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Where and when? Combining dental wear and death seasons to improve paleoenvironmental reconstruction through ungulate diets

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ABSTRACT

Dental meso- and microwear are proxies that allow the diet to be reconstructed. Applied to herbivores, these proxies provide information on vegetation structure and composition. Several studies on fossil populations have proposed environmental reconstructions based on these methods. These studies often focus on a few selected taxa and rarely consider the total variability of ungulate diets at sites in contexts where the seasonality of occupations is often not estimated. The variability of the ungulate diet associated with a better knowledge of the moment of their death can greatly improve the quality and resolution of the environmental interpretation at the scale past hominins experienced. In this paper, we propose a new approach to dental wear to reconstruct environments. We recommend including all available ungulates according to their abundance in the faunal spectrum to consider as many habitats as possible. The combination of dental meso- and microwear allows us to address two scales of time and space–the regional scale over several years and the local scale over one season, respectively. Applied to Teixoneres Cave (Units IIIa and IIIb, Spain) and Pié Lombard (Ensemble II, France), the results confirm previous microfauna analysis and make it possible to characterize the intensity of seasonal turnover.

1. Introduction

Dental wear analysis, a proxy for diet (and paleodiets), makes it possible to connect the structure of vegetation and the composition of the environment with animal behaviour. Dental wear methods can be used to measure the contribution of dicots and monocots in the diet of herbivores, indicating their presence in the environment (Fortelius & Solounias, 2000; Mainland, 2000, 1998; Semprebon et al., 2004; Solounias & Semprebon, 2002). Moreover, it is one of the few proxies that benefit from strict contemporaneity between several agents of an ecosystem, from vegetation to the predator–accumulator through the herbivore. Thus, environmental reconstruction based on herbivores provide also, an accurate context for their accumulator, carnivores or hominins. In fossil assemblages, paleoenvironmental reconstructions can be based on the study of pollen or microfauna amongst others (Carrión et al., 2022; López-García et al., 2021a, 2021b; Ochando et al., 2022). These approaches allow the accurate reconstruction of environmental and climatic parameters, but the accumulation is generally not due to hominin behaviour. Interactions between herbivores and their predators, are often the origin of the accumulation of herbivores (mainly ungulates) in the Pleistocene fossil record. Thus, environmental reconstructions from ungulate dental wear directly link the predators to their ecosystems. Therefore, dental wear analyses are very regularly used to propose environmental reconstructions based on the food preferences and adaptations of different species (Merceron & Madelaine, 2006; Rivals et al., 2017, 2023; Strani, 2021).

Many factors play a role in defining the diet of a taxon. These include intra- and inter-specific competition (Arsenault & Owen-Smith, 2002; de Boer & Prins, 1990; Loison et al., 1999; Rivals et al., 2017) and the preferences and adaptations of some taxa. For example, researchers have described browsers as “obligatory non-grazers” that avoid grasses to a much higher degree than grazers avoid browsing, since the morphology of their teeth would have prevented them at one stage from following a too-abrasive diet (Clauss et al., 2003). Dental wear studies are often limited to the analysis of the diet of one or a few taxa (Berlioz et al., 2023; Catz et al., 2020). Given the variability of factors involved in defining a cohort’s diet, this can be misleading (Ungar et al., 2020).

In addition, tooth wear corresponds to two scales of analysis: dental meso- and dental microwear. While dental mesowear gives an indication of the diet of ungulates over several years (Ackermans et al., 2020;

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Fortelius & Solounias, 2000; Uzunidis et al., 2023), dental microwear provides information on a much shorter period of life that can be subject to significant seasonal variation (Rivals et al., 2009; Winkler et al., 2020). Thus, combining dental wear and the estimation of the season of death of individuals could improve the scope of these analyses, as some studies have pointed out (Livraghi et al., 2022; Sánchez-Hernández et al., 2014, 2016, Sánchez-Hernández et al., 2020a).

Herbivores taxa that tend to be better represented in South European Pleistocene archaeo-/palaeontological sites are often similar: red deer, a large bovid, often *Bos primigenius* and horses (Brugal et al., 2022). They can all have very flexible behaviours and adopt distinct diet corresponding to their ability to occupy various environment (Rivals & Lister, 2016; Sokolowski et al., 2023; Strani & DeMiguel, 2023; Ungar et al., 2020; Uzunidis, 2021; Uzunidis et al., 2022). For these ecotone taxa, in Southern Europe, their relative abundance tend to be more impacted by environmental changes than their presence/absence (Álvarez-Lao et al., 2017; Álvarez-Lao & Méndez, 2016; Brugal et al., 2022). In this present study, we hypothesized that the study of the variability of the diet of the ungulates must be weighted by their abundance to be more indicative of the environmental features. We propose a new approach to dental meso- and microwear data that improves the accuracy of environmental reconstructions. We take into account all the ungulates available according to their abundance at a site and compare dental wear with seasonality estimates. The relationship between the relative abundance of known grazing or browsing ungulates and the vegetation structure may not be direct, at least not in the current South African environment (Negash & Barr, 2023). Thus, we control and compare our results using other palaeoenvironmental proxies that are available for each assemblage. We also answer methodological questions raised by the combination of the two proxies (meso- and micro), each of which have different resolutions within the life of the animal.

Two archaeological sites were selected for the present study. Pié Lombard and Teixoneres have a high diversity of taxa represented by large numbers of individuals. In addition, they have been the subject of environmental reconstruction studies using different proxies such as pollen analysis or microfauna, which can be compared with our findings.

2. Archaeological sites

2.1. *The Pié Lombard rock shelter*

Pié Lombard (Tourrettes-sur-Loup, Alpes-Maritimes, France) is a small rock shelter that was discovered in 1962 (Lumley, 1969) (**Supplementary data 1**). The site is located at the foot of a rather steep cliff at a relatively low altitude (250 m above sea level). It is surrounded by the Mediterranean Sea 12 km to the south, the Loup River to the east and the north, and very close mountainous areas rising to more than 1000 m (Texier et al., 2011). A three-metre-thick archaeological sequence was excavated from 1971 to 1996 (with interruptions) under the direction of P.-J. Texier (Texier, 1974; Texier et al., 2011). It 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 20,167 cal BP or 22,581–22,073 cal BP (Tomasso, 2014). It was attributed to the Epipaleolithic culture and yielded very few faunal remains (for more details, see Pelletier et al., 2019).
- Ensemble II is a Mousterian complex dated to a transitional phase between MIS 5 and 4 based on a thermoluminescence (TL) date of 70 ± 8 kyr BP (Valladas et al., 1987). Stalagmites supporting Mousterian sediments yielded two electron spin resonance (ESR) dates of 147 ± 10 kyr and 130 ± 20 kyr BP (Yokoyama et al., 1983). The present study focuses on this ensemble.

Carnivores were recovered along with the ungulates (Table 1): *Ursus arctos*, *Felis silvestris*, *Lynx* sp., *Panthera pardus*, *Canis lupus*, and some remains from *Vulpes vulpes* and *Cuon* sp.. Smaller species are also very well represented, including 225 rabbits (*Oryctolagus cuniculus*) and various bird species represented by at least 86 individuals. Zooarchaeological studies suggest that the accumulation was due primarily to human activity, with ungulates and small game, in particular, being exploited for their meat, skin, and feathers (Pelletier et al., 2019; Romero et al., 2017). Also, two Neanderthal deciduous incisors were found (Lumley (de), 1976; Texier et al., 2011). The Mousterian lithic industry produced local and semi-local finished tools, which supports the view that the site was a seasonal hunting camp (Porraz, 2005, 2009; Roussel et al., 2021; Texier et al., 2011).

The description of the paleoenvironment of the Pié Lombard Mousterian ensemble is based on palynological and microfauna proxies. The fauna-based proxies suggest a wooded and diverse environment under a Mediterranean climate (Texier et al., 2011). The pollen study, however, indicates a dry and cooler climate compared with the current one and an open environment dominated largely by grassland (Renault-Miskovsky & Texier, 1980; Texier et al., 2011). All the environmental proxies for Pié Lombard depict diverse biotopes comprising a diversity of landforms (riversides, cliffs, mountains, and plateaux).

2.2. *Teixoneres cave*

Teixoneres Cave (Moià, Barcelona, Spain) is part of the Toll caves karst complex (**Supplementary data 2**). It was discovered in the 1950s by a local speleological group. Different research teams carried out several excavation seasons up until the 1990s, and since 2003, the cave has been excavated by a team from the *Institut Català de Paleoecologia Humana i Evolució Social* (IPHES-CERCA; Rosell et al., 2008, Rosell et al., 2010a, 2010b, 2014).

A six-metre-deep sedimentary sequence with eight stratigraphic units separated into sub-units has been described in the literature (Rosell et al., 2008, 2010b,; Zilio et al., 2021). They have been dated by U-series: Unit I has an age of ca. 14–16 ka and unit IV, ca. 100.3 ± 6.1 ka (Tissoux et al., 2006). Unit II has been radiocarbon dated to 44,210 to 33,060 cal BP (Talamo et al., 2016) and separated into two subunits: IIa

Table 1
Summary of the total number of herbivores from Teixoneres IIIa (Tx_IIIa), Teixoneres IIIb (Tx_IIIb), and PL (Pié Lombard): the minimum number of individuals (MNI), the number of individuals that were used to build the seasonality estimation, and the number of teeth that were used for dental meso- and microwear per taxa.

