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Environment and hunting territories for Late Neanderthals in central Italy: new palaeoecological data from Grotta dei Santi (Monte Argentario – Tuscany, Italy)☆

Juan Ochando [a,b,c,*], Federico Di Rita [b], Donatella Magri [b], Jacopo Crezzini [c], Allegra Burgassi [c], Giulia Marciani [c,d], Francesco Berna [c,f], Francesco Boschin [c,e], Adriana Moroni [c,e,g,1], Vincenzo Spagnolo [c,d,1]

[a] University of Murcia, Department of Plant Biology (Botany Area), Faculty of Biology, Campus de Espinardo, 30100 Murcia, Spain
[b] Sapienza University of Rome, Department of Environmental Biology, Piazzale Aldo Moro 5, 00185 Rome, Italy
[c] University of Siena, Department of Physical Sciences, Earth and Environment, Strada Laterina, 8, 53100 Siena, Italy
[d] University of Bologna, Department of Cultural Heritage, Via Degli Ariani 1, 48121 Ravenna, Italy
[e] Centro Studi sul Quaternario, Via Nuova dell'Ammazzatoio, 7, 52037 Sansepolcro, Italy
[f] Simon Fraser University, Department of Archaeology, Burnaby, British Columbia, Canada
[g] Istituto Italiano di Paleontologia Umana, Piazza Ruggero Bonghi, 2, 03012 Anagni, Italy

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ABSTRACT

The Italian peninsula is a key biogeographical region in southern Europe, which acted as a refugium for flora and fauna and favoured the persistence of human groups during the Late Pleistocene. This study uses pollen analysis of coprolites from the Late Mousterian site of Grotta dei Santi, (Monte Argentario Promontory, Tuscany, Italy), in which the Palaeolithic human presence is chronologically constrained between ~ 48 and 44 ka BP. The vegetation landscapes during Marine Isotope Stage (MIS) 3 were reconstructed and compared with other palaeoenvironmental proxies from the same site. Palynological analyses revealed a semi-forested/forested environment within the Mediterranean landscape, with a relatively high diversity of woody taxa, including conifers, mesophytic angiosperms, elements of Mediterranean forest and of xerothermic scrub. The most remarkable result is the persistence of temperate climatic conditions throughout the studied sequence, even at the beginning of Greenland Stadial 12, as shown by both pollen and microfaunal records. This allowed the local maintenance of an unchanged availability of environmental resources. In this light, we assume that the definitive abandonment of the cave by Mousterian people cannot be linked to environmental stress. In other words, other factors must be taken into account to explain the possible demographic gap that seems to have occurred in the coastal area of southern Tuscany between the last Mousterian groups and the arrival of early modern humans at the nearby site of Grotta La Fabbrica. In a broader perspective, our work contributes to adding a new piece to the debate on the complex dynamics associated with the demise of Neanderthals in Europe.

1. Introduction

From a palaeoecological perspective, the Italian Peninsula – stretching more than a thousand kilometres into the Mediterranean Sea – has been, especially during past glacial phases, a phytodiversity reservoir (Magri, 2010; Magri et al., 2017), highlighted by a significant number of woody taxa typical of the southern European glacial refugia (Follieri et al., 1998; Magri, 1999; Magri and Sadori, 1999; Giardini, 2007; Pini et al., 2010; Badino et al., 2020). Pollen analysis of coprolites, food remains, and sediments, recovered from archaeological contexts, has proven to be a valuable method to reconstruct the plant components of past ecosystems in contexts crucial for the human evolution (Scott, 1987, 1994; Carrión, 1992; Carrión et al., 2004, 2006, 2007, 2011, 2019a, 2019b, 2019c, 2022a; Finlayson and Carrión, 2007; Bonnefille,

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* Corresponding author at: University of Murcia, Department of Plant Biology (Botany Area), Faculty of Biology, Campus de Espinardo, 30100 Murcia, Spain.
E-mail address: juan.ochando@um.es (J. Ochando).

[1] These authors share the last name.

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2010; Messager et al., 2011; Marais et al., 2015; De Porras et al., 2017; McGee and DeMenocal, 2017; Ochando et al., 2019, 2020a, 2020b, Ochando et al., 2020c, Ochando et al., 2020d, Ochando et al., 2022a, 2022b, 2022c). However, despite the interest associated with pollen analysis, there is still a lack of palynological studies from Pleistocene caves, rock shelters, and open-air sites within the Mediterranean Basin (Carrión et al., 2009, Carrión et al., 2022b, Carrión et al., 2024a), often due to the bad preservation of this environmental proxy in the sedimentological record. Fossil faeces from archaeological contexts, especially those of hyena, are considered to be one of the best sources of pollen (Scott, 1987; Horwitz and Goldberg, 1989; González-Sampériz et al., 2003; Carrión et al., 2004, 2008, 2018, 2019c, 2024b; Gatta et al., 2016; Daura et al., 2017; Djamali et al., 2020; Ochando et al., 2020b, Ochando et al., 2024a, Ochando et al., 2024b), because their hardness hampers oxidation of the grains (Larkin et al., 2000; Scott et al., 2003). In addition, pollen from coprolites often complements other palaeobotanical records, as it may better represents entomophilous species, which are uncommon in biogenic sediments whose pollen spectra are mainly derived from aquatic and airborne transport (Carrión, 2002; Carrión et al., 2018, 2019a, 2019b, 2019c).

Additionally, the coprolites' pollen composition represents the variety of the local environment, often with various habitats coexisting in a

