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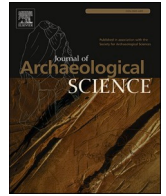
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# Neanderthal hunting grounds: The case of Teixoneres Cave (Spain) and Pié Lombard rockshelter (France)

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## ABSTRACT

The study of Neanderthal-Environment interactions very often lacks precise data that match the chrono-geographical frame of human activities. Here, we reconstruct Neanderthals' hunting grounds within three distinct habitats using dental microwear analysis combined with zooarchaeological data. The predation patterns toward ungulates are discussed in term of frequency (NISP/MNI) and potential meat intake (MAM). Unit IIIa of Teixoneres Cave (MIS 3, NE Spain) corresponds to a mosaic landscape, Unit IIIb was more forested, and, in the "Ensemble" II of Pié Lombard (MIS 4, SE France), forest cover dominated. At Pié Lombard, Neanderthals rely on a high diversity of taxa from closed and semi-open hunting grounds, mostly two ungulate species as well as rabbits and several bird taxa. At Teixoneres Cave, mainly open areas are exploited in summer with a predation mostly focused on large gregarious ungulates. The larger size of ungulate herds in open spaces may have allowed Neanderthals to restrict their subsistence behaviour only to very few species, in specific hunting strategies. In Unit IIIa, they do not appear to have made any selection within the most abundant species, while in Unit IIIb, they focused on aurochs and also opportunistically and heavily on newborn red deer. Neanderthal subsistence strategies seem, therefore, only partially linked to the hunting grounds they had access to. While it impacted the diversity of the prey they selected, Neanderthal groups were able to develop distinct hunting strategies within similar environments.

## 1. Introduction

The subsistence behaviours of human populations during the Middle Palaeolithic are commonly attributed to the intricate connection

between cultural and biotic factors (Discamps and Royer, 2017; Gaudzinski-Windheuser and Roebroeks, 2011; Hardy et al., 2012; Rolland and Dibble, 1990; Tzedakis et al., 2007; Vettese et al., 2022). The latter factor is investigated through the reconstruction of environmental

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parameters using a wide range of proxies such as pollen from long terrestrial and deep-sea sedimentary sequences (e.g., Pons and Reille, 1988; Sánchez Goñi et al., 2008), pollen from archaeological sequences (Carrión et al., 2018, 2022a, 2022b; Ochando et al., 2020a, 2020b, 2022), or small mammals (e.g., Discamps and Royer, 2017; Fernández-García et al., 2022; López-García et al., 2021). The accuracy of the correlations suggested by these proxies between the reconstructed environments and those experienced by humans can greatly vary depending on their resolution. Indeed, the chronological framework they address (millennial to yearly) never corresponds fully to the period of the site occupation by human groups. Likewise, the size of the territory they cover varies significantly, ranging from continental, regional to local scales. Proxies that reconstruct environmental contexts on large scales may overlook the diversity of local landscapes that hunter-gatherer groups had access to (Uzunidis and Rivals, 2023).

Neanderthals have exploited a wide range of resources present in various habitats. Populations that inhabited woodland consumed a higher proportion of plant food (El Zaatari et al., 2011; Hlusko et al., 2013), while the ones from cold steppe environments had a higher meat intake (El Zaatari et al., 2011, 2013; Lalueza-Fox and Pérez-Pérez, 1993; Williams et al., 2018). In terms of predation, the most common prey found in Neanderthal camp, in general, were large and medium-sized ungulates (Gamble, 1999; Mellars, 1996; Rivals et al., 2022). In Southern Europe, these hunts were completed with a significant acquisition of small game, while it appears less common in the Northern territories (Blasco et al., 2022). In the Western Mediterranean region notably, birds and leporids were commonly preyed upon to access both meat and pelt/feather (Blasco et al., 2013; Blasco and Fernández Peris, 2009; Fiore et al., 2020; Martínez Valle et al., 2016; Morin et al., 2019). Thus, Neanderthal dietary and predation habits are strongly dependent on climatic and environmental contexts. Accurate environmental reconstructions at the local scale are then essential to comprehensively grasp the impact of biocoenosis on Neanderthal subsistence strategies.

Approaches based on the study of ungulates benefit from the strict contemporaneity between the archaeological site occupation and the accumulation of prey resulting from hunter-gatherer activities. While environmental reconstructions based on large mammals can be misleading due to the high ecological flexibility of many of these taxa (Rivals et al., 2010, 2015a; Rivals and Lister, 2016; Ungar et al., 2020; Uzunidis, 2021; Uzunidis et al., 2022), approaches based on biogeochemical and dental wear analyses have emerged. These methods enable the examination of different life stages of the animals, allowing for the inclusion of their inherent variability (Bocherens et al., 2005, 2016; Britton, 2018; Britton et al., 2023; Sánchez-Hernández et al., 2016). Dental microwear stands out among these methods as a tool capable of reconstructing an individual's diet from a few days to a month prior to its death (Solounias and Semperebon, 2002; Winkler et al., 2020). Consequently, it provides a way to explore past ecologies, vegetal structure and to infer paleoenvironments within the biome where ungulates were present when and where they were preyed upon.

In this study, our aim is to provide insights into the subsistence strategies of late Middle Palaeolithic Neanderthals, focusing on three distinct archaeological units. Specifically, we examine Teixoneres Cave Units IIIa and IIIb (MIS 3, Spain) and Pié Lombard rockshelter (MIS 4, France), where Neanderthals inhabited environments ranging from mosaic to forested biome habitats (Fernández-García et al., 2022; Ochando et al., 2020a; Renault-Miskovsky and Texier, 1980; Texier et al., 2011; Uzunidis and Rivals, 2023). Our approach involves reconstructing the hunting grounds selected by Neanderthal groups within their environment and comparing them to the species and individuals they targeted as prey. The objective is to assess the diversity of Neanderthal subsistence strategies, considering the potential influence of environmental contexts and discerning the role of selective choices in shaping these strategies.

## 2. Archaeological sites

### 2.1. Pié Lombard rock shelter

Pié Lombard rock shelter (Tourrettes-sur-Loup, Alpes-Maritimes, France) is an archaeological site located near the city of Nice (Fig. 1), discovered in 1962 (Lumley, 1969) and excavated between 1971 and 1986 under the supervision of P.-J. Texier (Texier, 1974; Texier et al., 2011). It is located at the foot of a rather steep cliff at a relatively low altitude: 250 m above sea level (a.s.l) in a very rugged area surrounded by the Mediterranean Sea to the south and the Loup River, along with mountainous areas exceeding 1000 m in elevation to the east and north. Throughout the Pleistocene, as it is today, its topographical situation gives rise to ecotone landscapes and conditions.

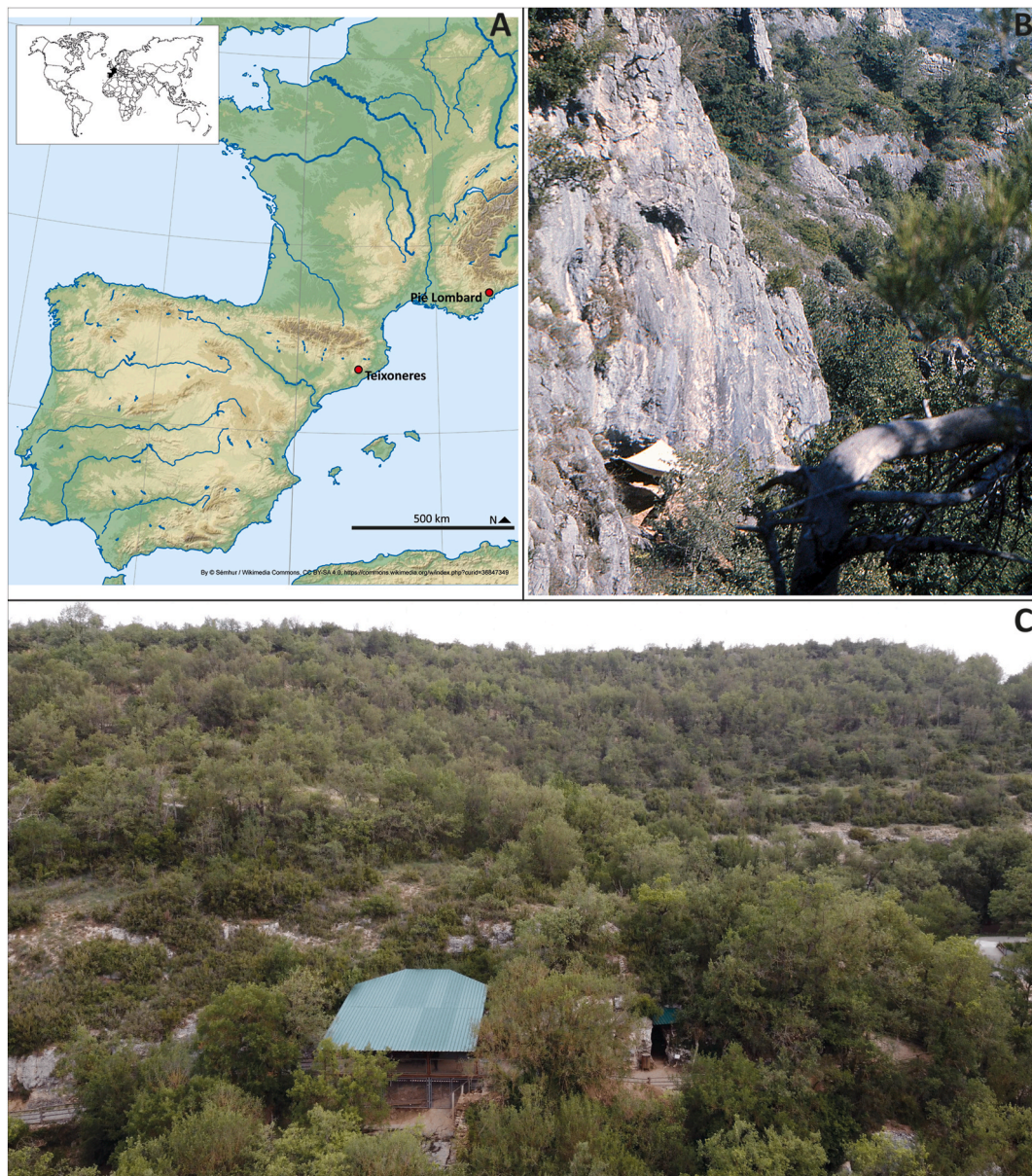
Pié Lombard has yielded a 3-m thick archaeological sequence that was separated into two main stratigraphic complexes, or *ensembles* (Texier et al., 2011).