	Minimum number of individuals			Number of individuals(seasonality estimation)			Number of teeth(dental mesowear)			Number of teeth(dental microwear)		
	Tx_IIIa	Tx_IIIb	PL	Tx_IIIa	Tx_IIIb	PL*	Tx_IIIa	Tx_IIIb	PL	Tx_IIIa	Tx_IIIb	PL
Bos primigenius	3	7	1	1	2			11	1	1	12	1
Capra sp.	1	4	23		4	17	2	10	141	1	6	30
Cervus elaphus	8	36	15	8	30	13	11	81	60	21	55	30
Capreolus capreolus	1	8	2		4		3	36	3	2	12	2
Equus caballus	11	9	2	8	9		20	10	1	41	23	2
Equus hydruntinus	3	4		1	4		5	5		6	14	
Rupicapra sp.	1		3						19			6

* The seasonality estimation of Pié Lombard ungulate was published by (Roussel et al., 2021).

and IIb. Unit III was radiocarbon dated from > 51,000 14C BP to 44,210 cal BP (Talamo et al., 2016) and was divided into two subunits on which the present study is focused: IIIa and IIIb. Unit IIIa is dated between 44,210 and 45,000 cal BP, unit IIIb starts at 45,000 and its base has a maximum age of 100,000 years BP (Ochando et al., 2020; Talamo et al., 2016; Tissoux et al., 2006).

Carnivores were recovered along with the ungulates (Table 1): *Ursus spelaeus*, *Crocuta crocuta*, *Canis lupus*, *Vulpes vulpes*, *Lynx spelaea*, and *Meles meles*. These occupied the cave in alternation with humans (Rosell et al., 2017; Rufà et al., 2014, 2016; Sánchez-Hernández et al., 2014, 2016). While carnivores occupied the inner parts of the cave, the human favoured the porch (Rosell et al., 2010a; Zilio et al., 2021). The remains of small prey remains (leporid and birds) were also found. Large herbivore mammals at the site display traces that can be attributed to Neanderthal and carnivore predation while leporid and bird remains are mainly due to predator activities (Rosell et al., 2017; Rufà et al., 2016, 2014). Finally, three deciduous human teeth and the molar of an adult were found in Unit IIIb. The Mousterian lithic industry used raw materials of local or semi-local origin and produced hunting and cutting tools for the early phases of butchery (Picin et al., 2020).

According to pollen analysis, the environment around Units IIIa and IIIb was highly forested, especially the former (arboreal pollen, IIIa = 87 %; IIIb = 60 %; Ochando et al., 2020). Micromammals and dental wear studies have shown an opposing tendency for Unit IIIb, where there was a wider forest cover than to Unit IIIa (Fernández-García et al., 2022; López-García et al., 2012a; Sánchez-Hernández et al., 2020a, Sánchez-Hernández et al., 2020b). The climate was cooler and wetter in Unit IIIa than in Unit IIIb, and in both cases, cooler and wetter compare with the current-day climate (Fernández-García et al., 2022; López-García et al., 2012a, López-García et al., 2012b).

3. Material and methods

Several methods were used to describe the dietary variability and the death period of the herbivores for both sites. Since the relative abundance of a species in a biome can by itself be indicative of the environmental context (Álvarez-Lao et al., 2017), it was important that the sampling for each method coincide with their abundance in each case. The sample size selected for dental wear analyses reflected the proportion of each species in the assemblage (based on the MNI), taking into account the taphonomic alteration and the specificities of each method (Table 1).

In both sites, the herbivores' teeth were mainly accumulated by human activities. Neanderthals are the main responsible for the accumulation at Pié Lombard (Romero et al., 2017; Roussel et al., 2021) and the Teixoneres material studied in this paper come from the outside part of the cave as it is identified by Zilio et al., 2021. Thus, human activities and the herbivores present are strictly contemporary but we cannot expect the depiction of the environment through human preys to be exhaustive. The better expressed ecological niches will be the ones favoured by Neanderthals for their prey acquisition.

Overall dental wear distribution can depend on (1) the ecological flexibility of the taxa or (2) their relative representation. We first compared the variability of the dental wear distribution of the most abundant taxa with the variability of the global distribution to establish the most effective bias and consider as many biomes as possible. Dental meso- and microwear have very different levels of resolution within the life of an individual, ranging from a few days to a few years before death. This difference also implies distinct scales of analysis. We therefore estimated the death period of the ungulates, since dental microwear is a very sensitive proxy that can be strongly influenced by seasonal changes.

3.1. Dental mesowear

Dental mesowear analysis is used to describe the wear patterns of ungulate teeth and to infer the abrasiveness of the diet of an individual (Fortelius & Solounias, 2000; Rivals et al., 2007). Very sharp buccal cusps correspond to low abrasion diets, while rounded and blunted cusps are found in high abrasion diets, since the sharpness and morphology of cusp apices correlate with relative attritive and abrasive dental wear. While exogenous grit can affect mesowear signatures (Kaiser et al., 2009), a high level of abrasion is more likely due to the consumption of siliceous grass than the ingestion of soil or dust (Kaiser et al., 2013; Saarinen & Lister, 2016). The individual life span covered by dental mesowear is still unclear. Recent research has suggested that it may correspond to a lifetime signal (Ackermans et al., 2020) but is more likely pluri-annual (Louys et al., 2012; Rivals et al., 2007; Ulbricht et al., 2015; Uzunidis et al., 2023).

In the present study, we examined the paracone of the second upper molar of well-preserved teeth, as recommended by Fortelius and Solounias (2000). Broken, unworn, and extremely worn ones were excluded (following Fortelius & Solounias, 2000; Rivals et al., 2007). The morphology of the cusps was analysed using the method proposed by Mihlbachler et al. (2011) and modified by Rivals et al. (2013). The method categorizes dental wear into seven groups (0 = high and sharp cusp; 1 = high, narrow angle and slightly rounded cusp; 2 = high, large angle and rounded cusp; 3 = medium high and very rounded cusp; 4 = low and round cusp; 5 = almost flat cups; 6 = blunt with no relief). The average value of mesowear data from a single sample is represented by a mesowear score (MWS; Mihlbachler et al., 2011), which has been applied to various Pleistocene assemblages (e.g., Rivals et al., 2017; Uzunidis, 2020). Browsers correspond to the categories 0 to 2, mixed-feeders: 1 to 2.5 and grazers cover from 2 to the category 6. We studied the MWS for each species and analysed the overall distribution including all the ungulates (i.e., the global mesowear distribution).

3.2. Dental microwear

The dental microwear analysis followed the protocol established by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned using acetone and 96 % alcohol. The surface was then moulded with high-resolution silicone (vinylpolysiloxane), and casts were made using clear epoxy resin. The transparent casts were observed with a stereomicroscope at a magnification of x35. Observations were restricted to a standard surface of 0.16 mm2 (using an ocular reticule), preferably on the upper tooth paracone and the lower tooth protoconid of each of the teeth, with the exclusion of the second and third premolar (Xafis et al., 2017). Microwear corresponds to a short time scale, that is, the last days or months of an individual's life (Hoffman et al., 2015; Merceron et al., 2016; Teaford & Oyen, 1989; Winkler et al., 2020).

Specimens with badly preserved enamel or significant taphonomic defects were excluded from the analysis (King et al., 1999). The morphology of each microfeature was systematically checked to quantify the ones relating to diet (Micó et al., 2023; Uzunidis et al., 2021). Several microwear features are usually observed on the enamel surface (Semprebon et al., 2004), but we only present the results for the number of scratches because these relate to seasonal changes in diet (Rivals et al., 2015, 2009; Solounias & Semprebon, 2002). Scratches are elongated microfeatures with parallel sides. Statistically, individuals with more than 17 scratches (in the 0.16 mm^2 reticule) are considered to have an abrasive diet (Rivals & Semprebon, 2010; Semprebon & Rivals, 2007; Solounias & Semprebon, 2002). As with mesowear, we examined the global microwear distribution.

3.3. Season of death

Since dental microwear signals are very sensitive to seasonal shifts in diet, we estimated the death period of the ungulates from Teixoneres Units IIIa and IIIb and Pié Lombard using several methods. Both the duration of the accumulation and its moment were investigated in order to detect any seasonal biases in the diet of the ungulates.

The first method, which was introduced by Rivals et al. (2015), evaluates the variability of scratches obtained through dental microwear studies that measured using the standard deviation (SD) and the coefficient of variation (CV) of their density in a population. The SD and the CV were plotted on a heat map divided into three areas corresponding to three types of accumulation event(s): [A] season-long or shorter time windows; [B] events longer than a season; and [C] separate events that occurred over different non-contiguous seasons. Black lines separate each area and the colour scale corresponds to the different error probabilities. Only the cohort that are displayed in white aeras are interpretable since we consider only an error of 0.05 to be statistically acceptable. This method will, thus, inform about the length of the accumulation event per species.