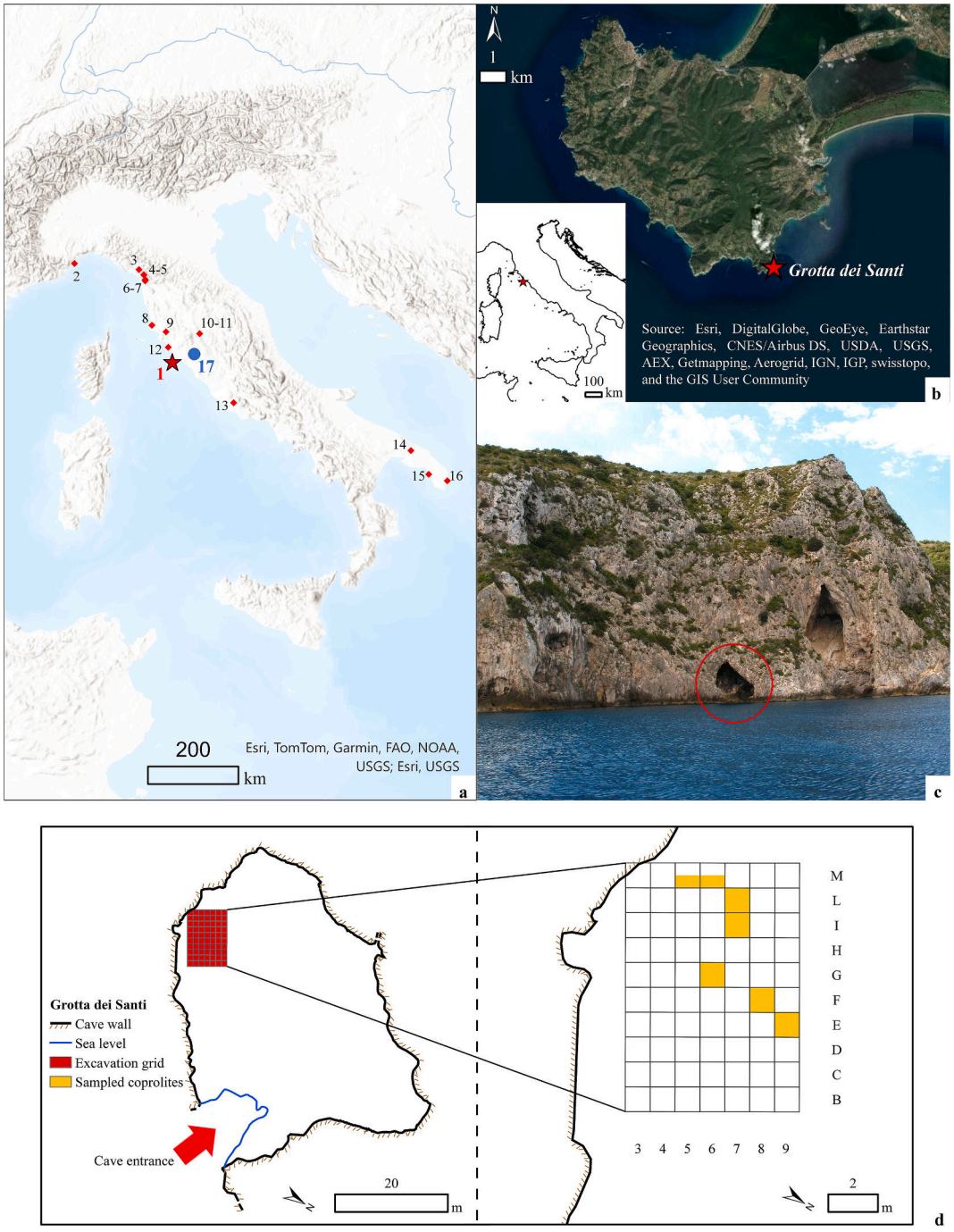

Fig. 1. Grotta dei Santi. a) Location of the sites quoted in the text (1 – Grotta dei Santi, 2 – Caverna delle Fate, 3 – Grotta and Tecchia di Equi, 4 – Buca della Iena, 5 – Grotta del Capriolo, 6 – Grotta all'Onda, 7 – Buca del Tasso, 8 – Botro ai Marmi, 9 – Riparo Cavanna, 10 – Grotta di San Francesco, 11 – Grotta di Gosto, 12 – Grotta La Fabbrica, 13 – Cava Muracci, 14 – Tana delle Iene, 15 – Grotta-Riparo di Uluzzo C, 16 – Grotta Romanelli, 17 – Lagaccione), b) location of Grotta dei Santi in frame of the Monte Argentario – Tuscany, c) cave entrance, d) planimetry of the cave with the sampling squares in the general excavation grid.

patchy landscape (Scott et al., 2003; Carrión et al., 2018). Besides, we should consider the fluctuating behaviour of the coprolite-producing animal when interpreting coprolite pollen species. According to previous research (Mills, 1989; Gutiérrez et al., 1998; Carrión et al., 2018; Ochando et al., 2024a), pollen might be incorporated into the hyaena coprolite through water consumption, accidentally from the air, attached to any food item, and through the prey's stomach contents.

Grotta dei Santi (Monte Argentario – Tuscany, Italy), located on the Tyrrhenian side of the Italian Peninsula (Fig. 1), is a key site for the study of the Middle Palaeolithic in central Italy, thanks to its high-resolution deposit, which has allowed us to zoom through the behavioural dynamics of human groups who lived in the area, and their relationship with the surrounding environment. According to radiocarbon and OSL chronology (Moroni et al. 2019; Conti et al., 2023), this cave's anthropogenic sequence covers a time period of a few thousand years, about 48–44 ka cal. BP, corresponding to the presence of Late Neanderthals in the region.

Grotta dei Santi has yielded large quantities of hyena coprolites due to the periodic use of the cave by this carnivore, alternating with humans. This paper presents the results of the palynological study carried out on several samples of hyena coprolites from different layers of the cave's deposit, with the aim of combining the palynological data with geochronological (Moroni et al., 2019; Conti et al., 2023), sedimentological (Moroni et al., 2019), magnetic susceptivity (Burgassi et al., 2024), palaeogeographical (Conti et al., 2023) and micro-/macrofaunal studies (Moroni et al., 2019), in order to reconstruct the vegetation landscapes and the environment with which the inhabitants of the cave interacted during mid-MIS 3.

2. The site and the regional context

Grotta dei Santi is located on the western coast of the Italian Peninsula (Tyrrhenian Sea; Fig. 1), which falls within the Mediterranean coastal climatic zone. The Mediterranean climate in the vicinity of the cave (Monte Argentario) is characterised by warm and dry summers, while winters and autumns are cool and rainy. The nearby meteorological station in Mt Argentario shows an annual average temperature of 17.5 °C (9 °C in the coldest month, 24.5 °C in the warmest month), which can reach maxima above 29–32 °C in summer, and annual average precipitation of 550–650 mm (https://weatherspark.com/y/68905/Average-Weather-in-Monte-Argentario-Italy-Year-Round).

Several authors have examined the characteristics, distribution, ecology, vegetation series, and habitats maps of the coastal vegetation in Tuscany (Cavalli, 1985; Arrigoni and Di Tommaso, 1997; Biondi et al., 2010; Arrigoni et al., 2001; Foggi et al., 2006a, 2006b, 2011; Blasi, 2010a, 2010b; Viciani et al., 2016, Viciani et al., 2017, Viciani et al., 2018). The local vegetation in the area surrounding the site is characterised by Mediterranean evergreen open forest growing on limestone substrates in the upper thermomediterranean bioclimatic belt (Baldini, 1995; Arrigoni and Di Tommaso, 1997). The vegetation in Mt Argentario has been severely disturbed by grazing, clearing land for agriculture, frequent anthropogenic fires, and, more recently, reforestation. According to Arrigoni and Di Tommaso (1997), the current vegetation is a mosaic of plant communities at various successional stages, influenced by both natural local factors like exposure, altitude, distance from the sea, and different substrata, as well as by previous land uses.

Grotta dei Santi is a karst cavity that opens on the eastern cliff of the Mt Argentario promontory, a few metres above the present sea level (Fig. 1). The cave consists of a large chamber, about 35x45 m wide. After the first scientific report by A.G. Segre (1959), Grotta dei Santi has been systematically investigated since 2006, by the Research Unit of Prehistory and Anthropology of the Department of Physical Sciences, Earth and Environment (University of Siena, Italy), in collaboration with the Italian Institute of Human Palaeontology. The research has brought to light several layers of human occupation which have yielded typical Mousterian lithic industries, traditionally associated with Neanderthals, macrofaunal, microfaunal and malacological remains, as well as living floors and hearths.

The infilling of the cave testifies to a complex sequence of formation processes at different time scales (Segre, 1959; Moroni et al., 2019). The abundance of short-term palimpsests and living floors separated by sterile sand and clay layers and the rapid formation times of the deposit, together with the exceptional preservation of most of the contexts, have provided the ideal setting to reconstruct the evolution of cultural and environmental events at very high-resolution and from multiple perspectives (Moroni et al., 2019; Spagnolo et al., 2020). Moreover, the wide availability and diversity of resources (not ubiquitously distributed) within the geomorphological variety of the Tuscan-Lazio palaeoenvironments and landscapes represented a favourable condition for the permanence of hunter-gatherer groups in the area and is a good premise to investigate their mobility and territory management (Conti et al., 2023).

The available radiocarbon and OSL chronology of Grotta dei Santi, in the context of the mid-MIS 3 (around 48–44 ka cal. BP), places this site in a crucial phase for the population history of Eurasia (Moroni et al., 2019; Conti et al., 2023), confirming that the dwellers of the cave were among the last Mousterian groups in the Italian peninsula, shortly before the arrival of *Homo sapiens* (Higham et al., 2024). Nearby, the presence of the early technocomplexes attributed to modern humans (the Uluzzian and the Protoaurignacian) is stratigraphically documented at Grotta La Fabbrica (about 20 km far from Grotta dei Santi, Fig. 1), where the Uluzzian is OSL dated to 40 ± 1.6 ka BP (Villa et al., 2018). At the same site, the most recent Mousterian layer (1a), separated from the overlying Uluzzian by an erosional surface, is OSL dated to 44 ± 2.1 ka BP (Villa et al., 2018), which is consistent with the chronology of the uppermost Middle Palaeolithic occupation at Grotta dei Santi (ca. 44 ka BP – Moroni et al., 2019). On the basis of these (still very preliminary) data, an age around 45–43 ka cal. BP could mark the definitive abandonment by Mousterian populations in the coastal areas of southern Tuscany, which were later recolonised, after a chronological hiatus, by Initial Upper Palaeolithic groups. The northwestern area of Tuscany, where the Uluzzian is absent, exhibits a different pattern with a cluster of Late Mousterian sites (Grotta all'Onda, Buca della Iena, Buca del Tasso, Grotta del Capriolo, Grotta and Tecchia di Equi), where a possible persistence of Mousterian groups up to ~ 41–40 ka cal. BP has been reported (Gennai, 2024, Gennai et al., preprint). In addition to the sites mentioned above, only a few other Mousterian sites in central and southern Tuscany are known to be stratigraphically documented from old excavations (Grotta di San Francesco and Grotta di Gosto, Cetona, Siena; Botro ai Marmi, Campiglia Marittima, Grosseto and Riparo Cavanna, Gavorrano, Grosseto – Galiberti, 1997) that are hypothetically dated to an earlier period than Grotta dei Santi, on the basis of geochronological assumptions.

