

Dental microwear of cave bear (*Ursus spelaeus*) reveals locally adapted foraging strategies in South-Eastern Europe during late MIS 3



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ABSTRACT

Cave bears (*Ursus spelaeus* sensu lato) represent a remarkable example of Late Pleistocene megafauna, whose ecology and extinction dynamics remain a subject of intense debate. This study investigates the short-term dietary ecology of Late Pleistocene (mainly late MIS 3) South-Eastern European cave and brown bear populations ($n = 316$) using dental microwear analysis (DMA) on specimens from Romanian Carpathians ($n = 160$), Moldavian Plateau ($n = 58$), Western Balkans and Western Rhodopes ($n = 65$) and Central Balkans ($n = 32$). By analysing and quantifying microwear features, this research captures the final days-to-weeks dietary behaviour prior to death, offering a high-resolution perspective complementary to isotopic and morphological analyses. Complementing the prevailing view of cave bears as highly specialized herbivores, our results suggest a seasonal ecology more comparable to that of extant northern hemisphere ursids, characterized by landscape-based dietary opportunism. This inferred dietary flexibility is further supported by local-scale niche partitioning, and possible regional niche overlap with contemporaneous southern refugia dwellers *U. arctos* populations. Evidence of dietary flexibility, closely tied to their immediate environment, supported by new radiocarbon dates ($n = 16$), with the youngest at 35 ka cal BP (Butești), calls for a reassessment of cave bear extinction dynamics. Ecological specialisation, particularly during resource-scarce seasons and in refugia areas, combined with pre-hibernation ecological pressures, likely contributed to a gradual, multifactorial extinction process. This localized dietary endemism may have limited the species' ability to adapt when climatic conditions deteriorated during MIS 3.

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1. Introduction

The *Ursus spelaeus* (order Carnivora) transitioned from an omnivorous diet towards a specialized herbivory during the Pleistocene (Jiangzuo and Flynn, 2020); a clear pattern inferred from both morphological traits (e.g., Mazza and Rustioni, 1994; van Heteren and Figueirido, 2019) and stable isotope analyses (e.g., Bocherens et al., 1994, 1997, 2006, 2011, 2014; Nelson et al., 1998; Vila-Taboada et al., 1999; Fernández-Mosquera et al., 2001; Münzel et al., 2011; Krajcarz et al., 2016; Naito et al., 2016; Bocherens, 2019; Ramírez-Pedraza et al., 2019; Kosintsev et al., 2024). Consequently, its ecology has been proven to have been plant-based, with a heavy year-round reliance on plant matter. Numerous stable isotopes studies involving large sample sizes have concluded that the cave bear's diet was relatively uniform over its lifespan (e.g., Bocherens, 2015; Krajcarz et al., 2016). This level of insight has been possible because cave bears hibernated in deep karstic cave systems, and their remains are among the most frequently recovered from cave fossil assemblages across Europe, likely due to individuals dying during dormancy (Kurtén, 1976; Rabeder, 1999; Rabeder et al., 2000; Grandal-d'Anglade et al., 2019). However, the seasonal ecology of cave bears differed from their overall annual dietary patterns (e.g., Ramírez-Pedraza et al., 2019). Individuals that died during hibernation reflect the physiological need for high caloric intake prior to dormancy, which resulted in a broadening of their diet before hibernation (e.g., Duñó-Iglesias et al., 2024a, 2024b). The pre-hibernation period is a key period for bears that determines the survival or extinction of offspring (Gende and Quinn, 2004). Interferences, such as competition for caves, hunting, or human presence might cause a shrinking of the regional population and even of a species (Stiller et al., 2010; Fortes et al., 2016; Robu et al., 2024).

The extinction of the cave bear has been mainly attributed to a decline in the availability of high-quality vegetation approaching the

Last Glacial Maximum (LGM) (Pacher and Stuart, 2009). The presence of other bears in the same landscapes have suggested local niche partitioning through both stable isotopes (e.g., Bocherens et al., 2011; Münzel et al., 2011; Frémondeau et al., 2020) and dental microwear analysis (e.g., Pappa, 2016; Ramírez-Pedraza et al., 2020, 2022; Duñó-Iglesias et al., 2024a, 2024b). The influence of other bear species on the decline of cave bears has been considered negligible based on life-span dietary proxies (i.e., stable isotopes) (Münzel et al., 2011); however, they may have exerted an ecological pressure at a seasonal scale (Duñó-Iglesias et al., 2024b).

In this study, we present a regional-scale dental microwear analysis of both *U. spelaeus* and *U. arctos* in South-Eastern Europe, including the Romanian Carpathians, expanding upon the dataset of Duñó-Iglesias et al. (2024a) with newly analysed individuals from Cioclovina and additional specimens from Urşilor and Muierilor caves, as well as newly sampled populations from the Moldavian Plateau, the Western Balkans, the Western Rhodope Mountains, and the Central Balkans regions.

The aim of this work is to assess the extent of seasonal dietary flexibility in *U. spelaeus* during the pre-hibernation period, and to evaluate niche relationships with *U. arctos*, in order to better understand ecological pressures that may have contributed to the decline of cave bears in South-Eastern Europe glacial refugia during the MIS 3.

2. Geographical context

This study includes populations from the Southeastern regions of the European continent (Fig. 1); from the Romanian Carpathians, Moldavian Plateau, Western Balkan Mountains and Western Rhodopes, and Central Balkans. The populations were grouped by regions based on geographical coherence. All populations are chronologically associated to the latter half of the Late Pleistocene, primarily during late MIS 3.

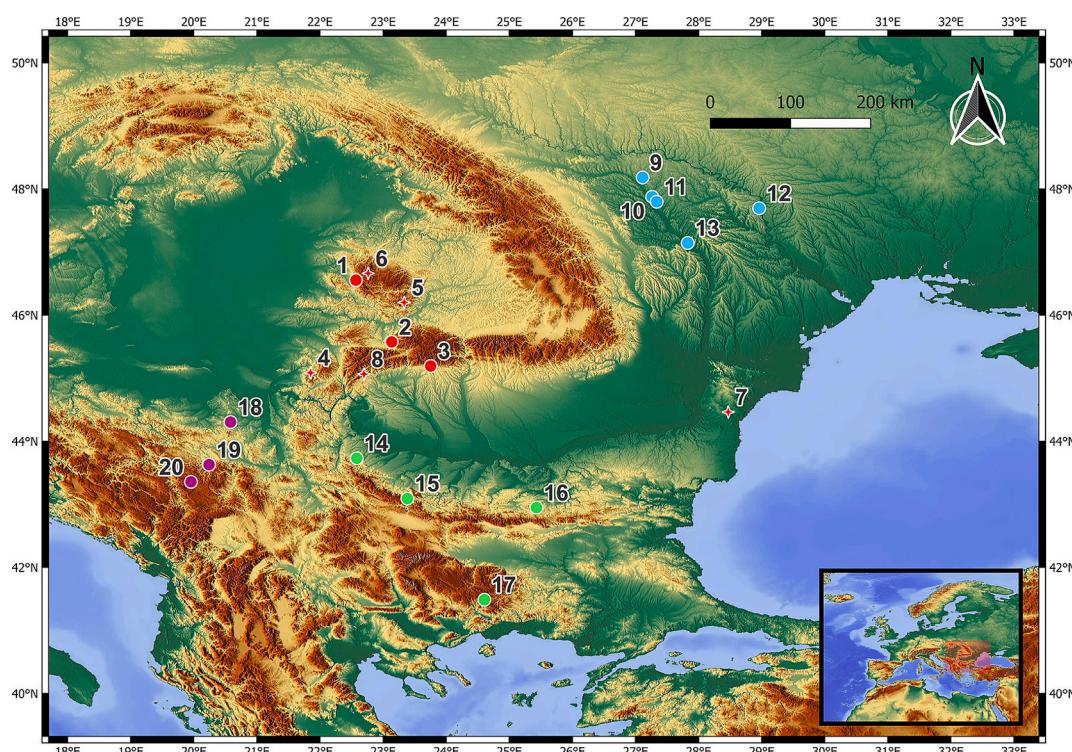


Fig. 1. Map of the sampled populations. *Romanian Carpathians* (red): 1. Urşilor, 2. Cioclovina Uscătă, 3. Muierilor, 4. Oase, 5. Biserica, 6. Oncea, 7. Adam, 8. ACCG. *Moldavian Plateau* (blue): 9. Trinca I, 10. Duruitoarea Veche, 11. Buteşti, 12. Saharna, 13. Buzdjeni. *Western Balkan Mountains and Western Rhodopes* (green): 14. Magura, 15. Lakatnik, 16. Bacho Kiro, 17. Borikovska. *Central Balkans* (purple): 18. Risovača, 19. Hadži Prodanova, 20. Ušačka. Stars indicate previously published sites, included for comparative purposes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1. Romanian Carpathians

Urşilor Cave ($46^{\circ} 55' 37''$ N, $22^{\circ} 56' 92''$ E), located on the western slope of the Apuseni Mountains (Western Carpathians), contains a rich Late Pleistocene cave bear (*U. spelaeus*) assemblage dated to 47–27.1 ka cal BP (Constantin et al., 2014; Robu, 2016; Duñó-Iglesias et al., 2024a).

Cioclovina Uscată Cave ($45^{\circ} 34' 27''$ N, $23^{\circ} 08' 10''$ E), in the Şureanu Mountains (Southern Carpathians), served as a hibernation site for *U. spelaeus* between 44.2 and 31.4 ka cal BP (Soficaru et al., 2007; Robu et al., 2019). Fauna includes *U. arctos*, *Canis lupus*, and *Panthera spelaea* (Rădulescu and Samson, 1959; Păunescu, 1980).

Muierilor Cave ($45^{\circ} 11' 29''$ N, $23^{\circ} 45' 14''$ E), in the Parâng Mountains (Southern Carpathians), yielded a diverse MIS 3 faunal assemblage (ca. 51–29 ka cal BP), dominated by *U. spelaeus* but also including *P. spelaea*, *C. lupus*, and *Cervus elaphus* (Mirea et al., 2021; Duñó-Iglesias et al., 2024a; Robu et al., 2024).

Further details on previously published comparative sites can be found in Duñó-Iglesias et al. (2024a).

