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Balkan Neanderthals: The Late Pleistocene palaeoecological sequence of Pešturina Cave (Niš, Serbia)

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ABSTRACT

The Central Balkans are a key biogeographical region in Southern Europe, influenced by a central European-Mediterranean climate, which acted as a refugium for flora and fauna, and favored the dispersion of Neanderthals and migration of modern human populations during Late Glacial Period. This study presents pollen analyses of sediment and hyaena coprolites from Pešturina Cave in Serbia to reconstruct the vegetation landscapes faced by Balkan Neanderthals and early Anatomically Modern Humans between MIS 5e-3. Between MIS 5e-5c (archaeological layers 4c and 4b) and MIS 5b-5a (layer 4a), semi-forested environments prevailed, characterized by *Pinus*, deciduous *Quercus*, *Tilia* and other angiosperm woody taxa, accompanied by heliophytes such as *Artemisia* and Poaceae. During MIS 4-3 (layers 3-2), the vegetation was dominated by *Artemisia*-Poaceae steppes with *Quercus* patches, conifers and legumes. Overall across the sequence, pollen assemblages are highly diverse and include a number of deciduous trees and sclerophylls. In addition, the occurrence of several herbaceous taxa reinforces the view that the Balkans were outstanding for endemicity. Neanderthals and early Upper Palaeolithic hominins lived in a highly diverse refugium, offering multiple opportunities for survival during the warm interstadials and, more critically, the cold stadials of the Pleistocene.

1. Introduction

The Balkan Peninsula displays a great variety and complexity of environments from a climatic, geological and vegetational perspective (Reed et al., 2004; Hewitt, 2011; Nieto Feliner, 2014; Španiel and Rešetnik, 2022). Solid geology is considered one of the most determining factors in defining the diversity and the refuge of autochthonous species of the present-day flora in the Balkans (Polunin, 1980; Thompson, 2005), at least since the Miocene, with the formation of the Carpatho-Balkan belt to the east and the Dinaric Alps to the west. Additionally, the climatic conditions of the Balkans are defined by their geomorphology, their particular geographical position and the broad platform coastline (Furlan, 1977; Martyn, 1992; Reed et al., 2004). Thus, in a series of works of crucial importance for European palaeoecology, several authors (Bennett et al., 1991; Tzedakis, 1994, 1999; Willis, 1994; Okuda et al., 2001; Magri, 2010; Pross et al., 2015; Sadori et al., 2016; Magri et al., 2017; Lang et al., 2023) have shown that the Balkan Peninsula acted as a unique phytodiversity reservoir for the

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Mediterranean Basin.

The Central Balkans served as a major natural corridor for the earliest migrations of archaic and modern humans into Europe (Conard and Bolus, 2003; Mihailović, 2009, 2020; Roksandic et al., 2018; Marín-Arroyo et al., 2023). Therefore, the Central Balkan Range is rich in Middle and Late Pleistocene archaeological sites (Mihailović et al., 2011, 2022a, 2022b; Roksandic et al., 2011, 2022; Marín-Arroyo, 2014; Mihailović and Bogićević, 2016; Skinner et al., 2016; Morin and Soulier, 2017; Marín-Arroyo and Mihailović, 2017). Pollen analysis has proven to be a valuable method to reconstruct the plant components of past ecosystems (Ritchie, 1995; Bennett and Willis, 2001; Birks, 2005), including hominin evolutionary contexts (García-Antón and Sáinz-Ollero, 1991; Carrión, 1992a, 1992b; Burjachs, 2001; Bonnefille et al., 2004; Finlayson and Carrión, 2007; Bonnefille, 2010; Carrión et al., 2011, 2019a, 2019b, 2019c; Messager et al., 2011; Bigga et al., 2015; McGee and deMenocal, 2017; Ochando et al., 2022a, 2020b; Saarinen et al., 2022). Nevertheless, there is still a lack of pollen records from that Pleistocene period, also due to the difficulties of conducting pollen analysis in caves, rockshelters and open-air sites. These include sedimentary discontinuities, selective preservation, preferential transport, and contamination by percolating water and bioturbation (Carrión and Scott, 1999; Carrión et al., 2009, 2022a).

Within materials recovered from archaeological contexts, coprolites and other foodstuffs have played a crucial role in the history of Quaternary palynology (Scott, 1994; Carrión et al., 1995a, 1995b, 1999a, 2006, 2007, 2022a,; Latorre et al., 2002; Yll et al., 2006; Marais et al., 2015; De Porras et al., 2017; Ochando et al., 2022c), particularly hyaena coprolites (Scott, 1987; Horwitz and Goldberg, 1989; González-Sampériz et al., 2003; Carrión et al., 2004, 2008, 2018; Gatta et al., 2016; Daura et al., 2017; Djamali et al., 2020; Ochando et al., 2020a). They often complement the palaeobotanical record as they incorporate strictly entomophilous pollen types that can rarely be found in biogenic sediments whose pollen spectra are largely derived from airborne pollen and aquatic transport (Carrión, 2002; Carrión et al., 2018, 2019a, 2019b, 2019c).

This paper presents a palynological study performed on sediment samples and on hyaena coprolites from Pešturina Cave (Niš, southern Serbia), with the aim of reconstructing the vegetation landscapes occupied by Balkan Neanderthals and early Anatomically Modern Human populations during MIS 5e-3.

2. The site: physical setting, excavations and chronology

Pešturina Cave is located about 20 km from the city of Niš (Serbia) (43°17′42″ N, 22°02′48″ E), a small tributary to the Nišava River, on the eastern edge of the Niš Basin (near the Sićevo Gorge) and on the western slopes of Suva Planina Mountain (Fig. 1). The mountain is situated in the south–east of Serbia and extends in a NW–SE direction. It is 45 km long, 15 km wide, and ranges between 250 m and 1810 m in altitude. The karst cave is set in the Upper Jurassic dolomites and reef limestones, with Paleozoic siliciclastic sediments below, and Neogene lacustrine sediments above the Jurassic sequence, about 330 m above sea level (Fig. 1). Pešturina Cave has a total length of 22 m, with an entrance 15 m wide and 3.5 m high (Figs. 1 and 2).

The Niš Basin is bordered to the north by the slopes of the Svrljig Mountains, and to the south by the slopes of the Suva Planina Mountain (Anđelković, 1982; Rakić and Dimitrijević, 1973; Vujisić and Navala, 1980). The Basin preserves multiple recorded caves on its vicinity and diverse Pleistocene emplacements, which could have served as human habitats in the past. The main communication routes linking the southern part of the Balkan Peninsula with Pomoravlje and the Carpathian Basin cross this area (Radović et al., 2019) (Fig. 1). Even more, the

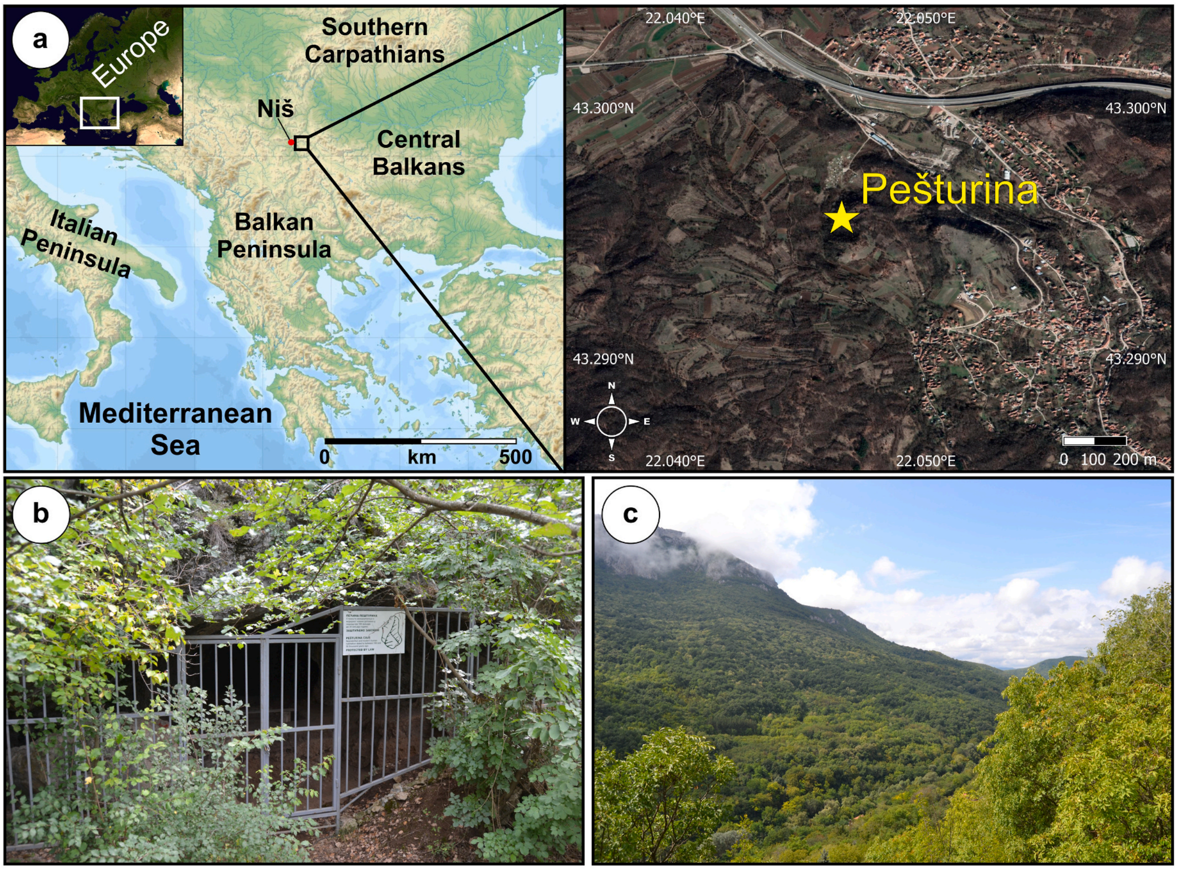

Fig. 1. Pešturina Cave. a) Location in the western Central Balkans (Niš, southern Serbia), b) cave entrance, c) area of access to the cave.

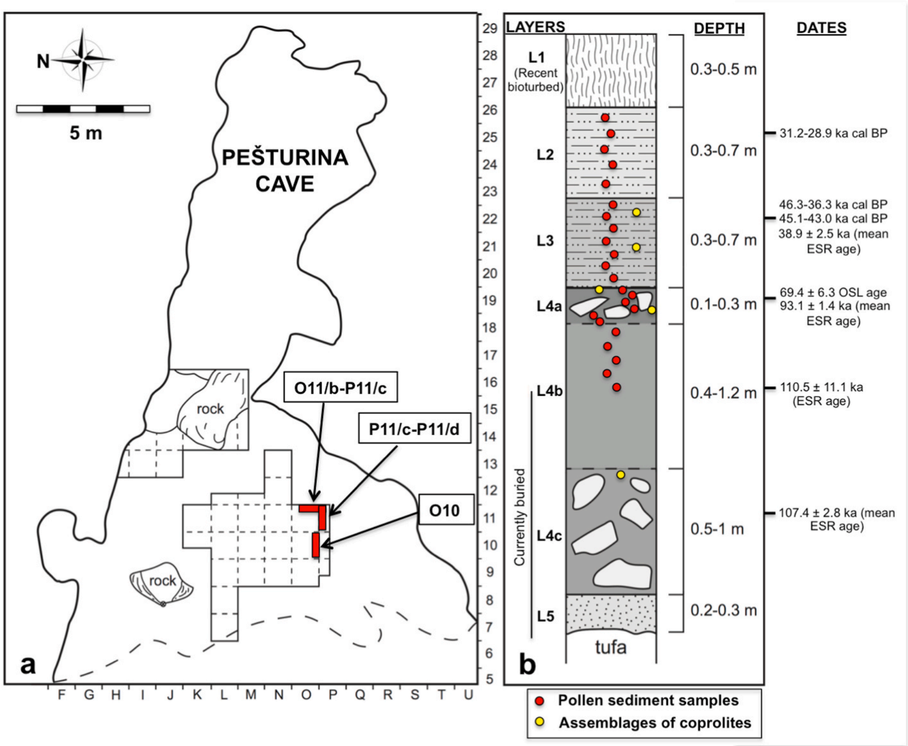

Fig. 2. a) Stratigraphy and profiles sampled for pollen analysis in Pešturina Cave, b) stratigraphy with the position of pollen sediment samples, assemblages of coprolites, and geochronological data (further details can be found in Tables 1 and 2).

position of the cave is located along a major cultural and biological migration route from Asia into northern Europe during the Middle-Late Pleistocene (Roksandic et al., 2011; Mihailović, 2020).

The cave was discovered in 2006. The initial excavations of a 2.5 × 1.5 m test pit by 1.3 m deep yielded only a dozen Palaeolithic artifacts. However in 2010, when the test pit was expanded after systematic excavations, Pešturina proved to have important deposits mainly belonging to the Middle and Upper Palaeolithic (Mihailović et al., 2022a). Since 2006, the excavated area has reached a surface of c. 24 m^2 and a depth of c. 3 m (Mihailović and Milošević, 2012; Mihailović, 2014; Mihailović et al., 2022a) (Fig. 2).

The multidisciplinary analysis of Pešturina Cave, which includes dating, Neanderthal and Anatomically Modern Humans fossils, lithic artifacts, and faunal remains, allowed to identify a stratigraphic

Table 1

Geochronological data for Pešturina Cave. Further details of the ^{14}C, ESR and OSL ages can be found in Alex and Boaretto (2014), Blackwell et al. (2014, 2018), Alex et al. (2019) and Mihailović et al. (2022a).

