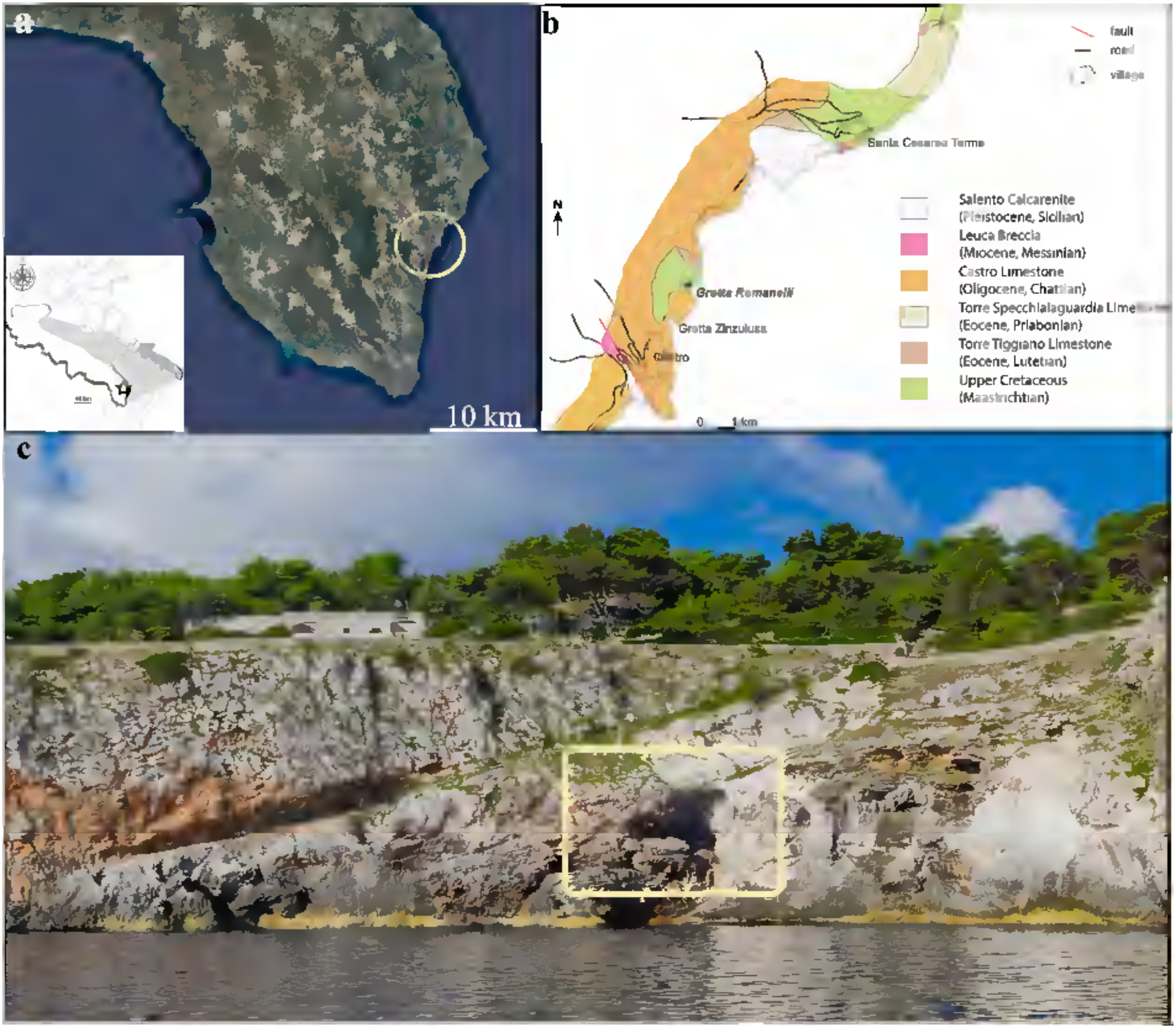
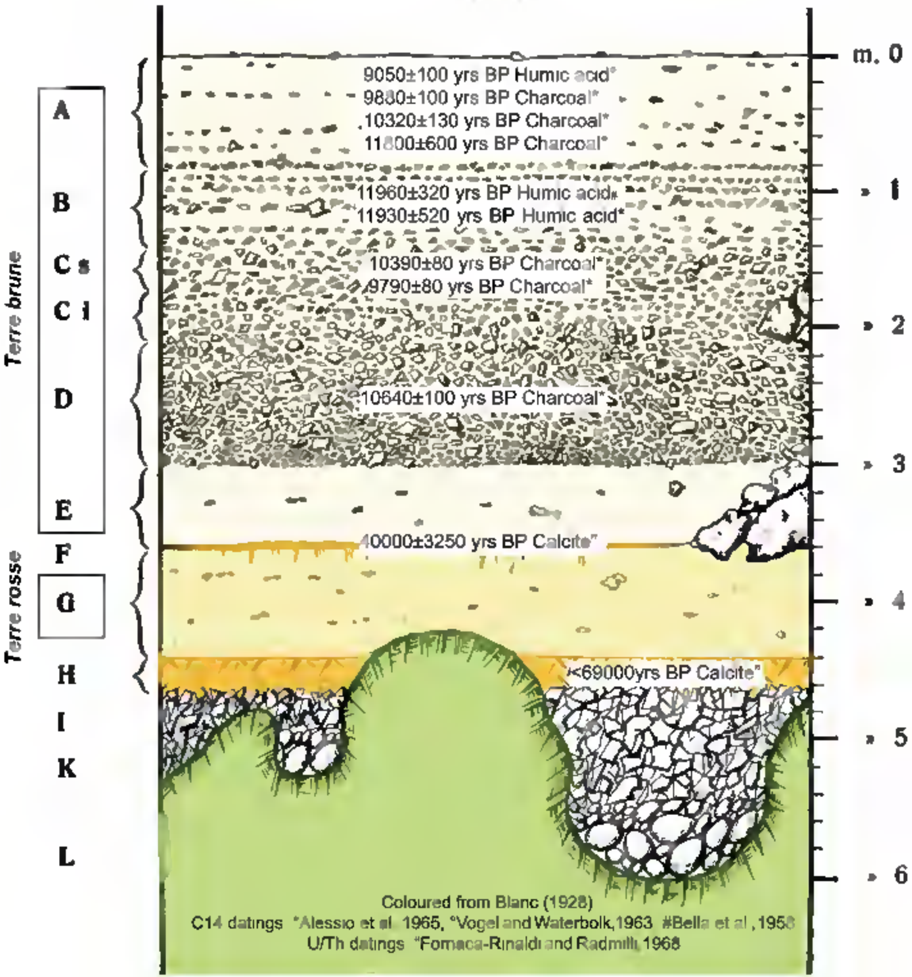