3. The stratigraphy

The cave infill can be schematically summarized in four macrophases (bottom to top). The first one is testified by an accumulation (about 10 m thick) of huge limestone blocks (coming from the ceiling of the cave due to breakdown processes, *sensu* Martini, 2011) present in most of the cavity (Unit 10.1 *sensu* Moroni et al., 2019), and some flowstone layers (Units 10.2–10.4 *sensu* Moroni et al., 2019), mainly visible in the outer part near the entrance (Table 1). Among these flowstone layers, Unit 10.4 (*sensu* Moroni et al., 2019) is the only one continuously present both in the outer and the inner part of the cavity (Fig. 2a). Moreover, at the entrance, thin strips of breccia containing sporadic bones seem to lie under the flowstone Unit 10.4, but a more detailed analysis is required for a better contextualization of these breccia strips. A U/Th date from a stalagmite core (CDS-C1) overlying the limestone blocks falls at about 375–345 ka (MIS 9), allowing us to establish a *terminus ante quem* for the breakdown event (Isola et al., 2016).

Table 1
Schematic overview of the sequence and main Units (see also Fig. 5 in Moroni et al. 2019 for the graphic scketch) attributed to the phases described here. Layer nomenclature follows Moroni et al. (2019). After Spagnolo et al. (2020), the Unit numbers of the inner sequence have been simplified by removing higher-rank annotations, keeping only archaeological Unit names.

Phase	Unit	Description
I	10.1	Accumulation (about 10 m thick) of huge limestone blocks
	10.2–10.4	Flowstone layers
II	10.5	Cemented beach deposits (MIS 5e Tyrrhenian transgression?)
III	20.2–1004-20.3.3–11	Sequence of sand-loam and clay layers (Pleistocene)
IV	20.4	Upper stalagmite (Holocene)
	20.5	Yellowish sands

Remnants of cemented beach deposits (Unit 10.5 *sensu* Moroni et al., 2019), adhering on both the collapsed blocks and the cave wall (up to about 4.5 m a.s.l.), are representative of the second phase, possibly identifiable with the MIS 5e Tyrrhenian transgression (Table 1). This event may have eroded a potential deposit prior to MIS 5e.

The third phase identified towards the bottom of the cave, consists of several stratigraphic components, including anthropogenic ones, and has been the main focus of systematic stratigraphic research at Grotta dei Santi (Table 1). The lowermost deposit includes, above Unit 10.4, a loamy sand level containing abundant cm-sized rounded pebbles and reworked marine shell fragments (also larval specimens). The subsequent horizon (Unit 1004, Fig. 2a, d), sedimentologically similar to the previous layer, is 20 cm thick and exhibits blackish-greyish-alternated layers with significant evidence of human activity (charcoals, ash, hearths, broken bones, marine shells, Mousterian lithics). The last component of this phase is a thick horizon of about 3 m. It starts with a 10 cm thick red clay layer (sealing the Unit 1004) and continues with several layers made by fining upwards cyclical sequences (greyish-sands-to-reddish-clays). This upper horizon consists of two sub-parts. The lower one (including Units 150, 125, 111, 110, 107, 105, and 100) is about 1 m thick and returned significant evidence of human camps and hyena dens (Spagnolo et al., 2020). The upper part is sterile of any anthropogenic evidence (Fig. 2a). As mentioned above, radiocarbon dates from the Units 1004 to 110 frame the human occupation of the cave within a narrow window of time, between 48–44 ka cal. BP (Moroni et al., 2019; Conti et al., 2023). Interestingly, despite the remarkable thickness (about 3 m) of the whole third phase, the time span covered is extraordinarily brief, as also shown by the OSL 1 date 35.6 ± 3.3 ka BP (Fig. 2a) obtained in layer 20.3.3–11 (*sensu* Moroni et al., 2019).

The fourth phase can be attributed to the Holocene and is represented by an extensive flowstone covered by sand deposits (respectively 20.4 and 20.5 *sensu* Moroni et al., 2019; Table 1; Fig. 2a), containing a Roman occupation referable, on the basis of some coins, to the 2nd century CE.

The anthropogenic sequence is as follows (in stratigraphic order bottom to top) (Fig. 2):

3.1. Unit 1004

Greyish-blackish loam with abundant rounded limestone skeleton, about 30–40 cm thick (Fig. 2a, d). It contains several blackish horizons rich in charcoal/ash matter and evidence of human occupations (e.g., living floors with hearths, faunal remains, marine shells and lithics). Only the upper part of this sequence (living floors 1004A and 1004B; Fig. 2d) has been excavated in a narrow area exposed by erosion. This Unit is sealed by a 10 cm thick sterile clay (Unit 900; Fig. 2a, c-d), followed by a sequence of unexcavated sands, about 40 cm thick, on which Unit 150, described below, lies.

3.2. Unit 150

Fine-grained reddish laminated sands about 10–15 cm, characterized by at least 3 living floors separated by sterile sediments (visible on the stratigraphic profiles; Fig. 2a-c) exhibiting different preservation state. The uppermost living floor (150 A) is the only one excavated so far (Spagnolo et al., 2020).

3.3. Units 125–120

Fine reddish sands about 5–7 cm thick (Unit 125). It is followed by a graded fining upward bedding made by greyish sands rich in millimetre-to-centimetre-scale limestone clasts covered by reddish loam ripples (sometimes on a multiple sequence), at place followed by a further level of fine yellowish sands, overall, 10 cm thick (Unit 121) (Fig. 2a-b). The Units 125 and 121 exhibit evidence of partially reworked human activity and traces of hyena den. This sequence is sealed by a finely laminated sterile reddish clay, about 5 cm thick (Unit 120).

3.4. Unit 111

Yellowish-to-greyish laminated sands sealed by a clay layer (about 15–20 cm thick), with at least 3 living floors separated by sterile sands (Fig. 2a-b). Several hearths (some in exceptional preservation state) with abundant evidence of human activity are recorded, while evidence of hyena frequentation is fragmented and sporadic. Sample for pollen analysis San-Cop 8 comes from this Unit.

3.5. Unit 110

Sequence of strata about 20–25 cm thick (Fig. 2a-b). The lower part of the Unit consists of an incompletely preserved brown loam level covered by a yellowish loamy sand. The upper part is a reddish fine sand-to-loam with thin layers of trampled coprolites. Granules are dispersed in sediments and sometimes organized in lenses. The main characteristic of this Unit is the repeated alternation of occupation episodes by spotted hyena (*Crocuta crocuta spelaea*) and humans, which sometimes can be distinguished at high temporal resolution. Samples for pollen analysis San-Cop 7 to 3 come from this Unit.

3.6. Unit 107

Greenish/yellowish grey medium-to-fine sands about 5–10 cm thick (Fig. 2a-b). An abundant component of femic volcanic minerals is present in the matrix. Limestone granules are dispersed within sediments. This Unit does not include any anthropogenic evidence but is rich in coprolites and microfaunal remains. Sample for pollen analysis San-Cop 2 comes from this Unit.

3.7. Unit 105

Reddish fine sands with clay/loam intercalations, about 5–10 cm thick (Fig. 2a-b). Lenses of greenish/yellowish sands similar to the underlying Unit 107 have been detected in the body of Unit 105, interbedded between the reddish sands. Limestone granules are rare. This Unit only includes coprolites and microfaunal remains. Sample for pollen analysis San-Cop 1 comes from this Unit.