Layer	Square	Laboratory code	Sample type	Technoculture	^{14}C kyr BP	^{14}C Ultrafiltration (ka cal BP 95.4% C.I.) (Alex and Boaretto, 2014; Alex et al., 2019)	ESR ages (ka ±1 σ and 2 σ) (Blackwell et al., 2014, 2018; Mihailović et al., 2022a)	OSL ages (Mihailović et al., 2022a)	MIS
2	L9b	RTD-7148	Bone	Gravettian	13.4 ± 60	16.3–15.9			MIS2
2	M9b	RTK-6446	Bone	Gravettian	26.1 ± 620	31.2–28.9			MIS3
2	N11c	RTK-6445	Bone	Gravettian	>37.8				MIS3
3	M7b	RTD-7231B	Bone	Charentian-like Mousterian	28.7 ± 180	33.4–32.0			MIS3
3/4	N10b	RTK-6450	Bone	Charentian-like Mousterian	36.2 ± 2200	46.3–36.3			MIS 3
3	N9b	RTD-7149	Bone	Charentian-like Mousterian	40.5 ± 590	45.1–43.0			MIS3
3	L9c	AT23	Tooth	Charentian-like Mousterian			38.9 ± 2.5		MIS3
4a	M11	OSL 4	Sediment	Charentian-like Mousterian				69.4 ± 6.3	MIS4
4a	M10d, N9a, N9d, O10c	AT22, ET5, AT32, AT66, AT65	5 Teeth, mean	Charentian-like Mousterian			93.1 ± 1.4		MIS5
4b	I14d	AT24	Tooth	Charentian-like Mousterian			110.5 ± 11.1		MIS5
4c	O10b, M10a	AT47, AT63	2 Teeth, mean	Mousterian			107.4 ± 2.8		MIS5

sequence that includes the Late Pleistocene and Holocene (Mihailović and Milošević, 2012; Mihailović, 2014; Radović et al., 2019; Lindal et al., 2020; Milošević, 2020; Mihailović et al., 2022a). Five stratigraphic layers have been identified. A simplified stratigraphic section is presented in Fig. 2b: Layer 1 (L1), the uppermost layer: loose humic silts with Bronze Age material (30–50 cm); Layer 2 (L2): light brown fine-grained silt, with Gravettian industry (30–70 cm); Layer 3 (L3): compact brown fine-grained silt with a Charentian-like Mousterian assemblage (30–70 cm). Layer 4 can be divided into three sub-layers of unequal thickness: (4a), slight red sediment with large blocks of bedrock (10–30 cm); (4b), loose dark red sediment with abundant limestone clasts (40–120 cm); (4c), loose dark brown sediment with large rock fragments (50–100 cm). The loose dark red sediment of horizon 4b contained the majority of human activities evidence (Radović et al., 2019). Layer 5 (L5): greyish sandy sediment with scarce finds, on tufa deposits that probably lie directly above the rocky bottom (20–30 cm) (Mihailović and Milošević, 2012; Mihailović, 2014; Radović et al., 2019; Lindal et al., 2020; Mihailović et al., 2022a).

Several methods were used in dating the archaeological materials and cave sediment (Table 1). Based on AMS Ultrafiltered on worked bones from Layer 2 (Table 2) there is evidence for modern human occupations at least between 16.3 and 15.9 ka cal BP, and between 31.2 and 28.9 ka cal BP (Alex and Boaretto, 2014). In addition, one AMS date from Layer 2 (Table 1), RTK-6445 > 37.8 ^{14}C ka BP, along with a date from Layer 3 between 33.4 and 32.0 ka cal BP, fits chronologically into the earliest Gravettian (Alex et al., 2019). Thus, it is most likely that around 30 ka cal BP (end of the MIS 3), Pešturina was occupied by modern humans producing Gravettian or Early Epigravettian industries, based on lithics assemblages and these dates (Alex and Boaretto, 2014; Alex et al., 2019).

Bones from Layer 3 with human modifications were dated to 45.1-43.0 ka cal BP by radiocarbon dating, likely indicating that the cave was used by late Middle Palaeolithic Neanderthals (Alex and Boaretto, 2014), while a tooth in Layer 3 was dated to 38.9 ± 2.5 ka by Electron Spin Resonance (ESR) method (Blackwell et al., 2014, 2018). According to conventional Optically Stimulated Luminescence of quartz (OSL), the sample OSL 4 provides a chronology of 69.4 ± 6.3 ka (Table 1). Hence, sediment in the upper portion of Layer 4, bordering with Layer 3, was potentially deposited during MIS 4 (boundaries: 74-59 ka; Martinson et al., 1987). Consequently, Layer 3 could correspond to MIS 4 or to early MIS 3, though changes over time in the cosmic dose rate and in the water content could have made the mean dose rate lower, leading to an older age estimate. Therefore, a MIS 5a age cannot be totally ruled out (Mihailović et al., 2022a).

Layer 4 is subdivided into three levels: Layer 4a, with a weighted mean age of 92.9 ± 5.2 ka; Layer 4b, with an average age of 101.9 ± 3.8 ka; Layer 4c, with an average age of 117.4 ± 6.6 ka (Blackwell et al., 2014). According to Blackwell et al. (2018), Layer 4a corresponds to MIS 5b, while Layer 4b corresponds to the end of MIS 5c. Additionally, Layers 4a, 4b and 4c were dated using ESR method (Mihailović et al., 2022a). Layer 4a, was dated to a mean age of 93.1 ± 1.4 ka (correlate with MIS 5b); Layer 4b, with only one tooth without being likely reworked to an age of 110.5 ± 11.1 ka (correlate with 5e-5c); Layer 4c, with an average of 107.4 ± 2.8 ka (correlate with 5e-5c). Mihailović et al. (2022a) suggest that Layers 4b and 4c could belong to the same geochemically uniform layer, just as the three teeth found not reworked at both layers (4b and 4c) correlate well with MIS 5e-5c.

It is clear from the former that there is no precise age model for the sedimentary sequence at Pešturina Cave, principally due to potential reworking of some teeth, as well as possible dating inaccuracies from the “lumpy” nature of the sediment. This can be appreciated mainly at Layer 3, which was significantly disturbed by erosion, bioturbation, and recent anthropogenic activities, causing inconsistent dates ranging from MIS 4 to MIS 3 (boundaries: 70-38 ka; Blackwell et al., 2014; Alex et al., 2019).

Preliminary studies have provided palaeoenvironmental proxies from Pešturina based on palaeontological and sedimentological characteristics of the archaeological layers (Milošević, 2016; Majkić et al., 2018; Boev and Milošević, 2020; Jovanović et al., 2020).

Table 2
NISP of anthropogenic modification, gnaw and digestion on animal remains per layer.

Layer	Cutmarks	Impact marks	Gnaw and digestion marks
2	8	7	252
3	13	16	327
4a	87	44	885
4b	9	9	219
4c	1	2	27

3. Human remains

Three human fossil remains from Pešturina Cave have been analysed so far (Roksandic et al., 2017; Radović et al., 2019; Lindal et al., 2020), namely a left lateral mass of an atlas (Pes-1), a juvenile radius shaft (Pes-2) and isolated tooth (Pes-3), all of them dating between MIS 5c and MIS 3. The fossil Pes-1 was found from the bottom of Layer 2. The layer is dated to 31-29 ka cal BP. Pes-1 was classified as Anatomically Modern Human, based on metric and non-metric morphological traits (Lindal et al., 2020). Thus, considering that the lithic material belongs to the Upper Palaeolithic (Gravettian) and that two of the four dates are consistent with it (Alex and Boaretto, 2014; Alex et al., 2019), the specimen is best dated to the end of MIS 3. The fossil Pes-2, a juvenile radius shaft, was recovered from the contact zone between Layers 3 and 4a. Based on the traits such as the teardrop-shaped cross-section and the apparently strong lateral curvature of the diaphysis, the analysis of the specimen suggested certain affinities with *Homo neanderthalensis* (Lindal et al., 2020; Mihailović et al., 2022a). Due to its stratigraphic position between Layers 3 and 4a, and based on the available dating, the fragment falls within a very wide chronological range of 92.9-38.9 ka (i.e., MIS 5b-3). The fossil Pes-3, an isolated upper first molar, was recovered from Layer 4b and dates to MIS 5c (Mihailović et al., 2022a). Previous analysis carried out on Neanderthal molars (Martin et al., 2017; Ortiz et al., 2017), as well as an excellent state of preservation (Radović et al., 2019), allowed to assign the specimen Pes-3 to Neanderthal.

4. 4. Lithic assemblages

Pešturina Cave lithic assemblages have not been published to the same extent. Artifacts from Layers 4a–4c, collected until 2017, were published in detail as a part of the same study (Mihailović et al., 2022a), while those from Layers 2 and 3, which originated from the initial excavations (2005–2011), were published only as a part of a single preliminary report (Mihailović and Milošević, 2012).

Lithic assemblages from Layers 4a–4c were attributed to the Central European Charentian (Mihailović et al., 2022a), and show a strong Quina component, which is primarily manifested in the knapping technology, and to a lesser extent in the repertoire of tools. Artifacts are made predominantly of quartzite and quartz (60–75%). In terms of the knapping products, there are cores and flakes struck via Quina, discoid and Levallois methods, while the most common tool types are side-scrapers, denticulated and notched pieces. Although the artifacts from Layer 3 were preliminarily attributed to Denticulated Mousterian (Mihailović and Milošević, 2012), subsequent (still unpublished) research showed that the structure of this assemblage does not differ significantly from Layer 4. The new analyses also showed that the (minute) differences between the assemblages from Layers 4b, 4a and 3 are not due to the presence of different types of Mousterian but are more likely resulting from differences in the duration and character of settlement.

The occupation intensity was somewhat more pronounced during the deposition of Pešturina Layer 4b, which yielded the highest number of artifacts and where cortical pieces are least represented. In contrast, artifact assemblages from Layers 4a and 3 (with significantly fewer finds) contain more cortical pieces, indicating a shorter occupation interval. In Layer 4, the highest concentration of finds was recorded in the central and southern parts of the cave, while in Layer 3, the eastern part that is closer to the cave entrance, showed the highest concentration.

Pešturina Layer 2 yielded relatively few finds (79 artifacts until 2012) which were all attributed to Gravettian. The largest number of artifacts from this layer originated from the southeastern part of the cave. All artifacts are made of chert. Among unretouched artifacts, unretouched flakes and blades predominate, while backed points and bladelets, truncated pieces and retouched blades predominate among the retouched tools. The number and character of finds from Layer 2 also indicate a short-term occupation.

5. Modern climate and vegetation

Pešturina is located on the hillock on the western slopes of the Suva Planina Mountain (Carpatho-Balkan mountain range; Fig. 1), which falls within a transitional zone between the Mediterranean and continental distinctive and contrasted climatic zones. The Mediterranean climate is characterised by warm and dry summers, while winters are mild and rainy. The central European climate is marked by rain falls throughout the year (with the maximum occurring in the summer months). In the south of the Balkan Range, in the plain of Thrace, a milder climate prevails under the influence of the Mediterranean air masses, while to the north the climate is sharply continental, with winters slightly colder than might be expected for these latitudes (Marinček et al., 1980; Polunin, 1980; Bohn and Neuhäusl, 2004).

The climate in the vicinity of the cave is mild, and generally warm and temperate. Suva Planina Mountain presents significant rainfall, even in the driest months, with most precipitation falling in winter. The nearby meteorological station in Niš shows an annual average temperature of 11.9 °C (−0.4 °C in the coldest month, 23.3 °C in the warmest month), which can reach maxima above 29 °C in summer, and annual average precipitation of 607 mm (https://es.climate-data.org/europe/serbia/nis/nis-1268/).

The hilly-montane landscape from Central Balkans, where numerous Middle and Upper Palaeolithic archaeological sites are located (the majority of them situated between 300 and 500 m elevation), is characterized by mostly lowland and some highland basins separated by canyons, gorges, and mountains (Mihailović, 2020). Suva Planina is a Tertiary fold mountain, being a southern extension of the Carpathians, together with the other Stara Planina mountains. They are largely composed of limestone, with some igneous and crystalline rocks exposed in the west and central areas (Polunin, 1980; Ager, 1980). The topography varies from river corridors below 200 m to peaks that do not exceed 2000 m, which limits the presence of persistent glaciations.

The Balkan Peninsula rises as the richest area of Europe by plant-life (Polunin, 1980; Stevanović et al., 2007; Hewitt, 2011). It has been considered that in the Balkans there are over 6530 species of native seed plants, of which >2650 are endemic (Turrill, 1944; Kryštufek and Reed, 2004; Stevanović et al., 2007; Tomović et al., 2014; Španiel and Rešetnik, 2022). These numbers are relevant with respect to the total number of native European species given in Flora Europaea (Tutin et al., 1964-1980), over 11000, about 3500–4000 of which are endemic to Europe.

The flora and vegetation of the Balkan region is mainly influenced by four factors: climate, altitude, soils and anthropogenic activity (Ellenberg, 1988; Reed et al., 2004; Thompson, 2005; Španiel and Rešetnik, 2022). In the same way, the richness of the Balkan flora is a result of several conditions: (1) the surviving Tertiary and Quaternary species, (2) the fragmentation, isolation, and migration of species due to changes in level and extent of the Mediterranean Sea, causing the formation of new habitats, (3) the gradual migration of species of other nearby floras, particularly the central European, Anatolian, and Pontic floras, (4) anthropic influence, introducing species from outside the Balkan Peninsula. Thus, the Balkans appear as one of the main refuge areas in Europe, along with the Iberian Peninsula and the Italian Peninsula, both for the formation of new species and for migration route of species.

The Suva Planina is mainly formed by central European vegetation (Bohn and Neuhäusl, 2004), as follows.

- **0-700 m:** mixed oak-hornbeam forest of *Quercus cerris*, *Q. frainetto*, *Q. robur*, *Q. petraea*, *Q. polycarpa* and *Carpinus betulus* with *Fagus sylvatica*, *Ulmus minor*, *U. glabra*, *Pyrus pyraster*, *Prunus avium*, *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Tilia tomentosa*, *T. cordata*, and *Fraxinus excelsior.* Commonly associated shrubs are: *Corylus avellana*, *C. colurna*, *Crataegus monogyna*, *Prunus spinosa*, *Euonymus europaeus*, *Frangula alnus*, *Cornus sanguinea*, *C. mas*, *Lonicera caprifolium*, *Ligustrum vulgare*, *Staphylea pinnata*, *Sambucus nigra*, and *Viburnum lantana.* Sweet chestnut woods may occur locally in this climatic region, widely mixed with oaks. Some of the most common herbaceous species are: *Helleborus odorus*, *H. dumetorum*, *Eranthis hyemalis*, *Epimedium alpinum*, *Vicia oroboides*, *Hacquetia epipactis*, *Cyclamen purpurascens*, *Lamium orvala*, *Knautia drymeia*, *Erythronium dens-canis*, *Convallaria majalis*, and *Galanthus nivalis.*
- **700–1700 m:** montane deciduous forests are mainly composed of beech forests of *Fagus sylvatica* in the northern and central Balkan region. Other trees often associated with these beech forests, but typically only as scattered individuals, are: *Abies alba*, *Picea abies*, *Pinus sylvestris*, *P. peuce*, *Populus tremula*, *Carpinus betulus*, *Corylus colurna*, *Ulmus glabra*, *Sorbus aucuparia*, *S. torminalis*, *S. aria*, *Acer platanoides*, and *A. pseudoplatanus.* Shrubs include: *Juniperus communis*, *Salix caprea*, *Alnus viridis*, *Ribes* spp., *Daphne laureola*, *D. mezereum*, *Vaccinium myrtillus*, and *Lonicera* spp. Montane coniferous forests are mostly formed of *Abies alba*, *Picea abies*, *Pinus nigra*, and *P. sylvestris.* They may occur mixed with *Ostrya carpinifolia*, *Fagus sylvatica*, *Sorbus aucuparia*, *S. torminalis*, *Acer opalus*, *A. platanoides*, *Tilia platyphyllos*, *Fraxinus excelsior*, or in stands of single species. Below 1000 m there are relict forests of *Fagus*, together with *Prunus laurocerasus.*
- **1700–3000 m:** Sub-alpine and alpine communities consist of *Pinus mugo*, *Juniperus communis* subsp. *nana*, *Alnus viridis*, and smaller shrubs such as *Rosa* spp., *Genista tinctoria*, and *Daphne oleoides.* Other remarkable species are: *Arctostaphylos uva-ursi*, *Bruckenthalia spiculifolia*, *Chamaecytisus hirsutus*, *C. heuffelii*, *Rhamnus alpinus*, *Vaccinium myrtillus*, *V. vitisidaea*, and *V. uliginosum.* Here are significant relict species such as *Rhynchocorys elephas*, *Haberlea rhodopensis*, *Primula frondosa*, and *Micromeria frivalszkyana.* Additionally, in these mountains the white-flowered *Daphne blagayana* as well as *D. oleoides* are found, and the primula-like *Cortusa matthioli*, which has a distribution as far east as the Himalaya. *Rhododendron myrtifolium*, a small shrub of the Carpathians, is also found in the central Stara Planina and in the eastern Rila Mountains.