The second method we employed was an analysis of the teeth eruption. This work was already done and published for Pié Lombard by Roussel et al., 2021, and was implemented in this paper. For Teixoneres, earlier studies already have estimated the mortality patterns of the ungulates (Sánchez-Hernández et al., 2020a, 2016). We have completed this work by including taxa and material from Unit IIIb that were not excavated at the time of these studies. Based on present-day ecology (Couturier, 1962; Roussel et al., 2021; Thimonier & Sempere, 1989) and in accordance with Roussel et al., 2021 and Sánchez-Hernández et al., 2020a, Sánchez-Hernández et al., 2016 we have considered the end of May to the beginning of June to be the birth period of the studied taxa. Red deer age was established on the fourth inferior decidual (d4) and the first lower molar (m1) using Steele's (2004) equation. Equid age was established using Fernandez's (2009) equations for the teeth, which are associated with a certainty rate above 85 %. For both taxa, unworn or very superficially worn decidual teeth were included in the 0–4-month group corresponding to summer, which allowed for the consideration of both adults and juveniles. The methods available for the other taxa relied on the wear pattern of decidual teeth and the eruption patterns of definitive ones meant that only individuals below 3 years of age could be taken into account. Also, only complete or sub-complete mandible and maxilla were used to analyse the relative eruption patterns of the teeth. Several works studies were used to describe the eruption and wear patterns for *Bos primigenius* (Brugal & David, 1993), *Capra* sp. (Pailhaugue, 2003; Pérez Ripoll, 1988), *Rupicapra* sp. (Pailhaugue, 1998), and *Capreolus capreolus* (Paulus, 1973). The death moment estimation aims at establishing which seasons are represented for each species in the assemblages.

3.4. Statistical analysis

Several statistical analyses comparing the mean and distribution of dental wear features were carried out using R Version 4.1.2 (R Core Team, 2014) and RStudio (RStudio Team, 2018). A 0.05 probability ($p < 0.05$) was considered significant. We used the Fisher (1935) test to examine the MWS distributions because it is better adapted to small samples with few categories—seven in the present case—than the chi-squared test (for example). Because the Fisher test tends to be conservative (Crans & Shuster, 2008), we combine it with a Monte Carlo simulation (10,000 times). To compare the distribution of the scratches at the dental microwear scale, we employed the Kolmogorov-Smirnov test, which compares the cumulative distribution to two datasets. While it is very sensitive to any changes in the distribution of quantitative data, it does not handle ties very well. In the present case, the quantity of scratches was not quantitative since we expected only integer numbers, so we used a modified version of the test with R package Matching; this provided coverage when the distributions were not continuous (Sekhon, 2011).

4. Results

4.1. Dental mesowear variability of the herbivores from Teixoneres and Pié Lombard

The dental mesowear means of ungulates from Teixoneres Unit IIIa display values that fall in the range of all dietary categories (Table 2; Fig. 1) with the cervids (*C. elaphus* and *C. capreolus*) characterized by low values (MWS = 0.87 and 0), *E. hydruntinus* by a medium one (MWS = 2.67), and *E. caballus* by the highest (MWS = 5.14). The mean of the MWS of all the ungulates for Unit IIIa is relatively high (MWS = 3.17) corresponding to a moderately abrasive diet. In Teixoneres Unit IIIb, the cervids display a more abrasive diet compared with Unit IIIa, with comparable values between them (*C. elaphus* = 1.6; *C. capreolus* = 1.59) and *C. pyrenaica* (MWS = 1.55). The mesowear value of *E. hydruntinus* in Unit IIIb is very similar to one in Unit IIIa (MWS = 2.5). *B. primigenius* and *E. caballus* have the highest values (MWS = 3.58 and 4.75, respectively). The general tendency shows that the diet is generally more focused on soft plants, and the global MWS is lower (1.42) than Unit IIIa. In Pié Lombard, most of the ungulates display a similar moderately abrasive diet, with *B. primigenius* (MWS = 2), *C. ibex* (MWS = 2.17), and *C. elaphus* (MWS = 2.27) being very alike. *R. rupicapra* (MWS = 1.47) display slightly weaker values and *E. caballus* (MWS = 3), slightly higher ones. The *C. capreolus* (MWS = 0) is very low (MWS = 0). The general tendency here is similar to Unit IIIb because the MWS is quite low (1.17).

We compared the distribution of the MWSs for the main species at both sites (Fig. 2). In Teixoneres, most of the *C. elaphus* display a score of 0, 1, or 2. In Unit IIIa, no higher scores are recorded, while a few specimens in Unit IIIb have scores between 3 and 5. The two distributions are statistically similar (Fisher test, $p = 0.38$). In Pié Lombard, the scores between 1 and 4 are almost equally represented and the other categories are either less well represented or absent. This distribution is significantly different from the others (Unit IIIa-PL, $p = 0.01$; Unit IIIb-PL, $p = <0.0001$), with a higher representation of the third and fourth categories and less of the category 0. In both Teixoneres Unit IIIb and Pié Lombard, the mesowear scores of *Capra* sp. range between 0 and 4. Both assemblages display a similar distribution, with the first three categories better represented. The MWS patterns of horses from Teixoneres Units IIIa and IIIb are also very similar and statistically identical. The highest values (i.e., between 4 and 6) are better represented. Categories 2 and 3 are rare and 0 and 1, absent. The global mesowear distribution for all ungulates in each site/unit, however, reveals significant differences (Units IIIa and IIIb, $p = <0.0001$; Unit IIIa-Pl, $p = <0.0001$; Unit IIIb-PL, $p = <0.0001$). In Teixoneres Unit IIIa, the distribution is dominated by 0, 2, and 6. The scores between 3 and 5, which correspond to a moderately abrasive diet, are scarce. In Teixoneres Units IIIa and IIIb, all the dietary categories are represented, with 0, 1, 2, and 3 dominating. The more abrasive ones (between 4 and 6) are scarce. In Pié Lombard, 5 and 6 (the most abrasive categories) are absent. The main categories are 1, 2, 3, and 4; 0 (representing a few very sharp teeth) is also represented.

In Teixoneres Unit IIIa, the better-represented MSWs (Fig. 2**D**) are in the two extremes of the dietary spectrum and correspond primarily to the browser and grazer categories. Most of the browsers are *C. elaphus* accompanied by *C. capreolus*, while the grazers are represented principally by *E. caballus* along with *E. hydruntinus* (Fig. 1). In Teixoneres Unit IIIb (Fig. 2**D**), the global mesowear distribution is different, especially regarding the presence of browsers and mixed feeders; grazers are scarce. The browsers and mixed feeders correspond here mainly to *C. elaphus*; *C. pyrenaica* and *C. capreolus* have similar MWSs. The main grazer is *E. caballus*, with some *B. primigenius* and *E. hydruntinus* (Fig. 1). In Pié Lombard, the browsers and mixed-feeders are also the most abundant, with almost no grazers represented (Fig. 2**D**). Here, almost all the species (*B. primigenius*, *C. ibex*, *R. rupicapra*, and *C. elaphus*) have MWSs that place them as mixed feeders. Only *C. capreolus* and *E. caballus* (which are represented by very few individuals) appear to have a more specialized diet, the first being a browser and the latter, a grazer (Fig. 1).

Table 2
Summary of dental meso- and microwear data of the ungulates from Teixoneres Units IIIa and IIIb and Pié Lombard. MWS = mesowear score with the number of teeth per category, the total number of teeth (n), the mean (m), and the standard deviation (s); scratches = number (n) of specimens with their mean (m), standard deviation (s) and coefficient of variation (cv). The raw data are given for the cohorts with an MWS below 3.

Site	MWS									Scratches	
	0	1	2	3	4	5	6				
Teixoneres_Unit IIIa											
B. primigenius										#6	21.5
C. pyrenaica		2						n	2	#21	6
								m	1		
C. elaphus	4	2	5					n	11	n	14
								m	1.09	m	17.64
								s	0.94	s	2.75
										cv	0.16
C. capreolus	3							n	3	#K16-53	4
								m	0	#N08-36	6
E. caballus			1	1	3	5	10	n	20	n	31
								m	5.10	m	22.48
								s	1.17	s	2.50
										cv	0.11
E. hydruntinus			2	2	1			n	5	n	5
								m	2.80	m	22.00
								s	0.84	s	7.20
										cv	0.33
Total: Teixoneres Unit IIIa	7	4	8	3	4	5	10	n	41	n	72
								m	3.17	m	20.61
								s	2.23	s	5.08
Teixoneres_Unit IIIb											
B. primigenius			2	4	4	1		n	11	n	12
								m	3.36	m	18.46
								s	0.92	s	6.84
										cv	0.37
C. pyrenaica	1	5	2	1	1			n	9	n	6
								m	1.67	m	8.75
								s	1.22	s	1.37
										cv	0.16
C. elaphus	12	29	30	8	1	1		n	81	n	62
								m	1.51	m	19.57
								s	0.99	s	4.03
										cv	0.21
C. capreolus	8	13	7	5	2	1		n	36	n	12
								m	1.53	m	10.25
								s	1.30	s	2.64
										cv	0.26
E. caballus				1	2	4	3	n	10	n	33
								m	4.90	m	20.80
								s	0.99	s	4.34
										cv	0.21
E. hydruntinus		1	2	1	1			n	5	n	14
								m	2.40	m	20.21
								s	1.14	s	5.94
										cv	0.29
Total: Teixoneres Unit IIIb	21	48	43	20	11	7	3	n	153	n	122
								m	1.90	m	18.14
								s	1.42	s	5.61
Pié Lombard											
B. primigenius			1					#F3-XVI	2		21
C. pyrenaica	5	37	44	39	16			n	141	n	29
								m	2.17	m	8.97
								s	1.06	s	2.93
										cv	0.33
C. elaphus	5	14	15	11	15			n	63	n	30
								m	2.27	m	15.70
								s	1.29	s	2.82
										cv	0.18
C. capreolus	3							n	3	#F3.2	6
								m	0.00	No ID	5
E. caballus				1				n	1	#F4-14bis	22.5
								m	3.00	#C4f-912	19
R. rupicapra	5	6	3	4	1			n	19	n	6
								m	1.47	m	6.50
								s	1.26	s	1.41
										cv	0.22
Total: Pié Lombard	18	57	63	55	32			n	225	n	71
								m	2.12	m	12.12
								s	1.17	s	4.81