2.2. Moldavian Plateau

Trinca I Cave ($48^{\circ} 10' 55''$ N, $27^{\circ} 06' 50''$ E), in the Edineț District, yielded *U. spelaeus*, and associated fauna (e.g., *U. arctos*, *P. spelaea*, *C. lupus*) of MIS 3 age, recovered from surface finds and old excavations.

Duruitoarea Veche Cave ($47^{\circ} 52'$ N, $27^{\circ} 15'$ E), Râșcani District, includes a diverse MIS 3 faunal assemblage with *U. spelaeus* dominant, but also including other taxa such as *Equus* sp., *Bison* sp., *C. elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *P. spelaea*, *Crocuta crocuta spelaea*, *C. lupus*, *Vulpes vulpes*, and *U. arctos*.

Buteşti Cave ($47^{\circ} 47' 46''$ N, $27^{\circ} 20' 13''$ E) contains *U. spelaeus* specimens attributed to the Late Pleistocene.

Saharna Cave ($47^{\circ} 41' 40''$ N, $28^{\circ} 57' 40''$ E), located near the Dniester River, is a karst containing Late Pleistocene *U. spelaeus* remains.

Buzdjeni I Cave ($47^{\circ} 08' 33''$ N, $27^{\circ} 49' 40''$ E) has a Late Pleistocene faunal sequence dominated by *U. spelaeus*, with associated remains of *E. ferus*, *B. priscus*, as well as *C. c. spelaea*, among others (Croitor and Burlacu, 2020; Vishnyatsky et al., 2020). The faunal deposits correspond to Late Pleistocene.

2.3. Western Balkan Mountains and Western Rhodopes

Magura Cave ($43^{\circ} 43' 41''$ N, $22^{\circ} 34' 57''$ E), in Western Balkan Mountains, preserves a Late Pleistocene assemblage dominated by *Ursus ingens*, accompanied by *U. arctos*, *C. lupus*, *C. c. spelaea*, *P. spelaea*, *E. hydruntinus*, and *C. elaphus*, among others (Ivanova et al., 2016). The cave bear remains date from more than >50 ka to ca. 35 ka (Ivanova et al., 2016).

Lakatnik Cave ($43^{\circ} 05' 21''$ N, $23^{\circ} 23' 05''$ E), in Western Balkan Mountains, includes Late Pleistocene *U. spelaeus* remains from Trench I, dating at between 40 and 31 ka BP (Ginter et al., 2000; Stuart and Lister, 2011).

Bacho Kiro Cave ($42^{\circ} 56' 48''$ N, $25^{\circ} 25' 49''$ E), in the Balkan Mountains, yielded *U. spelaeus* remains, associated with a diverse Late Pleistocene fauna, *E. ferus*, *E. hydruntinus*, *Megaloceros giganteus*, *Capra ibex* and *Rupicapra rupicapra*, *Mammuthus primigenius* among others and dating to 61–51 ka BP (Fewlass et al., 2020; Pederzani et al., 2021; Martisius et al., 2022).

Borikovska Cave ($41^{\circ} 29' 08''$ N, $24^{\circ} 36' 21''$ E), located in the Rhodope Mountains, preserves a rich MIS 3 faunal assemblage dominated by *U. spelaeus*, alongside *U. arctos*, *Lynx lynx*, and *C. c. spelaea*, belonging to MIS 3 (Petrov and Stoev, 2007; Boev, 2021).

2.4. Central Balkans

Risovača Cave ($44^{\circ} 18' 07''$ N, $20^{\circ} 34' 56''$ E), in Šumadija (Balkans, central Serbia), near the city of Arandelovac, includes Late Pleistocene

faunal remains dominated by *U. spelaeus*, along with remains of *U. arctos*, *C. c. spelaea*, *P. spelaea*, *M. primigenius*, *Dicerorhinus hemitoechus*, *E. ferus*, *E. hydruntinus*, *Sus scrofa*, *C. elaphus*, etc. (Dimitrijević, 1997; Forsten and Dimitrijević, 1995).

Hadži Prodanova Cave ($43^{\circ} 37' 41''$ N, $20^{\circ} 14' 25''$ E), central Serbia, near the city of Ivanjica, contains a faunal assemblage dominated by *U. spelaeus*, among other mammal species; *C. ibex*, *C. lupus*, *U. arctos*, *R. rupicapra*, *C. elaphus*, *L. lynx* and *C. c. spelaea* (Mihailović and Mihailović, 2006; Bogićević et al., 2017). The analysed cave bear specimens derive from upper stratigraphic levels assigned to late MIS 3 based on associated rodent and large mammal assemblages (Bogićević et al., 2017).

Ušacka Cave ($43^{\circ} 21' 16.2''$ N, $19^{\circ} 57' 15.2''$ E), part of the Usacki Cave System, southwestern Serbia, near the city of Sjenica, yielded abundant Late Pleistocene *U. spelaeus* remains, with few remnants of *U. arctos*, *C. c. spelaea* and *C. elaphus* (Dimitrijević, 1997).

3. Materials and methods

3.1. Dental microwear

A total of 495 lower first molars (m1; $n = 495$; published $n = 92$, from Duñó-Iglesias et al., 2024a, newly added $n = 403$) of different ursid species have been selected for this work, from a wide range of individuals, including juveniles, prime adults, and old adults of both sexes, hence, ensuring a comprehensive and reliable assessment of the population's variability. The m1 specimens comprise teeth preserved within mandibles as well as isolated teeth. The studied Pleistocene Ursidae fossil collection taxonomically contains two different species: *U. spelaeus* ($n = 489$), and *U. arctos* ($n = 6$). The specimens belong to 16 populations, from 15 different bone assemblages distributed across 4 different regions: Romanian Carpathians ($n = 246$; published $n = 92$, newly added $n = 154$), Moldavian Plateau ($n = 96$), Western Balkan Mountains and Western Rhodopes ($n = 99$), Central Balkans ($n = 54$) (see Table 1 in Supplementary Materials; see Duñó-Iglesias, 2025 for the raw data).

For the microwear analysis, the preparation of the sample followed the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). For a detailed visual description of the process see Supplementary Materials, section 2.1. The features examined include counts of fine (characterized by narrow and shallow marks) and coarse (characterized by wider and deeper marks) scratches, small and large pits (circular or semicircular shapes of similar length and width, which can be classified as either small pits, which are characterized by being shallow and appearing as shiny, bright, white dots, or large pits, which are wider and deeper, and reflect less light), puncture pits (very deep and symmetrical crater-like morphology with regular edges), gouges (crater-like but with irregular edges), SWS (0 = predominant fine scratches, 1 = mixed of fine and coarse, 2 = predominantly coarse scratches) and hypercoarse scratches (very deep and wider than fine and coarse scratches, resulting in very low reflectivity and appearing as dark features, they have a distinctive "trench-like" shape with symmetrical edges; presence counted from >4).

Our findings were compared with the reference dataset of extant bear species established by Pappa et al. (2019) to reconstruct the palaeodiet of the fossil populations. The reference collection allowed us to directly compare extinct ursids with their closely related living counterparts, such as *U. arctos* from different regions including Kamchatka, Greece, Central Europe, Northern Europe, and North America, as well as *Ursus americanus* from North America. Both species show a wide range of dietary preferences, which include the consumption of vertebrates and invertebrates as well as a hard mast and soft mast diet. In addition, the hyper-carnivorous *Ursus maritimus* and the hyper-herbivorous *Ailuropoda melanoleuca* were added to the comparison. To avoid the possibility of inter-observer error, a single observer (PDI) performed the analysis on all specimens.

Photomicrographs were captured using an Invenio 5SII digital

Table 1

Samples which were AMS ^{14}C dated (mandible bone). The radiocarbon dates were calibrated using the IntCal13 calibration dataset (Reimer et al., 2013). The table includes data from multiple sites (e.g., Duruitoarea Veche, Butești, Buzdujeni, Saharna, and Urșilor), with most samples identified as *U. spelaeus* and one as *U. arctos* (Butești). Collagen yield (%), and calibrated radiocarbon ages (median, mean, and $2\sigma/95.4\%$ ranges in cal BP), C:N ratio and Cb% and Nb% are reported where available.

#Collection	#FTMC	#IPHES	Species	Material	Bone type	Site	Coll. Yield (%)	cal BP age (median)	Age range cal BP (2σ ; 95.4 %)	C:N ratio	%Cb	%Nb	
Valid													
Bx-B-63-5	FTMC-SJ30-6		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	6.71	42,585	42,891	3.18	44.81	16.43	
669	FTMC-NO87-5	23	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	4.98	42,464	42,723	3.15	30.09	11.15	
671	FTMC-NO87-3	24	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	2.67	40,044	40,534	3.11	31.93	11.96	
10,704/149	FTMC-TW42-2	73	<i>U. spelaeus</i>	Bone	Mandible	Butești	2.96	41,704	41,985	3.18	41.6	15.26	
10,704/185	FTMC-TW42-3	79	<i>U. arctos</i>	Bone	Mandible	Butești	4.17	41,333	41,702	3.19	34.21	12.53	
10,704/147	FTMC-TW42-6	75	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.37	34,972	35,298	3.27	45.76	16.33	
GB/2	FTMC-PH50-2	33	<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	7.15	43,713	44,350	3.18	40.13	14.71	
GB/5	FTMC-TW42-8		<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	12.37	43,599	44,145	3.18	46.9	17.23	
GB/7	FTMC-PH50-1		<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	3.7	43,508	44,161	3.19	42.39	15.52	
GB/1	FTMC-TW42-7		<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	1.58	42,399	42,582	3.19	47.18	17.26	
4	GB/4	FTMC-NO87-2	32	<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	2.5	40,557	40,974	3.13	34.5	12.86
GB/21	FTMC-PH50-3		<i>C. c. spelaea</i>	Bone	Mandible	Buzdujeni	3.59	46,576	47,776–45,725	3.14	31.29	11.63	
SH/8	FTMC-TW42-11		<i>U. spelaeus</i>	Bone	Mandible	Saharna	3.54	42,960	43,228	3.18	48.06	17.65	
SH/4	FTMC-TW42-10	15	<i>U. spelaeus</i>	Bone	Mandible	Saharna	2.9	42,353	42,517	3.2	46.87	17.09	
SH/31	FTMC-TW42-13		<i>U. spelaeus</i>	Bone	Mandible	Saharna	6.84	41,313	41,700	3.2	46.26	16.86	
SH/18	FTMC-TW42-12		<i>U. spelaeus</i>	Bone	Mandible	Saharna	3.18	41,306	41,712	3.2	47.11	17.15	
Discarded													
674	FTMC-NO87-4	22	<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	1.73	40,603	41,035	3.1	15.03	5.65	
670	FTMC-SJ30-4		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	2.14	36,677	37,101	3.16	23.76	8.76	
60 Kg2511-75	FTMC-SJ30-2		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	1.54	36,249	36,724	3.18	24.28	8.91	
673	FTMC-SJ30-3		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	1.16	31,859	32,224	3.23	26.03	9.39	
Kg 28 H2	FTMC-SJ30-1		<i>U. spelaeus</i>	Bone	Mandible	Duruitoarea Veche	1.36	31,020	31,161	3.24	13.45	4.85	
SH/11	FTMC-PH50-5	2	<i>U. spelaeus</i>	Bone	Mandible	Saharna	0.78	27,620	27,790	3.21	11.56	4.2	
SH/10	FTMC-PH50-4		<i>U. spelaeus</i>	Bone	Mandible	Saharna	2.02	37,228	37,737	3.13	17	6.33	
GB/3	FTMC-TW42-9		<i>U. spelaeus</i>	Bone	Mandible	Buzdujeni	0.29	40,883	41,222	3.23	44.51	16.09	
10,704/180	FTMC-TW42-1	57	<i>U. spelaeus</i>	Bone	Mandible	Butești	0.41	37,432	38,240	3.17	21.18	7.8	
10,704/189	FTMC-TW42-5	65	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.05	38,066	39,008	3.13	12.41	4.62	
10,704/168	FTMC-TW42-4	61	<i>U. spelaeus</i>	Bone	Mandible	Butești	1.31	35,335	35,713	3.2	18.71	6.83	