In the west region of the Stara Planina, nearly Suva Planina, the following species are found: *Aconitum firmum*, *Vicia truncatula*, *Daphne laureola*, *D. oleoides*, *Primula halleri*, *Androsace obtusifolia*, *A. hedraeantha*, *Symphyandra wanneri*, *Scutellaria alpina*, and *Ramonda serbica*. In the westernmost part, on the hills of Vrška Čuka, there are some interesting species including *Eranthis hyemalis* var. *bulgaricus* and *Centaurea atropurpurea*.

6. Materials and methods

The sampling of the sediment samples was conducted on a vertical stratigraphic profile, as it is indicated for archaeological deposits (Girard, 1975), during the 2021 and 2022 fieldwork campaigns. The samples were taken from three archaeological profiles (samples ID Pes-Sed1 to Pes-Sed23) at the Southern sector, in Layers 2, 3, 4a and 4b (squares P11/c-P11/d, O11/b-P11/c, O10 of the excavation grid; Figs. 2 and 3;

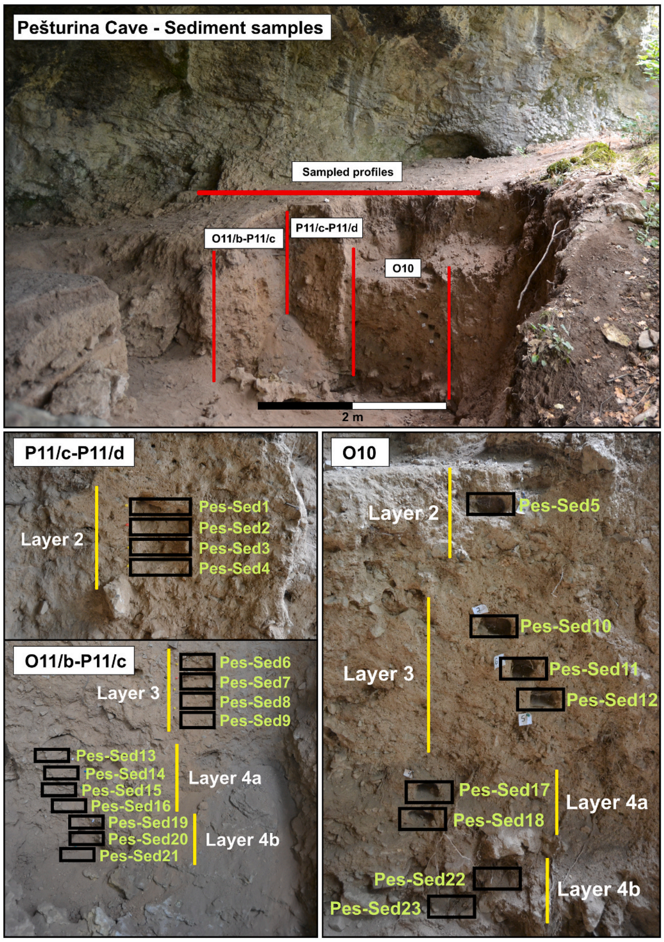

Fig. 3. Lithostratigraphical layers and profiles sampled for pollen analysis in Pešturina Cave with the position of pollen sediment samples.

Table 3). Exposed sediment surface was cleaned back and discarded to a depth of 10–15 cm, to avoid potential sources of contamination and/or recent bioturbation. In Layer 1 sampling was not carried out due to the presence of material disturbed by recent human activities. Similarly, it was not possible to take samples from the lower part of Layer 4b, and from Layers 4c and 5, since these profiles were and remain buried.

The coprolite assemblage analysed was recovered at Pešturina Cave during the 2021 and 2022 fieldwork campaigns (samples ID Pes-Cop1 to Pes-Cop16), from Layers 3, 4a, 4b and 4c (squares H11/c, H12/d, I12/a, I12/b, L11, M11, M12, M12/a, M12/d, O10, O11, O11/b, P10, P11/c of the excavations grid; Fig. 4; Table 3). These large coprolites have been associated as belonging to carnivores (Mihailović et al., 2022a), the morphology of these fragments being consistent with the ice age spotted hyaena (*Crocuta crocuta spelaea*) coprolite granulates from the European Pleistocene (Diedrich, 2012). Indeed, their association with bone fragments of spotted hyaena, whose remains are the most numerous among the carnivores, mainly in Layer 4 (Milošević, 2020; Mihailović et al., 2022a), confirms their attribution to hyaena. The colour of the coprolites varied on the outside from pale yellow to brown, and inside from pale brown to white (Fig. 4), similar to other hyaena-associated coprolites from the European Pleistocene (Carrión et al., 2001, 2007, 2008, 2018, 2019a; Ochando et al., 2020a).

In the laboratory, (1) the surface layer of each coprolite was cleaned using distilled water under pressure; (2) the surface layer was cut opened with a steel spatula; and (3) material from inside was scraped out to minimize contamination from external face. After the samples were weighed, both sediment and coprolites (Table 3), 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 evaluate the quality of the laboratory processing, we added three tablets of *Lycopodium* spores (BATCH No. 177745.500) to each sediment sample and one tablet of *Lycopodium* spores (BATCH No. 710961.500) to each coprolite sample. After the chemical treatment, the samples were mounted on slides with the use of liquid paraffin. The palynological identification was made by conventional microscopy (400× and 1000×) using an optical microscope. We used the palynomorph reference collection of the Department of Environmental Biology (Sapienza University of Rome) and of the Department of Plant Biology (University of Murcia). Along with spores and NPPs (Non-Pollen Palynomorphs), we excluded from the total pollen sum the counts of Asteroideae, Cichorioideae, *Centaurea*, and *Echinops*, assuming they might be overrepresented due to taphonomic and preservation processes (Havinga, 1984). The pollen count data was treated with the Tilia Graph 1.7.16 program in order to plot the pollen diagrams.

The pollen group established for *Pinus* taxa should be clarified. Pine pollen grains $>50\ \mu$ m were generally included within the *Pinus halepensis - pinea* type, except for grains $>50\ \mu$ m with thickenings in the distal exine, which belong to *Pinus pinaster* (Desprat et al., 2015). Pine pollen grains $<50\ \mu$ m were normally included in the *Pinus nigra – sylvestris* type. However, due to a large number of intermediate pollen morphotypes ($\sim 50\ \mu$ m), we decided to group them into a single taxon called *Pinus*, which may represent several species (*Pinus halepensis*, *P. pinea*, *P. nigra*, *P. sylvestris*, *P. mugo* and *P. heldreichii*).

7. Palynological results

7.1. Sediment samples

All the analysed sediment samples (23 out of 23 samples; ID Pes-Sed1 to Pes-Sed23) contained pollen grains (Figs. 5–7). A total of 8840 palynomorphs were identified, including 8203 pollen grains and 637 spores. The percentage of indeterminable grains is lower than 7% (Table 3), and the preservation is generally good. The number of pollen types per sample varies between 14 and 39, with a total of 83 recognized taxa. The pollen concentration varies between 222 and 278,760 grains/g (Table 3). Pollen diagrams, divided into arboreal pollen (AP), non-arboreal pollen (NAP) and spores, were plotted (Figs. 5 and 6; Supplementary Fig. 1) together with a synthetic diagram with the main taxa and ecological groups (Fig. 7). Conifers include *Pinus*, *Juniperus*, *Abies*, *Cedrus*, and *Taxus*. Mesophytes include deciduous *Quercus*, *Tilia*, *Betula*, *Corylus*, *Acer*, *Carpinus betulus*, *Ulmus/Zelkova*, *Alnus*, *Castanea*, *Fraxinus*, *Ilex*, *Juglans*, *Carpinus orientalis/Ostrya*, *Populus*, *Celtis*, *Sambucus nigra*, *Fagus*, *Salix*, *Daphne* t., and *Ribes*. Thermophytes include *Cistus*, *Buxus*, *Olea*, *Erica*, *Pistacia*, *Myrtus*, *Phillyrea*, *Viburnum*, and *Sambucus ebulus*. Xerophytes include *Artemisia*, Amaranthaceae, Lamiaceae, and *Asphodelus* (Figs. 7 and 11).

7.1.1. Layer 4b

In the lower half of the layer (samples Pes-Sed23-Pes-Sed22), a predominance of non-arboreal pollen appears (72–76%), while in the upper half (samples Pes-Sed21-Pes-Sed19), an increase in the amount of arboreal pollen occurs (51–58%) (Figs. 5–7). The most remarkable aspect in the lower half is the abundance of Amaranthaceae (40–42%), Poaceae (14–16%), *Artemisia* (7–8%), *Plantago* (3–4%), and Caryophyllaceae (1–3%). NAP includes also Lamiaceae, Apiaceae, Boraginaceae, Cannabaceae, *Epilobium*, *Typha*, Urticaceae, and Cyperaceae. In the AP it is important to emphasise the presence of deciduous *Quercus* (8–10%) and *Pinus* (7–9%). In addition, *Juniperus*, *Betula*, *Corylus*, *Tilia*, *Ulmus/Zelkova*, *Olea*, and Genisteae are also common. In the upper half of the layer, *Tilia* (4–15%) is abundant, reaching its maximum here. Deciduous *Quercus* fluctuates between 16 and 18%, while *Pinus* is around 11%. *Juniperus*, *Betula*, *Fraxinus*, *Ulmus/Zelkova*, *Rhamnus*, Genisteae, *Daphne*, *Cistus*, and Rosaceae undiff. are present in significant amounts, while *Abies*, *Taxus*, *Acer*, *Carpinus betulus*, *Castanea*, *Corylus*,

Table 3
Summary of palynological features at the Pešturina sequence.

Sample	Layer	Square	Material bag	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	[a]Pollen sum	Number of taxa (Pollen)	Spores sum
Sediment Samples											
Pes-Sed1	2	P11/c-P11/d	4	28.00	11.40	63,745	3.46	378	231	14	29
Pes-Sed2	2	P11/c-P11/d	3	28.00	9.90	52,795	1.90	375	210	17	127
Pes-Sed3	2	P11/c-P11/d	2	28.00	11.30	34,808	3.38	642	207	18	45
Pes-Sed4	2	P11/c-P11/d	1	28.00	10.00	43,471	2.26	577	221	22	25
Pes-Sed5	2	O10	78e	50.10	29.10	278,760	0.74	291	270	23	0
Pes-Sed6	3	O11/b-P11/c	4	28.50	11.20	63,428	3.98	395	226	21	25
Pes-Sed7	3	O11/b-P11/c	3	28.30	11.90	47,484	5.91	375	237	25	20
Pes-Sed8	3	O11/b-P11/c	2	28.40	12.80	7731	4.50	339	222	23	57
Pes-Sed9	3	O11/b-P11/c	1	28.60	11.90	10,781	4.31	382	209	25	115
Pes-Sed10	3	O10	77e	50.20	28.20	72,710	2.79	331	251	31	8
Pes-Sed11	3	O10	76e	50.50	26.40	3850	2.10	319	242	31	5
Pes-Sed12	3	O10	75e	50.00	23.50	10,021	1.75	283	228	28	4
Pes-Sed13	4a	O11/b-P11/c	4	28.70	13.80	11,638	5.19	314	212	24	23
Pes-Sed14	4a	O11/b-P11/c	3	28.20	14.80	13,146	4.39	342	228	21	28
Pes-Sed15	4a	O11/b-P11/c	2	28.50	15.10	9095	4.04	303	223	26	11
Pes-Sed16	4a	O11/b-P11/c	1	28.80	15.10	15,771	6.52	299	230	29	14
Pes-Sed17	4a	O10	74e	50.60	23.20	7193	1.86	437	376	32	18
Pes-Sed18	4a	O10	73e	50.10	24.80	5225	1.65	344	303	39	8
Pes-Sed19	4b	O11/b-P11/c	3	28.7	15.20	14,626	6.31	323	222	33	13
Pes-Sed20	4b	O11/b-P11/c	2	28.7	14.20	13,383	3.81	317	210	33	27
Pes-Sed21	4b	O11/b-P11/c	1	28.7	13.30	8156	5.10	358	217	35	29
Pes-Sed22	4b	O10	72e	50.20	26.10	222	1.80	230	222	22	3
Pes-Sed23	4b	O10	71e	50.20	20.90	382	1.31	249	229	19	3
								TOTAL 8203	5426		637
Coprolites											
Pes-Cop1	3	O11/b-P11/c	1	8.33	8.33	2998	4.29	237	210	16	0
Pes-Cop2	3	O10	2	4.39	4.39	46,031	4.98	277	241	21	1
Pes-Cop3	3	M11	81e	15.67	15.67	2882	1.83	224	218	13	1
Pes-Cop4	3	M12	104e	18.63	18.63	821	2.43	223	206	24	2
Pes-Cop5	3	M12/a	122e	16.14	16.14	2541	3.32	227	211	23	0
Pes-Cop6	4a	O11/b-P11/c	3	3.56	3.56	24,465	1.16	288	258	17	0
Pes-Cop7	4a	M11	111e	8.52	8.52	2005	1.86	221	215	13	6
Pes-Cop8	4a	O11	157e	9.74	9.74	10,890	1.72	246	233	15	4
Pes-Cop9	4a	O11/b-P11/c	4	5.12	5.12	4682	2.74	274	219	16	8
Pes-Cop10	4a	P10	146e	4.50	4.50	9068	2.38	220	210	17	21
Pes-Cop11	4a	M12/d	129e	17.22	17.22	409	3.40	224	206	17	2
Pes-Cop12	4a	M12/d	129e	13.09	13.09	1265	2.52	257	238	22	4
Pes-Cop13	4a	I12/b	155e	15.60	15.60	1117	3.27	218	214	19	0
Pes-Cop14	4a	H12/d	178e	14.60	14.60	328	4.93	208	203	16	20
Pes-Cop15	4a	H12/d	178e	14.17	14.17	1947	2.80	234	214	13	1
Pes-Cop16	4c	I12/a	210e	12.92	12.92	718	2.39	222	209	21	0
								TOTAL 3800	3505		70
Sterile Coprolites											
1	2/3	O11	57e	3.67	3.67	–	–	Sterile	–	–	Sterile
2	4	L11	110e	8.83	8.83	–	–	Sterile	–	–	Sterile
3	4a	M12/d	129e	15.48	15.48	–	–	Sterile	–	–	Sterile
4	4b	H11/c	184e	24.36	24.36	–	–	Sterile	–	–	Sterile