- “Ensemble” I: dated by accelerator mass spectrometry (AMS) to between 20,639 and 22,073 cal BP (Tomasso, 2014). This “ensemble” has been attributed to the Epigravettian culture and yielded very few faunal remains (for more details, see Pelletier et al., 2019).
- “Ensemble” II, identified as Mousterian complex, is dated to a transitional phase between Marine Isotope Stage (MIS) 5 and 4 based on a thermoluminescence (TL) date of  $70 \pm 8$  kyr BP (Valladas et al., 1987). Stalagmites underlying the Mousterian sediments yielded two electron spin resonance (ESR) dates of  $147 \pm 10$  kyr and  $130 \pm 20$  kyr BP (Yokoyama et al., 1983). The present study focuses on this ensemble.

Several ungulate species are present at Pié Lombard. *Capra ibex* and *Cervus elaphus* are the main represented large herbivore species while *Bos primigenius*, *Capreolus capreolus*, *Equus caballus*, and *Rupicapra rupicapra* are less abundant (Texier et al., 2011; Uzunidis et al., 2022; Uzunidis and Rivals, 2023). Few remains of carnivores were also identified belonging to *Ursus arctos*, *Felis silvestris*, *Lynx* sp., *Panthera pardus*, *Canis lupus*, and some remains from *Vulpes vulpes* and *Cuon* sp. (Texier et al., 2011). Small game is very well represented, including 225 rabbits (*Oryctolagus cuniculus*) and at least 86 individuals from various bird species (Pelletier et al., 2019; Romero et al., 2017). Zooarchaeological and taphonomical studies indicate that both ungulates and small game were exploited for meat, skin, and feathers, while carnivores were not exploited (Pelletier et al., 2019; Romero et al., 2017; Roussel, 2023). While there is no evidence of carnivore denning at Pié Lombard, some bones exhibit marks of carnivore activities suggesting their partial involvement in the accumulation of the caprid remains (Roussel, 2023). Additionally, two Neanderthal deciduous incisors were discovered (Lumley de, 1976; Texier et al., 2011). The Mousterian lithic industry, produced from various raw materials like flint, chert and quartzite, originates from both local and semi-local origin. Most raw materials come from the littoral area, with already finished tools abandoned at the site (Porraz, 2005, 2009). The “ensemble” II of Pié Lombard is interpreted as a seasonal camp, with limited carnivore incursions, primarily dedicated to hunting activities of both small game and ungulates by Neanderthals (Porraz, 2005, 2009; Roussel et al., 2021; Texier et al., 2011) that occurred mostly in autumn but also in spring (Roussel, 2023; Roussel et al., 2021; Uzunidis and Rivals, 2023).

### 2.2. Teixoneres Cave

Teixoneres Cave, located in Moià (Barcelona, Spain), is part of the Toll caves karstic system (Fig. 1). It was discovered as an archaeological site in the 1950s and some intermittent excavation seasons by different researchers took place until the 1990s. Since 2003, annual excavations have been conducted by a team from the *Institut Català de Paleocologia Humana i Evolució Social* (IPHES-CERCA; Rosell et al., 2008; 2010a;



**Fig. 1.** A: Geographical position of the site of Pié Lombard rockshelter and Teixoneres Cave, B: General view of Pié Lombard rockshelter within its current environment (Photo: Pierre-Jean Texier); C: General view of Teixoneres cave within its current environment (Photo: Gabriel Cifuentes-Alcobendas).

2010b, 2014). The Toll caves karstic system is located 780 m a.s.l. Nowadays, the landscape around Teixoneres Cave corresponds to small hills and minor streams, with the exception of the Llobregat River to the south and the Ter River to the north, which border the area (Rosell et al., 2017), implying a more homogenous environment compared to the partitioned landscape at Pié Lombard.

Teixoneres cave has yielded a 6-m deep sedimentary sequence divided into eight stratigraphic units, further categorized into sub-units (Rosell et al., 2008, 2010b; Zilio et al., 2021). At the top of the sequence, Unit I has an age of ca. 14–16 ka (Tissoux et al., 2006). Unit II has been radiocarbon dated between 44,210 and 33,060 cal BP and Unit III was radiocarbon dated from >51,000 BP to 44,210 cal BP (Talamo et al., 2016). Unit III, the focus of this study, is the richest unit in Teixoneres. Two sub-units are identified in Unit III: Unit IIIa, dated between 44,210 and 45,000 cal BP, and Unit IIIb dated to 45,000 cal BP at the top and its base has an age of >52,000 years BP (Ochando et al., 2020a; Talamo et al., 2016; Tissoux et al., 2006).

Both sub-units, IIIa and IIIb, exhibit a similar representation of

ungulate species, including *Bos primigenius*, *Capra pyrenaica*, *Cervus elaphus*, *Capreolus capreolus*, *Equus caballus*, *Equus hydruntinus*, and *Coelodonta antiquitatis*. The species diversity is higher in Unit IIIa where few remains of *Rupicapra pyrenaica* and *Mammuthus primigenius* were identified (Álvarez-Lao et al., 2017; Uzunidis et al., 2022; Uzunidis and Rivals, 2023). Carnivores are present in both sub-units: *Ursus spelaeus*, *Crocota crocuta*, *Canis lupus*, *Vulpes vulpes*, *Lynx spelaea*, and *Meles meles* (Rosell et al., 2017), along with remains of leporids and birds (Rufà et al., 2014, 2016). Several Neanderthal remains of both juveniles and adults were found in sub-unit IIIb. Carnivores seem to have occupied the inner parts of the cave in alternation with Neanderthals who had favoured the porch area (Rosell et al., 2010a, 2017; Rufà et al., 2014, 2016, 2014; Sánchez-Hernández et al., 2014, 2016; Zilio et al., 2021). Despite occasional human action, non-human predators are mainly responsible for the accumulation of small game (Rufà et al., 2014, 2016), while ungulate bones display evidence of anthropogenic activities (Rosell et al., 2017). The lithic raw materials are mostly of local origin (Muñoz del Pozo et al., 2023). The Mousterian industry consists of hunting and

cutting tools used in the early phases of butchery (Picin et al., 2020). Porch areas of units IIIa and IIIb were interpreted as Neanderthal hunting camps (Rosell et al., 2017) predominantly occupied during the summer (Sánchez-Hernández et al., 2014, 2016, 2020; Uzunidis and Rivals, 2023).

### 3. Material and methods

In both sites, specific-level identification of ungulates was successfully achieved for some cranial and post-cranial elements. However, the identification of post-cranial elements is notably limited due to a high fragmentation rate, particularly in Teixoneres Cave. Consequently, the analysis heavily relies on dental elements.