4. Palynological methods

The coprolite assemblages, sampled in a sub-stratigraphic order, were recovered from Grotta dei Santi during the 2010, 2015, 2016 and 2017 fieldwork campaigns (samples ID San-Cop1 to San-Cop8), from Units 111, 110, 107 and 105 (squares M5/II-III, M6/II-III, E9, G6, E9/IV, I7/I, F8 of the excavations grid; Fig. 1d; Table 2). These large coprolites have been ascribed to *Crocuta crocuta spelaea* (Crezzini and Moroni,

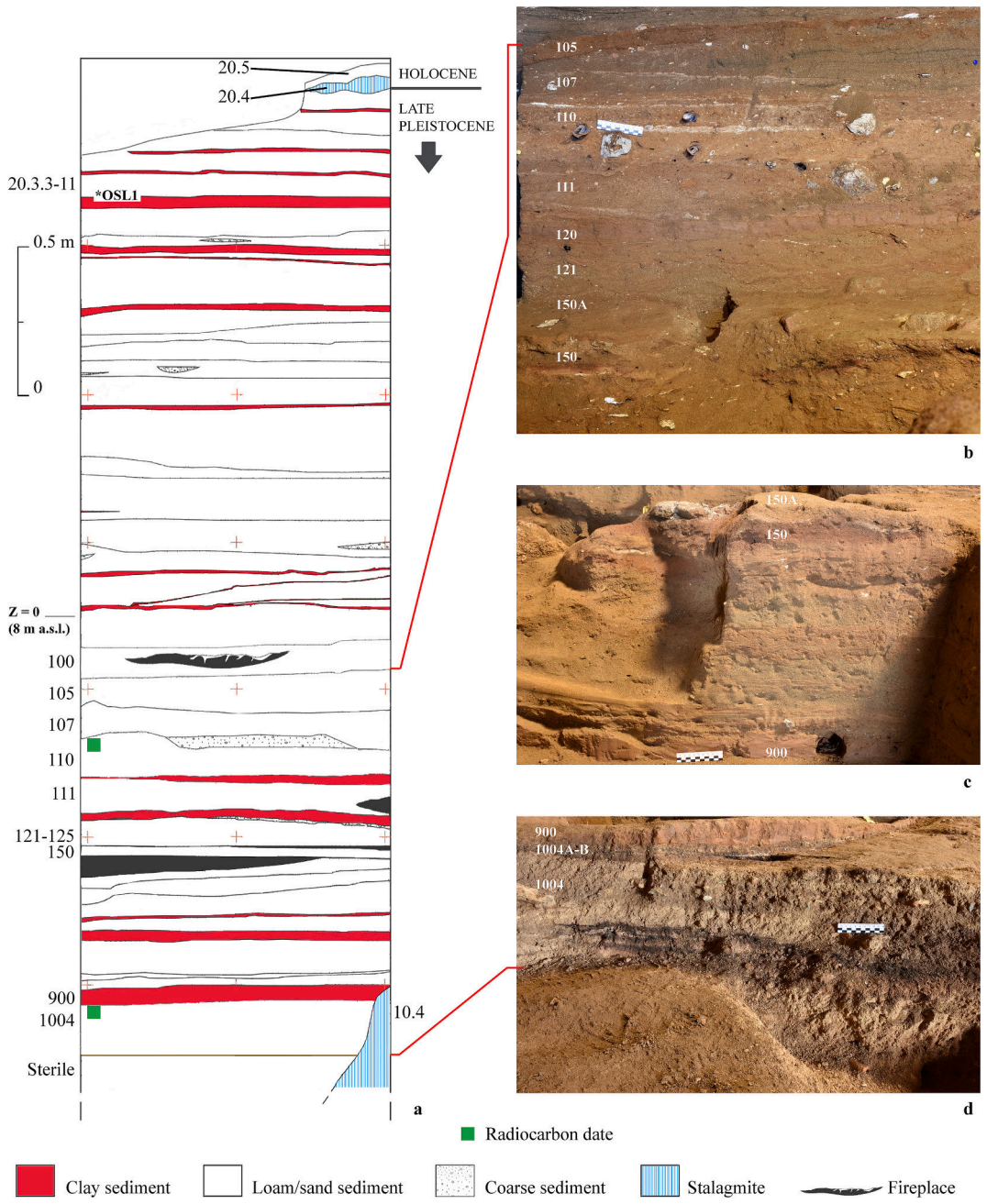

Fig. 2. A) Synthetic stratigraphic column of the sequence at Grotta dei Santi, b-d) view of the clastic sequence exposed and profiles studied for pollen analysis in Grotta dei Santi.

2012; Moroni et al., 2019), due to their shape and size consistent with those of the ice age spotted hyaena from the Pleistocene of Europe (Diedrich, 2012). The colours of the coprolites vary from pale yellow to brown on the outside and from pale brown to white on the inside, like other hyaena coprolites from the European Pleistocene (Carrión et al., 2001, 2007, 2008, 2018, 2019c; Ochando et al., 2020a, Ochando et al., 2024a; Fig. 3).

In the laboratory, the surface layer of each coprolite was cleaned with distilled water under pressure, then the surface layer was cut open using a steel spatula, and finally, material from the inside was scraped to reduce contamination from the outside face. After the coprolite samples were weighed (Table 2), 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). To calculate pollen concentration, we added one tablet of *Lycopodium* spores (batch No. 710961.500) to each coprolite sample (Stockmarr, 1971). 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. We used the palynomorph reference collection of the Department of Environmental Biology (Sapienza University of Rome). We excluded from the total pollen sum the counts of Asteroideae and Cichorioideae, assuming they might be overrepresented due to selective preservation in sediments, as it is the case in many archaeological samples (Havinga, 1984; Table 2). The pollen count data was treated with the Tilia Graph 1.7.16 program in order to plot the pollen diagrams (Grimm, 2011).

The pollen groups established for Lamiaceae should be clarified. Lamiaceae have been divided in two groups: pollen grains with three colpi (3C) and pollen grains with six colpi (6C).

Table 2
Summary of palynological features of the Grotta dei Santi coprolites ([a]Asteroideae and Cichorioideae excluded).

Sample	Unit/ spit	Square	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	[(a)]Pollen sum	Number of taxa (Pollen)
San-Cop1	105/1	M5	4.57	4.57	6,273	3.86	237	233	15
San-Cop2	107/1	M6	7.73	7.73	1,350	2.38	213	210	18
San-Cop3	110/2	E9	26.86	26.86	179	3.75	115	80	13
San-Cop4	110/3	G6	8.30	8.30	964	1.89	217	212	13
San-Cop5	110/3	E9	8.01	8.01	1,325	2.34	232	214	18
San-Cop6	110/3	I7	6.40	6.40	548	3.61	84	83	10
San-Cop7	110/ base		8.52	8.52	1,130	3.33	216	210	15
San-Cop8	111/0	F8	8.06	8.06	1,046	8.43	83	83	8
							TOTAL 1,397	1282	
Sterile Coprolites									
1	105	L7	33.97	33.97	–	–	Sterile	–	–