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

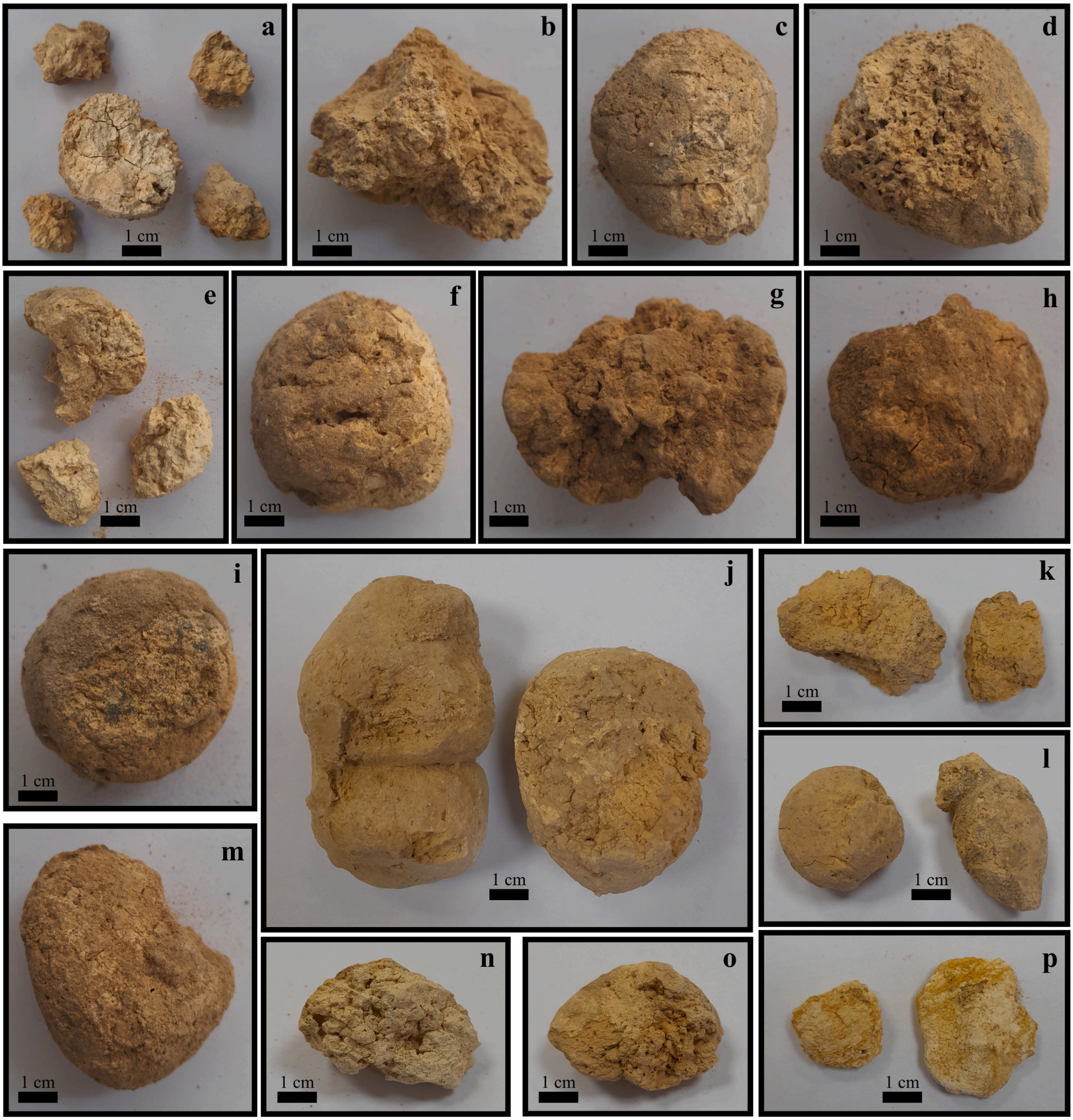

Fig. 4. Coprolite specimens from Pešturina Cave (Pes-Cop1 to Pes-Cop16) from Layers 3, 4a and 4c (a–p).

Fagus, *Celtis*, *Ilex*, *Sambucus ebulus*, *Buxus*, *Myrtus*, *Pistacia*, *Phillyrea*, and *Ribes* show discontinuous occurrences. In NAP, Poaceae (17–21%) and *Artemisia* (9–14%) are abundant. Amaranthaceae falls to below 3%. Additionally, Caryophyllaceae, Asteroideae, Cichorioideae, *Anthyllis*, *Vicia*, Apiaceae, *Armeria*, *Plantago*, Brassicaceae, Dipsacaceae, *Epilobium*, Lamiaceae, and Rubiaceae are frequent. The abundance of *Microsporonites* and *Monoporisporites* is noticeable (Supplementary Fig. 1). Trilete spores, *Inapertisporites*, *Pluricellaesporites*, *Polycellaesporonites*, Zygnemataceae, and Bryophyta appear.

7.1.2. Layer 4a

This layer includes samples Pes-Sed18 to Pes-Sed13 (Figs. 5–7). AP consistently presents levels >60%, with peaks >80%. This layer is characterised by high percentages of deciduous *Quercus* (19–40%), *Pinus* (10–22%), and *Tilia* (6–13%). *Juniperus* does not exceed 3%, while Genisteae reaches almost 6%. Accompanying AP are *Betula*, *Carpinus betulus*, *Castanea*, *Corylus*, *Ulmus/Zelkova*, *Rhamnus*, Ericaceae, *Cistus*, and Rosaceae undiff. It is noteworthy the occasional appearance of *Abies*, *Acer*, *Alnus*, *Carpinus orientalis/Ostrya*, *Fagus*, *Juglans*, *Fraxinus*, *Salix*, *Celtis*, *Ilex*, *Viburnum*, *Buxus*, *Olea*, *Phillyrea*, *Ligustrum*, and *Crataegus*. In NAP, Poaceae (6–20%) and *Artemisia* (5–11%) dominate.

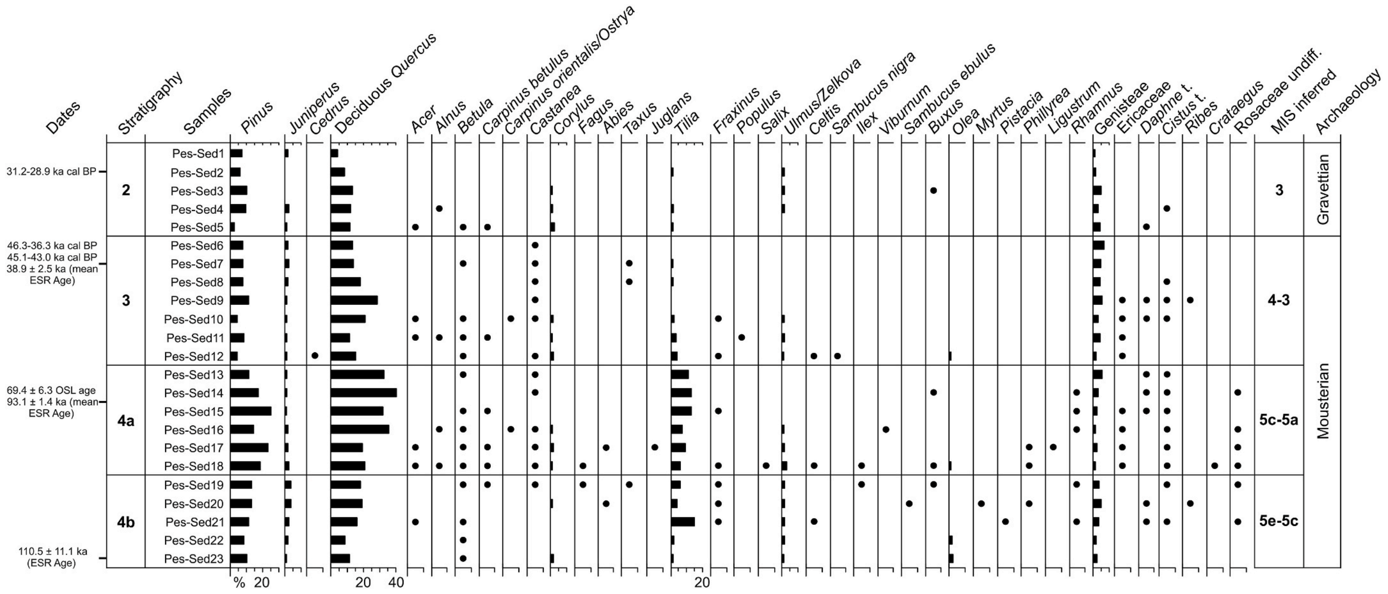

Fig. 5. Percentage pollen diagram of the woody component from sediment samples of Pešturina Cave. Black dots for percentages <3%. Black lines for divisions between lithostratigraphical layers.

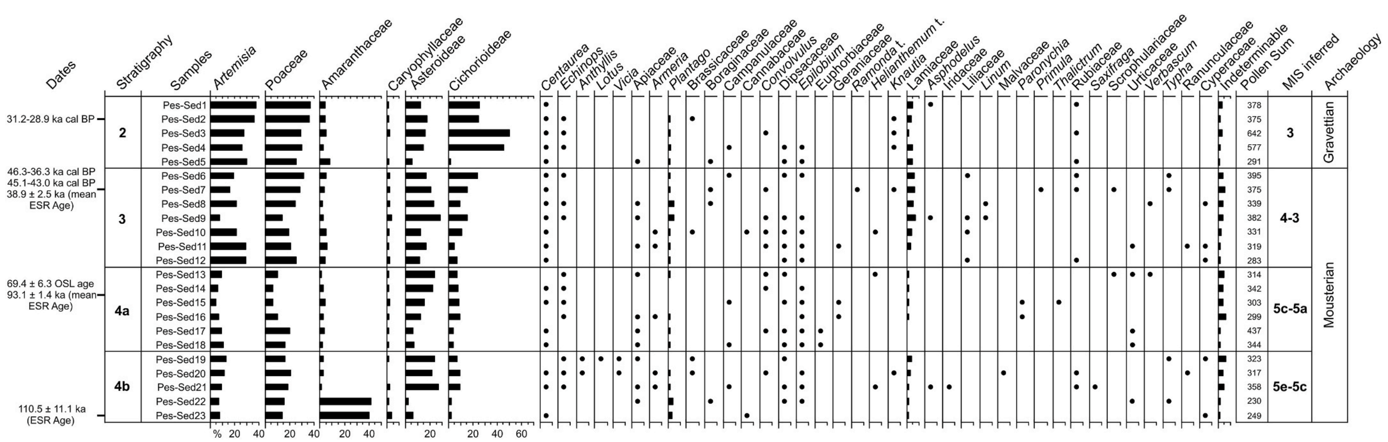

Fig. 6. Percentage pollen diagram of the non-arboreal elements from sediment samples of Pešturina Cave. Black dots for percentages <3%. Black lines for divisions between lithostratigraphical layers.

Amaranthaceae, Caryophyllaceae, Asteroideae, Cichorioideae, Apiaceae, *Plantago*, Campanulaceae, *Convolvulus*, Dipsacaceae, *Epilobium*, Euphorbiaceae, Lamiaceae, *Paronychia*, and Urticaceae are also common. The presence of *Monoporisporites* and *Microsporonites* stands out (Supplementary Fig. 1). Similarly, other algal spores, Zygnemataceae, Bryophyta, and Pteridophyta Trilete spores are present.

7.1.3. Layer 3

This layer includes pollen samples Pes-Sed12 to Pes-Sed6 (Figs. 5–7). NAP is dominant with total values of 50–70%, being characterised by high percentages of Poaceae (14–31%), *Artemisia* (8–29%), Lamiaceae (2–7%) and Amaranthaceae (2–6%). The highest percentages of *Plantago* (1–5%) and Caryophyllaceae (1–4%) are recorded. Asteroideae, Cichorioideae, Apiaceae, *Convolvulus*, Dipsacaceae, *Epilobium*, Liliaceae, Rubiaceae, and Cyperaceae are highly represented throughout the whole layer. Furthermore, *Armeria*, Brassicaceae, Boraginaceae, Campanulaceae, Cannabaceae, Geraniaceae, *Ramonda*, *Helianthemum*, *Knautia*, *Asphodelus*, *Linum*, *Primula*, Ranunculaceae, Scrophulariaceae, *Typha*, Urticaceae, and *Verbascum* appear. In AP, it is worth highlighting the presence of deciduous *Quercus* (10–28%), *Pinus* (4–10%), and Genisteae (2–6%). AP also include *Juniperus*, *Betula*, *Castanea*, *Corylus*, *Tilia*, *Ulmus/Zelkova*, Ericaceae, and *Cistus*, as well as a limited presence (<2%) of *Cedrus*, *Taxus*, *Acer*, *Alnus*, *Carpinus betulus*, *Carpinus orientalis/Ostrya*, *Fraxinus*, *Populus*, *Celtis*, *Sambucus nigra*, *Olea,* and *Ribes*. Pteridophyta Trilete spores, *Monoporisporites*, *Microsporonites*, other algal spores, and Zygnemataceae are frequent (Supplementary Fig. 1).

7.1.4. Layer 2

This layer includes samples Pes-Sed5 to Pes-Sed1 (Figs. 5–7). The NAP is dominant, reaching levels close to 88%, with high frequencies of *Artemisia* (26–38%), Poaceae (26–37%), and Amaranthaceae (3–9%), accompanied by Caryophyllaceae, Asteroideae, Cichorioideae, *Plantago*, Dipsacaceae, *Epilobium*, *Knautia*, Lamiaceae, and Rubiaceae. Apiaceae, Brassicaceae, Boraginaceae, Campanulaceae, *Convolvulus*, and *Asphodelus* are also present. Within AP, deciduous *Quercus* (3–13%), *Pinus* (2–9%), and Genisteae (1–5%) should be noted. *Juniperus*, *Corylus*, *Tilia*, and *Ulmus/Zelkova* are very well represented throughout the sequence, while *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Buxus*, *Daphne*, and *Cistus* show sporadic occurrences. The presence of Pteridophyta Trilete spores, *Monoporisporites*, *Microsporonites*, Zygnemataceae, and other fungal spores is significant (Supplementary Fig. 1).