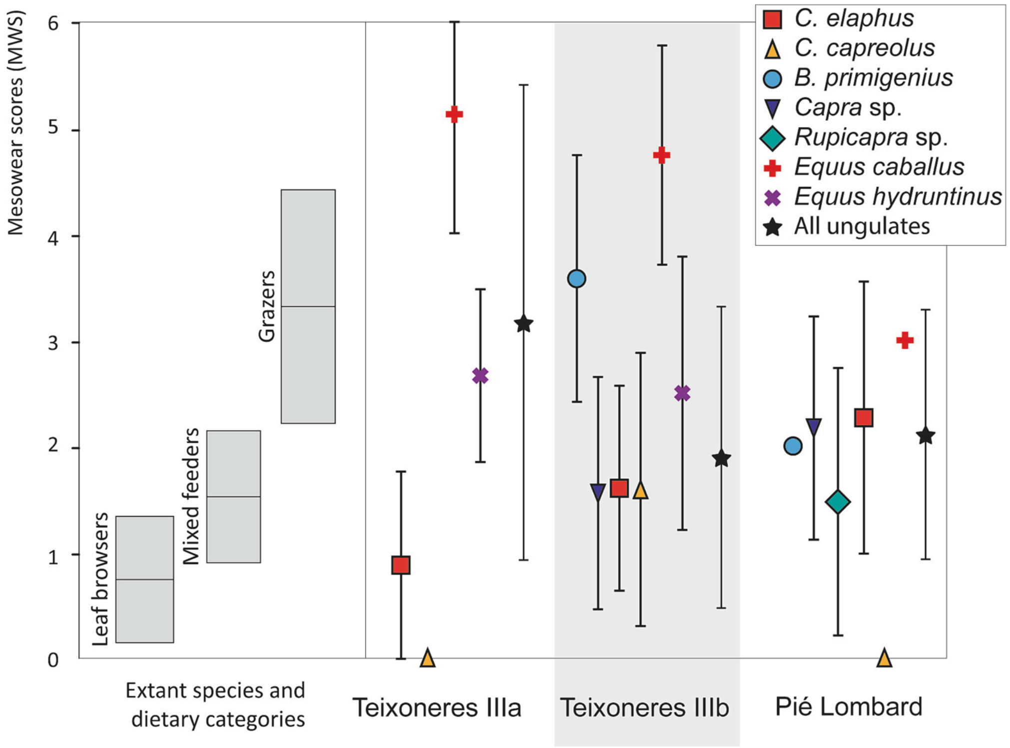

Fig. 1. Mesowear score (MWSs) of the ungulates from Teixoneres Units IIIa and IIIb and Pié Lombard. The total MWSs of all herbivores are compared with the values of recent ungulates published by Fortelius and Solounias (2000), Solounias and Semprebon (2002), and Rivals et al. (2010, 2014).

Dental mesowear distributions of *C. elaphus* between the Teixoneres units and Pié Lombard differ significantly (see above). In the former, they rank with the mixed-feeders, with no or almost no high abrasion scores. The latter features mixed-feeders with a grazing tendency (Fig. 1 **and** Fig. 2**A**). In Teixoneres, no difference was observed both for the mean and the distribution for *E. caballus*. They always rank with the grazers, with most of their teeth being highly abrased (Fig. 1 **and** Fig. 2**C**). Only one tooth was available at Pié Lombard, so a comparison was not possible. The two *Capra* sp. cohorts from Teixoneres Units IIIb and Pié Lombard are also very similar (Fig. 1 **and** Fig. 2**B**): they fall into the mixed-feeder diversity category, with abrasion patterns covering all types of variability, excepting the highest abrasion categories. Some species are not sufficiently well represented to allow statistical or distribution analysis. Amongst them (Fig. 1), *C. capreolus* is a browser in Teixoneres Unit IIIa and Pié Lombard, while it is a mixed feeder in Unit IIIb. In the latter, *B. primigenius* plots with the grazer, while the individual in Pié Lombard is a mixed feeder. In Teixoneres Units IIIa and IIIb, *E. hydruntinus* is always a grazer overlapping hugely with the mixed feeders.

4.2. Dental microwear variability for the herbivores from Teixoneres and Pié Lombard

In Teixoneres Unit IIIa, most of the ungulates display a high number of scratches (more than 17; Table 2; Fig. 3). This is the case for *E. caballus*, *E. hydruntinus*, and *B. primigenius*. The mean number of scratches of *C. elaphus* is above 17. Only *C. pyrenaica* and *C. capreolus* have a soft diet and a small number of scratches. The global microwear distribution of the Teixoneres Unit IIIa ungulates is dominated by an abrasive feeding pattern, with the majority of the individuals above 17 scratches ($M = 20.83$). In Teixoneres Unit IIIb, the mean number of scratches for the majority of taxa is around 20, with a distribution extending on either side to 17. This is the case for *B. primigenius*, *C. elaphus*, *E. caballus*, and *E. hydruntinus*. The global microwear distribution follows the trend ($M = 18.14$). Only *C. pyrenaica* and *C. capreolus* display a lower number of scratches (both around 10). In Pié Lombard, the opposite trend can be observed, with a majority of species displaying fewer than 17. This is the case for *C. ibex* (with a trend comparable with *C. pyrenaica*), *R. rupicapra*, and *C. capreolus* ($M \approx 7$). *C. elaphus* also has a low abrasive diet, with fewer than 17 scratches but with a higher number (around 15). Only *B. primigenius* and *E. caballus* display a more abrasive diet with high scratch means (around 19). The global microwear distribution of Pié Lombard ungulates is dominated by a low quantity of scratches ($M = 12.12$).

The distribution of the scratches of the main species and the global microwear distribution at both sites was compared (Fig. 4). In Teixoneres Units IIIa, the number of scratches amongst *C. elaphus* is almost equally distributed around 17, with more individuals displaying a greater number in Unit IIIb. In Pié Lombard, the majority of the specimens have a low number of scratches. The distribution of the number of scratches was compared using the Kolmogorov-Smirnov test (**Supplementary data**); there was no difference between Units IIIa and IIIb ($p = 0.13$). The distribution in both units is wider than in Pié Lombard (IIIa-PL, $p = 0.02$; IIIb-PL, $p = <0.0001$), where the distribution lies primarily between 13 and 21. The distribution pattern of scratches in horses varies between Teixoneres Units IIIa and IIIb. Most of the specimens with more than 17 scratches are present in Unit IIIa, with the majority bearing between 21 and 24. In Unit IIIb, most of the specimens' teeth have more than 17 scratches, with an almost repartition (between 14 and 25). The distribution is significantly different ($p = <0.0001$). The global microwear distribution displays significant differences between all the units/sites (IIIa-IIIb, $p = <0.0001$; IIIa-Pl, $p = <0.0001$; IIIb-PL, $p = <0.0001$). In Teixoneres Unit IIIa, the repartition is quite wide and organised around a peak of between 22 and 24 scratches, with a majority of the individuals possessing more than 17. In Teixoneres Unit IIIb, the repartition is even wider, organized around a peak of 20, with an almost equal repartition under and above 17. In Pié Lombard, the majority of the individuals have less than 17 scratches; these are organized around three peaks (7, 15, and 19).