In the case of Teixoneres Cave, the studied material exclusively originates from the outer area of the cave, following the definition by Zilio et al. (2021). Thus, the analysis was restricted to the anthropic part of the site.

The material from Pié Lombard material is curated at the Maison Méditerranéenne des Sciences de l'Homme (Aix-en-Provence, France) and the Teixoneres Cave collection is located at the Institut Català de Paleocologia Humana i Evolució Social (Tarragona, Spain).

#### 3.1. Quantification of ungulate representation

The representation of the ungulates in each accumulation was evaluated using two indices for comparative purposes: Minimum Number of Individuals (MNI) (Badgley, 1986) and the total Number of Identified Specimens (NISP) (Lyman, 2008). The NISP was calculated by considering all elements that were complete enough to secure anatomical and specific identification, including both post-cranial and cranial remains. The MNI is derived only from dental elements, which were the best-preserved and most represented. The calculation is based on the most abundant tooth from either the left or right side and includes age class attributions. MNI for Teixoneres cave were previously published by Uzunidis and Rivals (2023) and for Pié Lombard it was re-evaluated since the studies of Uzunidis and Rivals (2023), Roussel (2023) and Pelletier et al. (2019).

Both NISP and MNI are indicative of Neanderthal predation toward precise individuals. It can blur, however, the potential contribution of each of them to meat intake. Thus, the representation of each species regarding their meat mass was estimated following several steps.

- 1) MNI was calculated for each cohort and individuals were categorized into two age groups (for the methodology associated to age estimation, see below): 'newborn' and 'grown'. The 'newborn' group comprises individual aged between 0 and 4 months, while the 'grown' group includes all other individuals. The distinction between these age groups aims to account for potential differences in meat quantity related to age-biased ungulate accumulation. Juveniles older than 4 months and sub-adult individuals are classified with the adults in the 'grown' group. Indeed, those age classes were very scarce in our samples and growing processes can vary significantly between populations according to several factors that are difficult to assess in Pleistocene studies (see for example Gidney, 2013; Poppi et al., 2018). As a consequence, the weight of growing individuals (juveniles older than 4 months and subadults) was over-estimated.
- 2) The body mass of the 'grown' age-group was estimated using Janis (1990) equations based on measurements from the second and third lower molars taken at the collar. In one case, for *B. primigenius* of Pié Lombard, since no permanent teeth were available to estimate the body mass, we used the transversal diameter of the metatarsal taken in the middle of the diaphysis and used the equations from Scott (1990). For each cohort, a mean mass was calculated by averaging the results.

- 3) The body mass of the 'newborn' age group was calculated using the mean mass of the 'grown' age group from each cohort and the equation published by Traill et al. (2021).
- 4) For the large ungulates, the proportion of meat available on carcasses was considered to be 60% of the live mass (Brugal, 2005; Lyman, 1979). This proportion was calculated both for the 'newborn' and 'grown' age groups.
- 5) The meat mass obtained for both the 'newborn' and the 'grown' age groups was multiplied by the MNI obtained for the 0–4 months age class and for the others, respectively.

This method presented provides a means to estimate the meat available from each archaeological cohort of ungulates. However, it operates under the assumption that all ungulates from Pié Lombard and the outer part of Teixoneres cave were preyed upon by Neanderthals. While most evidence supports the idea that these assemblages were primarily accumulated by Neanderthals (Pelletier et al., 2019; Rosell et al., 2017; Roussel, 2023; Rufà et al., 2014, 2016), other occasional contributions from other predators cannot be entirely ruled out. Also, the sedimentary layers likely encompass several distinct occupation periods over time, but are concatenated here within each assemblage: 'Ensemble' II of Pié Lombard and Units IIIa and IIIb of Teixoneres. Additionally, the method does not account for potential selection of specific body parts that may have occurred at the kill site. Indeed, it assumes that the entire carcass contributed to the Neanderthal diet. Also, as explained in the methodology above, the weight of the juvenile individual above 4 months and of the subadult was purposely over estimated. Therefore, this approach should be interpreted as an approximation of the Maximum Available Meat (MAM) from the ungulate cohorts, acknowledging its limitations and assumptions.

#### 3.2. Estimation of the age at death

The estimation of the age at death of the ungulates was conducted based on the identification of dental remains, including isolated teeth for equids and cervids, as well as teeth on maxilla and mandibles for the other taxa. The age estimation for red deer and equids involved the use of specific equations. We followed the work of Steele (2004) to establish the age of red deer based on the fourth lower deciduous tooth and the first lower molar. For equids, we employed the equations published by Fernandez (2009). Both methods provide an estimation of the individual age associated with a certainty rate. We include in this study only the teeth with a certainty rate above 85%. For both taxa, unworn or very slightly worn deciduous teeth were included into the 0–4 month age group. For the other taxa, we used methods based on tooth eruption and wear patterns: *B. primigenius* (Brugal and David, 1993), *Capra* sp. (Pailhaugue, 2003; Pérez Ripoll, 1988), *Rupicapra* sp. (Pailhaugue, 1998) and *Capreolus capreolus* (Paulus, 1973).

#### 3.3. Dental microwear

Dental microwear involves studying the microscopic marks on tooth occlusal surfaces, which are produced by food and masticatory processes. In herbivores, these dietary micro-traces, such as scratches and pits, result from the presence of phytoliths (Rivals et al., 2015b; Walker et al., 1978). The quantification of these traces provides insights into three dietary types: grazers (consuming grass), browsers (consuming ligneous and herbaceous plants), and mixed-feeders (consuming both categories seasonally or not). When applied to a diverse range of herbivorous taxa from the same site, dental wear analysis can indicate the contribution of dicots and monocots to the environment (Mainland, 1998, 2000; Semprebon et al., 2004b; Solounias and Semprebon, 2002; Uzunidis and Rivals, 2023). Dental microwear helps reconstruct the diet of an individual a few days before its death (Hoffman et al., 2015; Teaford and Oyen, 1989; Winkler et al., 2020). Indeed, it serves as a valuable proxy for discussing the environmental setting of Neanderthal

groups at the moment of their prey acquisition (Uzunidis and Rivals, 2023).

The study followed the protocol established by Solounias and Semprebon (2002) and Semprebon et al. (2004a). The occlusal surface of each tooth was cleaned using acetone, then 96% ethanol, followed by moulding using high-resolution silicone (vinylpolysiloxane). Transparent casts were created using epoxy resin and observed with a stereomicroscope at x35 magnification. The microwear features were identified and quantified on a standard surface of 0.16 mm<sup>2</sup> using an ocular reticule, preferably on the upper tooth paracone and the lower tooth protoconid, excluding the second and third premolars (Xafis et al., 2017). Individuals deemed too old or too young individuals and teeth bearing taphonomic damages were discarded (Fortelius and Solounias, 2000; King et al., 1999; Rivals et al., 2007). Microscopic taphonomical defects were also discarded following the morphological descriptions of Micó et al. (2023); Uzunidis et al. (2021). For the identification of the microwear features, the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004a) was followed, quantifying pits (small and large), scratches (fine, coarse and hypercoarse), and gouges. The scratch width score (SWS) was also estimated, giving a score of '0' to teeth with predominantly fine scratches, '1' to those with mixed fine and coarse scratches, and '2' to those with predominantly coarse scratches. Microwear features are compared to a referential of present-day herbivores with known diet (Solounias and Semprebon, 2002).

## 4. Results

### 4.1. Representation of the species in Teixoneres Cave Units IIIa/IIIb and Pié Lombard

In Teixoneres Cave Unit IIIb, *C. elaphus* represents 55.88% of the NISP and 52.94% of the MNI (Table 1; Fig. 2). *E. caballus* and *C. capreolus* follow as the second most represented species, accounting for 14.57% and 12.17% of the NISP and 13.23% and 11.76% of the MNI, respectively. *B. primigenius* and *C. pyrenaica* (NISP = 6.79%; MNI = 10.29% and 5.88%, respectively) are slightly more represented than *E. hydruntinus* (NISP = 3.79%; MNI = 5.88%). A significant part of the *C. elaphus* cohort comprises very young individuals below 4 months (Table 2; Fig. 3), strongly influencing the MAM. *B. primigenius* dominates the MAM with 50.72%, followed by *C. elaphus* at 27.6%. The other species have a more limited contribution: *E. caballus*, 10.36%, *E. hydruntinus*, 6.73%, *C. pyrenaica*, 2.96% and *C. capreolus*, 1.60% (Table 1; Fig. 2).