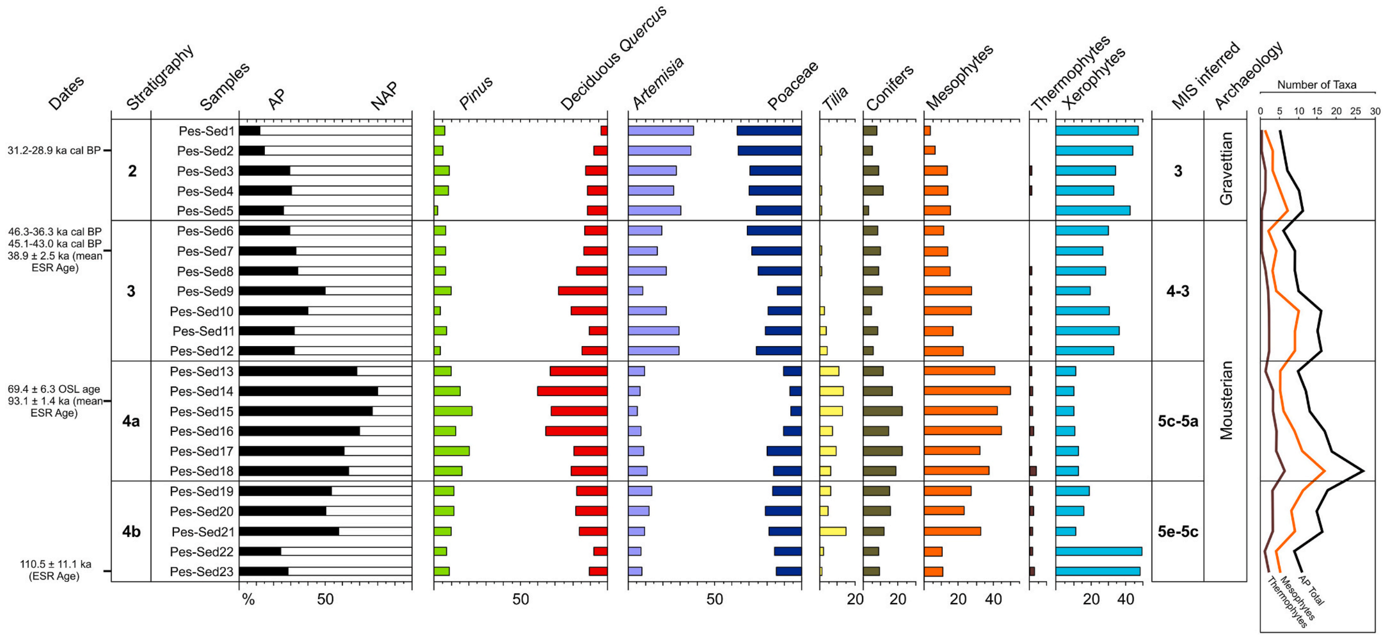

Fig. 7. Synthetic pollen diagram of ecological groups and the main pollen contributors from sediment samples of Pešturina Cave.

7.2. Coprolites

A total of 20 coprolites were analysed, 16 being polleniferous (samples ID Pes-Cop1 to Pes-Cop16) and four being sterile coprolites (Figs. 8–10). A total of 3875 palynomorphs were identified (3800 pollen grains and 75 spores). The percentage of indeterminable types is <5% (Table 3). The number of pollen types varies between 13 and 24, with a total of 52 identified taxa. The pollen concentration ranges between 328 and 46,031 grains/g (Table 3). Palynological diagrams represent AP, NAP, together with a synthetic diagram with the main taxa and ecological groups (Figs. 8–10). Conifers include *Pinus*, *Juniperus*, and *Cedrus*. Mesophytes include deciduous *Quercus*, *Tilia*, *Betula*, *Corylus*, *Acer*, *Carpinus betulus*, *Ulmus/Zelkova*, *Alnus*, *Castanea*, *Fraxinus*, *Ilex*, *Juglans*, *Carpinus orientalis/Ostrya*, *Populus*, *Sambucus nigra*, *Fagus*, and *Salix*. Thermophytes include *Cistus*, *Buxus*, *Olea*, *Erica*, *Pistacia*, and *Myrtus*. Xerophytes include *Artemisia*, Amaranthaceae, and Lamiaceae (Figs. 10 and 11). The number of spores present in the coprolites was low (see Spore Sum in Supplementary Fig. 1).

7.2.1. Layer 4c

This layer only includes coprolite Pes-Cop16 (Figs. 8–10). The AP is >60%, with dominance of *Pinus* (37%). Deciduous *Quercus* is 18%, while *Pistacia* does not exceed 2%. AP also includes *Juniperus*, *Betula*, *Corylus*, *Juglans*, *Sambucus nigra*, *Myrtus*, Genisteae, Ericaceae, and *Cistus*. NAP is

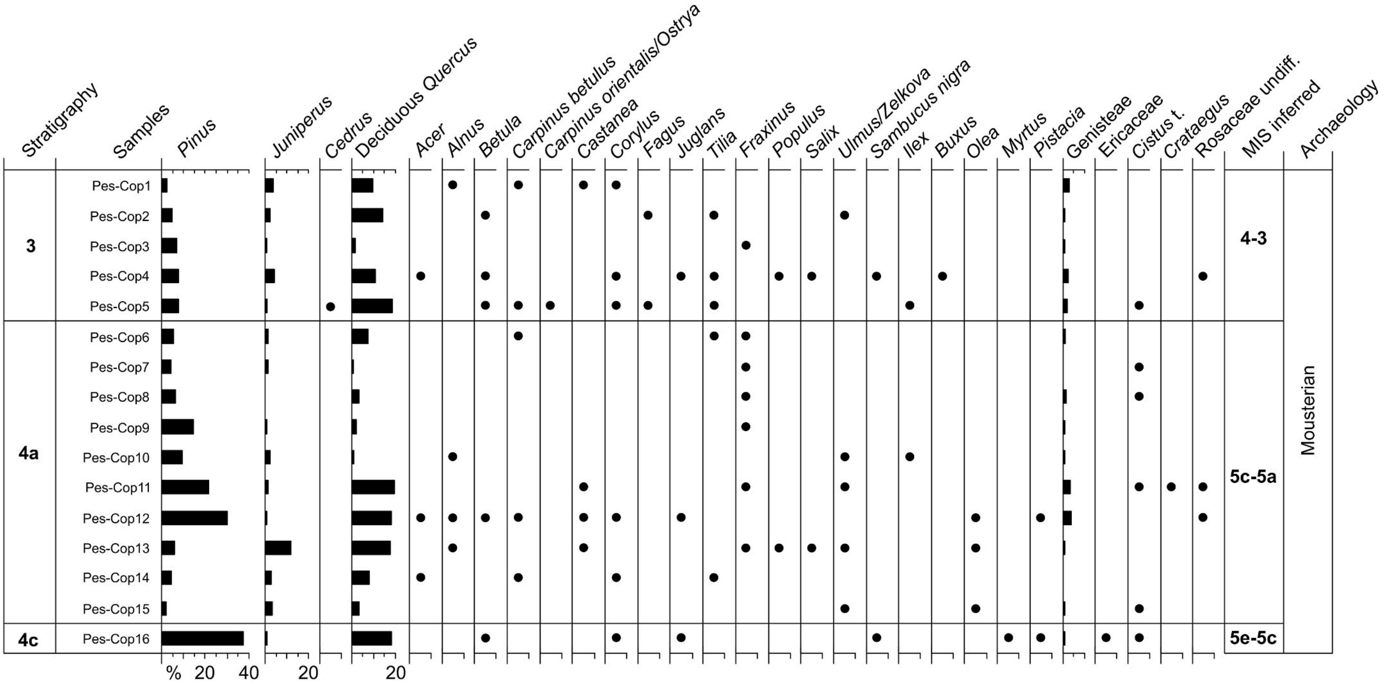

Fig. 8. Percentage pollen diagram of the woody component from the coprolites of Pešturina Cave. Black dots for percentages <3%. Black lines for divisions between lithostratigraphical layers.

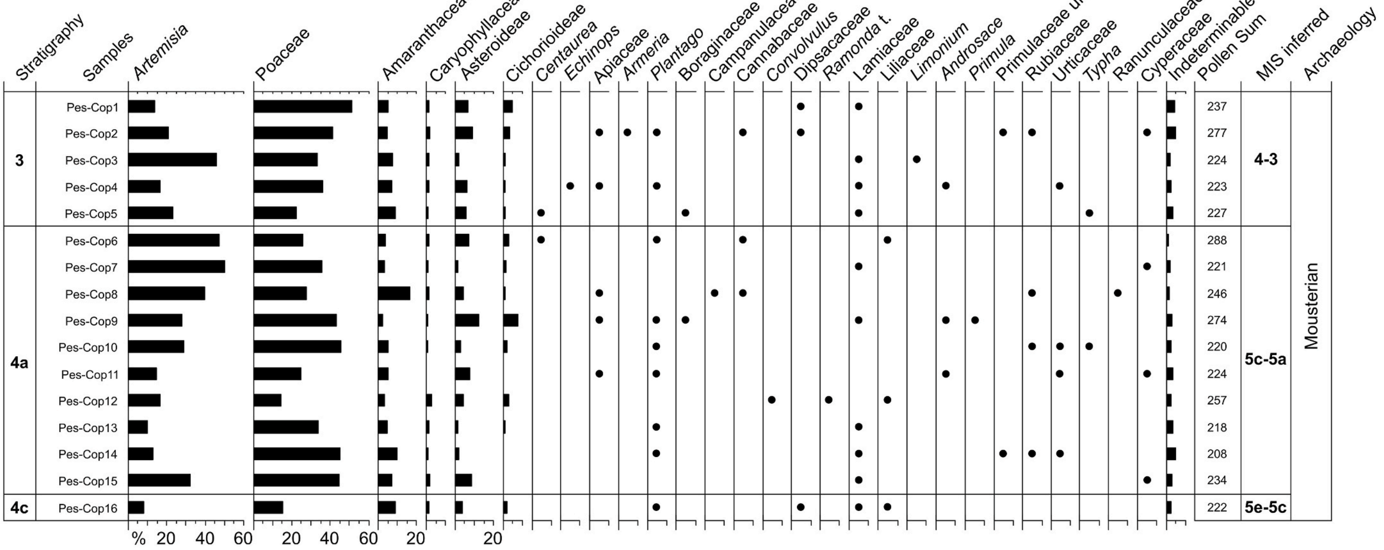

Fig. 9. Percentage pollen diagram of the non-arboreal elements from the coprolites of Pešturina Cave. Black dots for percentages <3%. Black lines for divisions between lithostratigraphical layers.

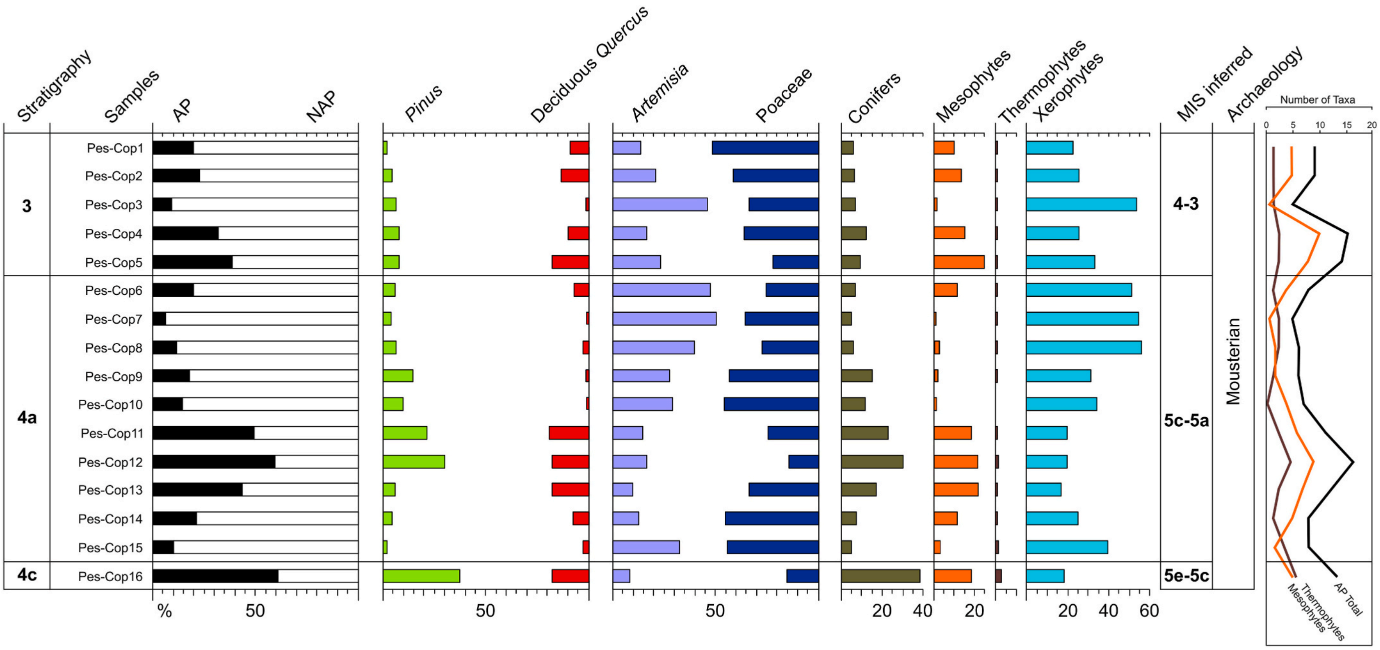

Fig. 10. Synthetic pollen diagram of ecological groups and the main pollen contributors from the coprolites of Pešturina Cave.

mainly composed of Poaceae (15%), Amaranthaceae (9%), and *Artemisia* (8%). Additionally, Caryophyllaceae, Asteroideae, Cichorioideae, *Plantago*, Dipsacaceae, Lamiaceae, and Liliaceae are frequent. Spores are absent (Supplementary Fig. 1).

7.2.2. Layer 4a

This layer includes coprolites Pes-Cop15 to Pes-Cop6 (Figs. 8–10). NAP is predominant across all samples, reaching values > 93%, except Pes-Cop12, in which the lowest percentage of NAP (40%) is recorded. The most noteworthy characteristic is the abundance of *Artemisia* (10–50%), Poaceae (14–46%), and Amaranthaceae (2–16%), while Caryophyllaceae does not exceed 3%. Other NAP includes Asteroideae, Cichorioideae, Apiaceae, *Plantago*, Lamiaceae, Rubiaceae, *Typha*, Urticaceae, and Cyperaceae. Among AP (Fig. 8), *Pinus* (2–30%), deciduous *Quercus* (1–19%), and *Juniperus* (1–12%) are remarkable. Occurrences of Genisteae, *Fraxinus*, *Ulmus/Zelkova*, and *Cistus* are also ecologically meaningful, as well as the occurrences of *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Castanea*, *Corylus*, *Juglans*, *Tilia*, *Populus*, *Salix*, *Ilex*, *Olea*, *Pistacia*, and Rosaceae undiff. Other fungal spores and *Microsporonites* are present (Supplementary Fig. 1).