a
10 km
b
fault
road
village
Santa Cesarea Terme
Salento Calcarenite
(Pleistocene, Sicilian)
Leuca Breccia
(Miocene, Messinian)
Castro Limestone
(Oligocene, Chattian)
Torre Specchialaguardia Lime
(Eocene, Priabonian)
Torre Tiggiano Limestone
(Eocene, Lutetian)
Upper Cretaceous
(Maastrichtian)
N
Grotta Romanelli
Grotta Zinzulusa
0 1 km
c

Figure 1



m. 0
1
2
3
4
5
6
A
B
C s
C i
D
E
F
G
H
I
K
L
Terre brune
Terre rosse
9050±100 yrs BP Humic acid*
9880±100 yrs BP Charcoal*
10320±130 yrs BP Charcoal*
11800±600 yrs BP Charcoal*
11960±320 yrs BP Humic acid#
11930±520 yrs BP Humic acid*
10390±80 yrs BP Charcoal*
9790±80 yrs BP Charcoal*
10640±100 yrs BP Charcoal*
40000±3250 yrs BP Calcite"
>69000yrs BP Calcite"
Coloured from Blanc (1928)
C14 datings *Alessio et al. 1965, °Vogel and Waterbolk,1963 #Bella et al.,1958
U/Th datings "Fornaca-Rinaldi and Radmilli, 1968