In Teixoneres Cave Unit IIIa, *E. caballus* and *C. elaphus* represent 42.35% and 35.29% of the NISP and 39.28% and 28.57% of the MNI, respectively (Table 1; Fig. 2). They are the most abundant species in this

unit followed by *Bos primigenius* and *E. hydruntinus*, representing 12.94% and 2.35% of the NISP, respectively, and both accounting for 10.71% of the MNI. Finally, *C. pyrenaica*, *C. capreolus* and *R. pyrenaica* are relatively scarce, each comprising 2.35% of the NISP and 3.57% of the MNI. In terms of available meat, *E. caballus*, *B. primigenius* and *C. elaphus* contributed the most to the MAM with 36.8%, 28.37% and 24.56%, respectively (Table 1; Fig. 2). They are followed by *E. hydruntinus* (7.56%), *C. pyrenaica* (1.04%), *R. pyrenaica* (1.02%) and *C. capreolus* (0.6%).

In Pié Lombard, *C. ibex* is the main represented species (NISP = 60.84%; MNI = 49%), followed by *C. elaphus* (NISP = 32.49%; MNI = 28.3%). The other species are less common with *R. rupicapra* (NISP = 4.6%; MNI = 11.32%), *B. primigenius* (NISP = 1.13%; MNI = 3.77%), *C. capreolus* (NISP = 0.47%; MNI = 3.77%) and *E. caballus* (NISP = 0.37%; MNI = 3.77%) (Table 1; Fig. 2). *C. elaphus* and *C. ibex* contribute most to the MAM representing 52.69% and 31.16%, respectively, followed by *B. primigenius* (8%), *E. caballus* and *R. rupicapra* (3.74%) and *C. capreolus* (0.63%).

### 4.2. Diet of the ungulates at Teixoneres Cave Units IIIa and IIIb and Pié Lombard at the moment of death

In Teixoneres Cave Unit IIIb, *B. primigenius*, *C. elaphus* and *E. caballus* exhibit a relatively high number of small pits and scratches, the presence of large pits, a mixed scratch texture and an absence of gouges (Fig. 4; Table 3). *Equus hydruntinus* displays the same characteristics but lacks large pits. Their diet is therefore considered abrasive and falls within the range of the extant mixed-feeders. *Capra pyrenaica* and *C. capreolus* are characterized by a low number of scratches and a fine scratch texture, indicative of a soft diet. The number of pits for *C. capreolus* is lower compared to *C. pyrenaica*, which could suggest the ingestion of dust for the latter, while the former may have focused on leaves (Semprebon et al., 2011; Uzunidis et al., 2022). Both species fall within the confidence ellipse of extant browsers.

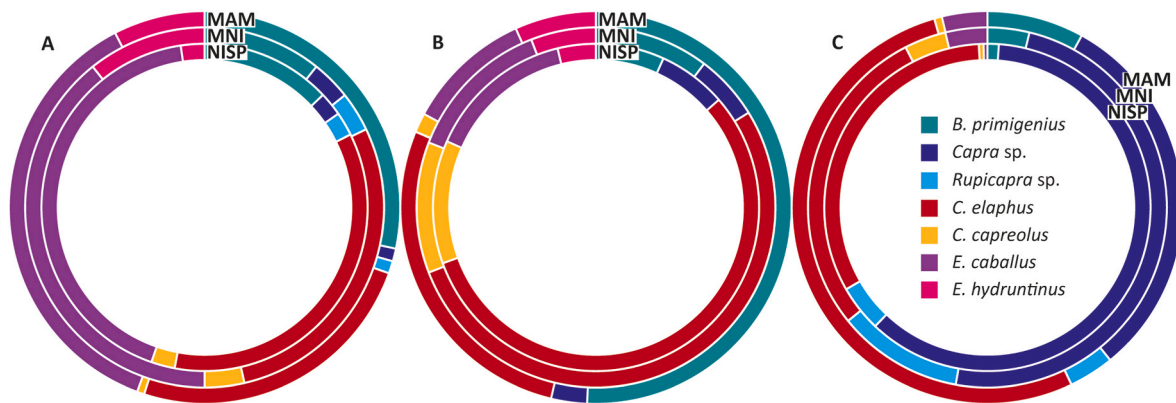
In Teixoneres Cave Unit IIIa, the species exhibit similar dietary patterns to those in unit IIIb, with *B. primigenius*, *C. elaphus*, *E. caballus* and *E. hydruntinus* showing an abrasive diet and falling within the mixed-feeder group, while *C. pyrenaica* and *C. capreolus* fall within the confidence ellipse of the extant browsers (Fig. 4; Table 3).

In Pié Lombard, *E. caballus* and *B. primigenius* exhibit a high number of scratches and a low number of pits, falling within the confidence ellipse of the extant grazers (Fig. 4; Table 3). *Cervus elaphus* is characterized by moderate values for both pits and scratches, along with the scarce presence of gouges and large pits, indicating a mixed-feeding diet. *Capreolus capreolus*, *R. rupicapra* and *C. ibex* display few scratches and pits, as well as a fine scratch texture, suggesting a soft browsing diet

**Table 1**

Representation of the species from Teixoneres Cave Units IIIa and IIIb and Pié Lombard in term of NISP (number of identified specimens), MNI (minimum number of individuals) and MAM (maximum of available meat, in kg).

| Site/species          | Teixoneres Cave - IIIa |           |           | Teixoneres Cave - IIIb |            |           | Pié Lombard    |             |           |                |
|-----------------------|------------------------|-----------|-----------|------------------------|------------|-----------|----------------|-------------|-----------|----------------|
|                       |                        | NISP      | MNI       | MAM                    | NISP       | MNI       | MAM            | NISP        | MNI       | MAM            |
| <i>B. primigenius</i> |                        | 11        | 3         | 954                    | 34         | 7         | 2731.76        | 12          | 2         | 317.86         |
|                       | %                      | 12.94     | 10.71     | 28.37                  | 6.79       | 10.29     | 50.72          | 1.13        | 3.78      | 8              |
| <i>Capra sp.</i>      |                        | 2         | 1         | 35                     | 34         | 4         | 159.61         | 649         | 26        | 1235.26        |
|                       | %                      | 2.35      | 3.57      | 1                      | 6.79       | 5.89      | 2.96           | 60.94       | 49        | 31.16          |
| <i>Rupicapra sp.</i>  |                        | 2         | 1         | 34.45                  | 0          | 0         | 0              | 49          | 6         | 148.36         |
|                       | %                      | 2.35      | 3.57      | 1                      | 0          | 0         | 0              | 4.6         | 11.32     | 3.74           |
| <i>C. elaphus</i>     |                        | 30        | 8         | 826                    | 280        | 36        | 1486.86        | 346         | 15        | 2088.42        |
|                       | %                      | 35.29     | 28.57     | 24.56                  | 55.89      | 52.94     | 27.6           | 32.49       | 28.3      | 52.69          |
| <i>C. capreolus</i>   |                        | 2         | 1         | 20.26                  | 61         | 8         | 86.3           | 5           | 2         | 25.16          |
|                       | %                      | 2.35      | 3.57      | 0.6                    | 12.17      | 11.76     | 1.6            | 0.47        | 3.78      | 0.63           |
| <i>E. caballus</i>    |                        | 36        | 11        | 1238.4                 | 73         | 9         | 558.34         | 4           | 2         | 148.62         |
|                       | %                      | 42.35     | 39.28     | 36.83                  | 14.57      | 13.23     | 10.37          | 0.37        | 2.78      | 3.75           |
| <i>E. hydruntinus</i> |                        | 2         | 3         | 254.26                 | 19         | 4         | 362.58         | 0           | 0         | 0              |
|                       | %                      | 2.35      | 10.71     | 7.56                   | 3.79       | 5.89      | 6.73           | 0           | 0         | 0              |
| <b>Total</b>          |                        | <b>85</b> | <b>28</b> | <b>3362.5</b>          | <b>501</b> | <b>68</b> | <b>5385.46</b> | <b>1065</b> | <b>53</b> | <b>3963.67</b> |



**Fig. 2.** Comparison of the representation of the ungulates from Teixoneres Cave Units IIIa (A) and IIIb (B) and Pié Lombard (C) based on the percentage of the NISP (number of identified specimens), MNI (minimum number of individuals) and MAM (maximum of available meat, in kg).