7.2.3. Layer 3

This layer includes coprolites Pes-Cop5 to Pes-Cop1 (Figs. 8–10). NAP oscillates between 61 and 91%. Poaceae (22–51%) reaches the maximum peak of the sequence in Pes-Cop1. We found high levels of *Artemisia* (14–46%) and Amaranthaceae (5–9%). Caryophyllaceae, Asteroideae, Cichorioideae, Apiaceae, *Plantago*, Dipsacaceae, and Lamiaceae are very well represented throughout the layer. In AP it is worth

Ecological groups	Taxa	Sediment pollen				Coprolite pollen		
		Layers				Layers		
		2	3	4a	4b	3	4a	4c
Conifers	*Pinus*	+	+	🟢	🟢	+	🟢	🔴
	Juniperus	+	+	+	+	+	+	+
	Abies	+	-	+	+	-	-	-
	Cedrus	-	+	-	-	+	-	-
	Taxus	-	+	-	+	-	-	-
Mesophytes	Deciduous *Quercus*	🟢	🔴	🔴	🔴	🟢	🟢	🔴
	Tilia	+	+	🔴	🟢	+	+	-
	Betula	+	+	+	+	+	+	+
	Corylus	+	+	+	+	+	+	+
	Acer	+	+	+	+	+	+	-
	Carpinus betulus	+	+	+	+	+	+	-
	Ulmus/Zelkova	+	+	+	+	+	+	-
	Alnus	+	+	+	-	+	+	-
	Castanea	-	+	+	+	+	+	-
	Fraxinus	-	+	+	+	+	+	-
	Ilex	-	-	+	+	+	+	-
	Juglans	-	-	+	-	+	+	+
	Carpinus orientalis/Ostrya	-	+	+	-	+	-	-
	Populus	-	+	-	-	+	+	-
	Celtis	-	+	+	+	-	-	-
	Sambucus nigra	-	+	-	-	+	-	+
	Fagus	-	-	+	+	+	-	-
	Salix	-	-	+	-	+	+	-
	Daphne t.	+	+	+	+	-	-	-
	Ribes	-	+	-	+	-	-	-
Thermophytes	*Cistus*	+	+	+	+	+	+	+
	Buxus	+	-	+	+	+	-	-
	Olea	-	+	+	+	-	+	-
	Erica	-	+	+	-	-	-	+
	Pistacia	-	-	-	+	-	+	+
	Myrtus	-	-	-	+	-	-	+
	Phillyrea	-	-	+	+	-	-	-
	Viburnum	-	-	+	-	-	-	-
	Sambucus ebulus	-	-	-	+	-	-	-

Ecological groups	Taxa	Sediment pollen				Coprolite pollen		
		Layers				Layers		
		2	3	4a	4b	3	4a	4c
Xerophytes	*Artemisia*	🔴	🔴	🟢	🟢	🔴	🔴	🟢
	Amaranthaceae	🟢	🟢	🟢	🔴	🟢	🟢	🟢
	Lamiaceae	🟢	🟢	+	🟢	🟢	🟢	+
	Asphodelus	+	+	-	+	-	-	-
Other significant shrubs and herbs	Poaceae	🔴	🔴	🟢	🟢	🔴	🔴	🟢
	Caryophyllaceae	+	+	+	+	+	+	+
	Apiaceae	+	+	+	+	+	+	-
	Campanulaceae	+	+	+	+	-	+	-
	Convolvulus	+	+	+	+	-	+	-
	Boraginaceae	+	+	-	+	+	+	-
	Epilobium	+	+	+	+	-	-	-
	Verbascum	-	+	+	-	-	-	-
	Geraniaceae	-	+	+	-	-	-	-
	Scrophulariaceae	-	+	+	-	-	-	-
	Primulaceae	-	-	-	-	+	+	-
	Primula	-	+	-	-	-	+	-
	Ramonda t.	-	+	-	-	-	+	-
	Androsace	-	-	-	-	+	+	-
	Linum	-	+	-	-	-	-	-
	Ligustrum	-	-	+	-	-	-	-
	Paronychia	-	-	+	-	-	-	-
	Thalictrum	-	-	+	-	-	-	-
	Euphorbiaceae	-	-	+	-	-	-	-
	Saxifraga	-	-	-	+	-	-	-
	Iridaceae	-	-	-	+	-	-	-
	Malvaceae	-	-	-	+	-	-	-
	Limonium	-	-	-	-	+	-	-
Other significant families	Genisteae	🟢	🟢	🟢	🟢	+	+	+
	Rosaceae undiff.	-	-	+	+	+	+	-

🔴 Dominance + Presence
🟢 Abundance - Absence

Fig. 11. Comparative results of sediment and coprolite pollen from Pešturina Cave.

noting deciduous *Quercus* (1–18%), *Pinus* (2–8%), *Juniperus* (1–4%), and Genisteae (1–3%), accompanied by *Cedrus*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Carpinus orientalis/Ostrya*, *Castanea*, *Corylus*, *Fagus*, *Juglans*, *Tilia*, *Fraxinus*, *Populus*, *Salix*, *Ulmus/Zelkova*, *Sambucus nigra*, *Buxus*, *Ilex*, *Cistus*, and Rosaceae undiff. Spores are represented by *Glomus*, *Dicellaesporites*, *Multicellites*, and Zygnemataceae (Supplementary Fig. 1).

8. Comparison of pollen in sediment samples and in coprolites at Pešturina Cave

Pollen samples recovered from the sediment of archaeological profiles may capture multi-decadal periods of sedimentation, while coprolite pollen would reflect the environmental conditions of shorter time periods. Additionally, sediment pollen would mostly describe the local environment in the vicinity of the cave, whereas the pollen composition of the coprolites may show the diversity of the regional environment, reflecting different habitats coexisting within a patchy landscape (Scott et al., 2003; Carrión et al., 2018), which is generally wider than 15 km but no more than 50 km from hyaena den (Argant, 2004; Argant and Dimitrijevic, 2007). Furthermore, the behaviour of the animals that produced the coprolites can be diverse (Scott, 1987; Scott and Brink, 1992; Scott et al., 2003), so that coprolites collected at the same depths might be reflecting a mosaic of different environments occupied by different animals rather than a temporal record of different vegetation stages (Carrión et al., 2008, 2018). As pointed out by Carrión et al. (1999b), the archaeological pollen records, which are often discontinuous and/or altered by humans, should not be used to assess vegetational and climatic fluctuations with the same confidence as when they are interpreted from continuous and pristine lacustrine or marshy pollen records. In this sense, taxonomic differences between sediment samples and coprolites must be taken with some caution.

The pollen content of sediments and coprolites from Late Pleistocene caves has been directly compared to shed light into past environments at Gorham's and Vanguard Caves, Gibraltar (Carrión et al., 2008, 2018), Carihuela Cave, Spain (Carrión, 1990, 1992a; Fernández et al., 2007; Carrión et al., 2019a; Ochando et al., 2020a), and Abrigo do Lagar Velho, Portugal (Queiroz, 1999; Queiroz et al., 2002; Ochando et al., 2022c). The combined sediment and coprolite pollen record from Pešturina provides an additional and unique opportunity to reconstruct the palaeoenvironment during the Late Pleistocene in relation to human occupations.

In the Pešturina vegetation sequence, mixed oak-pine open forests with a conspicuous presence of *Tilia*, strongly inertial throughout MIS 5 (Layers 4a, 4b and 4c), are a characteristic feature. These forests are especially revealed by sediment samples (Fig. 11; Supplementary Figs 2 and 3). The coprolites of MIS 5 reflect more open landscapes with characteristics typical of parkland or even steppe environments (Fig. 11; Supplementary Figs 2 and 3), with the dominance of Poaceae and *Artemisia*, along with *Pinus* and *Quercus*. Abundance of grasses, and particularly high diversity of herbaceous types, may reflect prey diet of hyaenas, as in Vanguard Cave (Carrión et al., 2018). At Pešturina, the combination of coprolites and sediment shows that different environments coexisted during the last interglacial (MIS 5). There was a high diversity of woody plants, including abundant *Pinus*, *Juniperus*, deciduous *Quercus*, *Carpinus betulus*, *Corylus*, *Ulmus/Zelkova*, and Genisteae, which were continuously accompanied by broad-leaved trees such as *Acer*, *Alnus*, *Betula*, *Carpinus orientalis/Ostrya*, *Castanea*, *Fagus*, *Juglans*, *Fraxinus*, *Populus*, *Salix*, and *Celtis*, as well as thermophytes taxa, such as *Viburnum*, *Sambucus ebulus*, *Buxus*, *Myrtus*, *Pistacia*, *Phillyrea*, *Rhamnus*, and *Cistus* (Fig. 11). The xerophytic component is mainly represented by *Artemisia*, Poaceae, Amaranthaceae, Asteraceae, and Lamiaceae (Fig. 11; Supplementary Fig. 3). Increments of xerophytes may reflect a general opening of the landscape or simply a change in some parts of the mosaic of landscapes.

Although only one coprolite is available (Pes-Cop16), Layer 4c and the lower parts of Layer 4b could tentatively correspond to MIS 5e (Supplementary Fig. 4), with warm-loving taxa (e.g., *Myrtus*, *Pistacia*, and *Cistus*) and absence of *Fagus*. Rare or sporadic occurrences of beech pollen are typical of Eemian sites in Europe (Magri et al., 2006). The mid Layer 4b (samples Pes-Sed22 and Pes-Sed23) would correspond to MIS 5d, with a notable increase in steppe, indicated by high values of Amaranthaceae (Supplementary Fig. 4). The uppermost part of Layer 4b (samples Pes-Sed21 to Pes-Sed19) and the lowermost part of Layer 4a (samples Pes-Sed18 and Pes-Sed17) could be associated with the warmer climatic conditions of MIS 5c, as shown by the predominance of mesophytes and mediterranean elements (Fig. 11; Supplementary Fig. 4). It should be noted the appearance of *Carpinus betulus*, *Fagus*, *Taxus*, *Buxus*, *Castanea*, and *Celtis*. The upper part of Layer 4a (samples Pes-Sed16 to Pes-Sed13) is difficult to attribute to MIS 5b or MIS 5a based of pollen, although according to Blackwell et al. (2018) Layer 4a was deposited during MIS 5b.

The large quantity of artifacts from Layer 4b suggests that human groups occupied the site for an extended period of time, while the decrease of artifact assemblages from Layers 4a and 3 indicates a succession of short-term human occupations. Anthropogenic evidence on faunal remains is identified in the form of cut-marks and impact marks, being more abundant in Layer 4b (Table 2). However, because of the bias caused by a smaller volume and area of excavated sediment than Layer 4a, the faunal remains from Layers 4b, and particularly 4c, should be interpreted with caution. The abundance of hyaena-associated coprolites and *Crocuta crocuta spelaea* bones was somewhat more pronounced in Layers 4a and 3, indicating more frequent visits than in Layer 4b.

The pollen results from Layer 4 of Pešturina are supported by the faunal remains. The impressive record of vertebrates includes typical avifaunal species of temperate forests (*Tetrao tetrix, Scolopax rusticola*, *Aegolius funereus*, *Sitta europaea*, *Fringilla coelebs*, *Garrulus glandarius*), steppe environments (*Perdix perdix*, *Coturnix coturnix*, *Crex crex*, *Otis tarda/Tetrax tetrax*) and warm habitats (*Petronia petronia*, *Ptyonoprogne rupestris*) (Boev and Milošević, 2020), as well as herpetofauna from multiple biotopes with relatively humid conditions (Jovanović et al., 2020), including wet grassland, shrubland, woodland, and rocky areas with water points. The small mammal assemblage includes typical woodland, moist meadows, xero-mesophilous, montane and petrophilous species, with a very limited presence of steppe and semi-arid species (Jovanović et al., 2020). The presence of *Testudo hermanni*, which preferably inhabited open and semi-open areas of Mediterranean type, is also noteworthy.

Among the large mammals, *Equus ferus germanicus*, *Equus hydruntinus*, *Cervus elaphus*, and *Crocuta crocuta spelaea* are the most common species identified, together with minor occurrences of *Dama dama*, *Sus scrofa*, *Capreolus capreolus, Rupicapra rupicapra*, *Bison priscus*, *Capra ibex*, *Megaloceros giganteus*, *Lepus europaeus*, *Canis lupus*, *Vulpes vulpes*, *Ursus spelaeus*, *Ursus arctos*, *Panthera spelaea*, *Panthera pardus*, *Coelodonta antiquitatis*, *Mammuthus* sp., *Castor fiber*, and *Hystrix vinogradovi* (Milošević, 2016, 2020; Majkić et al., 2018; Dimitrijević, 2021). The presence of horse and bison herds suggests the existence of open woodlands near the cave; red deer and roe deer would dwell in temperate forests, while ibex and chamois would inhabit rocky cliffs. Mihailović and Milošević (2012) point out that the high frequencies of *Equus ferus germanicus* and *Equus hydruntinus* in the bottom of Layer 4 (4c and lower part of 4b) could indicate a warmer climate than the following Layers 3 and 2, as also suggested by a larger presence of thermophilic and forest faunal species (Mihailović et al., 2022a). Layer 4 shows the highest number of potential woodland inhabitants from Pešturina, in agreement with the pollen record. The occurrence of typical steppe fauna in the upper part of Layer 4 suggests a cold period of the final MIS 5 or the early MIS 4 (Mihailović et al., 2022a), as also reflected by an increase of steppe taxa in the pollen record of the coprolites from the upper part of Layer 4 (Figs. 9 and 10).

The pollen record of Layer 3 may reflect one or more episodes of MIS 4-3 (Alex and Boaretto, 2014; Blackwell et al., 2014; Alex et al., 2019; Mihailović et al., 2022a). A diverse landscape can be inferred, with Poaceae-*Artemisia* steppes, *Quercus*-Poaceae parklands/open woodlands, shrubby grasslands with patches of conifers and mesophytes, and heliophytic shrublands (Fig. 11; Supplementary Figs 2 and 3). Interestingly, the pollen spectra of coprolites and sediment shows a considerable consistency, with all ecological groups and the main pollen contributors presenting similar percentages in both types of samples (Fig. 11; Supplementary Fig. 3). Pollen assemblages display a general landscape stability with semi-open woodland, showing abundant Poaceae, *Artemisia*, deciduous *Quercus*, Asteroideae, Amaranthaceae, Genisteae, Lamiaceae, *Juniperus*, *Pinus*, and *Tilia* (Fig. 11) and occurrence of *Acer*, *Betula*, *Carpinus betulus*, *Castanea*, *Corylus*, *Fraxinus*, *Ulmus/Zelkova*, Ericaceae, *Cistus*, Caryophyllaceae, *Centaurea*, Apiaceae, *Plantago*, Dipsacaceae, *Epilobium*, Liliaceae, Rubiaceae, and Cyperaceae (Fig. 11). Although the number of mesophytes and thermophytes taxa is still well represented, the loss of some taxa present in Layer 4 (4a, 4b and 4c) marks the beginning of Layer 3, including *Viburnum*, *Sambucus ebulus*, *Myrtus*, *Pistacia*, *Phillyrea*, *Ligustrum*, *Rhamnus*, *Daphne*, *Crataegus*, *Anthyllis*, *Lotus*, *Vicia*, Euphorbiaceae, Iridaceae, Malvaceae, *Paronychia*, *Thalictrum* and *Saxifraga* (Fig. 11; Supplementary Fig. 2). In addition, it should be noted the appearance of exclusive taxa for Layer 3, such as *Cedrus*, *Limonium*, and *Linum*. *Cedrus* (<2%) is probably of distant origin, being currently present in Anatolia.