camera in extended focus mode and the Helicon Focus software to combine the images acquired at different focal planes to create a single image with an increased depth of field. The scale bars were incorporated using ImageJ software. Maps were generated using ArcGIS version 10.6.1 (Esri, 2018), while graphs, statistical tests, and analyses were performed using RStudio version 4.1.2 (RStudio Team, 2021).

3.2. Radiocarbon dating

For radiocarbon dating, we sampled cave bear ($n = 25$), brown bear ($n = 1$) and cave hyena ($n = 1$) mandible bones from: Buteşti ($n = 6$: *U. spelaeus*, $n = 5$, *U. arctos*, $n = 1$), Buzdujeni ($n = 6$: *U. spelaeus*, $n = 5$, *C. c. spelaea*, $n = 1$), Saharna ($n = 6$) and Duruitoarea Veche ($n = 9$). The AMS ^{14}C dating was performed at the Center for Physical Sciences and Technology (FTMC), in Vilnius (Lithuania). The preparation of bone samples involved standard acid-base-acid (ABA) procedure and collagen extraction. Firstly, bone samples were ultrasonicated in ultrapure water, dried, grinded and sieved to get the appropriately sized sample fraction (0.5–1 mm). Then samples were treated with 0.5 M hydrochloric acid (~18 h), 0.1–0.2 M sodium hydroxide (30 min–1 h), and 0.5 M hydrochloric acid (1 h). Bone collagen gelatinization was performed in pH 3 solution at 70 °C for 20 h. Gelatine solution was filtered using a cleaned Ezee-filter and freeze-dried. As quality of collagen is a critical factor in radiocarbon dating, it was monitored by carbon and nitrogen content in collagen, atomic C/N ratio determination and collagen yield. Samples were dated if the collagen yield was above 1 % and the C:N ratio of the collagen was between 2.9 and 3.5. The samples that deviate from these ratios were discarded. The obtained radiocarbon data were calibrated using the OxCal v4.4 software (Bronk Ramsey, 2009, 2020) against the INTCAL20 radiocarbon calibration curve (Reimer et al., 2020).

4. Results

4.1. Radiocarbon dating

A total of 27 AMS radiocarbon dates were obtained from the Moldavian Plateau region, including specimens of *U. spelaeus* ($n = 25$), *U. arctos* ($n = 1$), and *C. c. spelaea* ($n = 1$). Of these, 24 radiocarbon dates yielded sufficient collagen ($\geq 1\%$) for reliable analysis, while 3 were discarded due to insufficient yield ($< 1\%$) or unavailable yield data (van Klinken, 1999; Brock et al., 2010). Moreover, of the remaining 24 dated samples, 8 exhibited poor chemical preservation, evidenced by %Cb values below 30 % and %Nb below 12 %, the lower thresholds for valid AMS collagen dating as recommended by van Klinken (1999) and van der Plicht and Palstra (2016), and were therefore discarded. Hence, 16 dates were thus retained as valid (Table 1; Fig. 2). Calibrated valid ages range from ca. 46 ka cal BP (Buzdujeni site) to ca. 35 ka cal BP (Buteşti).

4.2. Dental microwear

A total of 315 lower first molars (m1) were selected for analysis out of 495 examined specimens from four regions across South-Eastern Europe (Table 2; Fig. 3). From the Romanian Carpathians, 160 m1s were suitable, including *U. spelaeus* from Ursilor ($n = 54$), Cioclovina ($n = 35$), Muierilor ($n = 32$), Oase ($n = 26$), Bisericuța ($n = 5$), Onceasa ($n = 3$), and La Adam ($n = 2$), as well as *U. arctos* from Bisericuța ($n = 1$) and ACCG ($n = 2$). In the Moldavian Plateau, 58 m1s were included, comprising *U. spelaeus* from Trinca ($n = 16$), Saharna ($n = 18$), Buzdujeni ($n = 11$), Duruitoarea Veche ($n = 6$), Buteşti ($n = 2$), and *U. arctos* from Trinca ($n = 5$). Western Balkan Mountains and Western Rhodopes yielded 65 suitable m1s, from *U. spelaeus/ingressus* individuals at Borikovska ($n = 48$), Magura ($n = 8$), Bacho Kiro ($n = 5$), and Lakatnik ($n = 4$). In Central Balkans, 32 m1s were included from *U. spelaeus* specimens at Ušacka ($n = 11$), Hadži Prodanova ($n = 11$), and Risovača ($n = 10$). Across all regions, 180 specimens were excluded due to the absence of wear facets in juvenile individuals (Rivals et al., 2007) or due to

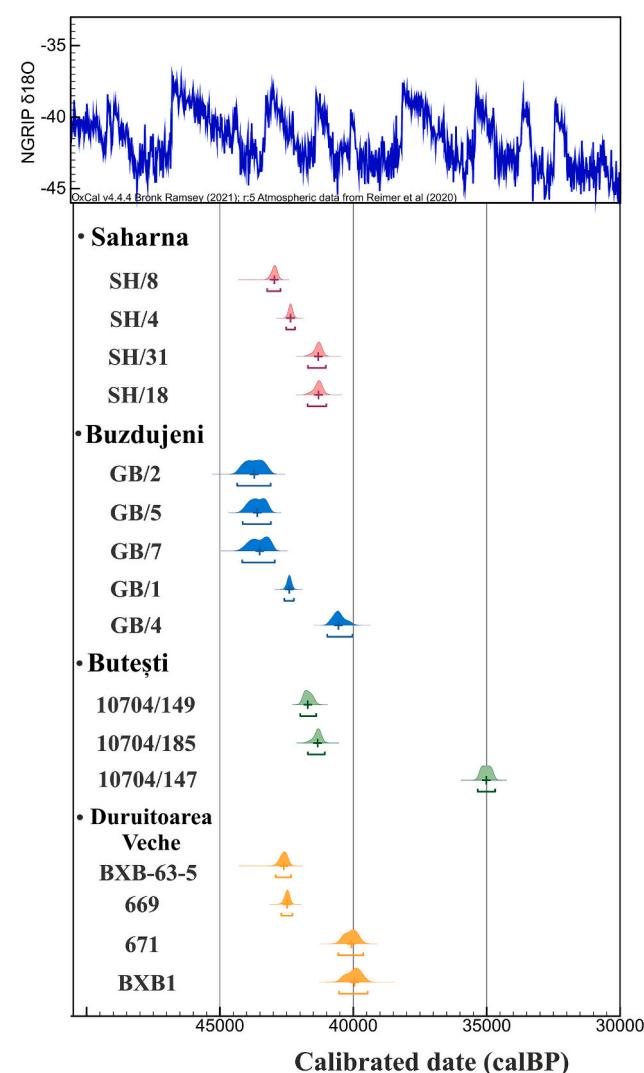


Fig. 2. Posterior probability distributions of calibrated AMS ^{14}C dates for *U. spelaeus* and *U. arctos* specimens from four key sites in Moldavian Plateau: Saharna (red), Buzdujeni (blue), Buteşti (green), and Duruitoarea Veche (orange). Calibrations were performed using OxCal v4.4 and the IntCal20 atmospheric curve (Reimer et al., 2020). The top panel shows the NGRIP $\delta^{18}\text{O}$ climate record as a proxy for palaeo-temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant taphonomic damage affecting occlusal surfaces (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2024). Excluded samples included *U. spelaeus* from Ursilor ($n = 16$), Cioclovina ($n = 12$), Muierilor ($n = 44$), Oase ($n = 8$), Onceasa ($n = 3$), ACCG ($n = 3$), Saharna ($n = 3$), Buzdujeni ($n = 8$), Duruitoarea Veche ($n = 4$), Buteşti ($n = 23$), Borikovska ($n = 28$), Magura ($n = 4$), Bacho Kiro ($n = 1$), Lakatnik ($n = 1$), Ušacka ($n = 7$), Hadži Prodanova ($n = 3$), and Risovača ($n = 12$).

The cave bear populations exhibit regional variation (Table 2; Fig. 3). A description of microwear patterns and their comparison with the reference dataset established by Pappa et al. (2019), organised by geographic region, is presented below, while a detailed population-level analysis is provided in the Supplementary Materials (section 3).