**Table 2**

Minimum number of individuals per age group of the ungulates from Teixoneres Cave Units IIIa and IIIb and Pié Lombard. The total number of individuals within the juvenile age class is given and, among them, the number of individuals between 0 and 4 months that correspond to the “Newborn” age group. The mass of available meat (in kg) per species for one carcass for the age group ‘newborn’ and ‘grown’ is also given.

| Site                   | Species               | Juvenile |            | adult | senile | Meat available per carcass (kg) |         |
|------------------------|-----------------------|----------|------------|-------|--------|---------------------------------|---------|
|                        |                       | Total    | 0–4 months |       |        | ‘Newborn’                       | ‘Grown’ |
| Teixoneres Cave - IIIa | <i>B. primigenius</i> | 1        | 1          | 2     |        | 27.16                           | 463.42  |
|                        | <i>C. pyrenaica</i>   |          |            | 1     |        | 5                               | 35.09   |
|                        | <i>C. elaphus</i>     | 4        | 3          | 4     |        | 10.70                           | 158.78  |
|                        | <i>C. capreolus</i>   |          |            | 1     |        |                                 | 20.26   |
|                        | <i>E. caballus</i>    | 4        | 2          | 5     | 2      | 9.45                            | 135.50  |
|                        | <i>E. hydruntinus</i> | 1        |            | 2     |        | 6.71                            | 84.76   |
|                        | <i>R. pyrenaica</i>   |          |            | 1     |        |                                 | 34.45   |
|                        | <i>R. rupicapra</i>   |          |            | 3     | 1      | 26.48                           | 450.88  |
| Teixoneres Cave - IIIb | <i>B. primigenius</i> | 3        | 1          | 1     |        | 26.48                           | 450.88  |
|                        | <i>C. pyrenaica</i>   | 1        |            | 3     |        | 5.47                            | 39.90   |
|                        | <i>C. elaphus</i>     | 26       | 24         | 9     | 1      | 7.96                            | 107.98  |
|                        | <i>C. capreolus</i>   | 3        | 2          | 5     |        | 3                               | 16.06   |
|                        | <i>E. caballus</i>    | 5        | 5          | 4     |        | 9.06                            | 128.26  |
|                        | <i>E. hydruntinus</i> |          |            | 3     | 1      | 7.03                            | 90.64   |
|                        | <i>R. pyrenaica</i>   | 1        |            | 1     |        | 18.30                           | 299.55  |
| Pié Lombard            | <i>B. primigenius</i> | 1        |            | 1     |        | 18.30                           | 299.55  |
|                        | <i>C. ibex</i>        | 6        |            | 15    | 5      | 6.11                            | 47.51   |
|                        | <i>C. elaphus</i>     | 6        | 2          | 8     | 1      | 10.72                           | 159.00  |
|                        | <i>C. capreolus</i>   | 1        | 1          | 1     |        | 3.31                            | 21.84   |
|                        | <i>E. caballus</i>    | 1        | 1          | 1     |        | 9.64                            | 138.98  |
|                        | <i>R. rupicapra</i>   | 3        | 1          | 2     | 1      | 4.61                            | 29.67   |

focused on leaves (Semprebon et al., 2011).

## 5. Discussion

### 5.1. Habitats of the ungulates from Teixoneres Cave Units IIIa and IIIb and Pié Lombard

*Teixoneres IIIb* (~45–100 ka): studies on ungulate dental mesowear and micromammals suggest a substantial amount of forest cover (Fernández-García et al., 2022; López-García et al., 2012a; Uzunidis and Rivals, 2023). Dental mesowear also indicates the presence of dicot meadows with few patches of grasslands (Uzunidis and Rivals, 2023). According to pollen analysis from the cave, the forest cover is still substantial but less developed compare to Unit IIIa, with a percentage of arboreal pollen (AP) of 60% (Ochando et al., 2020a). Strong environmental variations occurred during the accumulation of Unit IIIb at Teixoneres Cave since it encompasses a wider period than Unit IIIa. For this timeframe, the regional forest cover appears to generally decrease from 60 ka to 48 ka, based on the decrease of the temperate forest pollen percentage from 59 to 6% documented by the deep-sea pollen record from the Gulf of Lion (Fourcade, 2022; Sánchez Goñi et al., 2020). At the moment of their death, *B. primigenius*, *C. elaphus*, *E. caballus*, and *E. hydruntinus* had a mixed-feeding diet (Fig. 4; Table 3). They fed on

both grass and ligneous plants, indicating the exploitation of an ecotone at the transition between forest and grassland or of a dicot meadow. The diet of *C. pyrenaica* and *C. capreolus* is focused on soft ligneous plants, suggesting their presence in forested areas.

*Teixoneres IIIa* (45,000– 44.210 cal BP): the general environmental context is characterized by the presence of both forested areas and grassland in the region of the site, as indicated by dental mesowear analysis (Uzunidis and Rivals, 2023). This description is further supported by studies on micromammals (Fernández-García et al., 2022; López-García et al., 2012a). Climatically, Unit IIIa experienced cooler and more humid conditions compared to Unit IIIb (Fernández-García et al., 2022; López-García et al., 2012a, 2012b). The pollen analysis of this unit, however, attests to a significant forest cover with more than 87% of arboreal pollen (AP) (Ochando et al., 2020a). Regional pollen data from the deep-sea sedimentary sequence MD99-2343 (40°29'N, 4°01'E, collected in the Gulf of Lion and partially fed by the terrestrial sediments transported by the Rhône and Ebro rivers) indicates that the pollen percentage of the temperate forest was 23% and the percentage of the grassland was 55 % at ca. 45.1 ka, contemporaneous with the formation of Unit IIIa. At 43.9 ka, the forest percentage was 7% and the grassland one was 66 % (Fourcade et al., 2024; Fourcade, 2022; Fourcade et al., 2024; Sánchez Goñi et al., 2020). These data indicate that forested and grassland areas co-existed at a regional scale. Overall, the

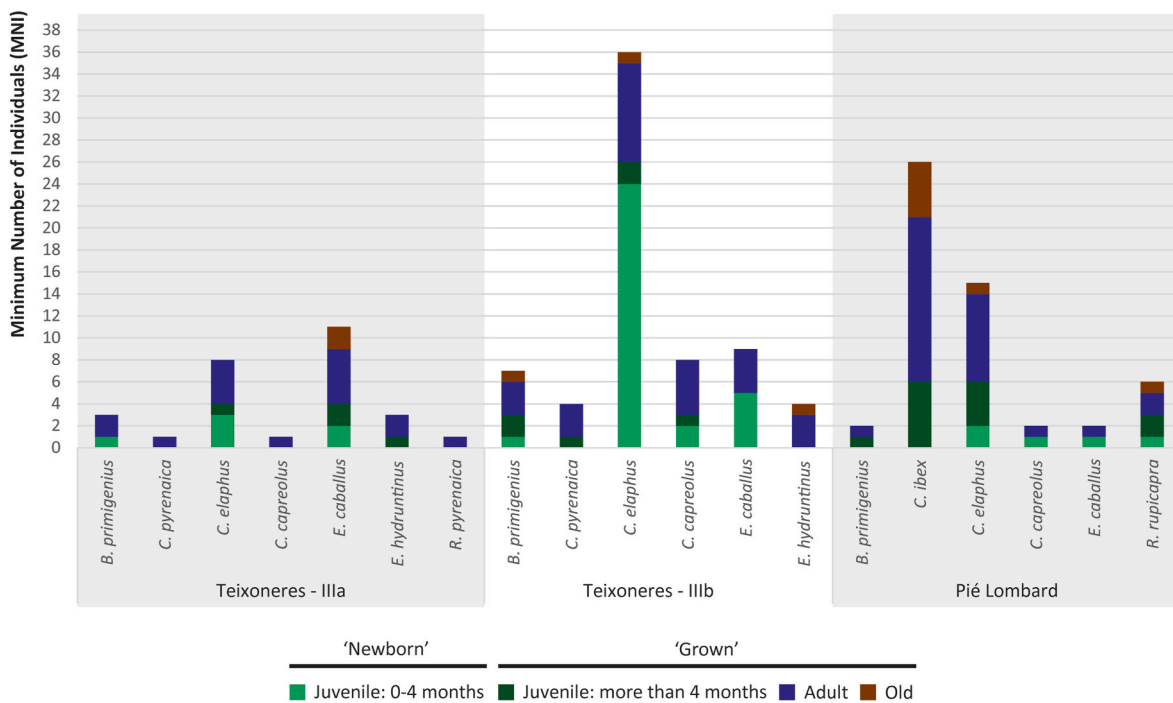


Fig. 3. Distribution of the age groups per species in Teixoneres Cave Units IIIa and IIIb and Pié Lombard in MNI.