The mammal fauna indicates drier and harsher climates in Layer 3 than in previous Layer 4 (Milošević, 2016, 2020; Majkić et al., 2018), as indicated by abundant fossils of horse (*Equus ferus germanicus* and *Equus hydruntinus*), bison (*Bison priscus*), and red deer (*Cervus elaphus*), matching the pollen record that shows dominance of steppes and loss in the diversity of woody elements. The most common carnivore is spotted hyaena (*Crocuta crocuta spelaea*), which could accumulate an important part of the recovered fauna record in Layer 3 (Table 2). The herpetofaunal taxa and the small mammals suggest that climate was probably drier (Jovanović et al., 2020), while the Taxonomic Habitat Index (THI) reflects presence of steppe with deciduous trees. Based on the range of habitats that extant species occupy, the THI is a cumulative index that assigns a score (Andrews, 1990). The purpose of this method is to evaluate habitat preferences, which accounts for the fact that most mammal species live in multiple biotopes (Evans et al., 1981). Thus, the bioclimatic analysis provides the permanence of relatively humid environments but drier than Layer 4 (Jovanović et al., 2020).

The pollen results of Layer 2 are defined exclusively by the sediment samples. The available dates estimate a chronology around 30 ka cal BP, corresponding to the end of the MIS 3 (Alex and Boaretto, 2014; Alex et al., 2019). Overall, there was a greater openness of the landscapes with an increase in steppes, mainly formed by xerophytic elements such as *Artemisia*, Poaceae, Amaranthaceae, Lamiaceae, and *Asphodelus* (Fig. 11). Nevertheless, a wide diversity of secondary landscapes in the vicinity of the site persisted, with *Quercus*-Poaceae open woodlands, oak open woodlands, shrubby grasslands with conifers, mesophytes patches and heliophytic shrublands (Fig. 11; Supplementary Fig. 3). Several woody taxa persisted, such as *Pinus*, *Juniperus*, deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Corylus*, *Tilia*, *Ulmus/Zelkova*, *Buxus*, Genisteae, and *Cistus* (Fig. 11). However, the overall floristic diversity decreased, mainly due to the desappearance of several mesophyte and thermophyte taxa, including *Taxus*, *Carpinus orientalis/Ostrya*, *Castanea*, *Fagus*, *Juglans*, *Fraxinus*, *Populus*, *Salix*, *Celtis*, *Sambucus nigra*, *Ilex*, *Olea*, Ericaceae, *Ribes*, Rosaceae undiff., *Armeria*, Cannabaceae, Geraniaceae, *Ramonda*, Liliaceae, *Androsace*, *Primula*, Primulaceae undiff., Scrophulariaceae, Urticaceae, *Verbascum*, *Typha*, Ranunculaceae, and Cyperaceae (Fig. 11; Supplementary Fig. 2).

In Pešturina, Layer 2 contains abundant bones of horse (*Equus ferus germanicus* and *Equus hydruntinus*), bison (*Bison priscus*), and ibex (*Capra ibex*), while wolf (*Canis lupus*) dominates the carnivores (Milošević, 2016, 2020; Majkić et al., 2018; Dimitrijević, 2021). Through the analysis of cut marks and impact marks (Table 2), it was possible to identify the anthropogenic use of the animals composing the assemblage. The abundance of artifacts from Layer 2 indicates a short-term occupation. Thus, part of the remains recovered could have been deposited by animals, as indicated by the analysis of gnaw and digestion marks (Table 2).

Herpetofauna and small mammals suggest a variety of different habitats with the predominance of woodland, moist meadows, xero-mesophilous, steppe, and semi-arid environments (Jovanović et al., 2020). The bioclimatic analysis offers a more humid climate compared to caves from Central Europe, although confirming substantial cold values (Jovanović et al., 2020). This is clear from the pollen record of Pešturina, where mesophytes taxa, which need some wet conditions, survived within the steppe and parkland formations.

In general, the pollen spectra of coprolites and sediment display an increasing frequency of xerophytes from the lower levels of Layer 4 (4c) to the upper levels of Layer 2, with the exception of the sediment samples from Layer 4a (Fig. 11; Supplementary Fig. 3). This trend can be observed mainly in the total sums of Poaceae and *Artemisia*, especially in Layers 3 and 2 (Supplementary Fig. 3). In parallel, there is a decrease in the frequencies of *Pinus*, deciduous *Quercus* and other Mediterranean woody taxa. The sediment samples from Layer 4a record the highest percentages of AP in the sequence and indicate the period with the optimum conditions for the development of deciduous *Quercus*, *Tilia*, mesophytes and Mediterranean woody taxa (Fig. 11; Supplementary Fig. 3).

The number of palynological types is greater in sediments than in coprolites, as sediments reflect a larger spatial and temporal window of pollen deposition than do coprolites. Thereby, 28 exclusive taxa have been found in sediment samples that have not been collected in coprolites (Fig. 11), including *Abies*, *Taxus*, *Celtis*, *Viburnum*, *Sambucus ebulus*, *Phillyrea*, *Ligustrum*, *Rhamnus*, *Daphne*, *Ribes*, *Anthyllis*, *Lotus*, *Vicia*, Brassicaceae, *Epilobium*, Euphorbiaceae, Geraniaceae, *Helianthemum*, *Knautia*, *Asphodelus*, Iridaceae, *Linum*, Malvaceae, *Paronychia*, *Thalictrum*, *Saxifraga*, Scrophulariaceae, and *Verbascum*. Likewise, 3 unique taxa have been identified in the coprolite samples (*Limonium*, *Androsace*, and Primulaceae undiff.) (Fig. 11).

According to Carrión (2002), occurrences of minor pollen taxa in coprolite spectra, possibly with a limited poor dispersal, are crucial for characterizing local floristic assemblages and recording plant taxa that are rarely listed in non-archaeological contexts (Carrión et al., 2018). Considering their current distribution, it is worth mentioning the possible local existence of some endemic Balkan species (Sarić, 1992; Niketič and Tomovič, 2008; Ranđelović et al., 2008; Petrova and Vladimirov, 2010) in Pešturina Cave at least during the Late Pleistocene. The occurrence of *Ribes*, *Daphne*, *Primula*, *Ramonda*, *Androsace*, *Vicia*, and *Knautia* is especially interesting since these genera/species, that may include endemics, were found during MIS 4-3 when climatic conditions were severe (Fig. 11). In addition, during the same time-period (Layers 2 and 3), a number of families were recorded that may embrace endemic species, such as Caryophyllaceae, Apiaceae, Asteraceae, Campanulaceae, Boraginaceae, Brassicaceae, Dipsacaceae, Ericaceae, Rosaceae, Genisteae, Scrophulariaceae, Poaceae, Primulaceae, Ranunculaceae, and Rubiaceae. Other pollen types (*Convolvulus*, *Epilobium*, *Verbascum*, *Linum*, *Ligustrum*, *Paronychia*, *Thalictrum*, *Saxifraga*, *Limonium*, Geraniaceae, Euphorbiaceae, and Malvaceae) may be associated to local floras in the Balkan Peninsula (Polunin, 1980; Bohn and Neuhäusl, 2004), although they do not include endemic species of the central Balkans. On the whole, these taxa show a greater expansion during the glacial stages of the Late Pleistocene than at present, which reinforces their naturalness in the Balkans that acted as a refugium for endemic taxa, and confirms the biogeographic importance of this region in maintaining the phytodiversity of the plant communities (Bennett et al., 1991; Tzedakis, 1994, 1999; Willis, 1994; Okuda et al., 2001; Magri, 2010; Pross et al., 2015; Sadori et al., 2016; Magri et al., 2017).

9. Palaeoenvironment during MIS 5-MIS 3 in the Central Balkans

Pešturina and other sites from the Balkan Peninsula are relevant to the issue of glacial refugia for temperate trees during the Late Pleistocene (Fig. 12). These sites contain deposits sometimes extending back to the Middle and Early Pleistocene, although many of them only cover the last stages of the last glacial period in MIS 2 (Fig. 12). In general, and also at Pešturina, the predominant xerophyte elements during the coldest and most arid phases of the glacial periods consisted of *Artemisia* and Amaranthaceae (Huntley and Birks, 1983; van Zeist and Bottema, 1991; Willis, 1994). In contrast to others sites from central and northern Europe, these sequences show continuous presence of both deciduous and coniferous tree taxa during the Late Pleistocene (Willis, 1994).

The Tenaghi Philippon sequence, in the Mediterranean Sea (NE Greece), has provided one of the most complete vegetation records of the European Quaternary (Wijmstra, 1969; van der Hammen et al., 1971; Greig and Turner, 1974; Wijmstra and Smit, 1976; Tzedakis et al., 2003; Fletcher et al., 2013), spanning the last 1.35 Ma (Tzedakis et al., 2006; Pross et al., 2015). In the last interglacial complex (MIS 5e-5a), the pollen data show a pattern of alternating development of forest, mainly in MIS 5e, 5c and 5a, and xerophytic steppe vegetation, in MIS 5d and 5b (Supplementary Fig. 4). The pollen record from Pešturina (Layers 4a, 4b and 4c) shows similar alternating landscapes, although MIS 5b and MIS 5a have not been clearly distinguished (Figs. 5 and 8). Dominant forest taxa at Tenaghi Philippon are *Quercus* and *Pinus*, while abundant deciduous *Quercus*, *Tilia*, and Poaceae are found at Pešturina. Mediterranean elements, such as *Pistacia*, *Olea*, *Phillyrea*, and *Fraxinus ornus*, are recorded at Tenaghi Philippon during the Eemian interglacial (Milner et al., 2016), as well as at Pešturina (Layer 4c), with the continued presence of *Olea*, *Myrtus*, *Pistacia* and *Cistus*.

In the Ioannina basin, north-west Greece, extending back ca. 430 ka, the vegetation of the last interglacial complex mainly consists of deciduous *Quercus*, *Carpinus betulus*, *Pinus*, *Ulmus/Zelkova*, *Abies*, and *Fagus*, with marked peaks of *Artemisia* and Poaceae in MIS 5d (Bottema, 1974; Tzedakis, 1993, 2000; Tzedakis et al., 2003; Lawson et al., 2004). These data show a general correspondence with the dynamics of MIS 5 in Pešturina, where *Carpinus betulus* and *Fagus* are also found during MIS 5c, although in low frequencies (Fig. 5).

The vegetation history of Lake Kopais, south-east Greece, extends from the Holocene back to MIS 11 (Tzedakis, 1999; Okuda et al., 2001). A remarkable study of the last interglacial shows substantial coincidence with the MIS 5e-5a phases at Pešturina (Supplementary Fig. 4).

The Lake Prespa record, reaching back 92 ka BP, indicates a climate variability in the south-western part of the Balkans (Panagiotopoulos et al., 2014). Three major phases of vegetation development are distinguished: the forested phases of MIS 5 dominated by deciduous trees, the pine-dominated open landscapes of MIS 4, and the open landscapes of MIS 3 with significant presence of temperate trees. The pollen record from Pešturina reveals a composition of the landscapes that is comparable to that of Lake Prespa, with some differences in the dynamics of the principal taxa, including *Quercus*, *Pinus*, *Artemisia*, Amaranthaceae, and Poaceae (Supplementary Fig. 4).

In Lake Ohrid, where a sequence spanning 1.36 Ma was studied (Donders et al., 2021), a detailed pollen record from approximately 160 to 70 ka (MIS 6 to MIS 4) shows high percentages of *Pinus*, *Quercus*, *Abies*, *Betula*, *Carpinus betulus*, *Corylus*, *Tilia* and *Ulmus*, as well as mediterranean taxa such as *Cistus*, *Fraxinus ornus*, *Olea*, *Phillyrea* and *Pistacia* for the last interglacial complex (Sinopoli et al., 2019). There is a general correspondence with Pešturina (Supplementary Fig. 4).

As regards MIS 4 and MIS 3, it is not easy to establish a well-defined correlation between the Pešturina record and the other Balkan sequences, although there is a fairly high degree of coincidence in the loss of forests, characterized by a decline of deciduous *Quercus* and other mesophytes, and a spread of steppes with *Artemisia*, Poaceae, and Amaranthaceae (Supplementary Fig. 4). In addition to the above-mentioned sites, the record of Xinias in Greece, spanning approx. the

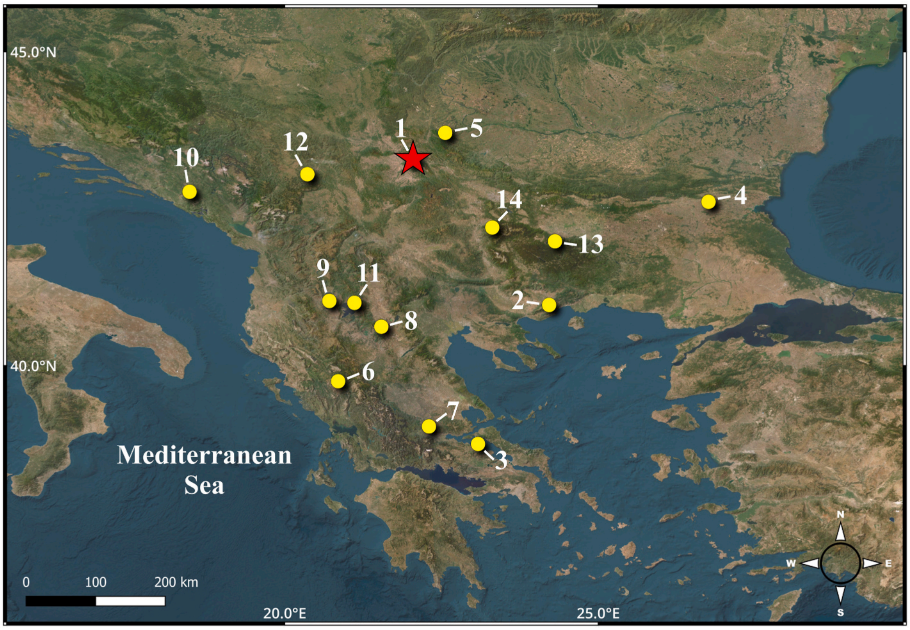

Fig. 12. Late Pleistocene pollen sites from the Balkan Peninsula mentioned in the text: 1. Pešturina (330 m; MIS 5e – end of MIS 3); 2. Tenaghi Philippon (42 m; 1350–0 ka; Milner et al., 2013, 2016; Pross et al., 2015); 3. Kopais (100 m; 500–2 ka; Okuda et al., 2021); 4. Straldzha (128 m; ~37.5–0 ka; Connor et al., 2013); 5. Magura (375 m; ~50–36 ka; Ivanova et al., 2015); 6. Ioannina (473 m; 430–0 ka; Tzedakis et al., 2003; Lawson et al., 2004); 7. Xinias (500 m; ~50–0 ka; Bottema, 1979; Digerfeldt et al., 2000); 8. Limni Zazari (606 m; 20–0 ka; Gassner et al., 2019); 9. Ohrid (693 m; 1360–0 ka; Donders et al., 2021); 10. Crvena Stijena (700 m; MIS 6 – MIS 1; Whallon, 2017); 11. Prespa (849 m; 92–0 ka; Panagiotopoulos et al., 2014); 12. Smolucka (945 m; MIS 5 – MIS 3; Jovanović et al., 2022); 13. Kupena (1356 m; 30–0 ka; Bozilova et al., 1989; Huttunen et al., 1992; Tonkov et al., 2014); 14. Trilistnika (2216 m; 20–1 ka; Tonkov et al., 2008).

last 50 ka (Bottema, 1979; Digerfeldt et al., 2000), has certain similarities with Layers 3 and 2 of Pešturina, with relatively high percentages (30–60%) of arboreal taxa, including deciduous *Quercus*, *Pinus*, *Ulmus*, *Corylus*, *Juniperus*, *Abies*, *Fagus*, *Carpinus betulus*, and *Carpinus orientalis/Ostrya*. In addition, as in Pešturina, the herbaceous vegetation is represented by remarkable values of Poaceae, *Artemisia*, and Amaranthaceae, and to a lesser extent of Asteroideae, Cichorioideae, *Centaurea*, and *Plantago* (Bottema, 1979). In Straldzha Mire (Bulgaria), spanning approx. the last ~ 37. 5 ka (Connor et al., 2013), the pollen data corresponding to MIS 3 shows persistence of cold steppe vegetation, with abundant *Artemisia* and Poaceae, consistent with Pešturina (Supplementary Fig. 4).