4.2.1. Romanian Carpathians

Microwear analysis of *U. spelaeus* from the Romanian Carpathians reveals notable variability among sites, for both number of total scratches (NTS) and number of total pits (NTP) (Fig. 4A). Furthermore,

Table 2

Comparison of the dental microwear results of the fossil populations of cave bear (*U. spelaeus*) and brown bear (*U. arctos*) from the Romanian Carpathians, Moldavian Plateau, Western Balkan Mountains and Western Rhodopes and Central Balkans with the reference dataset of extant bear species of *U. arctos*, *U. americanus*, *A. melanoleuca* and *U. maritimus* established by Pappa et al. (2019). Abbreviations: N = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

Region	Site	Species	N	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct												
Romanian Carpathians												
	Urşilor	<i>U. spelaeus</i>	54	10.58	8.84	19.55	1.04	2.31	20.04	1.27	23.59	0.94
	Cioclovina	<i>U. spelaeus</i>	35	15.29	5.33	20.88	0.37	1.67	27.17	2.34	31.3	1.03
	Muierilor	<i>U. spelaeus</i>	32	16.75	3.81	21.24	0.22	1.64	30.34	3.14	35.17	1.34
	Oase	<i>U. spelaeus</i>	26	13	10.05	23.05	1.04	3.6	19.35	2.87	25.81	1.12
	Bisericuṭa	<i>U. spelaeus</i>	5	14.27	9.1	23.37	0.8	2.8	19.03	2.5	24.33	0.6
		<i>U. arctos</i>	1	6	21	27	2	27	9	2	38	1
	Onceasa	<i>U. spelaeus</i>	3	15.17	10	25.17	1	5	17.33	1	23.17	0
	La Adam	<i>U. spelaeus</i>	2	16	4	20	0.5	2	25	2	29	0
	ACCG	<i>U. arctos</i>	2	10.5	14.75	25.25	1.5	5.5	14.25	1.5	21.25	1
Moldavian Plateau												
	Trinca	<i>U. spelaeus</i>	16	19.91	0.63	20.53	0	0.5	11.05	0.44	11.99	0.09
		<i>U. arctos</i>	5	16.7	3.6	20.2	0.4	2	18.8	0.4	21.2	1.7
	Saharna	<i>U. spelaeus</i>	18	16.54	1.97	18.45	0.06	0.5	33.4	3.11	36.47	0.28
	Buzdujeni	<i>U. spelaeus</i>	11	17.41	3.82	27.45	0.36	0.68	24.59	2.59	27.45	0.14
	Duruitoarea Veche	<i>U. spelaeus</i>	6	19	3	22	0.29	2.42	30.21	0.64	33.28	0.57
	Buteşti	<i>U. spelaeus</i>	2	19.25	5	24.25	0.5	0.5	36.5	0.25	37.25	0
W-Balkans and W-Rhodopes												
	Borikovska	<i>U. spelaeus</i>	48	11.53	2.55	14.07	0.19	2.34	30.63	0.64	33.61	1.48
	Magura	<i>U. ingressus</i>	8	11.94	4.38	15.06	0.38	1.44	25.4	1.31	28.15	1.29
	Bacho Kiro	<i>U. spelaeus</i>	5	10	3.6	14.1	0.2	2	31.67	1.7	35.37	0.9
	Lakatnik	<i>U. spelaeus</i>	4	11.88	0.38	12.5	0	0.25	20.63	0.13	21	0.5
Central Balkans												
	Ušačka	<i>U. spelaeus</i>	11	10.41	5.14	15.48	0.64	1.09	20.14	0.05	21.27	0.27
	Hadži Prodanova	<i>U. spelaeus</i>	11	13.86	2.27	16.29	0	1.23	22.02	0.14	23.38	0.59
	Risovača	<i>U. spelaeus</i>	10	17.35	0.9	18.15	0	0.65	28	0.3	28.95	0.4
Extant												
	North America	<i>U. americanus</i>	9	13.56	2.56	16.12	0	5.44	19	3	27.44	0
	Greece	<i>U. arctos</i>	4	13	7	20	0.5	9.25	8.5	2.25	20	2
	Central Europe	<i>U. arctos</i>	10	17.5	3.4	20.9	0	5.4	22.5	8.3	36.2	2.1
	North America	<i>U. arctos</i>	8	18.25	3	21.25	0	6.75	18.38	3.25	28.38	0.25
	Kamchatka	<i>U. arctos</i>	23	16.22	3.83	20.05	0.1	6.96	19.78	4.78	31.52	0.35
	Northern Europe	<i>U. arctos</i>	9	15.78	3.78	19.56	0	6.44	23.33	2.67	32.44	0.22
	Eastern Asia	<i>A. melanoleuca</i>	4	19.25	0	19.25	0	8.5	46.25	0	54.75	0
	Polar circle	<i>U. maritimus</i>	13	11	3.21	14.23	2.79	4.5	16.21	0.07	20.15	0

all populations presented puncture pits (NPP) and gouges (NG) (Fig. 3A-B-C). A detailed description of dental microwear patterns can be found in the Supplementary Materials, section 3.1., along with extended population-level comparisons. Multivariate analysis of microwear patterns (i.e., NFS, NCS, NSP, NLP, SWS, NG and NPP) using PERMANOVA revealed significant differences between populations from the Romanian Carpathians ($R^2 = 0.276$, $p = 0.001$), indicating marked dietary variation across sites. Importantly, the lack of significant differences in within-group dispersion ($p = 0.174$) suggests that these differences reflect genuine shifts in population-level dietary preferences rather than variation in dietary breadth within populations. Permutation-based tests further confirmed that no individual population exhibited unusually high or low intra-population variability (all $p > 0.1$), reinforcing the conclusion that dietary divergence occurred primarily between, rather than within, populations in the Romanian Carpathians (see Duñó-Iglesias (2025) for underlying statistical information).

When compared with extant bear populations, the microwear scores (NTS, NTP, NG, NPP) and the distribution of scratches (coarse vs fine) and pits (small vs large) size are similar to omnivorous *U. arctos* from Greece, Central and Northern Europe, Kamchatka and North America as well as *U. americanus* from North America (a detailed population by population description of similarities with reference dataset bear populations can be found in Supplementary Materials, section 3.1.1.).

The Pleistocene *U. arctos* from Bisericuṭa displays notable differences with contemporaneous *U. spelaeus* populations as well as with reference ursids, due to displaying a predominance of coarse over fine scratches (opposed to *U. spelaeus* and extant omnivorous bears). Finally, the two

Holocene-age *U. arctos* from ACCG, present similarities with fossil *U. spelaeus*, due to a predominance of fine scratches over coarse and small pits over large ones (see Supplementary Materials, Fig. 3).

The fossil populations occupy distinct eco-regions within the bivariate plot (Fig. 4A). Urşilor, Bisericuṭa, and Oase are primarily distributed within the soft mast-dominated region, situated near the omnivorous *U. arctos* population from Greece. However, their error bars extend into regions associated with omnivorous bears exhibiting vertebrate-dominated diets, overlapping with populations from northern latitudes, such as *U. arctos* from North America. Notably, Oase displays the most extensive extension into the vertebrate-dominated region, overlapping with *U. arctos* populations from Kamchatka and Northern Europe. The Cioclovina population falls within the vertebrate-dominated region but its error bars extend into both the soft mast- and hard mast-dominated regions, exhibiting the most extensive variability among populations. This wide range mirrors the dietary breadth displayed by *U. arctos* from Kamchatka and Northern Europe, which are characterized by highly variable omnivorous diets. Finally, the Muierilor population is located within the vertebrate-dominated eco-region, overlapping with northern omnivorous bears, while its error bars extend significantly into the hard mast-dominated region, overlapping with *U. arctos* from Central Europe.

The extinct ursid populations exhibit distinct distributions within the CA plot (Fig. 4B). The *U. spelaeus* from the Romanian Carpathians displays a wide range of distribution, in comparison to any other species represented in the analysis. The different *U. spelaeus* populations show variability in their placement on the plot, reflecting differences based on

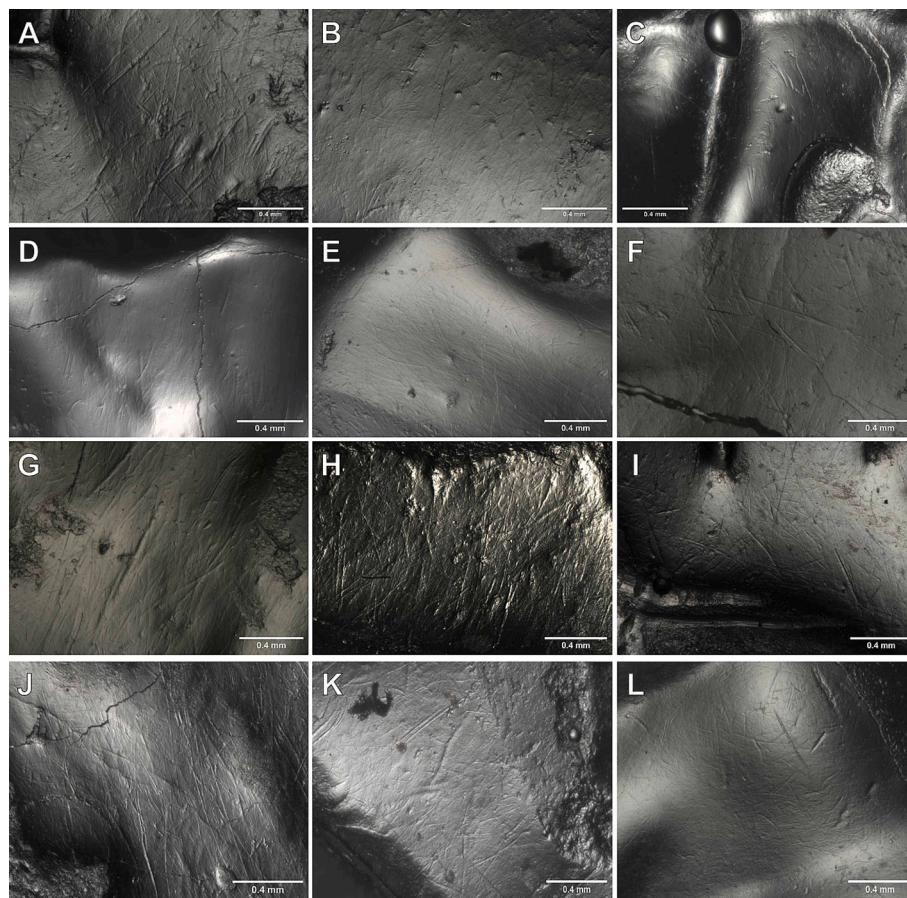


Fig. 3. Photomicrographs (at $\times 35$ magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* sensu lato from: Romanian Carpathians. A: Muierilor (#PM/R6-0-I-X6) individual displaying gouges; B: Cioclovina (#18il/107) individual displaying puncture pits; C: Cioclovina (#18il/101) individual displaying puncture pits. Moldavian Plateau. D: Trinca (#Tr-I-80-41) individual displaying puncture pits and a pattern dominated by fine over coarse scratches; E: Saharna (#SH/3-31/55) individual exhibiting puncture pits and predominantly fine scratches; F: Buzdjeni (#ERIS-25) individual displaying high counts of coarse scratches as well as presence of gouges. Western Balkan Mountains and Western Rhodopes. G: Borikovska (#116C) individual displaying hypercoarse and coarse scratches, along with small and large pits; H: Magura (#MII/53) individual exhibiting gouges, large pits and a clear predominance of coarse over fine scratches; I: Măgura (#M3/1532) individual exhibiting both coarse and fine scratches, along with large and small pits, and gouges. Central Balkans. J: Risovača (#RIS92/284) individual, displaying fine and coarse scratches. K: Ušačka (#85/1048) specimen displaying a mix of coarse and fine scratches, as well as gouges. L: Hadži Prodanova (#HPP04/172/5) specimen, exhibiting fine and coarse scratches and one hypercoarse scratch. Scale bar = 0.4 mm.