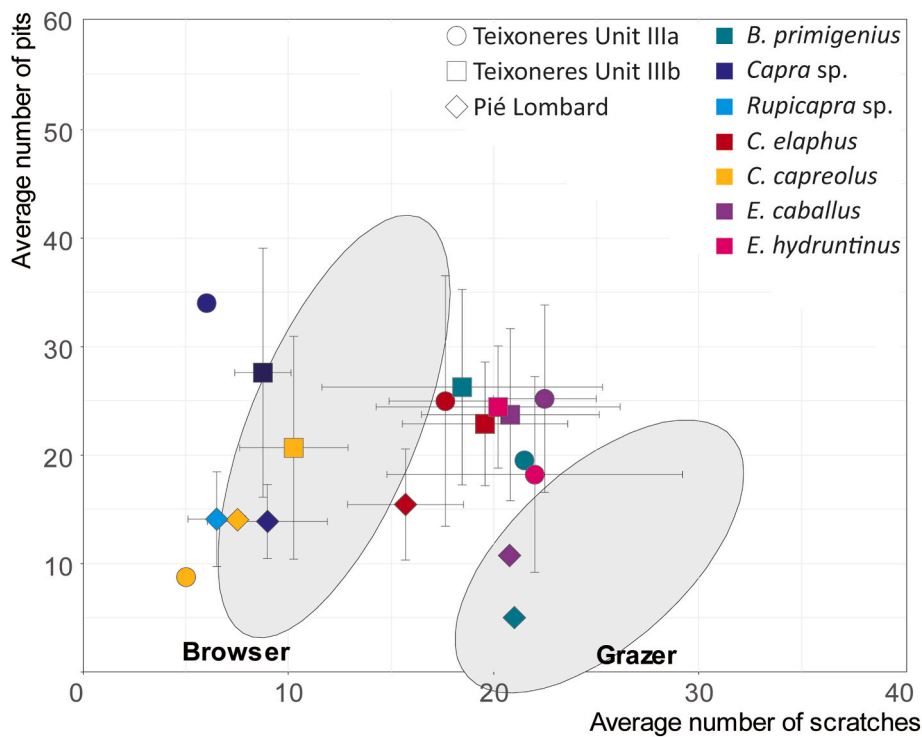


Fig. 4. Bivariate plot of the mean number of pits and scratches for the ungulates from Teixoneres Cave Units IIIa and IIIb and Pié Lombard. The error bars correspond to the standard deviation ( $\pm 1$  SD). The ellipses correspond to the Gaussian confidence ellipse ( $p = 0.95$ ) on the centroids of extant grazers and browsers based on the dataset published by (Solounias and Sempebon, 2002).

forest cover is regionally less important within the Unit IIIa time-span compared to Unit IIIb. At the moment of their death, *B. primigenius*, *C. elaphus*, *E. caballus*, and *E. hydruntinus* had a mixed-feeding diet. Bovids and equids displayed more grazing trends, while cervids showed more browsing tendencies (Fig. 4; Table 3). The inclusion of grass in their diet indicates that they occupied grasslands and open areas in the

surrounding habitats of Teixoneres Cave. In contrast, *C. capreolus* and *C. pyrenaica* had a diet focused on soft ligneous plants, suggesting their presence in the forested areas of the habitat.

*Pié Lombard, ensemble II (~70 ka)*: dental mesowear analysis suggests a forest-dominated environment with dicot meadows and very few grasslands (Uzunidis and Rivals, 2023). Studies based on herpetofauna,



**Table 3**

Summary of dental microwear data of the ungulates from Teixoneres Cave Units IIIa and IIIb and Pié Lombard. Abbreviations: n = Number of specimens; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width score; %HC = Percentage of specimens with hypercoarse scratches; %XS = Percentage of specimens with cross scratches; n = number of specimens; m = mean; sd = standard deviation.

| Site/species              | n  | Microwear |       |        |       |      |       |        |
|---------------------------|----|-----------|-------|--------|-------|------|-------|--------|
|                           |    | NP        | NS    | %LP    | %G    | SWS  | %HC   | %XS    |
| Teixoneres Cave Unit IIIa |    |           |       |        |       |      |       |        |
| <i>B. primigenius</i>     | 1  | 19.50     | 21.50 | 100.00 | 0.00  | 1.00 | 0.00  | 100.00 |
| <i>C. pyrenaica</i>       | 1  | 34.00     | 6.00  | 100.00 | 0.00  | 0.00 | 0.00  | 0.00   |
| <i>C. elaphus</i>         | m  | 24.96     | 17.64 | 78.57  | 0.00  | 0.71 | 7.14  | 64.28  |
|                           | sd | 11.54     | 2.75  |        |       |      |       |        |
| <i>C. capreolus</i>       | m  | 8.75      | 5.00  | 50.00  | 0.00  | 0.00 | 0.00  | 50.00  |
| <i>E. caballus</i>        | m  | 25.18     | 22.48 | 74.19  | 3.22  | 0.74 | 6.45  | 77.19  |
|                           | sd | 8.63      | 2.50  |        |       |      |       |        |
| <i>E. hydruntinus</i>     | m  | 18.20     | 22.00 | 0.00   | 0.00  | 0.60 | 0.00  | 60.00  |
|                           | sd | 9.02      | 7.20  |        |       |      |       |        |
| Teixoneres Cave Unit IIIb |    |           |       |        |       |      |       |        |
| <i>B. primigenius</i>     | m  | 26.25     | 18.46 | 25.00  | 16.67 | 1.00 | 16.67 | 50.00  |
|                           | sd | 9.00      | 6.84  |        |       |      |       |        |
| <i>C. pyrenaica</i>       | m  | 27.58     | 8.75  | 33.33  | 0.00  | 0.67 | 16.67 | 16.67  |
|                           | sd | 11.48     | 1.37  |        |       |      |       |        |
| <i>C. elaphus</i>         | m  | 22.87     | 19.57 | 74.19  | 17.74 | 0.91 | 14.51 | 78.68  |
|                           | sd | 5.70      | 4.00  |        |       |      |       |        |
| <i>C. capreolus</i>       | m  | 20.66     | 10.25 | 16.67  | 0.00  | 0.83 | 0.00  | 8.33   |
|                           | sd | 10.27     | 2.64  |        |       |      |       |        |
| <i>E. caballus</i>        | m  | 23.71     | 20.8  | 42.42  | 0.00  | 0.84 | 6.00  | 54.54  |
|                           | sd | 7.93      | 4.34  |        |       |      |       |        |
| <i>E. hydruntinus</i>     | m  | 24.43     | 20.21 | 42.86  | 0.00  | 0.86 | 14.28 | 57.14  |
|                           | sd | 5.62      | 5.94  |        |       |      |       |        |
| Pié Lombard               |    |           |       |        |       |      |       |        |
| <i>B. primigenius</i>     | 1  | 5.00      | 21.00 | 0.00   | 0.00  | 0.00 | 0.00  | 100.00 |
| <i>C. ibex</i>            | m  | 13.86     | 8.96  | 20.69  | 10.34 | 0.48 | 0.00  | 72.42  |
|                           | sd | 3.41      | 2.92  |        |       |      |       |        |
| <i>R. rupicapra</i>       | m  | 14.08     | 6.50  | 16.67  | 83.3  | 0.17 | 0.00  | 83.30  |
|                           | sd | 4.36      | 1.41  |        |       |      |       |        |
| <i>C. elaphus</i>         | m  | 15.43     | 15.70 | 16.67  | 23.33 | 0.84 | 3.33  | 70.00  |
|                           | sd | 5.12      | 2.82  |        |       |      |       |        |
| <i>C. capreolus</i>       | m  | 14.00     | 7.50  | 50.00  | 0.00  | 0.50 | 0.00  | 50.00  |
| <i>E. caballus</i>        | m  | 10.75     | 20.75 | 50.00  | 50.00 | 1.00 | 50.00 | 0.00   |

malacofauna, micromammals and avifauna indicate a correlation with a Mediterranean-temperate forested habitat (Texier et al., 2011). However, the pollen analysis of the site suggests an open landscape dominated by grassland and a cold and dry climate (Renault-Miskovsky and Texier, 1980; Texier et al., 2011). In contrast with the pollen analysis of Pié Lombard, the pollen analysis of the deep-sea core from the Gulf of Lion shows a high amount of forest cover in the adjacent northwestern Mediterranean landmasses during MIS 4 (Fourcade, 2022; Fourcade et al., 2024). At the moment of their death, *E. caballus* and *B. primigenius* had an abrasive diet oriented toward grass, indicating that they occupied the scarce open areas in the vicinity of the site (Fig. 4; Table 3). The diet of *C. elaphus* falls within the variability of the mixed-feeders with few scratches, allowing them to be characterized as browse-dominated mixed-feeders. The topography around the site implies an ecotone zone with influences both from the valleys and the mountainous areas. The habitat was mostly forested with some grassy areas or a meadow rich in dicot plants. *Capreolus capreolus*, *C. ibex*, and *R. rupicapra* were browsers that fed on ligneous plants in the forested areas.