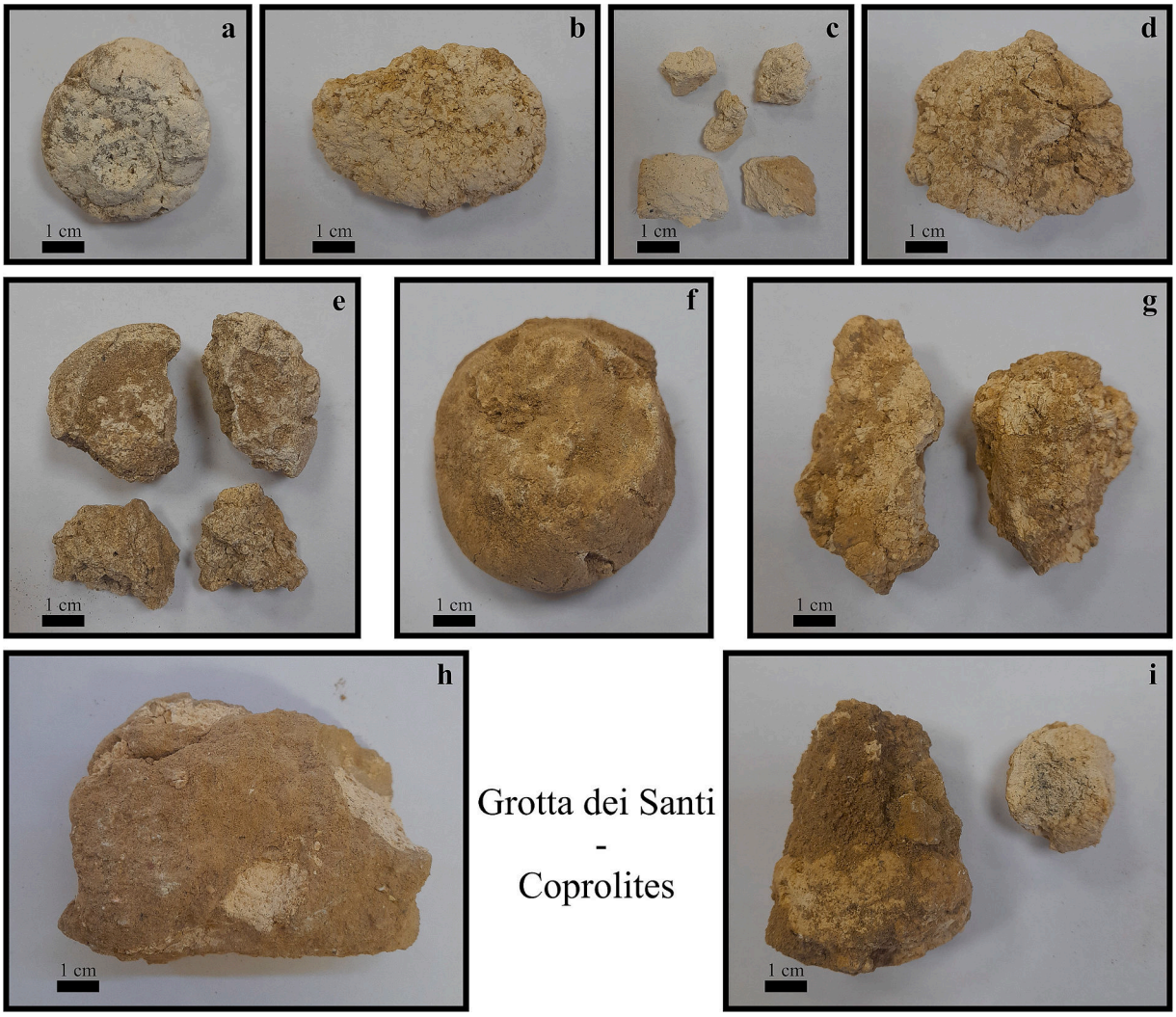

Fig. 3. Coprolite specimens from Grotta dei Santi (San-Cop1 to San-Cop8) from Units 105, 107, 110 and 111 (a-d, f-i) and one sterile coprolite from Unit 105 (e).

5. Palynological results

A total of nine coprolites were analysed; eight of them preserved pollen (samples ID San-Cop1 to San-Cop8) and one was barren from Unit 105 (Table 2). A total of 1,395 pollen grains were identified. The percentage of indeterminable grains is < 9 % (Table 2). The number of pollen types varies between 8 and 18, with a total of 32 identified taxa. The pollen concentration ranges between 179 and 6,273 grains/g (Table 2). Palynological diagrams represent AP (Arboreal Pollen)-NAP (Non-Arboreal Pollen), together with a synthetic diagram including the main taxa and ecological groups (Figs. 4-5).

5.1. Unit 111

This unit only includes coprolite San-Cop8 (Figs. 4-5). AP is 78 %, with dominance of *Pinus halepensis/pinea* (37 %) and deciduous *Quercus* (23 %). Evergreen *Quercus* (5 %) reaches the maximum peak of the sequence. Occurrences of *Pinus nigra/sylvestris* and *Juniperus* are also ecologically meaningful. NAP is exclusively composed of Poaceae (14 %) and Amaranthaceae (6 %).

5.2. Unit 110

This unit includes coprolites San-Cop7 to San-Cop3 (Figs. 4-5). AP is predominant across all samples, reaching values > 93 %, except San-Cop4 (47 %) and San-Cop7 (38 %), in which the lowest percentage of AP is recorded. The most noteworthy characteristic is the abundance of *Pinus halepensis/pinea* (16–57 %), *Pinus nigra/sylvestris* (3–29 %), deciduous *Quercus* (2–12 %), and *Juniperus* (1–6 %), while evergreen *Quercus* does not exceed 4 %. Other AP includes *Fraxinus*, *Buxus*, *Abies*, *Picea*, *Cedrus*, *Acer*, *Alnus*, Genisteae, *Erica*, and Rosaceae. Among NAP (Fig. 4), Poaceae (3–39 %), *Artemisia* (1–19 %), and Amaranthaceae (1–18 %) are remarkable. Additionally, Asteroideae, Cichorioideae, and *Plantago* are frequent.

5.3. Unit 107

This unit only includes coprolite San-Cop2 (Figs. 4-5). The NAP is 54 %, with high frequencies of Poaceae (28 %), *Artemisia* (12 %), and Amaranthaceae (9 %), accompanied by Caryophyllaceae, Asteroideae, *Plantago*, Brassicaceae, *Knautia*, and Rubiaceae. Within AP, *Pinus halepensis/pinea* (15 %), *Pinus nigra/sylvestris* (11 %), and deciduous *Quercus* (11 %) should be noted. AP also includes *Juniperus*, *Alnus*, evergreen *Quercus*, *Ulmus*, and *Pistacia*.

5.4. Unit 105

This unit only includes coprolite San-Cop1 (Figs. 4-5). AP is 74 %, with dominance of deciduous *Quercus* (61 %) reaching the maximum frequencies of the sequence. We found significant values of evergreen *Quercus* (4 %). Other AP are *Pinus halepensis/pinea*, *Pinus nigra/sylvestris*, and *Juniperus*. In NAP, Poaceae (9 %), *Artemisia* (9 %), and Amaranthaceae (4 %) dominate. Other NAP includes Asteroideae, Cichorioideae, Rubiaceae, Caryophyllaceae, *Plantago*, and Lamiaceae 3C.

6. Discussion

6.1. Vegetation history and palaeoecological inferences

The human presence at Grotta dei Santi is recorded between 48 and 44 ka BP (Fig. 6a; Moroni et al., 2019; Conti et al., 2023). Therefore, it begins during a stadial phase (Heinrich event 5), develops throughout the Greenland Interstadial (GI) 12 and ends at the beginning of Greenland Stadial (GS) 12 (Rasmussen et al., 2014). The lake cores from Lagaccione (Fig. 6b; Magri, 1999), Lago di Vico (Magri and Sadori, 1999) and Valle di Castiglione (Follieri et al., 1988) help to reconstruct the environmental dynamics in central Italy during this time window. During GI-12, the open environments of the preceding GS-13 are replaced by a long-lasting dominance of open deciduous forests with pine, which are then replaced by open environments during GS-12 (Badino et al., 2020).

In the Grotta dei Santi vegetation sequence, mixed oak-pine open forests with continuous presence of *Juniperus* are a characteristic feature of Units 111, 110, 107 and 105 (Figs. 4-5), in association with abundance of grasses (Poaceae). A high diversity of herbaceous types may reflect prey diet of hyaenas, as suggested for other caves (e.g., Gorham's Cave – Carrión et al., 2008, Vanguard Cave – Carrión et al., 2018, and Pešturina Cave – Ochando et al., 2024a). At Grotta dei Santi there was also a relatively high diversity of woody plants, including abundant *Pinus halepensis/pinea*, *Pinus nigra/sylvestris*, *Juniperus*, deciduous and

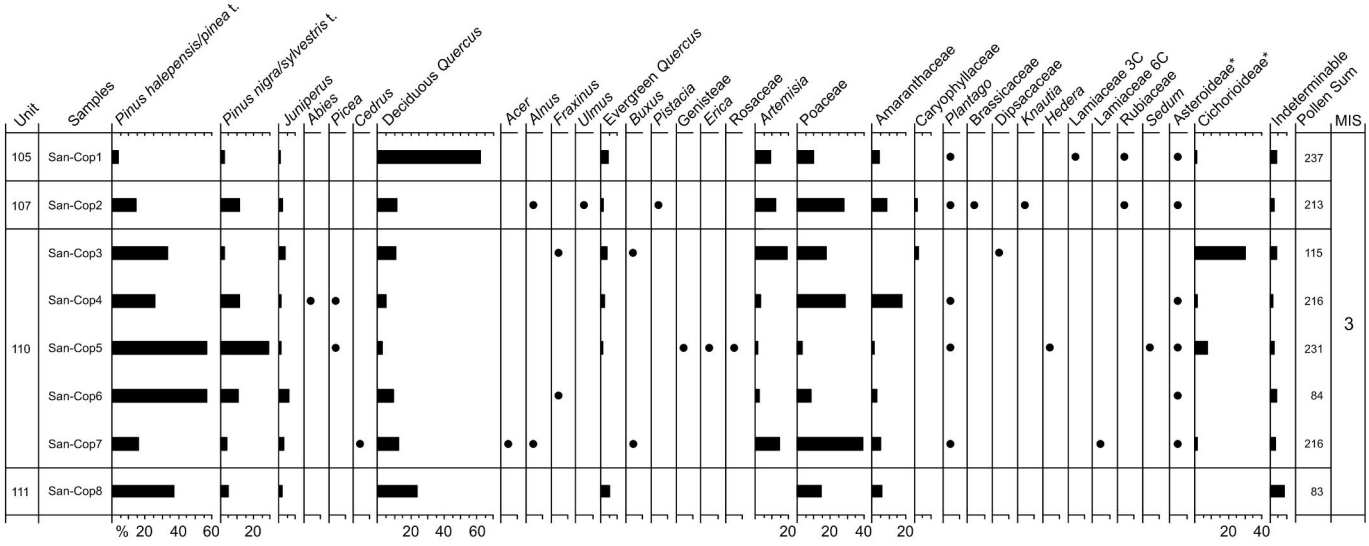

Fig. 4. Percentage pollen diagram of the coprolites from the Mousterian units at Grotta dei Santi including Trees, Shrubs, and Herbs. Black dots for percentages below 3%.