At the microwear scale, in Teixoneres Unit IIIa, the majority of the

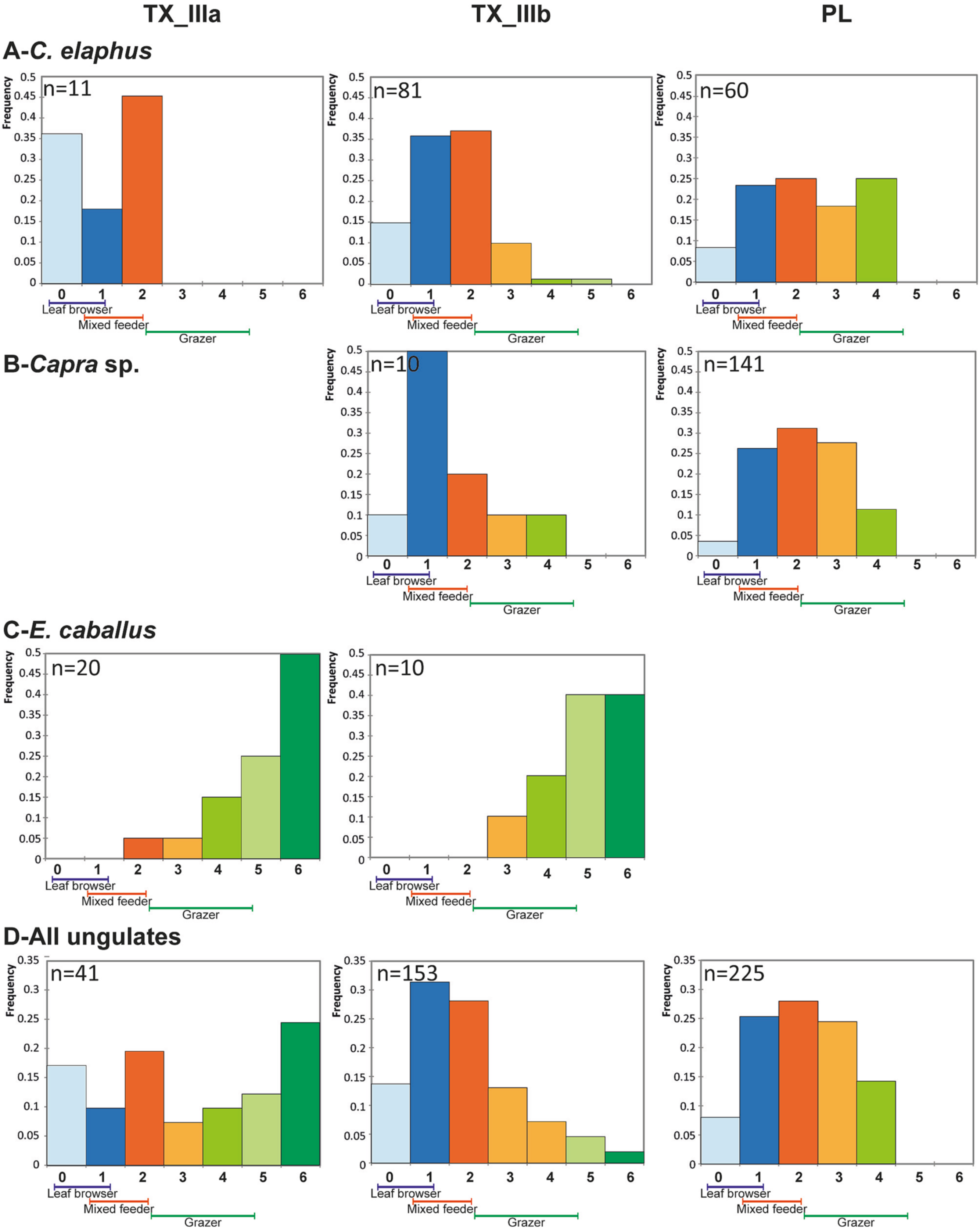

Fig. 2. Distribution of the mesowear scores (MWSs) of the principal ungulates from Teixoneres Units IIIa (TX_IIIa), Units IIIb (Tx_IIIb), and Pié Lombard (PL): A: *C. elaphus*; B: *Capra* sp.; C: *E. caballus*; D: all ungulates.

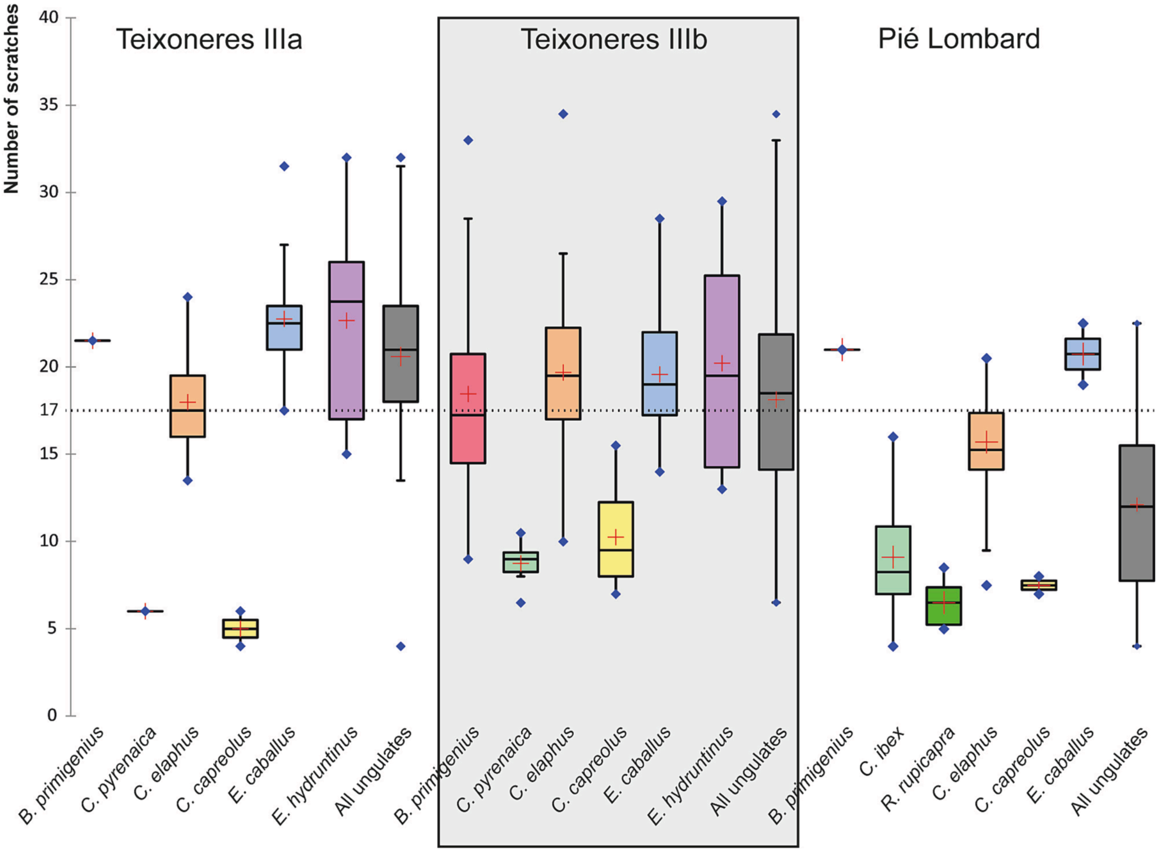

Fig. 3. Box plots of the number of scratches amongst the ungulates from Teixoneres Units IIIa and IIIb and Pié Lombard. At Value 17, a line separates the most abrasive diets from the softer ones.

ungulates have more than 17 scratches (Fig. 4**C**). This is due largely to the abundant presence of *E. caballus* and *E. hydruntinus*, both of which have an abrasive diet (Fig. 3 **and** Fig. 4**B**). The scratch distribution of *C. elaphus* of around 17 scratches corresponds to a mixed-feeder diet with a grazing tendency (Fig. 4**A**). Only *C. capreolus* have browser values (Fig. 3). In Teixoneres Unit IIIb, the global microwear distribution is almost equally distributed around 17 scratches (Fig. 4**C**). Indeed, *C. elaphus* and *E. caballus* (along with the less well-represented herbivores) display similar scratch values corresponding to a mixed feeder diet (Fig. 3 **and** Fig. 4**A and B**). Only *C. pyrenaica* and *C. capreolus* have lower values (similar to browsers; Fig. 3). In Pié Lombard (Fig. 3 **and** Fig. 4**C**), the global microwear distribution is divided into three groups: (1) around 7 scratches (*C. ibex*, *R. rupicapra*, and *C. capreolus*), corresponding to browsers; (2) around 15 scratches (*C. elaphus* – a mixed feeder); and (3) around 19 scratches (*B. primigenius* and *E. caballus*, which are grazers). The browsers and mixed feeders (principally *C. elaphus* and *C. ibex*) are the better represented diet categories.

At this scale (Fig. 3 **and** Fig. 4**A**), the values and distributions of *C. elaphus* differ amongst and between the Teixoneres units and Pié Lombard. The number of scratches in Teixoneres Units IIIa and IIIb is higher, with individuals distributed on either side of 17. In Pié Lombard, most of the individuals display less than 17 scratches. *E. caballus* in Teixoneres Units IIIa and IIIb, are mixed-feeders with a grazing tendency but with a more abrasive diet in IIIa and almost no individual exhibiting fewer than 17 scratches. In Unit IIIb, more individuals display fewer than 17 scratches. Of the less well-represented herbivores (Fig. 3), *B. primigenius* have an abrasive diet in Teixoneres Unit IIIa and Pié Lombard. In Teixoneres Unit IIIb, they appear to be less focused on abrasive plants, with a mixed feeder diet and a grazing tendency. *Capra* sp., *R. rupicapra* and *C. capreolus* have a reduced number of scratches and a soft browsing diet. *E. hydruntinus* has an abrasive diet, with almost all the individuals in Teixoneres Unit IIIa above 17 and a repartition in Unit IIIb, where more individuals have more than 17.

4.3. Seasonality of the herbivores of Teixoneres and Pié Lombard

Since microwear is a short-time window proxy for the diet of the last meals of an individual (Sánchez-Hernández et al., 2016; Semprebon et al., 2004; Winkler et al., 2020), it is strongly influenced by the duration of cohort mortality events in a sedimentary layer. The present study estimated dental microwear and dental eruption patterns for ungulates in Teixoneres and Pié Lombard. As can be seen in the heat map (Fig. 5), all the herbivore cohorts from Teixoneres Unit IIIa fall into the black, red, or yellow areas ($p > 0.05$), so the findings could not be interpreted. For Teixoneres Unit IIIb, *C. pyrenaica*, *E. caballus*, *C. elaphus*, and *B. primigenius* are located in the white areas ($p \leq 0.05$). The accumulations of *C. pyrenaica* appear to be uniseasonal, with *B. primigenius* appearing during non-contiguous seasons. The accumulations of *E. caballus* and *C. elaphus* correspond to several contiguous seasons. In Pié Lombard, only three species display enough teeth for the duration of their mortality events to be estimated: *C. elaphus*, *C. ibex*, and *R. rupicapra*. Amongst them, only the position of the two caprids could be interpreted. The accumulations of *R. rupicapra* appear to be uniseasonal, with *C. ibex* corresponding to several contiguous seasons.