## 5.2. Neanderthal environmental exploitation for prey acquisition in Teixoneres Cave Units IIIa-IIIb and Pié Lombard

*Teixoneres IIIb*: the most represented species is *C. elaphus* in term of NISP and MNI. The MAM is dominated by *B. primigenius* (Fig. 2). The most important species for Neanderthal subsistence strategy, therefore, occupied open or semi-open landscape areas (Fig. 5B, 5B', 5B'').

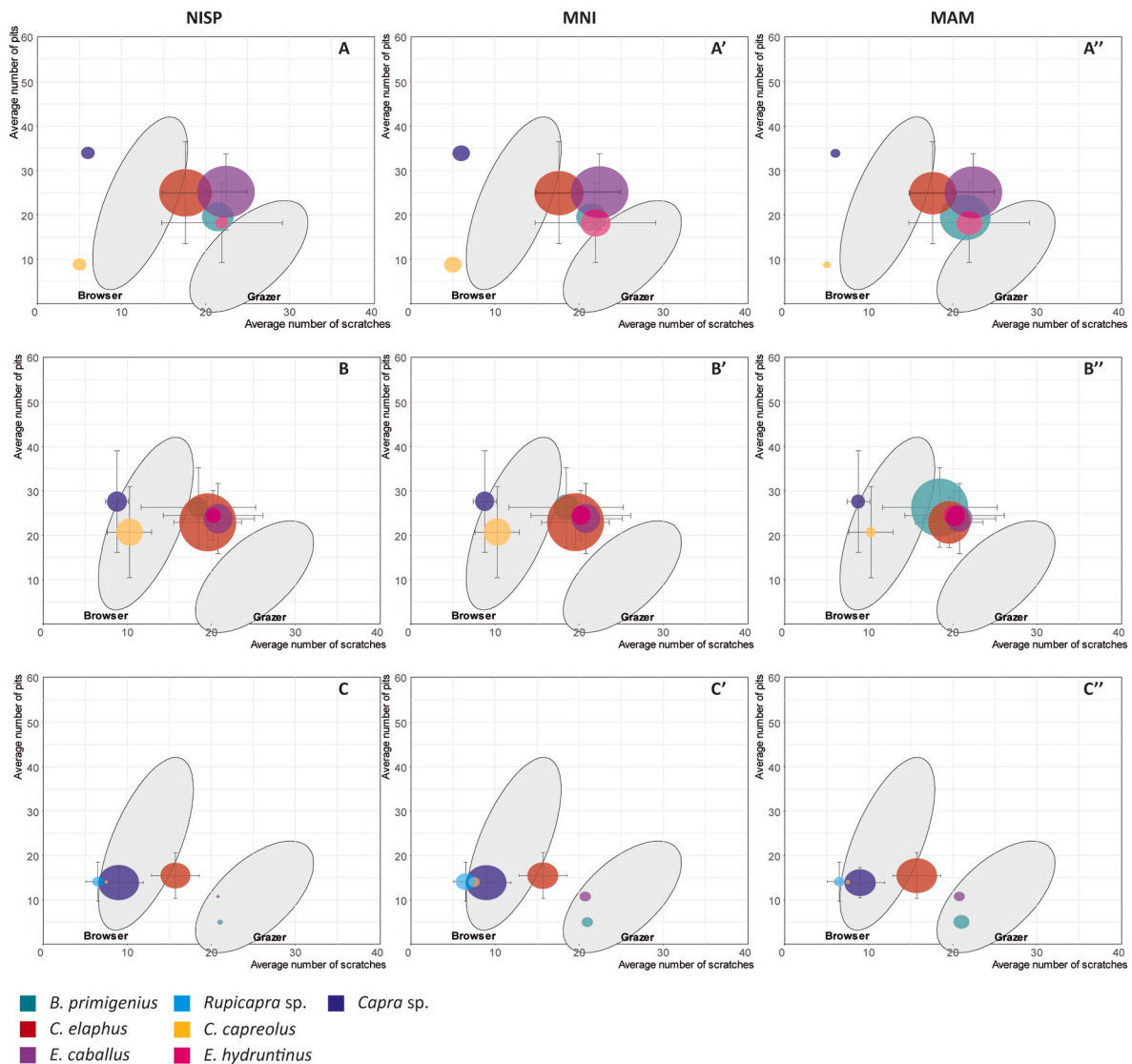
*Bos primigenius* are mainly adults and also few juvenile and senile individuals (Fig. 3). *Cervus elaphus* are mainly represented by juvenile individuals, most of them under 4-month-old. This pattern is known in

other Mousterian sites from the Iberian Peninsula, such as Abric Romaní level I (Marín et al., 2017), Cova Beneito levels XII-X (Tortosa et al., 2002), and Gabasa (Steele, 2004). This type of accumulation has been interpreted as a specialized hunt (Marín et al., 2017), where human groups took advantage of predictive doe behaviour with newborn red deer (Rendu, 2010). In the Unit IIIb, newborns seem to have been trapped or ambushed while does were generally spared since adults are not as well represented as the juveniles.

*Teixoneres IIIa*: *C. elaphus* and *E. caballus* were the most numerous prey species preyed upon by Neanderthals, both in terms of NISP and MNI. The MAM is distributed between *E. caballus*, *B. primigenius*, and *C. elaphus* (Fig. 2). Thus, in both cases, the species that most contributed to Neanderthal subsistence strategies inhabited open landscapes, probably grasslands (Fig. 5A, A', 5A'').

Mainly adults *B. primigenius* and *C. elaphus* are represented, with few juvenile and no senile individuals (Fig. 3). The *Bos primigenius* mortality pattern is quite similar to the one in Unit IIIb while the one for *C. elaphus* is very distinct. *Equus caballus* is represented mainly by adults although very few senile individuals are present. This age distribution is similar to that described for instance at level Ja of Abric Romaní (Marín et al., 2017). Since adult individuals are the main represented age class in a herbivore living population, hunter-gatherers will capture them more frequently (Bunn and Gurtov, 2014). The age distribution of the main ungulates from Unit IIIa is consistent with a non-selective hunt by Neanderthal groups based on age criteria.

*Pié Lombard, ensemble II*: *C. ibex* and *C. elaphus* are the most numerous ungulates in NISP and MNI, and they are also the two species that contributed the most to the MAM (Fig. 2). Here, the species that were most frequently preyed upon occupied forested and semi-open



**Fig. 5.** Bivariate plot of the mean number of pits and scratches of the ungulates from Teixoneres Cave Units IIIa (A) and IIIb (B) and Pié Lombard (C). The error bars correspond to the standard deviation ( $\pm 1$  SD). The ellipses correspond to the Gaussian confidence ellipse ( $p = 0.95$ ) on the centroids of extant grazers and browsers based on the dataset published by Solounias and Semperebon (2002). The size of the circle for each cohort represents its frequency in terms of number of identified specimens (NISP), minimum number of individuals (MNI) and of maximum of available meat (MAM) as they are indicated in Table 1.

landscapes (Fig. 5C, C', 5C''). The age distribution follows the same pattern as the main ungulates from Teixoneres Cave Unit IIIa, indicating an opportunistic hunting strategy.

### 5.3. Predation pattern and selective choice

In the two units of Teixoneres Cave, Neanderthals primarily exploited open environments to acquire ungulates. While other species lived in this habitat, only some of them are well represented at the site: *C. elaphus*, *B. primigenius* and *E. caballus* in Unit IIIa; and only the first two in Unit IIIb. *Equus hydruntinus* is consistently rare both in terms of frequency and meat available despite having also inhabited open landscapes. The scarcity of this species could be attributed to several reasons: (1) It might be indicative of human choices that may have avoided this species for cultural reasons; (2) *E. hydruntinus* may have not been abundant in Western Europe (Özkan et al., 2023; Uzunidis et al., 2024), and thus, the small amount of hunted individuals in Teixoneres Cave may reflect its weak representation in the environment; or (3) *E. hydruntinus* may have exhibited an erratic behaviour compared to gregarious animals, making it more difficult to hunt (Burke et al., 2003).

In Unit IIIb, *E. caballus* is not as well represented as in Unit IIIa despite having inhabited open landscape, as observed for *C. elaphus* and *B. primigenius*. This could reflect a reduction in the horse population in relation with the habitats that were more forested in Unit IIIb compared to Unit IIIa as suggested by dental mesowear and micromammals analyses (Fernández-García et al., 2022; López-García et al., 2012a; Uzunidis and Rivals, 2023). Horses, however, are very flexible and can adopt a mixed feeding and even a browsing diet to adapt to seasonal changes and various habitats (Rivals et al., 2009; Rivals and Lister, 2016; Strani and DeMiguel, 2023; Uzunidis, 2021). It could, therefore, reflect a selective choice by human groups. Otherwise, since most of the deposits of both units occurred in summer (Sánchez-Hernández et al., 2014, 2016, 2020; Uzunidis and Rivals, 2023), the scarcity of equids may reflect seasonal movements and their absence around the site during the occupation of Unit IIIb.