Figure 2

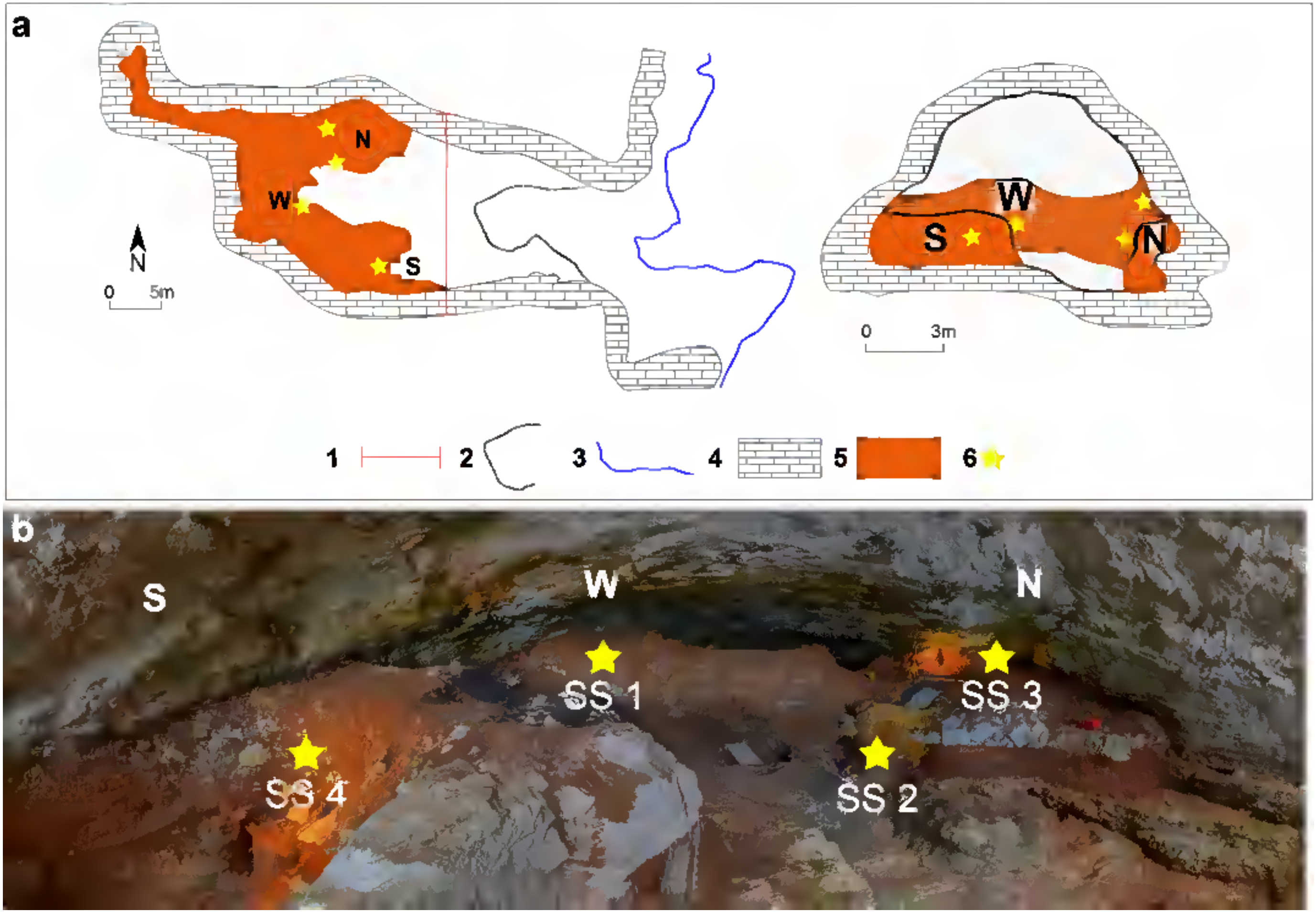


Figure 3

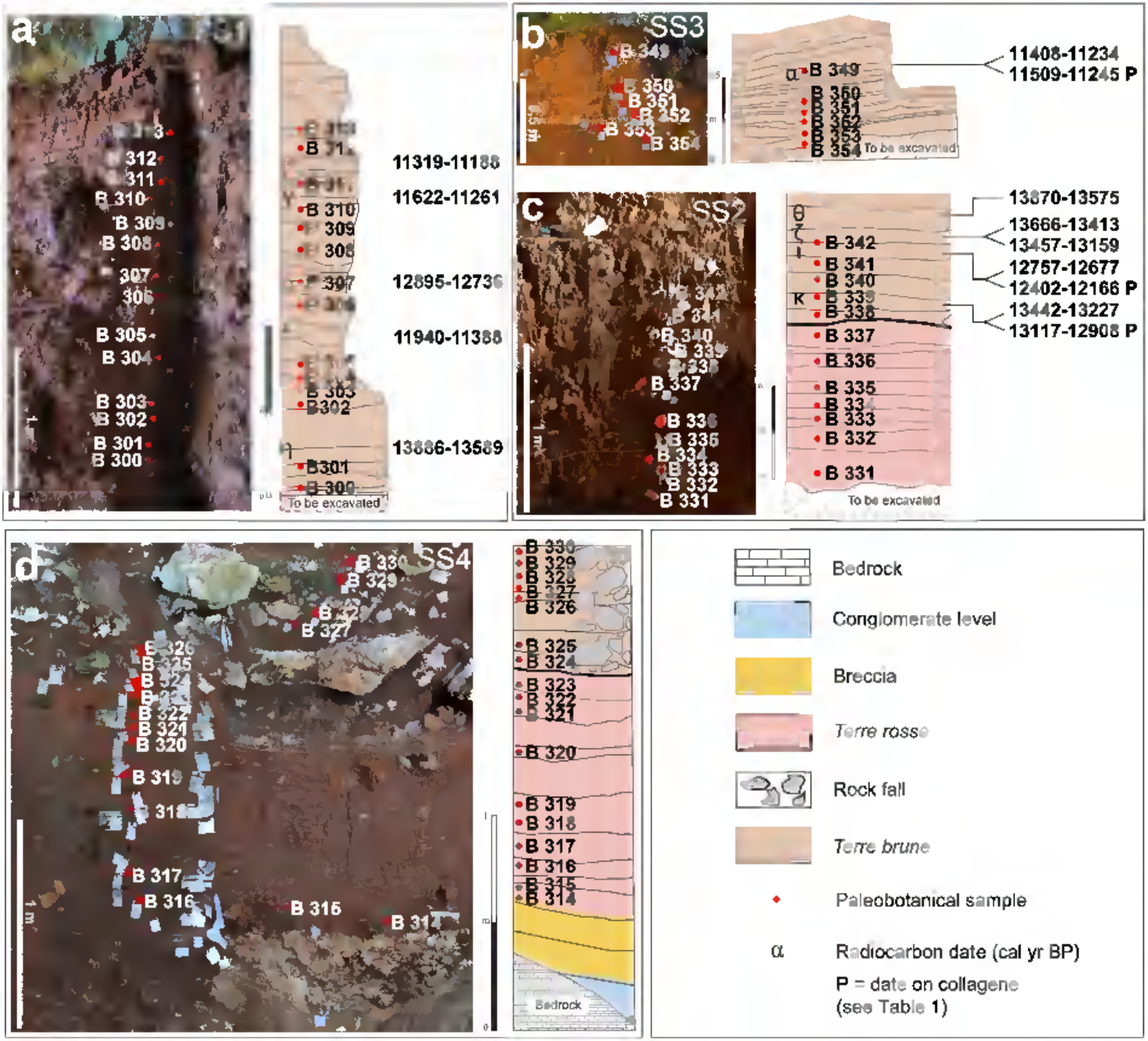

a
b
SS3
c
SS2
d
SS4
11319-11188
11622-11261
12895-12736
11940-11388
13886-13589
To be excavated
11408-11234
11509-11245 P
13870-13575
13666-13413
13457-13159
12757-12677
12402-12166 P
13442-13227
13117-12908 P
B 349
B 350
B 351
B 352
B 353
B 354
B 342
B 341
B 340
B 339
B 338
B 337
B 336
B 335
B 334
B 333
B 332
B 331
B 330
B 329
B 328
B 327
B 326
B 325
B 324
B 323
B 322
B 321
B 320
B 319
B 318
B 317
B 316
B 315
B 314
B 310
B 309
B 308
B 307
B 306
B 305
B 304
B 303
B 302
B 301
B 300
1 m
Bedrock
Conglomerate level
Breccia
Terre rosse
Rock fall
Terre brune
Paleobotanical sample
α Radiocarbon date (cal yr BP)
P = date on collagene
(see Table 1)