their cave of origin. Within each cave population, some groups cluster tightly, indicating more uniform diets, while others are more dispersed, suggesting greater dietary diversity. The fossil *U. arctos* populations, are positioned to the right along the x-axis and above the y-axis (Fig. 4B). This placement indicates a higher number of coarse scratches relative to fine scratches, and a relatively high number of large pits in comparison to most *U. spelaeus* individuals. However, there is a certain degree of overlap between MIS 3 *U. arctos* and *U. spelaeus* from the Romanian Carpathians.

When compared to extant bear populations, the majority of *U. spelaeus* specimens from the Urşilor and Oase populations cluster on the right side of the x-axis, separating from the extant omnivorous bear populations (*U. arctos* and *U. americanus*) while some of them display an overlap with *U. maritimus* (Fig. 4B). This positioning can be attributed to their higher number of coarse scratches and, consequently, a higher SWS compared to the omnivorous reference bears, i.e., a higher preference for hard object consumption. However, a significant portion of the individuals from the Urşilor ($n = 6$: 11.1 %) and Oase ($n = 6$: 23.1 %) populations overlap with extant omnivorous bear species.

Although there is a certain degree of differentiation from extant bears, and some populations overlap with *A. melanoleuca* (with a graminivorous tough diet), a significant proportion of *U. spelaeus* individuals fall within the range of *U. americanus* and *U. arctos* populations

from Kamchatka, North America, and the northern regions of Europe, as well as with the central European population (Fig. 4B); all with a shared omnivorous nature including a wide range of items in their diets (soft and hard mast plants, as well as vertebrates). Finally, some individuals overlap with *U. maritimus* with a higher number of coarse scratches (see Supplementary Materials, section 3.1.3. for a detailed population by population description).

The *U. arctos* individual from Bisericuța ($n = 1$; dating to the Pleistocene), plot on the right side, overlapping with certain Oase and Urşilor cave bear individuals (Fig. 4B). Among extant reference bears, this directional placement is exclusively associated with the hypercarnivorous *U. maritimus*, whose diet is characterized by a high proportion of vertebrates. Thus, we infer that the *U. arctos* individual analysed here similarly consumed a diet rich in hard objects, as driven by their high SWS. Nevertheless, two individuals from ACCG ($n = 2$) which date of medieval times, present a more diverse distribution, with one falling closer to the left side of the plot, while the other falls not far from the Pleistocene *U. arctos* from Bisericuța within the right side of the plot (Fig. 4B). Nevertheless, all *U. arctos* analysed tend to differentiate from Pleistocene cave bears and extant reference bears. Furthermore, due to their statistically null ($n = 1$) in case of Bisericuța and statistically insignificant ($n = 2$) due to low number of ACCG, their ecological niche cannot be inferred properly as lacking more individuals.

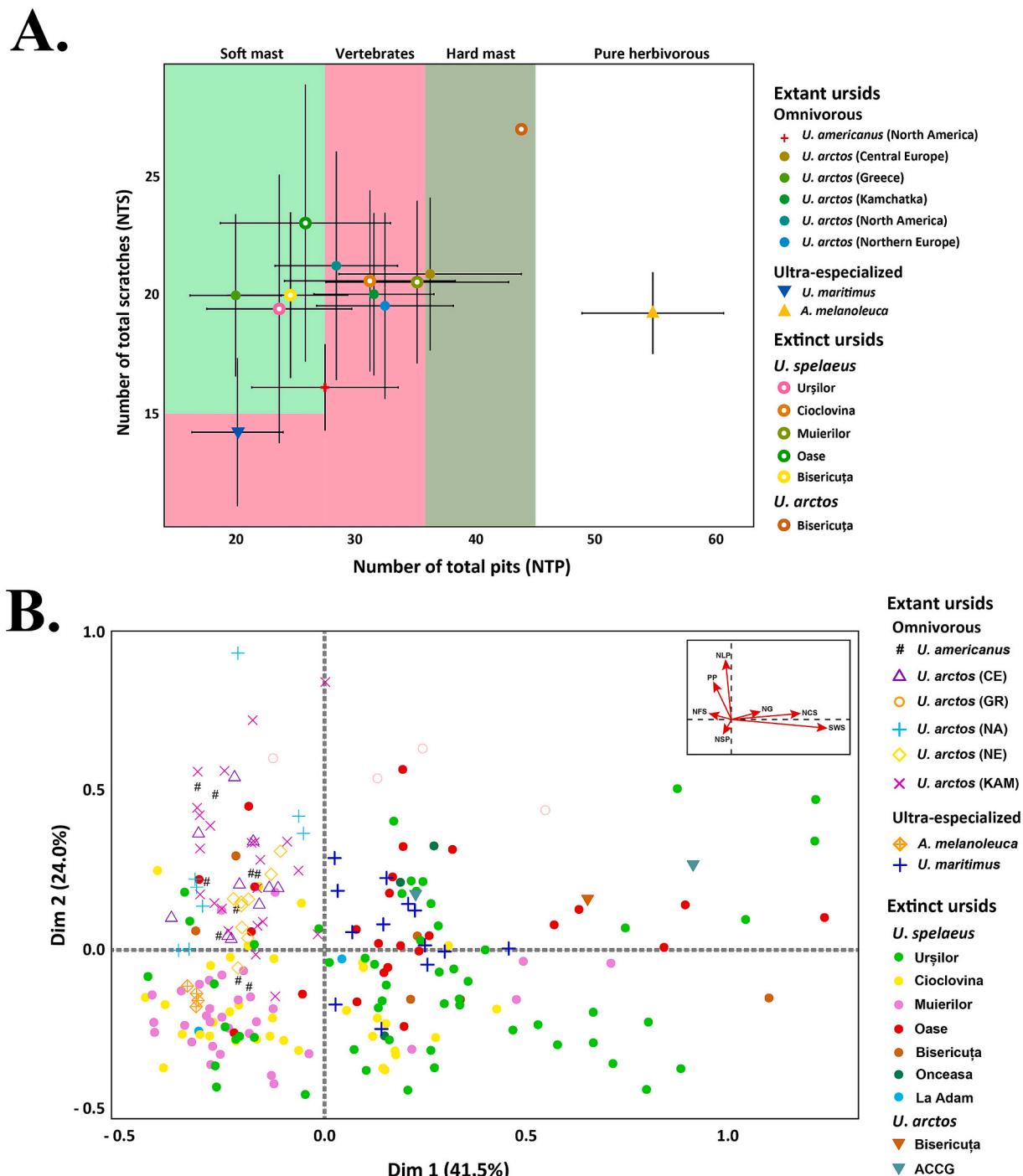


Fig. 4. Romanian Carpathians: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from the Romanian Carpathians with a reference dataset of extant ursids established by Pappa et al. (2019). Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2.2. Moldavian Plateau

Microwear analysis of *U. spelaeus* from Moldavian Plateau reveals notable differences between cave sites, regarding NTS and NTP (Table 2). However, the predominance of fine over coarse scratches results in consistently low SWS across all populations (Table 2). Microwear analysis of fossil bear populations from the Moldavian

Plateau also reveals substantial inter-population variability in both the total number of scratches (NTS) and total number of pits (NTP). A detailed description of dental microwear patterns can be found in the Supplementary Materials, section 3.2, along with extended site-level comparisons.

Multivariate analysis of microwear variables (NFS, NCS, NSP, NLP,

SWS, NG, and NPP) using PERMANOVA showed statistically significant differences between populations ($R^2 = 0.412$, $p = 0.001$), suggesting marked dietary variation across sites. However, the test for homogeneity of dispersion yielded significant results ($p = 0.021$), implying that differences among populations may be partially influenced by variation in dietary breadth. Nevertheless, post hoc permutation tests for intra-population variance revealed that none of the individual populations displayed significantly high or low variability (all $p > 0.1$), suggesting that the observed differences likely reflect genuine shifts in dietary preferences across sites. These findings highlight the complexity of ecological behaviours among fossil bear populations in the region (see Duñó-Iglesias (2025) for underlying statistical information).

Regarding puncture pits, Saharna (NPP = 3.11) and Buzdujeni (NPP = 2.59) recorded high values, while Duruitoarea Veche (NPP = 0.64), and Buteşti (NPP = 0.25) also displayed them. Regarding gouges, all populations exhibit values ranging from low gouge counts, such as Duruitoarea Veche (NG = 0.57) and Saharna (NG = 0.28), to negligible levels: Trinca (NG = 0.09), Buzdujeni (NG = 0.14). While no gouges were observed in Buteşti (NG = 0.00). The microwear patterns of *U. spelaeus* populations from the Moldavian Plateau exhibit strong similarities to those of omnivorous bears, specifically *U. americanus* and *U. arctos* from North America, Kamchatka, and Central Europe (see Supplementary Materials, section 3.2. for a more detailed site by site description).