In a second step, the season of death was estimated using dental eruption patterns (Fig. 6) that allowed to include more taxa while focusing on juveniles and sub-adults (except for the equids and red deer that also included adults). In Teixoneres, the seasonality of red deer has been estimated by previous authors (Sánchez-Hernández et al., 2020a, Sánchez-Hernández et al., 2016), but we have incorporated other ungulate species and material from new excavation campaigns. In Units IIIa and IIIb, *C. elaphus* and *E. caballus* are present in all seasons. In Unit

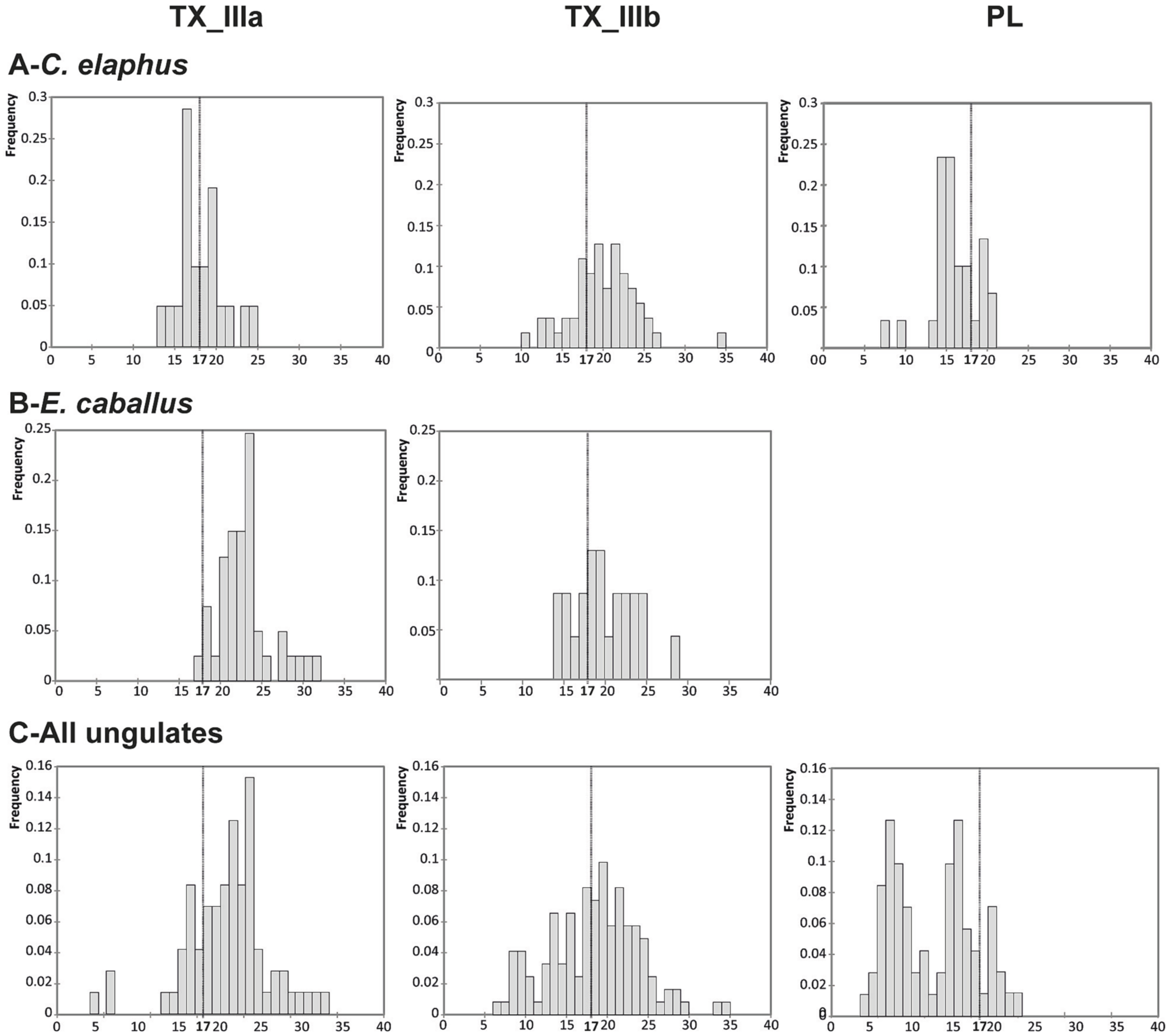

Fig. 4. Distribution of the number of scratches of the principal ungulates from Teixoneres Unit IIIa (TX_IIIa), Teixoneres Unit IIIb (Tx_IIIb), and Pié Lombard (PL): A: C. elaphus; B: E. caballus; C: all ungulates. At Value 17, a line separates the most abrasive diets from the softer ones.

IIIa, the higher diversity of species occurs in summer, when *B. primigenius* and *E. hydruntinus* are also present. In Unit IIIb, both of these species are present in summer, along with *C. capreolus*. The specific diversity is lower in autumn and spring; in addition to *C. elaphus* and *E. caballus*, *C. capreolus* and *E. hydruntinus* are present in autumn and the latter in spring. *C. pyrenaica*, *C. capreolus*, *E. hydruntinus*, *B. primigenius*, and the two main represented species are present in winter. Although all the seasons are represented in Teixoneres, *E. caballus* and *C. elaphus* are dominant in summer, with approximately 50 % of the individuals dying then. In Pié Lombard also, an imbalance can be observed in seasonal representativeness, with a majority of individuals (around 60 %) dying in autumn (Roussel et al., 2021).

5. Discussion

5.1. *Description of the habitats using dental wear: Individual or collective variability?*

Intra-species diet diversity is relatively low at the dental mesowear scale and higher at the dental microwear scale. This is probably due to the time-scale analysed by the two proxies. Mesowear refers to an average diet of several years, while microwear refers to the last days of an individual. Microwear is therefore more sensitive to punctual parameters such as seasonality (Sánchez-Hernández et al., 2016), inter-species competition (Rivals et al., 2017), and resource availability (Uzunidis, 2021). The global dental wear distributions are significantly different. The intra-species diet diversity is quite low in comparison, which may be due to the abundance of the species that contribute to the global distribution. Thus, both at the meso- and microwear scales, taking all the ungulates from an assemblage into account and weighting their importance by their relative abundance allows us to consider as many ecological niches as possible and evaluate their environmental representativeness. The relationship between the relative abundance of known grazing or browsing ungulates and vegetation structure may not be direct, however, at least at the scale of the animal life and in current South African environment (Negash & Barr, 2023).