Figure 4

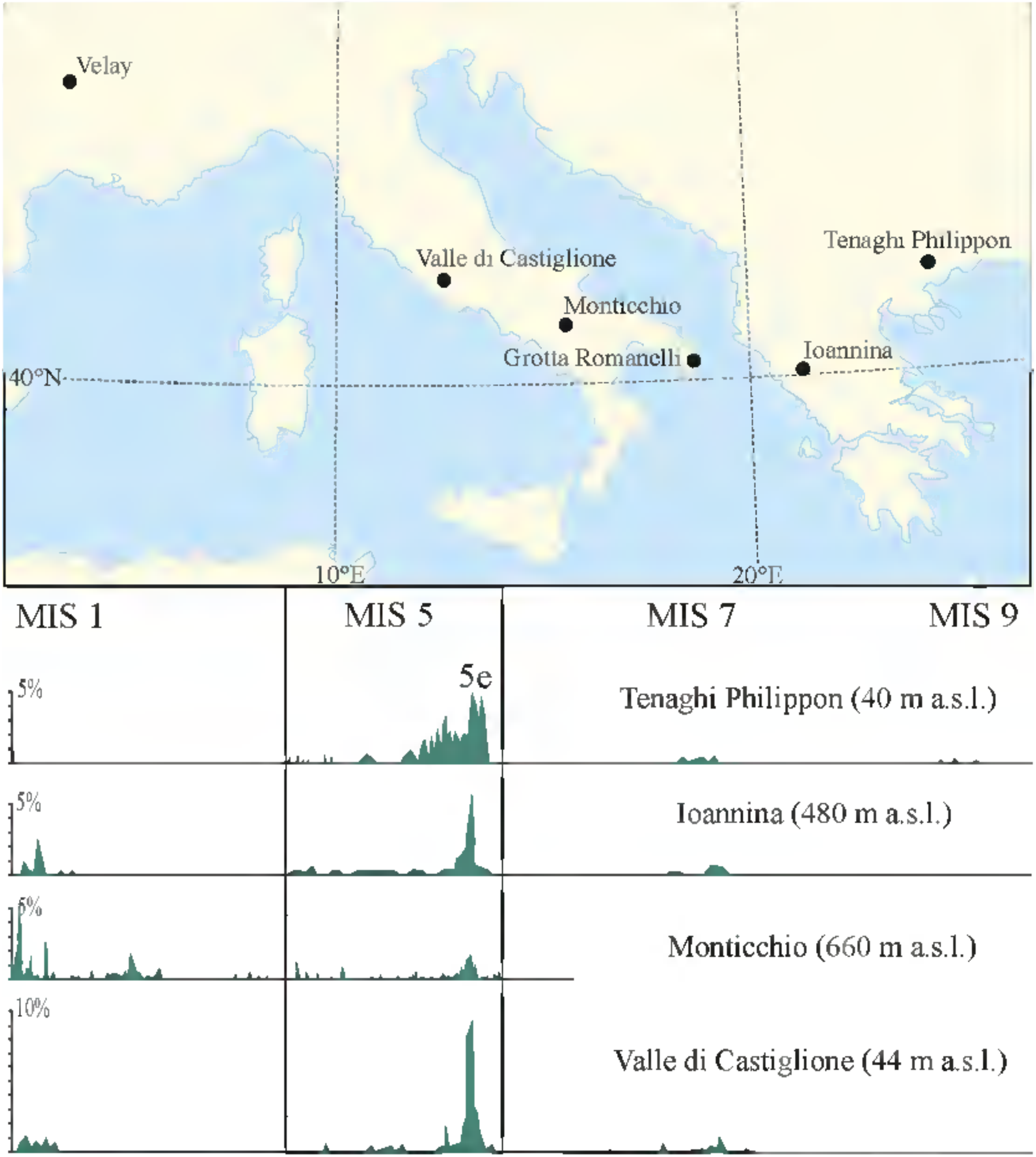

Velay
Valle di Castiglione
Monticchio
Grotta Romanelli
Tenaghi Philippon
Ioannina
40°N
10°E
20°E
MIS 1
MIS 5
MIS 7
MIS 9
5e
5%
Tenaghi Philippon (40 m a.s.l.)
5%
Ioannina (480 m a.s.l.)
5%
Monticchio (660 m a.s.l.)
10%
Valle di Castiglione (44 m a.s.l.)

Figure 5