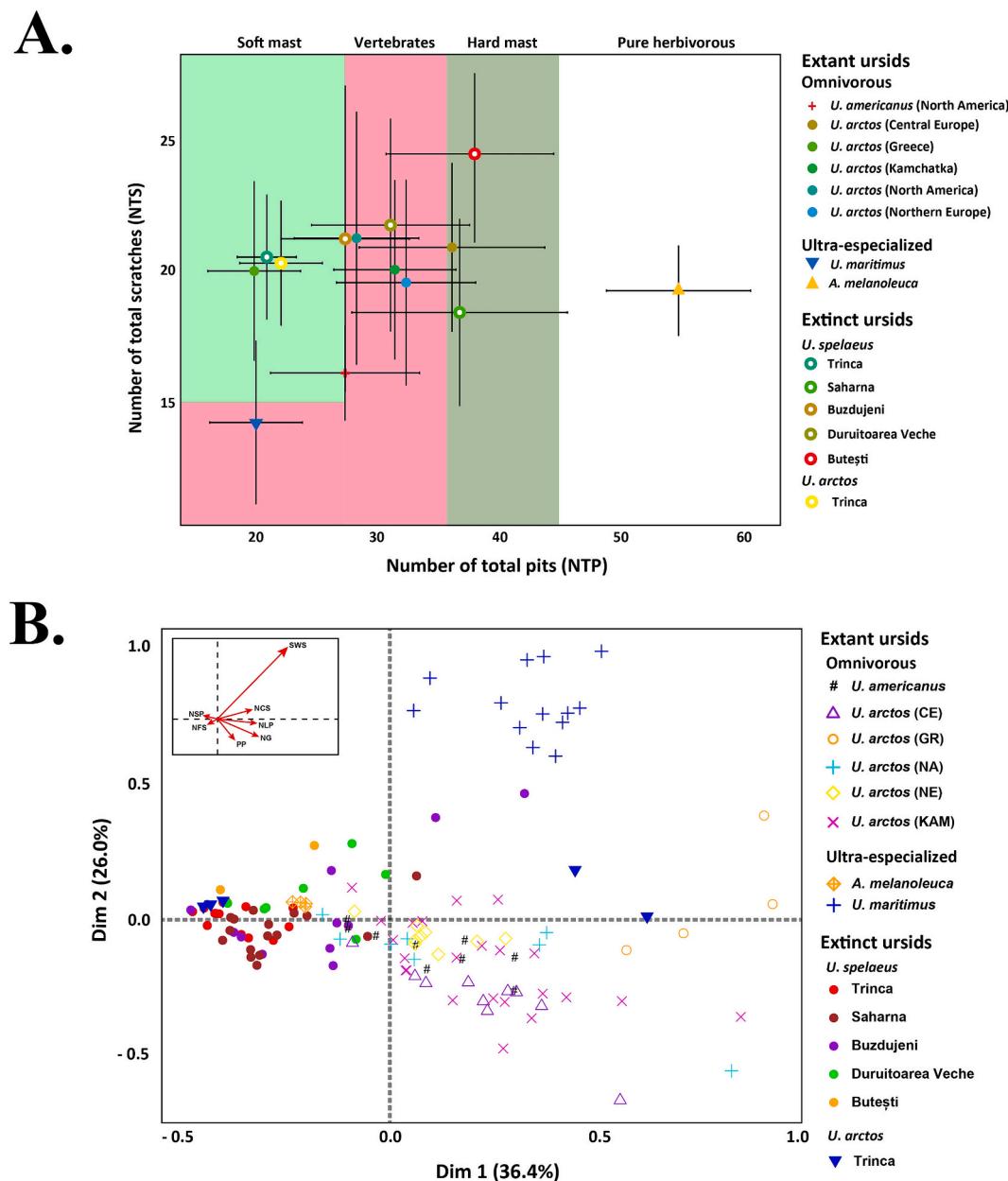


Fig. 5. Moldavian Plateau: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* and *U. arctos* from the Moldavian Plateau with a reference dataset of extant ursids established by Pappa et al. (2019). Auxiliary plot in the upper left illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Despite the limited sample size ($n = 5$), the *U. arctos* population from Trinca shows a different microwear pattern than co-occurring *U. spelaeus* from Trinca (regarding SWS and NTP), but comparable with contemporaneous populations of *U. spelaeus* of the same region. In comparison to referential bears, it shows similar values to omnivorous *U. arctos* populations.

The fossil populations from the Moldavian Plateau are distributed across distinct ecological regions in the bivariate plot (Fig. 5A). *U. spelaeus* and *U. arctos* from Trinca fall within the soft mast-dominated

region, closely aligning with omnivorous *U. arctos* from Greece. *U. spelaeus* from Buzdjeni lies near the soft mast–vertebrate boundary, close to *U. arctos* from Kamchatka, which consumes high amounts of vertebrates within a soft mast-based omnivorous diet. Buzdjeni overlaps with *U. americanus* from North America, with an omnivorous diet including soft mast and vertebrates, particularly fish. *U. spelaeus* from Duruitoarea Veche is positioned in the vertebrate-dominated region, overlapping with *U. arctos* from Northern Europe and Kamchatka, with error bars extending into the soft and hard mast regions, overlapping

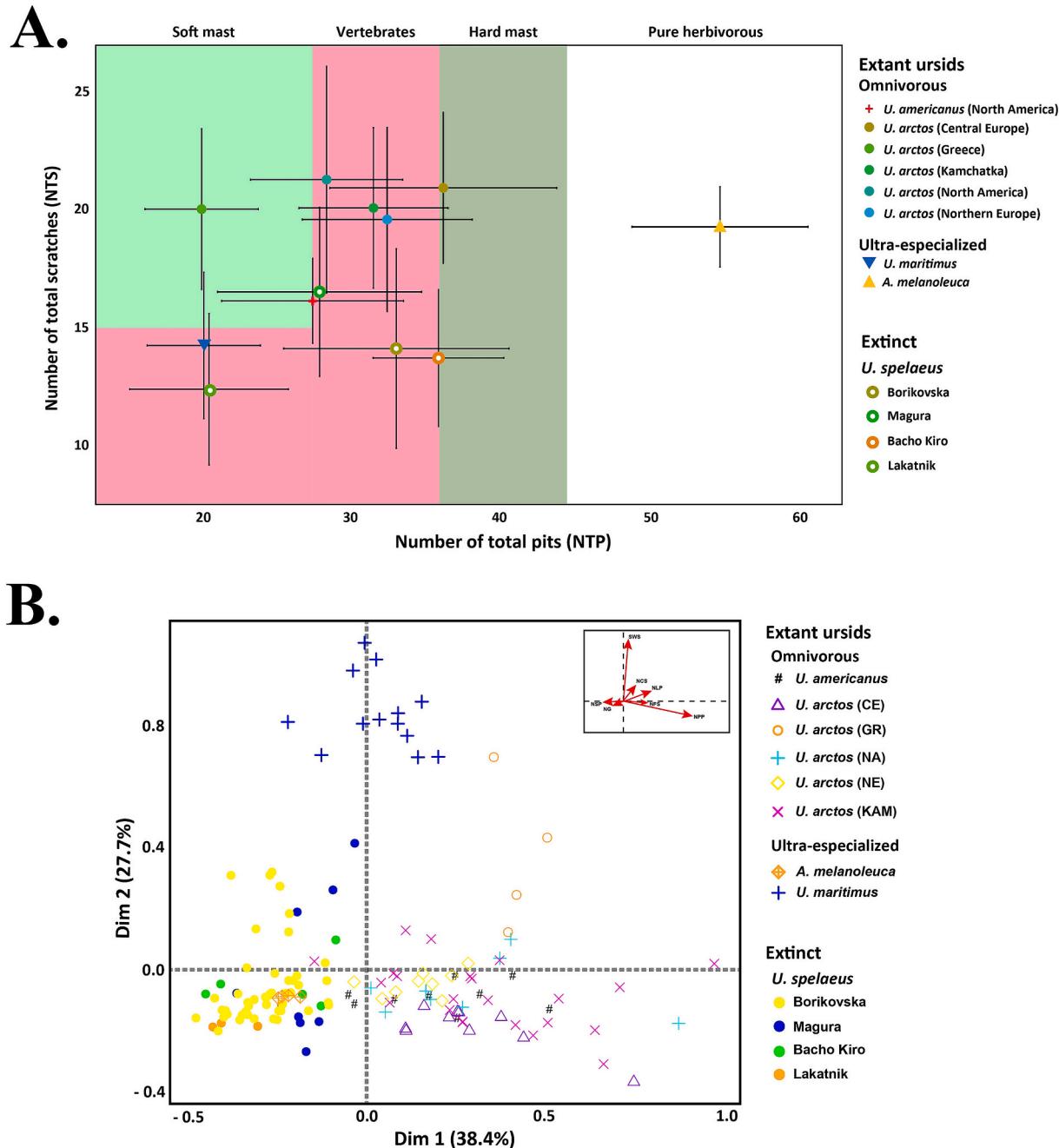


Fig. 6. Western Balkan Mountains and Western Rhodopes: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* from the Western Balkan Mountains and Western Rhodopes with a reference dataset of extant ursids established by Pappa et al. (2019). Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with *U. arctos* from Central Europe, with variable omnivorous diet rich in vertebrates. *U. spelaeus* from Saharna and Butești fall within the hard mast-dominated region, overlapping with *U. arctos* from Central Europe and extending into the vertebrate region, with omnivorous northern hemisphere bears with high vertebrate intake. While Saharna aligns more closely with *U. americanus*, Despite the small sample size ($n = 2$), the elevated scratch counts and high pit density of the Butești population suggest a hard mast-based omnivorous diet (Fig. 5A).

The fossil populations of *U. spelaeus* exhibit a clustered (and concentrated) distribution within the CA plot, with most *U. spelaeus* individuals positioning in the lower-left quadrant of the plot, distinguishing them from extant omnivorous bears and overlapping them close to *A. melanoleuca* with a graminivorous diet based on abrasive foliage. While the *U. spelaeus* population from Trinca clusters close to *A. melanoleuca* (Fig. 5B), indicating a uniform diet focused on soft mast consumption, the populations from Saharna, Duruitoarea Veche, and particularly Budzujeni exhibit a broader distribution, extending towards the right side of the plot, overlapping with the dietary range of omnivorous bear species (Fig. 5B; see Supplementary Information, section 3.2.3. for a detailed comparison). This distribution further supports the presence of dietary variability within the *U. spelaeus* populations from Moldavian Plateau. The fossil *U. arctos* population from Trinca exhibits a broad distribution on the CA plot (Fig. 5B). While three individuals cluster near *A. melanoleuca*, alongside other *U. spelaeus* specimens, two individuals deviate significantly towards the lower-right region of the plot, overlapping with the dietary range of omnivorous bear species. The *U. arctos* population from Trinca ($n = 5$) displays a microwear pattern distinct from the coexisting *U. spelaeus*, with notably higher values in scratch width (SWS), number of pits (NTP), and gouges (NG), despite similar total scratch counts. These results suggest dietary differences between the two taxa at the same site, as can be observed in the CA plot (Fig. 5B; see Supplementary Information, section 3.2.2 and 3.2.3. for a detailed comparison).