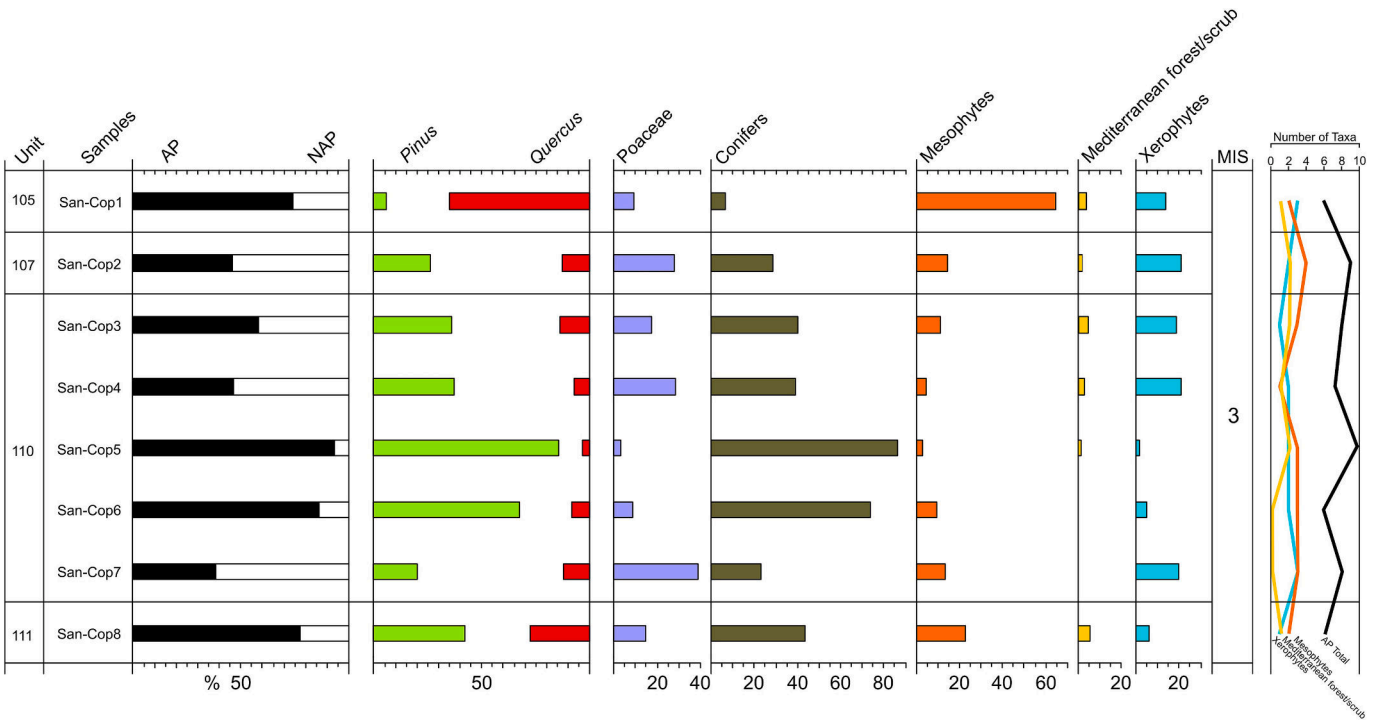

Fig. 5. Synthetic pollen diagram representing main pollen contributors (*Pinus*, *Quercus*, and Poaceae) and ecological groups (Conifers, Mesophytes, Mediterranean forest/scrub, and Xerophytes), together with the sum of arboreal pollen (AP) and non-arboreal pollen (NAP). Conifers include *Pinus*, *Juniperus*, *Abies*, *Picea*, and *Cedrus*. Mesophytes include deciduous *Quercus*, *Acer*, *Alnus*, *Fraxinus*, *Ulmus*, and Rosaceae. Mediterranean forest/scrub include evergreen *Quercus*, *Buxus*, *Pistacia*, and *Erica*. Xerophytes include *Artemisia*, Amaranthaceae, Lamiaceae 3C and 6C. Asteroideae and Cichorioideae are out of the main sum.

evergreen *Quercus*, which were always accompanied by broad-leaved *Acer*, *Alnus*, *Fraxinus*, *Ulmus*, and Rosaceae, as well as by Mediterranean taxa, such as *Buxus*, *Pistacia*, and *Erica*. The xerophytic component is mainly represented by *Artemisia*, Asteraceae, Amaranthaceae, and Lamiaceae (Fig. 4). The presence of xerophytes may indicate a generally open landscape or merely an herbaceous patch within a mosaic of semi-forested landscapes (Carrión et al., 2018; Ochando et al., 2019, Ochando et al., 2024a).

The pollen results from Units 111 and 110 (containing human occupations) of Grotta dei Santi are supported by the faunal remains, confirming the existence of a mosaic of environments. The macromammal assemblage from Unit 111 includes *Cervus elaphus*, *Capreolus capreolus*, and large bovids. In addition, Unit 110 includes *Dama dama*, *Crocuta crocuta spelaea*, *Panthera pardus*, and *Equus ferus* (Moroni et al., 2019). Thus, a high frequency of cervids characterizes both units, which suggests a woodland environment, while the presence of horse and large bovid herds suggests the existence of open woodlands near the cave. The micromammal assemblage includes typical woodland species, dominated by *Apodemus* (*Sylvaemus*), together with *Eliomys quercinus* and *Nyctalus noctula* (Moroni et al., 2019), while *Microtus arvalis* preferably inhabited open areas of temperate climate.

The pollen record of Units 107 and 105 show a considerable consistency with Units 111 and 110, with all ecological groups and the main pollen contributors presenting similar percentages, with the exception of the high frequencies of deciduous *Quercus* in Unit 105 and the parallel decline of *Pinus*. Micromammals suggest a shift towards more open environments, especially in Unit 105, while the percentages of microfaunas in Unit 107 remain comparable to the preceding Units 111 and 110. For Units 107 and 105, no large mammal data is available.

Through the Habitat Weighting and Hernández Fernández Methods (see Moroni et al., 2019) carried out on microfaunal remains, Units 111, 110 and 107 present interstadial conditions, while Unit 105 would be associated with colder conditions, with an expansion of the open-dry habitat and loss of forest areas. However, it should be emphasized that the micromammals' assemblage from Unit 105 should be considered with caution, due to its limited size (33 specimens, Moroni et al., 2019). Conversely the pollen spectra of coprolites display a general landscape stability, within a temperate interstadial, with *Quercus*-Poaceae parklands/open woodlands, Poaceae-*Artemisia* steppes, shrubby grasslands with patches of conifers and mesophytes, and heliophytic shrublands (Figs. 4-5).

According to Burgassi et al. (2024), the results of high-resolution analysis of magnetic susceptibility performed at Grotta dei Santi show low χ_{mass} values in Units 111, 110, 107, and 105, suggesting a deposition during cold and arid settings. Thus, although pollen data reflects moderately humid and mild conditions for these units, an increase in typical steppe taxa in the upper part of Unit 110 and Unit 107 suggests a trend towards more arid conditions (but not extreme). According to pollen data, Unit 105, characterized by abundant oak, documents a temperate climate, suitable for the development of a deciduous broad-leaved woodland. When considering these inconsistencies, especially among micromammal and palynological results on the one hand and magnetic susceptibility on the other, it must be borne in mind that sediments take time to be pedogenised, eroded and then deposited in the cave (Boschin et al., 2022 *and reference therein*), so that the responses of the vegetation and mammal communities are not necessarily contemporaneous with those of the sediments, and their palaeoecological signals can be considered more accurate than other proxies and consistent with the archaeological evidence (Boschin et al., 2022).