Layers dated to MIS 2 are missing from Pešturina Cave, but information about the vegetation of the Balkan Peninsula during the last glacial maximum can be obtained from a number of pollen records (Fig. 12), including Limni Zazari (Gassner et al., 2019), Kupena (Bozilova et al., 1989; Huttunen et al., 1992; Tonkov et al., 2014), Trilistnika (Tonkov et al., 2008), Tenaghi Philippon (Milner et al., 2013, 2016; Pross et al., 2015), Kopais (Okuda et al., 2021), Straldzha (Connor et al., 2013), Ioannina (Tzedakis et al., 2003; Lawson et al., 2004), Xinias (Bottema, 1979; Digerfeldt et al., 2000), Ohrid (Donders et al., 2021), and Prespa (Aufgebauer et al., 2012; Panagiotopoulos et al., 2014). These sequences collect evidence of woody taxa, which reinforces the refuge status of the Balkan Peninsula for mesophytes and Mediterranean elements, including *Pinus*, *Juniperus*, *Abies*, *Picea*, *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Carpinus orientalis/Ostrya*, *Castanea*, *Corylus*, *Fagus*, *Juglans*, *Tilia*, *Fraxinus*, *Ulmus*, *Salix*, *Olea*, *Phillyrea*, and *Pistacia* (Supplementary Fig. 4).

Bennett et al. (1991) suggest that low but persistent pollen percentages from thermophytes and mesophytes tree taxa during the glacial period are likely to have originated from local refugial populations. Additionally, Willis (1992) points out that these populations were probably in microenvironmentally favorable areas, located especially in the mountains. The continuous permanence throughout the Pešturina sequence, and particularly in the final phases of MIS 3, of a diverse assemblage of woody taxa (*Pinus*, *Juniperus*, deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Corylus*, *Tilia*, *Ulmus/Zelkova*, *Buxus*, Genisteae, and *Cistus*), confirms that the Central Balkans were a refuge area for the mesothermophilic component.

The high frequencies of *Tilia* throughout the Pešturina pollen sequence are remarkable, especially because lime pollen is poorly dispersed (mainly entomophily) and consequently is underrepresented (Andersen, 1970; Środoń, 1991; Kupryjanowicz et al., 2004). Lime is a mesophilous taxon adapted to moist conditions under warm temperate climates, mainly in plains and on the lower slopes of hills and mountains (De Benedetti et al., 2022). Three species of *Tilia* occur today in the Balkan Peninsula, whose pollen cannot be easily distinguished (Bińka et al., 2006): *Tilia cordata* Miller (currently widespread in Western Europe; Eaton et al., 2016), *T. tomentosa* Moench (extending in SE Europe; Atalay and Efe, 2010), and *T. phatyphyllos* Scopoli (reaching the westernmost parts of the East European Plain; Pigott, 2020). While Late Pleistocene pollen records of *Tilia* from the Balkan Peninsula are scarce and generally discontinuous (Bottema, 1974; Tzedakis, 1993; Willis, 1994; Milner et al., 2013, 2016; Pross et al., 2015; Sinopoli et al., 2019; De Benedetti et al., 2022; Lang et al., 2023), Pešturina Cave stands out as the site with the highest presence of *Tilia* in the Central Balkan Peninsula, where valley gorges could have been a glacial refuge for lime trees (De Benedetti et al., 2022), as well as a biodiversity hotspot (Carrión et al., 2011).

The occurrence of pollen of *Zelkova* at Pešturina during MIS 5 is probable but, due to the poor conservation state of pollen grains, it was not distinguished from *Ulmus* (Figs. 5 and 8). Most Pleistocene palynological records from the Balkan Peninsula fail to show any separation between *Zelkova* and *Ulmus*, which makes it difficult to reconstruct its history (Magri et al., 2017). Nevertheless, evidence for *Zelkova* during the Eemian interglacial at Ioannina (Tzedakis et al., 2003) and until 77 ka BP at Lake Ohrid (Donders et al., 2021) supports the finding at Pešturina and the existence of a refuge in the Central Balkans during the Late Pleistocene (Lang et al., 2023).

10. Palaeoecological implications for survival of human populations in the Central Balkans

Kozlowski (1998) highlights the importance of the Balkan Peninsula as a pivotal area for the dispersal of hominids, as hominin occupations may have been preferentially distributed across regions with high levels of topography and orography variability, favouring the maintenance or the movement of Neanderthals and Anatomically Modern Human populations (Conard, 2002; Van Andel et al., 2003; Mellars, 2011; Mihailović et al., 2011; Marín-Arroyo and Mihailović, 2017; Mihailović, 2020; Carvalho and Bicho, 2021; Karavanić et al., 2022; Marín-Arroyo et al., 2023).

Pešturina Cave represents the first systematically excavated site dated from MIS 5e to MIS 3 in the Central Balkan Range, and the only site within the Balkan interior where Neanderthal fossil remains have been discovered. There are some relevant hominid sites of the Middle Pleistocene in the Balkan Peninsula (Mihailović et al., 2022a), such as Mala Balanica, dated to >400 ka (Roksandic et al., 2011; Rink et al., 2013; Skinner et al., 2016; Mihailović et al., 2022b) and Velika Balanica, dated to MIS 9-7 (Mihailović and Bogićević, 2016; Mihailović et al., 2022b; Roksandic et al., 2022). Other significant Palaeolithic sites, chronologically situated in the Middle to Late Pleistocene are: Kozarnika Cave (Bulgaria; MIS 6; Guadelli et al., 2005; Tillier et al., 2017), Zobište (northern Bosnia; MIS 5a to MIS 4; Montet-White et al., 1986; Baumler, 1988), Šalitrena Pećina (Serbia; MIS 4 to MIS 3; Marín-Arroyo and Mihailović, 2017; Marín-Arroyo et al., 2023), Tabula Traiana (Serbia; MIS 3; Borić et al., 2022), Baranica (Serbia; MIS 3; Mihailović et al., 2011), Hadži Prodanova (Serbia; MIS 3 to MIS 2; Milošević, 2016; Alex et al., 2019), Dubočka-Kozja caves (Serbia; MIS 3 to MIS 2; Borić et al., 2022), and Theopetra (Greece; MIS 3 to MIS 1; Karkanas et al., 2015). In the site of Crvena Stijena (Montenegro; MIS 6 to MIS 1; Whallon, 2017), charcoal analysis from layer XXIV (toward the end of MIS 5a) has allowed the identification of at least twelve woody taxa (*Pinus*, *Abies*, *Juniperus*, *Buxus*, *Cornus*, *Prunus*, *Sambucus*, *Fagus*, *Fraxinus*, *Juglans*, *Acer*, and *Tilia*) used by the rock shelter inhabitants. These taxa are consistent with Layer 4a in Pešturina (MIS 5b-5a) (Fig. 11; Supplementary Fig. 3). In the Magura Cave, north-west Bulgaria, extending back ca. 50-36 ka, the pollen composition of the coprolites mainly consists of *Pinus*, Poaceae, and *Artemisia* (Ivanova et al., 2015), which shows a general correspondence with MIS 3 in Pešturina Cave. In Smolućka cave (Serbia), dated from MIS 5 to MIS 3 (Jovanović et al., 2022), the application of a bioclimatic analysis and the Taxonomic Habitat Index to the Late Pleistocene rodent assemblages indicates climate conditions favorable for a large species diversity during MIS 5, not too severe during MIS 4, and temperate-humid during MIS 3. The bioclimatic results obtained for the same period at Pešturina show similar alternating environments (Jovanović et al., 2020), consistent with the pollen record.

From a palaeoecological perspective, the Pešturina site appears as a unique palaeofloristic record in the Balkans, in relation to the Neanderthal palaeoenvironment, highlighted by a permanent open forested habitat, with high plant diversity, typical of the glacial refugia in the southern European regions. Similar situations were found in the Iberian Peninsula (Carrión et al., 1999b, 2003a, 2008, 2018, 2022b; González-Sampériz et al., 2010; Manzano et al., 2017; Ochando et al., 2019, 2020b, 2020c, 2020d, 2022a; Verdú et al., 2020; Amorós et al., 2021), in the Italian Peninsula (Follieri et al., 1998; Magri, 1999; Magri and Sadori, 1999; Giardini, 2007; Pini et al., 2010), and the Lesvos Island (Margari et al., 2009). Finlayson et al. (2011) found a conspicuous association between *Homo* and ecologically rich, semiopen woodlands in ecotonal and mosaic landscapes. This wide diversity of habitats, as in the southern Iberian Peninsula (Carrión et al., 2008, 2018; Finlayson and Carrión, 2007; Ochando et al., 2020b) could have favored a propitious environment for a long permanence of Neanderthals and the early Anatomically Modern Human populations (Carrión et al., 2011). Thus, the palynological record of Pešturina Cave emerges as an optimal mesothermic refuge.

According to Vidal-Cordasco et al. (2022, 2023), Neanderthals were influenced by the abundance of herbivores, which were an important part of their daily subsistence. The search for ungulates caused the Neanderthals to follow them, which determined environmental conditions suitable for survival by providing opportunities for hunting, collecting, and sheltering (Finlayson and Carrión, 2007; Carrión and Walker, 2019; Stewart et al., 2019). This is confirmed by the palaeoecological indicators of wetlands in Pešturina, which might have developed around the cave and nearby riverine ecosystems, dominated by *Alnus*, *Fraxinus*, *Populus*, *Salix*, *Ulmus*, and Cyperaceae, among others. The presence of riparian species near the site is in itself an evidence for fresh water availibility both for human populations and hunted animals that frequented the region (Ochando et al., 2022a, 2022b, 2022c).

The Neanderthals and modern human groups that inhabited Pešturina were undoubtedly expert of open woodland ecosystems, along with wooded ravines, in areas that combined the middle mountain and the plain towards the valley, as demonstrated by the stable isotope signatures of the macromammals from Šalitrena Pećina (Marín-Arroyo et al., 2023). They had a deep knowledge of their environment (Nabais and Zilhão, 2019; Spikins et al., 2019; Stewart et al., 2019), where diverse and rich conditions allowed them to develop different subsistence strategies (Spagnolo et al., 2019), and to obtain greater adaptability by means of a tremendous structural complexity (Carrión et al., 2011). Although hyaenas were likely the main agents of bone accumulation to the site, especially in Layers 4 and 3 (Milošević, 2016), large mammmal remains, like woolly rhinoceros and mammoth, together with lithic tools show that some remains were brought to the site by humans (Mihailović and Milošević, 2012). Thus, these human groups, mainly the Neanderthal populations from Layer 4 (MIS 5), processed and consumed a wide diversity of animal species, including *Equus ferus germanicus*, *Cervus elaphus*, *Dama dama*, *Bison priscus*, *Sus scrofa*, *Capreolus capreolus*, and *Ursus spelaeus*. Through the analysis of cut marks, dismemberment, filleting, long/extensive bone breakage and bones with traces of burning, it was possible to identify anthropogenic activities composing the assemblage (Camarós et al., 2013; Milošević, 2016, 2020; Majkić et al., 2018; Mihailović et al., 2022a). Likewise, the use of plant materials for food and technological items cannot be disregarded (Ward et al., 2012a, 2012b; Hardy, 2018; Zilhão et al., 2020), especially since Fellows Yates et al. (2021) demonstrated the presence of bacteria involved in starch digestion within the oral microbiome of the Pes-3 Neanderthal from Layer 4 in Pešturina. Besides, a number of recent investigations highlight how relevant plants were for Neanderthal diet (Barton et al., 1999; Carrión et al., 2008, 2018; Hardy et al., 2012; Ochando et al., 2019, 2020a, 2020b, 2020c, 2020d). Thereby, we can add to the human diet the possibility of a broad spectrum of edible plants that likely grew in the proximity of Pešturina, such as chestnut (*Castanea sativa*), hazelnut (*Corylus avellana*), walnut (*Juglans regia*), Mediterranean hackberry (*Celtis australis*), elderberry (*Sambucus nigra*), olive (*Olea europaea*), and probably wild Rosaceae.

The new palynological study of Pešturina cave reinforces our understanding of the adaptation and persistence of Neanderthals and early Anatomically Modern Humans in mosaic environments within Mediterranean ecotones. The Mousterian-Gravettian pollen record of Pešturina depicts a diverse vegetation landscape, which may well represent the Central Balkan Range for this period (MIS 5e-MIS 3). Thus, the pollen results presented here provide new insights into the biogeography of the Mousterian-Gravettian populations that used the present-day thermo-meso-mediterranean and continental European belts as corridors.

CRediT authorship contribution statement

Juan Ochando: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Supervision, Validation, Writing – review & editing. **José S. Carrión:**

Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Donatella Magri:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Ana B. Marín-Arroyo:** Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Federico Di Rita:** Software, Supervision. **Manuel Munuera:** Investigation, Methodology, Resources, Software, Supervision. **Fabrizio Michelangeli:** Software, Supervision. **Gabriela Amorós:** Software, Visualization. **Stefan Milošević:** Supervision, Validation, Writing – review & editing. **Katarina Bogićević:** Supervision, Validation, Writing – review & editing. **Vesna Dimitrijević:** Supervision, Validation, Writing – review & editing. **Draženko Nenadić:** Supervision, Validation, Writing – review & editing. **Mirjana Roksandic:** Project administration, Resources, Supervision, Validation, Writing – review & editing. **Dušan Mihailović:** Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.108600.

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