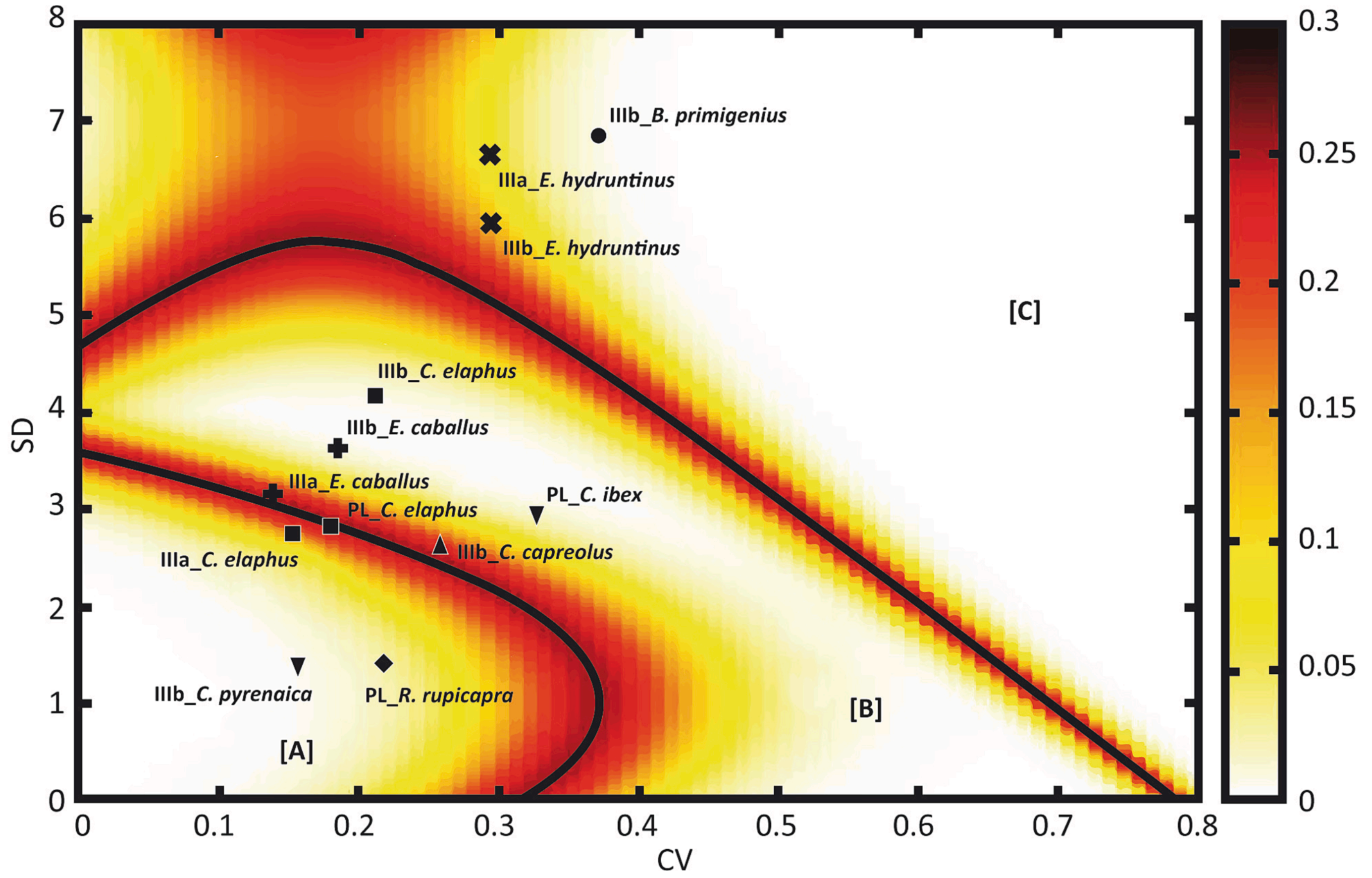

Fig. 5. Microwear data of the ungulates from Teixoneres Units IIIa and IIIb and Pié Lombard. Bivariate plot: standard deviation (*SD*) and coefficient of variation (*CV*) are calculated based on the number of scratches. Boundary lines between the three areas with the error probability (heat map). A = seasonal or shorter events; B = longer than one season; C = at least two separate events that occurred in different non-consecutive seasons.

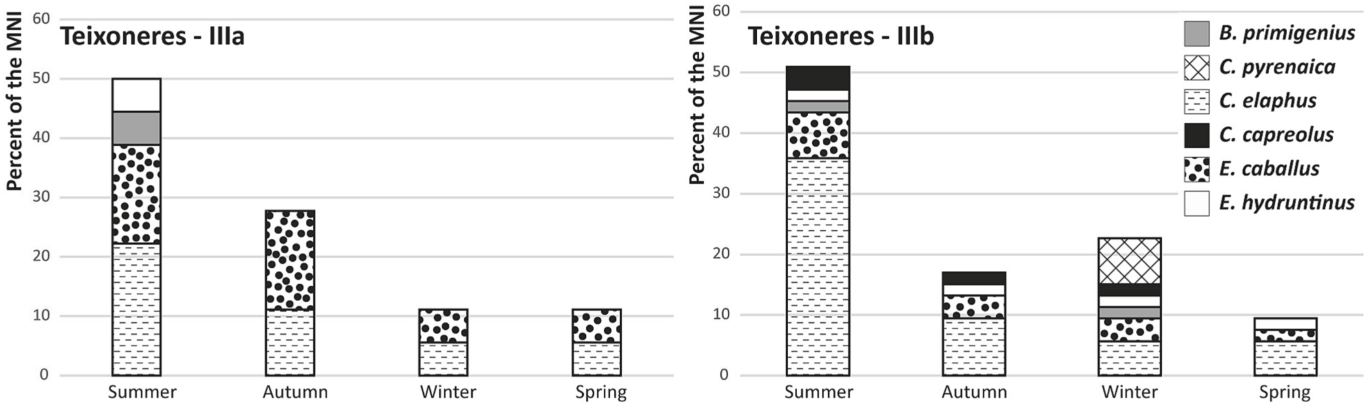

Fig. 6. Repartition of the ungulates from Teixoneres Units IIIa and IIIb per season in percent of the minimum number of individuals (MNI).

5.2. *Spatial and temporal frames of Teixoneres and Pié Lombard dental wear*

The meso- and microwear global distributions are not reflecting the same environmental conditions in either Teixoneres or Pié Lombard. In Teixoneres Unit IIIa, mesowear values reveal an abundance of both browsers and grazers, with very few mixed feeders; microwear values are dominated by grazers. In Teixoneres Unit IIIb, mesowear indicates an overrepresentation of browsers and mixed feeders and a scarcity of grazers. Microwear suggests an equal representation of high- and low-abrasive diets. In Pié Lombard, mesowear and microwear point to the presence of browsers and mixed feeders and the almost complete absence of grazers. The two proxies correspond to two different time scales of the life of an individual (Sánchez-Hernández et al., 2016), which implies the registration of different temporal and spatial resolutions.

The intra- and inter-specific sizes of the territory occupied by a palaeontological cohort can vary greatly. Such is the case with one of the main species of the corpus, *C. elaphus*. Currently, its annual home ranges vary from 1 km^2 on the Isle of Rhum (Clutton-Brock et al., 1982) to 94.8 km^2 in the Carpathian forest (Kropil et al., 2015). Some populations can be sedentary, with other migratory groups occupying generally low elevations in winter and high ones in summer (Luccarini et al., 2006; Mysterud et al., 2001). *E. caballus* is also usually well-represented; current feral horse populations also display highly diverse home ranges, from 0.8 km^2 up to 303 km^2 annually (McCort, 1984; Miller, 1983; Salter & Hudson, 1982). Groups can exhibit very different territorial behaviour within the same area; for example, territories from 12.4 km^2 to 90 km^2 in Alberta forest, Canada (Girard et al., 2013) and 1.3 km^2 up to 24 km^2 in the Hustai National Park, Mongolia (King & Gurnell, 2005). At the seasonal scale, the home range is smaller than the annual one for the two above-mentioned species (Bahloul et al., 2001; Carranza et al., 1991; Catt & Staines, 1987; Kamler et al., 2008; Miller, 1983; Schoenecker et al., 2023). The size of the seasonal territory varies according to several factors. For example, it may be larger in winter because of the scarcity of resources (King & Gurnell, 2005; Kropil et al., 2015; Schoenecker et al., 2023) or the need to avoid too much energy loss (McCort, 1984; Schoenecker et al., 2023). For migratory populations, especially red deer, the autumn territory is usually larger since it corresponds to the displacement period (Kropil et al., 2015; Luccarini et al., 2006). Currently, the largest territories appear to be correlated with environments where resources are scarce, dispersed, or unpredictable in terms of abundance (Clutton-Brock & Harvey, 1978). These conditions are difficult to establish for the Pleistocene, and the size of the territory of fossil cohorts cannot be extrapolated. Currently, however, whatever the behaviour of the groups, migratory or sedentary, the territories covered in one season are always smaller than the annual territories. Dental mesowear (which can be used to record the diet over several years) averages the biomes travelled within the annual home range. Dental microwear, by recording the diet shortly before death, fits into the seasonal territory. The first proxy corresponds to an indefinite regional scale that is larger than the second proxy, which describes an equally undefined local scale.

The short scale of dental microwear within an individual's life also implies a high temporal resolution within the year and a sensitivity to seasonal turnovers (Gogarten & Grine, 2013; Merceron et al., 2010, 2004; Rivals et al., 2015; Sánchez-Hernández et al., 2016). In Teixoneres and Pié Lombard, the herbivore accumulations last the whole year but, in each case, one season is favoured. In Teixoneres Units IIIa and IIIb, most of the accumulations occur during summer, and in Pié Lombard, autumn. *C. elaphus* and *E. caballus* are amongst the main represented species in Teixoneres and Pié Lombard. Currently, feral horses graze throughout the year (McInnis & Vavra, 1987; Scasta et al., 2016; Sietses et al., 2009; Zielke et al., 2019). In some cases, this species does not experience huge changes in diet across the seasons (Scasta et al., 2016; Zielke et al., 2019). Other populations, however, have shown seasonal variations by selecting more graminoid in summer and more bark in winter (McInnis & Vavra, 1987; Ohtsu & Takatsuki, 2021; Putman et al., 1987; Sietses et al., 2009). Horse diets follow the patterns of the habitats selected; for instance, individuals can encounter problems accessing grass in winter snow (Crane et al., 1997). Present-day red deer are classified as intermediate feeders (Gebert & Verheyden-Tixier, 2001). They focus ordinarily on soft plants, with around 30 % of their intake being grass (García-González & Cuartas, 1992; Gebert & Verheyden-Tixier, 2001; Ismaili et al., 2018; Ohtsu & Takatsuki, 2021). Some populations can, however, have a diet generally or seasonally based on grasses (Berlioz et al., 2017; Gordon & Illius, 1989; Jayasekara & Takatsuki, 2000; Sherlock & Fairley, 1993; Sietses et al., 2009). Red deer diets appear to change according to the availability of resources (Groot Bruinderink & Hazebroek, 1995; Ismaili et al., 2018; Latham et al., 1999; Sietses et al., 2009; Storms et al., 2008); individuals tend to focus on monocots when their environment lacks less fibrous plants (Berlioz et al., 2017; Gebert & Verheyden-Tixier, 2001). In short, during the year, the feeding behaviour of these two species can change according to the seasons and the resources available. The apparent contradiction between the results of dental mesowear and microwear at Teixoneres may reflect a strong seasonal alternation, whereas the correspondence between the two proxies at Pié Lombard would indicate a homogeneity of environmental parameters on several scales.