In Pié Lombard, Neanderthals exploited forested and semi-open biomes for ungulate acquisition within a partitioned environment of cliff, plateau and valley floor. They focused on *C. elaphus* from semi-open habitats and *C. ibex* from forested ones in term of NISP, MNI and MAM. While having very similar dietary characteristics to *C. ibex*,

*C. capreolus* and *R. rupicapra* were not as frequently preyed upon. This last species is often considered challenging to hunt and more commonly found in sites corresponding to occupations by anatomically modern humans (Freeman, 1973; Gamble, 1995; Straus, 1987). Recent studies, however, have shown that Neanderthal groups were able to hunt this species (Rodríguez-Gómez et al., 2022; Yravedra and Cobo-Sánchez, 2015). *Capreolus capreolus* is also regularly represented in Neanderthal sites (Gaudzinski-Windheuser and Roebroeks, 2011; Livraghi et al., 2022; Romandini et al., 2023; Terlato et al., 2021). Pié Lombard ungulate accumulation occurred mainly in autumn (Roussel, 2023; Roussel et al., 2021; Uzunidis and Rivals, 2023) which can lead to seasonally-biased accumulation. The scarcity of species can, therefore, reflect either species selection by Neanderthal groups or periodical absence and presence in the vicinity of the site due to seasonal movements.

In the open-area hunting grounds corresponding to the two Teixoneres Units, Neanderthal subsistence strategies relied on a few species. In this site, two to three taxa, including red deer, horse and aurochs, constitute the main basis of the meat intake. The presence of large mammal herbivores organized in herds tend to increase in open habitats (Evans, 1979; Geist and Walther, 1974; Gerard et al., 2002; Jarman, 1974; Lagory, 1986; Leuthold, 1970), impacting hunter-gatherer choice and prey selection. In open habitats, other Neanderthal groups have also specialized their hunting practices toward large ungulates, such as large bovine (*Bos/Bison*) or cervids (*Cervus/Rangifer*) (Berlioz et al., 2023; Gaudzinski-Windheuser and Roebroeks, 2011). While occupying Units IIIa and IIIb at the same season and targeting large ungulates within an open environment, Neanderthal groups did not develop similar strategies. In Unit IIIa, they focused on three species without targeting a specific age group when in Unit IIIb they focused mostly on one species (*B. primigenius*) and supplemented their meat intake by opportunistically preying on newborn red deer. At this stage, more information concerning occupation patterns and butchering activities is needed to suggest hypotheses explaining such differences in subsistence strategies.

In the forested hunting ground around Pié Lombard, Neanderthal predation toward ungulates was primarily focused on *C. elaphus* and *C. ibex*. Beside the forested environment not being suitable for large herds, the scarcity of *B. primigenius* and *E. caballus* could be related to the topographic situation of Pié Lombard. Its position on a cliff in a mountainous area may not be suitable for aurochs or horse herds either. The main preyed upon taxa, however, in terms of NISP/MNI were the rabbits (MNI = 225) and several bird species (MNI = 86) (Pelletier et al., 2019; Texier et al., 2011). Both bear anthropic marks, and a study on the rabbit remains revealed that they were targeted for both their skin and their meat (Pelletier et al., 2019). If rabbit contribution to the meat intake remains limited (7%), they were far more frequently eaten than the ungulates. The higher diversity of the species exploited in Pié Lombard is related to the forest cover, preventing access to large herds. In other forested landscape, the exploitation of other small game species (i.e. turtles, rabbits or beavers) is documented, such as in Taubach, Weimar Parktravertin (Gaudzinski-Windheuser and Roebroeks, 2011) or in Arbreda level G (Kehl et al., 2014; Lloveras et al., 2016).

Moreover, dietary behaviours of Neanderthal populations living in forested areas includes both meat as well as a high proportion of plant food (El Zaatari et al., 2011; Hlusko et al., 2013). The diversity of the species preyed upon, including large mammals, birds and rabbits, implies subsistence strategies relying on multiple resources. In mixed habitats, the proportion of plants in the Neanderthal diet is lower, and, finally, in open habitats, the Neanderthal diet appears more restricted to meat consumption (El Zaatari et al., 2011, 2013; Harvati et al., 2013; Lalueza-Fox and Pérez-Pérez, 1993; Williams et al., 2018, 2019). Food acquisition practices may have then been very oriented toward a narrow range of resources. The toolkits from Teixoneres and Pié Lombard exhibit typical features of the Middle Paleolithic, characterized by dominant discoid and Levallois reduction sequences. Both sites feature a combination of local and semi-local raw materials. Semi-local raw

materials commonly include finished tools with some retouching activities, primarily for tool maintenance. In contrast, local raw materials, especially in Teixoneres, show a higher proportion of cores and knapping activities. At Teixoneres, tools appear primarily dedicated to hunting or cutting activities, whereas in Pié Lombard, they were used for cutting and processing meat and likely plant materials. Across all three occupations, lithic tools suggest a consumption-based economy rather than one focused on lithic tool production (Porraz, 2005; Texier et al., 2011; Picin et al., 2020; Muñoz del Pozo et al., 2023). Despite the relatively similar habitats, prey, and seasons associated with similar lithic toolkits and knapping activities, acquisition strategies differ between Units IIIa and IIIb. Unit IIIa shows a more opportunistic approach, while Unit IIIb is more selective. Despite the relatively similar habitat occupied by quite similar prey in the same season associated with similar lithic toolkit and knapping activities, acquisition strategies differ between Units IIIa and IIIb, with the first being more opportunistic and the latter more selective. Thus, Neanderthal subsistence strategies are greatly diverse although only partially related to the biome they lived in. While the paleoethology of the prey related to the environmental conditions, notably the organization in herds, other factors, such as procurement goals or intrinsic factors (cultural), are involved in the prey acquisition patterns of Neanderthal groups.

## 6. Conclusions

In Teixoneres Cave Units IIIa and IIIb and Pié Lombard, Neanderthals exploited distinct hunting grounds. Here, prey acquisition mostly occurred in an open landscape despite the presence of forested areas around the cave, while it occurred in a more forested landscape around Pié Lombard. Distinct procurement strategies can be identified according to the foraged biome. In open areas, Neanderthal groups focused on two or three large ungulate species, while in closer habitats, they exploited chiefly two species of ungulates along with several species of small game (rabbit and birds), surely reflecting their abundance in the environment. The lowest specific diversity in sites with open-area hunting grounds can be the consequence of a modification in ungulate ethology: gregarious species occurring commonly in large herds, while their herds are reduced in closed landscapes. While focusing on large gregarious ungulates, Neanderthal groups developed distinct strategies in the two units of Teixoneres Cave. In Unit IIIa, they did not make any selection regarding the age of prey. In Unit IIIb, their potential main meat intakes are based on aurochs of all age groups, but they also opportunistically and clearly preyed upon newborn red deer. Since the two units were mainly occupied at the same season (summer) Neanderthal groups had access in both case to the same age groups. Therefore, the differences in their prey acquisition patterns may reflect Neanderthal choices rather than their environmental constraints.

## Data availability

Data are available to the link <https://dataverse.csuc.cat/dataset.xhtml?persistentId=doi:10.34810/data734>.

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## Authors' contributions

AU collected the data; designed and conducted the research; wrote the main manuscript; and prepared all the figures, tables, and supplementary information. FR, RB, ARu were responsible of the excavation in Teixoneres caves, and PJT of the ones in Pié Lombard. TF, MSG and JO provided data about terrestrial and deep-core pollen. AR and JPB provided zooarchaeological information for Pié Lombard fauna. All the authors have discussed the integration of zooarchaeological, paleoecological, and palynological data throughout the study. All authors reviewed, commented and participated in improving the manuscript.

## CRediT authorship contribution statement

**Antigone Uzunidis:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ruth Blasco:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Jean-Philip Brugal:** Writing – review & editing, Validation, Project administration. **Tiffanie Fourcade:** Writing – review & editing, Investigation, Formal analysis. **Juan Ochando:** Writing – review & editing, Formal analysis. **Jordi Rosell:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Audrey Roussel:** Writing – review & editing, Formal analysis. **Anna Rufà:** Writing – review & editing, Project administration. **Maria Fernanda Sánchez Goñi:** Writing – review & editing, Supervision, Formal analysis. **Pierre-Jean Texier:** Writing – review & editing, Project administration. **Florent Rivals:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

## 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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