6.2. *Palaeoenvironment during MIS 3 in the Italian Peninsula*

The pollen analysis on coprolites from Grotta dei Santi provides an additional and unique opportunity to reconstruct the palaeoenvironment encountered by Late Italian Mousterian groups during MIS 3.

Considering the geographical features and the temporal trend of vegetation responses to the climatic processes associated with D-O cycles, the pollen data from Grotta dei Santi is consistent with the

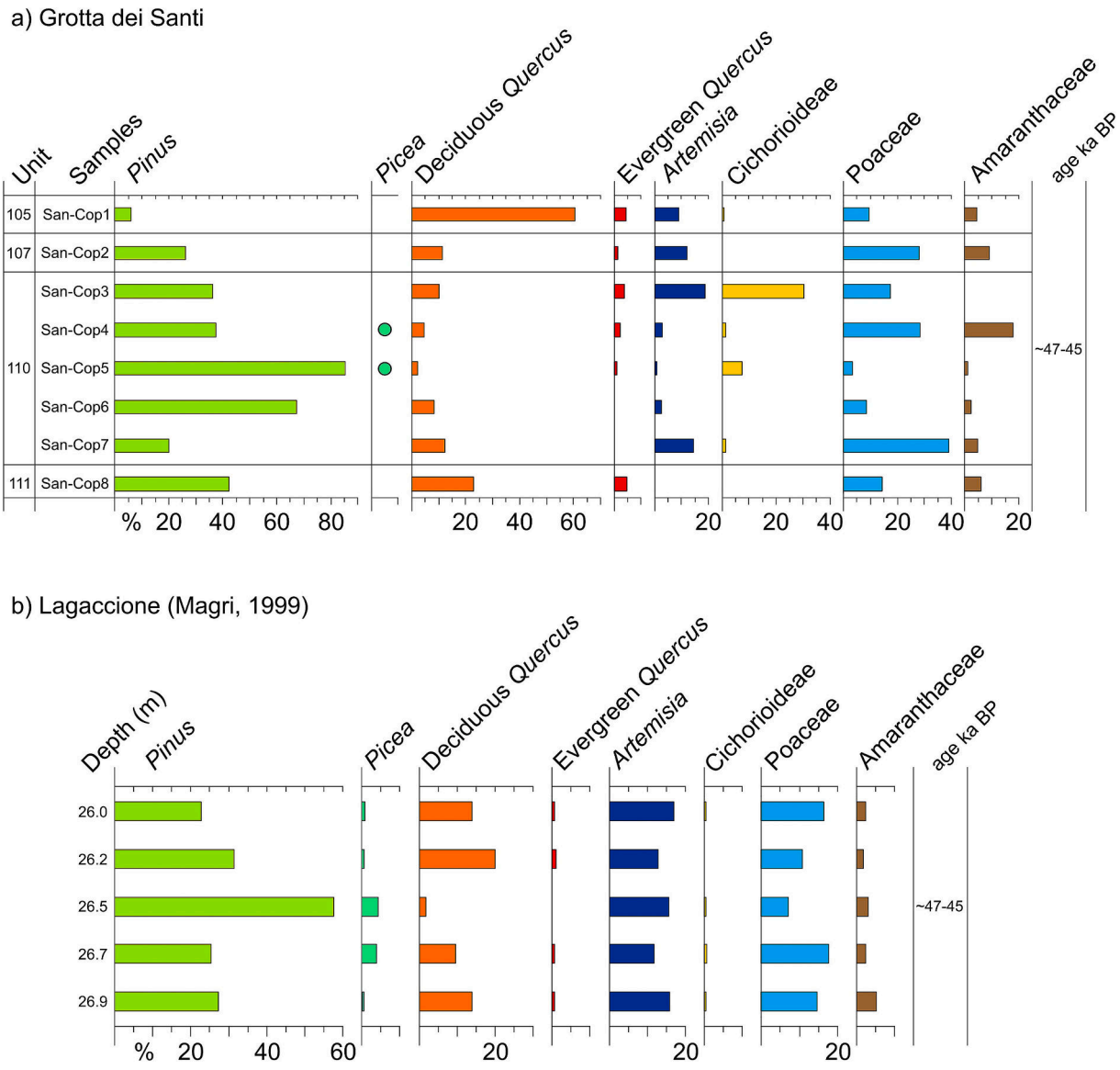

Fig. 6. Tentative correlation between the pollen sequences of: a) Grotta dei Santi (this study) and b) Lagaccione (Magri, 1999), framed in the GI-12 (ca. 47–45 ka BP).

vegetation characters documented in the Lagaccione pollen record during GI-12, which has an age of ca. 47–45 ka BP (Magri, 1999; Fletcher et al., 2010; Fig. 6a-6b). Since Lagaccione is a continuous sequence, the intensity of the climatic/forest pulses and the alternation of vegetation composition during MIS 3 provide a biostratigraphical frame for interstadial phases beyond the reach of radiocarbon dates. At Lagaccione, the GI-12 oscillation is characterized by a peculiar pattern of alternating development of deciduous *Quercus* – *Pinus* – deciduous *Quercus* (Fig. 6b), which is different from the previous and following interstadial phases. The same alternating development of deciduous *Quercus* – *Pinus* – deciduous *Quercus* is revealed by the pollen record from Grotta dei Santi (Fig. 6a). Besides, other taxa, such as *Picea*, evergreen *Quercus*, *Artemisia*, Poaceae, and Amaranthaceae, exhibit similar trends in the levels of GI-12 at Lagaccione and at Grotta dei Santi.

The preceding (GS-13) and following (GS-12) stadial phases at Lagaccione are characterized by an open and strongly xerophytic environment not recorded in the pollen assemblages from Grotta dei Santi. Thus, our data derived from the coprolite analyses strongly support a correlation of Units 111 to 105 with only GI-12, excluding any stadial climate phase. Thus, the chronology of these Units can be restricted to ca. 47–45 ka (Fig. 7).

Coprolites from Late Pleistocene caves, primarily Cava Muracci, Lazio (Gatta et al., 2016), Tana delle Iene, Apulia (Petrucci et al., 2005; Gatta et al., 2016), and Caverna delle Fate, Liguria (Karatsori et al., 2005), can be directly compared with Grotta dei Santi in terms of pollen assemblages. However, as regards MIS 3, it is not easy to establish well-defined correlations, since Palaeolithic sites contain discontinuous deposits sometimes extending back to different periods of the Late Pleistocene.

The Caverna delle Fate record, dating back to MIS 5e, indicates a temperate climate in the north-western part of the Italian Peninsula (Karatsori et al., 2005). Four major vegetation phases are distinguished from MIS 5 to MIS 3: a forested phase dominated by *Pinus*, evergreen *Quercus*, deciduous *Quercus*, and *Corylus* tentatively correlated with an interstadial phase of MIS 5 (5e, 5c, or 5a); a pine-dominated open landscapes of an interstadial period between MIS 5a and MIS 4; a semi-forested vegetation of a second interstadial period between MIS 5a and MIS 4; and a forested landscapes of MIS 3 with significant presence of *Pinus*, evergreen *Quercus*, and deciduous *Quercus*. During MIS 3, the pollen record reflects semi-forest to forest vegetation, indicating a