5.3. Paleoenvironmental parameters of Teixoneres and Pié Lombard according to dental wear

Our results indicate that dental mesowear can be used to ascertain the annual diets of herbivores over a regional geographical scale and dental microwear, seasonal diets over a local geographical scale. In Teixoneres Units IIIa and IIIb, summer is the main season represented, and in Pié Lombard, autumn. The differences between the two proxies in Teixoneres may indicate strong seasonal variations. These are less expressed in Pié Lombard.

Human activities are the main factor that lead to the accumulation of ungulate remains at both sites (Rosell et al., 2010a; Texier et al., 2011; Zilio et al., 2021). It is then unlikely, that the herbivores dental wear parameters reflect the whole available environmental diversity but rather the niches favoured by Neanderthals in their meat acquisition.

The global mesowear distribution in Teixoneres Unit IIIa (Fig. 2**D**) is based on the contribution of *C. pyrenaica*, *C. elaphus*, *C. capreolus*, *E. caballus*, and *E. hydruntinus*. Amongst them, *C. elaphus* and *E. caballus* are the main contributors. In this unit, the browser and grazer diet categories are well-represented and the mixed-feeders less so, which would imply the presence of both forested areas and grassland. Herbaceous dicot meadows would not be well-represented in the region, a "mosaic environment" facilitating a well-defined segregation, especially between horses and red deer. In Teixoneres Unit IIIb (Fig. 2**D**) the mesowear distribution is built on *B. primigenius*, *C. pyrenaica*, *C. elaphus*, *C. capreolus*, *E. caballus*, and *E. hydruntinus*, with *C. elaphus* the main species. In this unit, the browsers and mixed-feeders are the most represented and the grazers are more scarce, implying a growth in forested and dicots meadow areas and a decline in open grassland. Those trends accord with micromammals studies that point towards a decrease in forest between Units IIIb and IIIa (Fernández-García et al., 2022; López-García et al., 2012a). They do not match, however, with pollen data that indicate an opposite tendency (Ochando et al., 2020), though this may be the result of the different scales recorded by the two proxies. The reduction of forest cover and an increase in grassland may have accompanied climatic change, with Unit IIIa becoming relatively colder and wetter (Álvarez-Lao et al., 2017; Fernández-García et al., 2022; Sánchez-Hernández et al., 2020a, Sánchez-Hernández et al., 2020b). Global microwear distributions in Teixoneres (Fig. 3**D**) rely on the contribution of *B. primigenius*, *C. pyrenaica*, *C. elaphus*, *C. capreolus*, *E. caballus*, and *E. hydruntinus* (mostly horses and red deer). A vast majority of the herbivores have an abrasive diet that indicates open areas in Unit IIIa. In Unit IIIb, the distribution disperses to cover all the dietary categories, indicating the presence of grass, herbaceous dicots, and forested areas (Table 3). In both units, the grazers are overrepresented at the microwear scale relative to the mesowear scale, which suggests a seasonal increase in grassland during summer that is in turn associated with a significant turnover of vegetation. Thus, at Teixoneres, herbivore acquisition by Neanderthals may had occurred preferentially in open landscapes.

The global mesowear distribution in Pié Lombard (Fig. 2**D**) relies on the contribution of *B. primigenius*, *C. ibex*, *R. rupicapra*, *C. elaphus*, *C. capreolus*, and *E. caballus*, with a majority of red deer and alpine ibex. Most of these individuals have a browsing or a mixed-feeding diet, and there are very few grazers. The overrepresentation of soft plant specialists is greater here than in Teixoneres Unit IIIb, which might indicate a more forested landscape with some herbaceous dicot meadows (Table 3). These results are consistent with studies of birds, herpetofauna, small mammals, and malacofauna that suggest the presence of a forest-dominated biome under a Mediterranean-dominated climate (Texier et al., 2011). Some taxa, however, such as *Marmota* cf. *marmota*, *Microtus nivalis* or *Lagopus* sp., are typical of colder conditions and may reflect the ecotone nature of the site (i.e., halfway between the valley and mountain peaks; Texier et al., 2011). As in Teixoneres, the

Table 3
Previous palaeoenvironmental approaches atTeixoneres units IIIa and IIIb and Pié Lombard and results from this work.

Site	Age	Pollen	Small mammals	Dental mesowear	Environmental interpretation - Mesowear	Main season of accumulation	Dental microwear	Environmental interpretation - Microwear
Teixoneres-Unit IIIa	44–45 ky	Forest-dominated biome [a]	Open woodland [b,c]	Browser and grazer abundant, Mixed-feeder scarcer [d]	Both forested areas and grassland [d]	Summer [d]	Overall diet very oriented toward abrasive plants [d]	Open grassland [d]
Teixoneres-Unit IIIb	45- > 51 ky	Less forested than previous layer [a]	Open woodland, more forested than IIIa [b,c]	Browser and mixed-feeder abundant, grazer scarcer [d]	Increase of forest and dicots meadow, decrease of grasslands [d]	Summer [d]	All dietary categories represented with a majority of grazers [d]	Open grassland with few forested aeras and dicot meadows [d]
Pié Lombard	70 ± 8 ky	Open landscape and rigorous climate [e,f]	Forest-dominated biome, Mediterranean-dominated climate [e]	Browser and mixed-feeder dominant, very few grazers [d]	Forested landscape with dicot meadows and very few grasslands [d]	Automn [g]	Browser and mixed-feeder dominant, very few grazers [d]	Forested landscape with dicot meadows and very few grasslands [d]

[a] (Ochando et al., 2020).

[b] (López-García et al., 2012a).

[c] (Fernández-García et al., 2022).

[d] this work.

[e] (Texier et al., 2011).

[f] (Renault-Miskovsky and Texier, 1980).

[g] (Roussel et al., 2021).

environmental description based on mesowear does not concur with pollen data that imply an open landscape and a rigorous climate (Renault-Miskovsky & Texier, 1980; Texier et al., 2011). The difference in scales might explain differences in the results. The scaleof dental mesowear would therefore be more comparable with proxies from microfauna in general. In the present site, the microwear distribution (Fig. 2**D**) is built on the same species as the mesowear one, with the same two main taxa represented: red deer and alpine ibex. The dental microwear scale shows the same tendency as the mesowear equivalent, with an overrepresentation of browsers and mixed-feeders and almost no grazers. As in Teixoneres, autumn is considerably more represented than the others. The correspondence between the two dental wear scales may indicate a weak seasonal turnover. Dental microwear makes it possible to observe three principal groups that are averaged at the mesowear scale. Each corresponds to abundant browsers and mixed-feeders and the rarer grazers. The clear segregation suggests a partitioned environment of distinct biomes dominated by forests and dicots that is consistent with the topography of the site. Thus, as is the case with microfauna (Texier et al., 2011), dental microwear indicates that species occupied different elevations around the site that were also exploited by Neanderthals.

Thus, while the herbivore dietary distribution is probably influenced by human prey selection, it still displays tendencies that are consistent with those observed by the analysis of micromammals. Dental mesowear, microwear and small mammals indicate a decrease of the forest cover from Pié Lombard to Teixoneres IIIa. The dietary habits of the ungulates in the human selected niches follow then the general tendencies of the forest cover evolution through time. Microwear scale still follow the chronological trends while being strongly influenced by seasonal changes.

6. Conclusions

By taking into account the distribution of dental MWSs and the number of dental microwear scratches of all herbivorous ungulates at the three sites, we were able to include as many habitats as possible. A consideration of the distribution of dental meso- and microwear features allowed us to put into perspective the presence of herbivorous dietary categories in terms of their abundance. The contribution of dicots and monocots in an environment can therefore be measured to provide an approximation of the past environment on several temporal and spatial scales. Dental mesowear provides a multi-year signal of the landscape on a regional scale, whereas the dental microwear signal is seasonal and corresponds to a smaller local scale. Combining these proxies with an estimation of mortality periods and seasonality enables dental microwear and environmental reconstructions to be contextualised at the seasonal level. The combination of dental meso- and microwear is thus a powerful environmental proxy that describes past seasonal alternations. The direct relationship between the presence of herbivores in Teixoneres and Pié Lombard and anthropic predation also makes it possible to establish a connection between these landscapes and Neanderthal activities. Thus, the landscapes that were occupied by herbivores and exploited by Neanderthal around Teixoneres were open habitats while there were more closed habitats in Pié Lombard. For each sites/unit, the different proxies (dental wear, micromammals and pollens) display distinct close/open environment ratio according to their scales of observation and the condition of accumulation. The faunal proxies, however, including those that are biased by anthropic activities (dental wear on prey) and those that are not (micromammals) indicate similar trends through time that suggest a reduction of the forest cover from MIS 4 to MIS 3.

Our approach involves several steps, each of which allows us to overcome technical issues: (1) a sample that follows the composition of the ungulate assemblage; (2) a meso- and microwear analysis of the teeth; (3) an estimation of the season of death of the respective individuals (with the contribution of grazers, mixed-feeders, and browsers to the distribution analysed using MWSs for mesowear and the number of scratches for microwear); and (4) combining the microwear distribution with the season of death, through which paleoenvironmental variations within the year can be measured.

Authors contributions

Antigone Uzunidis: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Florent Rivals:** Conceptualization, Supervision, 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

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

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Appendix A. Supplementary materials

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2023.104258.

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