4.2.3. Western Balkan Mountains and Western Rhodopes

The microwear analysis of the cave bear populations from Western Balkan Mountains and Western Rhodopes reveals that the total number of scratches (NTS) and the total number of pits (NTP) varies significantly among the different cave populations, likewise in puncture pits (NPP) and gouges (NG) (Table 2; see Supplementary Materials, section 3.3. for a more detailed site by site description). It is important to note that the Borikovska cave bear specimens exhibited a notable presence of hypercoarse scratches (Fig. 3G), with a mean value of 0.5, observed in 30 % of the individuals ($n = 48$).

Microwear analysis of fossil bear populations from the Western Balkans and Western Rhodopes reveals considerable variability in both total scratches (NTS) and pits (NTP) (Fig. 6A). Multivariate analysis of microwear features (NFS, NCS, NSP, NLP, SWS, NG, and NPP) using PERMANOVA identified statistically significant differences between populations ($R^2 = 0.195$, $p = 0.003$), suggesting notable dietary divergence across sites. Importantly, the test for homogeneity of dispersions was not significant ($p = 0.156$), indicating that these differences are unlikely to result from variation in dietary breadth within populations. This interpretation is supported by permutation-based tests of intra-population variance, which showed no population exhibited significantly high or low variability (all $p > 0.1$). While the degree of inter-population divergence is slightly lower than that observed in the Romanian Carpathians and Moldavian Plateau, the results nonetheless point to consistent patterns of regional dietary differentiation among *U. spelaeus* populations (see Duñó-Iglesias (2025) for underlying statistical information).

Regarding the comparison with the extant bears reference dataset, the *U. spelaeus* populations from the Western Balkans and Western Rhodopes most closely resemble extant *U. arctos* from Central, Northern Europe, Kamchatka, and Greece, particularly in their high pit counts and moderate to high coarse scratch and gouge values, indicating similar

omnivorous diets including hard and soft mast, while vertebrate consumption cannot be ruled out. Additionally, their low NFS and NPP counts align them more closely with *U. maritimus*, suggesting reduced abrasive plant matter consumption relative to the compared extant omnivorous bears (see Supplementary Materials, section 3.3.1. for a more detailed population by population description).

The cave bear populations from Western Balkan Mountains and Western Rhodopes display intra-population variability among them (Fig. 6A), although they predominantly cluster within the vertebrate-dominated region of the bivariate plot (see Supplementary Materials, section 3.3.2. for a more detailed site by site description). Regarding the CA plot, the fossil cave bear populations from this region are clustered in the lower-left region of the plot, occupying the negative space along both the x- and y-axes (Fig. 6B). This placement differentiates them from extant omnivorous bears and makes them fall close to *A. melanoleuca* and *U. arctos* from Northern Europe and *U. americanus*. Nevertheless, those exhibit partial overlap along the y-axis (explaining 27.7 % of the variance) with omnivorous bear populations such as *U. arctos* from Kamchatka, Central Europe, North America, Northern Europe and *U. americanus* (see Supplementary Materials, section 3.3.3. for a more detailed site by site description).

4.2.4. Central Balkans

Microwear analysis of *U. spelaeus* populations from the Central Balkans reveals that the total number of scratches (NTS) and pits (NTP) varies among different cave populations (Table 2). Variation is also observed in the scratch width, pit size, puncture pits (NPP), and gouges (NG). PERMANOVA results reveal statistically significant differences between populations ($R^2 = 0.522$, $p = 0.001$), indicating the strongest inter-population divergence observed among the regions analysed. Importantly, the test for homogeneity of dispersion was not significant ($F = 0.38$, $p = 0.687$), confirming that the observed differences reflect genuine shifts in population-level dietary preferences, rather than variation in dietary breadth within populations. This interpretation is further supported by permutation-based tests for intra-population variance, which showed that no population exhibited significantly high or low variability (all $p > 0.05$). Notably, while the Romanian Carpathians, Moldavian Plateau as well as the Western Balkans and Western Rhodopes also exhibited significant dietary variation with similarly non-significant dispersion (i.e., all populations showed comparable levels of within-group dietary consistency). These findings position the Central Balkans as a region of strong dietary differentiation among fossil bear populations while dietary consistency was maintained within the same localities (see Duñó-Iglesias (2025) for underlying statistical information).

Finally, regarding hypercoarse scratches, those were only displayed by Risovača population specimens, although in low numbers ($n = 3$: 30 %), as well as for Ušačka ($n = 1$: 9 %; Fig. 3K). The *U. spelaeus* populations from the Central Balkans show the greatest similarity in microwear scores with *U. americanus*, and *U. arctos* from Greece, Kamchatka, and Central Europe, as well as with *U. maritimus* (see Supplementary Materials, section 3.4.1. for a more detailed population by population description).

The *U. spelaeus* populations from Central Balkans exhibit a degree of intra-population variability (Fig. 7A); however, their distribution on the bivariate plot remains clustered near the boundary between vertebrate-dominated and soft-mast-dominated dietary regions (see Supplementary Materials, section 3.4.2. for a more detailed population by population description).

The *U. spelaeus* populations from Hadži Prodanova and Ušačka are positioned in the lower-most section of the soft-mast-dominated region, with total pit values (x-axis) overlapping those of *U. arctos* from Greece and *U. maritimus* (Fig. 7A). Additionally, the error bars for Hadži Prodanova extend into the range of *U. americanus* within the soft-mast-dominated region. Despite this, their relatively low total scratch counts (y-axis) bring them closer to *U. maritimus*, while their error bars

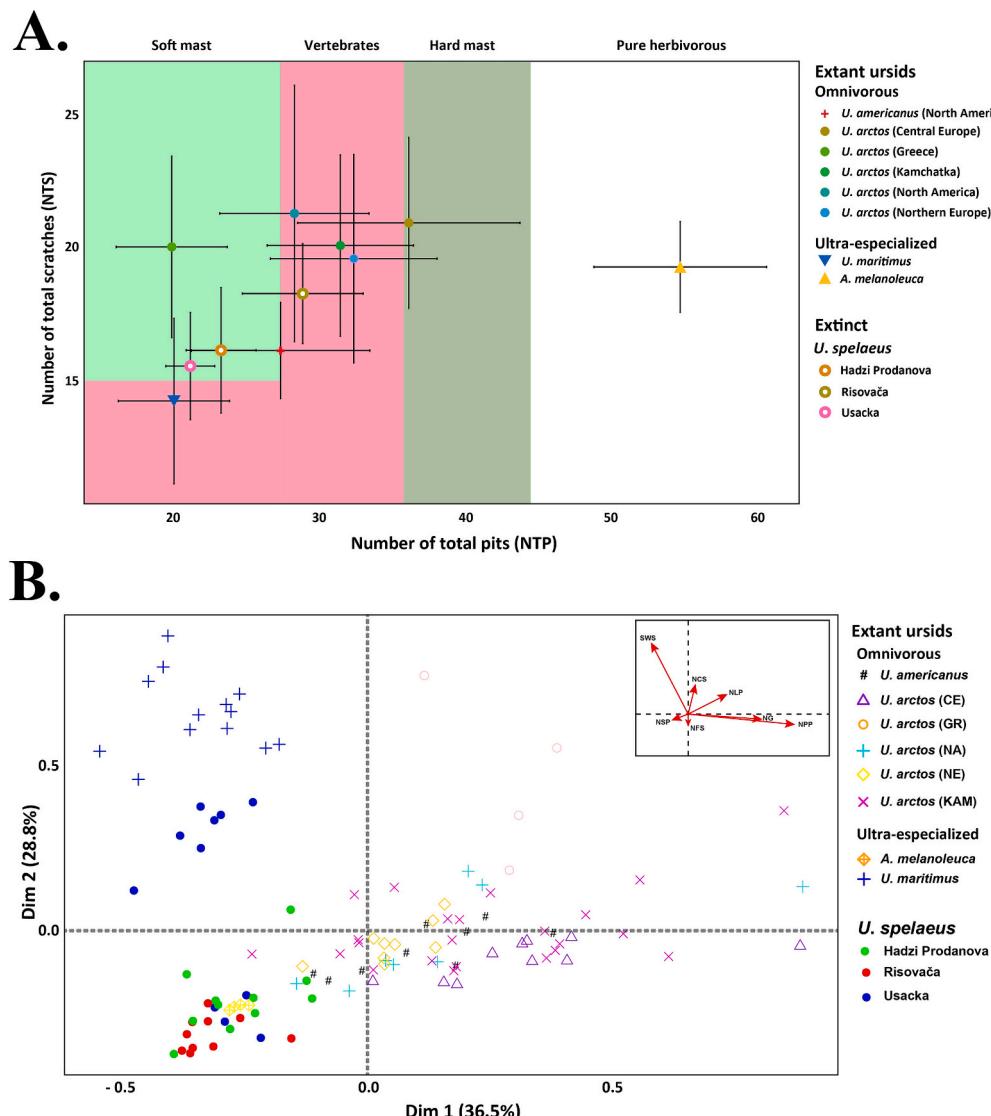


Fig. 7. Central Balkans: A. Bivariate plot of the number of total pits (NTP) and the number of total scratches (NTS) comparing the extant bear populations and the fossil populations. Highlighted are four distinct eco-regions (soft mast, hard mast, vertebrates, and pure herbivorous) based on the predominant diet of extant bear populations as established by Pappa et al. (2019). B. Correspondence analysis (CA) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares fossil populations of *U. spelaeus* from the Central Balkans with a reference dataset of extant ursids established by Pappa et al. (2019). The direction and contribution of the variables in the CA plot are depicted in the top-right inset of the figure. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. Abbreviations: CE = Central Europe; GR = Greece; NA = North America; NE = Northern Europe; KAM = Kamchatka. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extend towards the vertebrate-dominated region. In contrast, the Risovača population falls within the vertebrate-dominated region, positioned higher on the y-axis, overlapping with *U. arctos* from Northern Europe, Kamchatka, and North America, as well as with *U. americanus* (Fig. 7A).