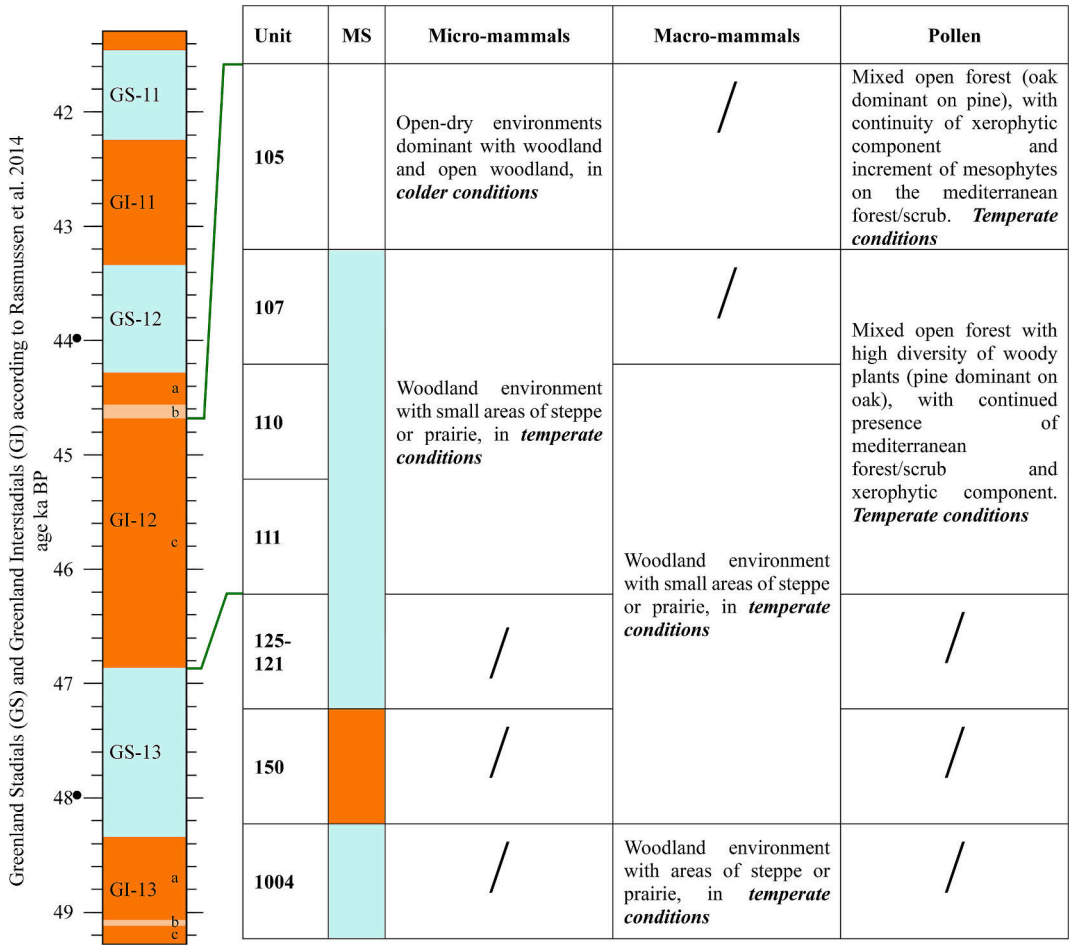

Fig. 7. General synthesis of the environmental data from magnetic susceptivity (MS: the pale blue indicates cold and arid settings, the orange indicates warm and humid settings), microfauna, macrofauna, and pollen samples, compared to the Greenland Interstadial (GI) and Greenland Stadial (GS) succession during the Neanderthal presence at Grotta dei Santi, according to Rasmussen et al. (2014). Data derived from the coprolite analyses support a correlation of Units 111 to 105 with only GI-12 (ca. 47–45 ka BP). The chronological period based on the known datings is indicated by the black dots at 48 and 44 ka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperate climate developed under Mediterranean influence, allowing the persistence of mesothermophilous taxa, similar to the pollen assemblage from Grotta dei Santi.

In Grotta di Cava Muracci (Cisterna di Latina), central Italy, a detailed coprolite pollen record from approximately 44 to 35 ka (MIS 3) shows a spread of steppes/grasslands with *Artemisia*, Poaceae, and Amaranthaceae, as well as a decline of deciduous *Quercus* and other mesophytes and thermophytes (Gatta et al., 2016). The chronology and the composition of this pollen assemblage corresponds to the steppe vegetation phase starting from GS-12, which is represented in the continuous record from Lagaccione and is missing at Grotta dei Santi (Fig. 6a-6b), where only a forested phase is documented.

In the Tana delle Iene, Apulia, south-east Italy, extending back from 60 to 40 ka (Giaccio and Coppola, 2000), the pollen assemblages from coprolites suggest a steppe/grassland environment with sporadic mesophilous and thermophilous trees (Petrucci et al., 2005; Gatta et al., 2016). As in Grotta dei Santi, the herbaceous vegetation is represented by remarkable values of Poaceae, *Artemisia*, Amaranthaceae, and Cichorioideae, and to a lesser extent of Brassicaceae and *Plantago* (Figs. 4-5). Tana delle Iene differs from Grotta dei Santi also from a palaeontological point of view, as equids and aurochs count for almost half of the ungulate remains, confirming the presence of open environments (Conti et al., 2012). This feature is common in Apulian sites (e.g. Crezzini et al., 2024; Boscato and Crezzini, 2012) and marks a clear difference between the Apulian and the northern Adriatic side of the peninsula (Boschin et al., 2022).

7. Conclusions

This study has allowed, for the first time, a detailed contextualisation of the environmental setting of the Argentario Promontory and the surrounding areas in mid-MIS 3 in relation to the presence of Late Mousterian groups, providing a fundamental piece in the reconstruction of the complex palaeoecological mosaic immediately preceding the disappearance of these populations in the Italian Peninsula.

The analysis of eight coprolites from Grotta dei Santi yielded a good pollen sample, revealing a vegetation spectrum with a significant presence of mixed forest (dominated by pine and oak, with a high diversity of woody plants), Mediterranean forest/bush and xerophytic/open environment components, suggesting the persistence of temperate climatic conditions throughout the period examined (from 111 to 105).

Our data from Grotta dei Santi confirms that, regardless of the relative influence of digestion processes of hyenas, depositional environment, and post-depositional pollen alteration, coprolite pollen assemblages closely reflect regional vegetation features. Coprolites, often the only depositional element preserving pollen in prehistoric caves, provide valuable palaeovegetational records that can be integrated with lacustrine sediments to set up biostratigraphic schemes at a regional scale. The comparison with the regional pollen record constrains the age of the pollen record to ca. 47–45 ka BP, corresponding to GI-12.

Except for faint traces of human presence (remnants of fire in the Unit 100), it is interesting to note that, as far as we know, after the Mousterian occupation of Unit 110 (Fig. 2), Grotta dei Santi seems to have been almost completely deserted by humans until the Roman period, although the cave was still accessible from the outside as evidenced by the continuation of sedimentation and the presence of hyena dens. Our data show that the climatic and environmental conditions did not change significantly after the Mousterian occupation, during the deposition of Unit 107, and even later, during Unit 105, suggesting that the availability of environmental resources was unchanged even after the end of the human occupation. In short, it seems that Mousterian populations did not abandon the cave and the surrounding area for environmental stress, since they were able to have access to the same variety and abundance of resources as before. This assumption is indirectly supported by the fact that, on the contrary, the Mousterian presence is still documented ~ 41–40 ka cal BP in northern Tuscany, in sites located at the foot of the Apennines, where environmental conditions may have been less favourable.

It is now well established that the demise of European Neanderthals occurred at different times and in different ways in different geographical regions (e.g., Higham et al., 2014, 2024; Picin et al., 2020; Timmermann, 2020; Devièse et al., 2021; Vidal-Cordasco et al., 2022; Dogandžić, 2023; Finlayson et al., 2023; Slimak et al., 2024). Consequently, it seems increasingly necessary to investigate the dynamics associated with this phenomenon in detail, down to the micro-regional level. In this sense, the results of our study open new windows on the ecological characteristics and behaviour of Late Neanderthals in central Italy.

8. Authors' contribution

J.O., A.M. and V.S. conceived and wrote the article; J.O., F.D.R., and D.M. studied the pollen record; J.C. and F.Bo. studied the macrofaunal remains and contributed to the revision of faunal data and comparison with pollen results; A.B. studied the magnetic susceptivity and contributed to the comparison with pollen results; F.Be. contributed to the evaluation of the hearths structures; V.S. and G.M. contributed to the site and stratigraphy contextualization; A.M. and V.S. directed the research fieldwork at Grotta dei Santi over the years and collaborated in writing the conclusions; All the Authors collaborated in writing the final revision of the article.

J.O. made the Figs. 3-6 and Table 2; V.S. made the Figs. 1-2 and 7 and the Table 1.

CRediT authorship contribution statement

Juan Ochando: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Federico Di Rita:** Writing – original draft, Validation, Supervision, Investigation, Formal analysis. **Donatella Magri:** Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis. **Jacopo Crezzini:** Validation, Supervision. **Allegra Burgassi:** Validation, Supervision. **Giulia Marciani:** Supervision, Project administration, Investigation. **Francesco Berna:** Writing – original draft, Validation, Supervision. **Francesco Boschin:** Writing – original draft, Validation, Supervision, Resources, Investigation. **Adriana Moroni:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Vincenzo Spagnolo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

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

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Data availability

Data will be made available on request.

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