The fossil *U. spelaeus* populations from Central Balkans exhibit a clustered distribution in the lower-left region of the plot, occupying negative values along both the x- and y-axes (Fig. 7B). This placement differentiates them from extant omnivorous bears, positioning them closer to *A. melanoleuca*, *U. arctos* from Northern Europe, and *U. americanus*. However, some individuals from Hadži Prodanova ($n = 3$: 27.27 %) extend towards the cluster of omnivorous bears from the northern-most hemisphere such as *U. arctos* from North America and Northern Europe, as well as *U. americanus* (Fig. 7B). Hence, Hadži Prodanova exhibits a degree of intra-population variability, which is associated with the presence of gouges and puncture pits, which are more

characteristic of extant omnivorous bears. Furthermore, most of the Ušacka population ($n = 7$: 63.63 %) deviates from this main cluster, positioning itself closer to *U. maritimus*. This differentiation is primarily driven by a higher scratch width score (SWS), indicating higher counts of coarse to fine scratches in comparison to other Central Balkans *U. spelaeus* populations (Fig. 7B).

4.2.5. Interregional analysis

In the interregional correspondence analysis of all populations (CA; Fig. 8A-B), the Romanian Carpathians exhibit the broadest distribution, indicating the highest degree of variability in the microwear pattern. This is clearly visible in the convex hulls plot (Fig. 8B), where all regional ellipses are nested within the Romanian Carpathians hull, although some individuals extend beyond its boundaries at the lower extremes. Furthermore, considerable overlap exists among the regions of Moldavian Plateau, Western Balkan Mountains and Western

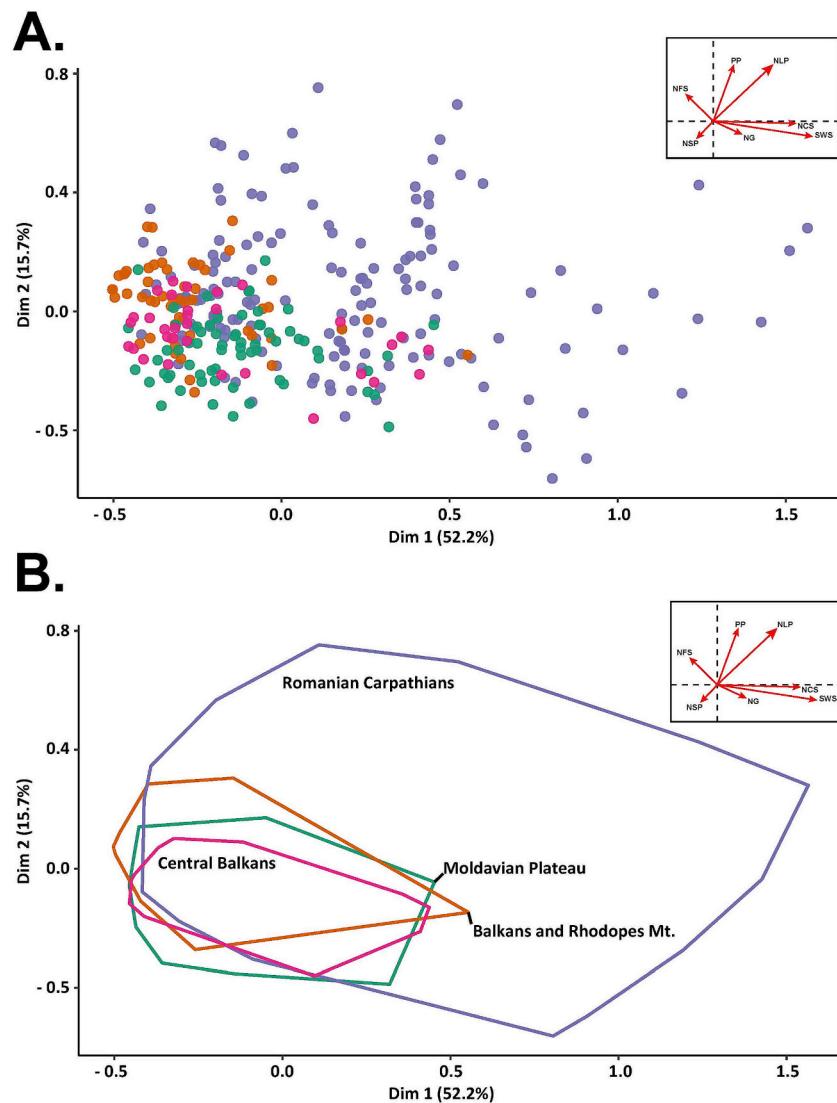


Fig. 8. Correspondence analysis (A) based on seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). The analysis compares cave bear (*U. spelaeus* sensu lato) populations from different regions: Romanian Carpathians (purple), Moldavian Plateau (green), Western Balkan Mountains and Western Rhodopes (orange) and Central Balkans (pink). A) Individual-level CA coloured by region. B) Same plot with group outlines (convex hulls) highlighting regional populations. Auxiliary plots in the upper right illustrate variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Rhodopes, and Central Balkans (Fig. 8B; see Supplementary Materials section 3.5. for a more detailed description).

The left area of the plot, where the bulk of Moldavian Plateau, Western Balkan Mountains and Western Rhodopes and Central Balkans cluster is characterized by a high number of small pits (NSP) and fine scratches (NFS), coupled with a relatively low number of coarse scratches (NCS), resulting in a low scratch width score (SWS). Additionally, puncture pits (NPP), gouges (NG), and large pits (NLP) exhibit moderate to low frequencies in this area, indicative of diets dominated by soft mast items. In contrast, some individuals of this populations partially extend towards the right side of the plot (Fig. 8). This right-side region is characterized by a higher prevalence of coarse scratches (NCS), thus resulting in elevated SWS values.

Finally, it is noteworthy that several individuals from the Romanian Carpathians extend into the uppermost area of the plot. This pattern reflects elevated values for puncture pits (NPP) and large pits (NLP), features that characterize and distinguish Romanian Carpathians cave bears from those of other regions. This microwear signature likely corresponds to a diet enriched with hard mast resources, such as seeds and

tough-coated fruits, a pattern characteristic of some Romanian Carpathian populations.

4.2.6. *U. spelaeus* and *U. arctos* dental microwear comparison during the MIS 3

To assess dietary differences and ecological interactions between cave bears (*U. spelaeus*) and brown bears (*U. arctos*) during MIS 3, as well as the dietary evolution of *U. arctos* from the Pleistocene to the Holocene, microwear patterns were analysed across all studied populations. These populations included *U. spelaeus* ($n = 307$) and *U. arctos* from MIS 3 ($n = 6$), as well as Holocene *U. arctos* from Romanian Carpathians ($n = 2$). Given the very limited sample size for *U. arctos*, these results must be interpreted with caution and should be considered preliminary.

Two correspondence analyses were performed, one with population averages and the other with individual species level (for more details about the CA see Supplementary Materials section 3.6.). When examining the correspondence analysis based on population averages, a clear pattern emerges (Fig. 9). Holocene *U. arctos* plots in proximity to large pits (NLP), coarse scratches (NCS), and scratch width score (SWS),

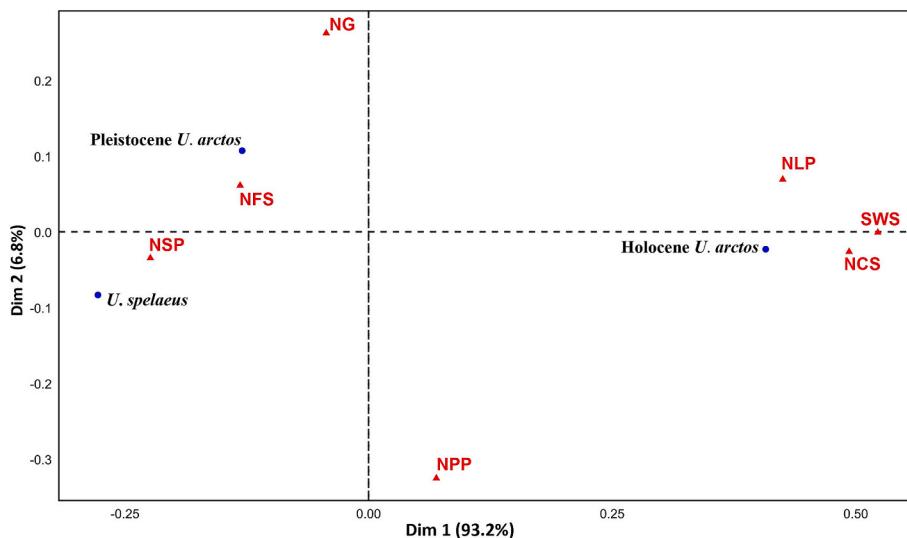


Fig. 9. Correspondence analysis (CA) showing the relationships between microwear variables (red triangles) and population means (blue circles) for *U. spelaeus* and *U. arctos* specimens. The analysis includes seven microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and the scratch width score (SWS). Population means were calculated using averaged individual scores per group. The plot includes Late Pleistocene *U. spelaeus* ($n = 307$), *U. arctos* from the same period ($n = 6$), and Holocene *U. arctos* ($n = 2$) from South-Eastern Europe (Romanian Carpathians). Dim 1 explains 93.2 % of the variation and primarily reflects the contrast between coarse/fine scratches and pit sizes (i.e., small versus large pits), while Dim 2 explains only 6.8 %, as the number of gouges and puncture pits contribute very little to the distribution of the populations in the space. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suggesting an association with harder or more resistant food items. However, the limited sample size ($n = 2$) precludes generalization and may instead reflect local dietary behaviour in the Romanian Carpathians, where Holocene *U. arctos* have been observed to consume harder items (Fig. 9). Furthermore, Pleistocene *U. arctos* and *U. spelaeus* cluster

in distinct regions, although both lie near fine scratches (NFS), more so in *U. arctos*, while small pits (NSP) are more frequent in *U. spelaeus*. Late Pleistocene *U. arctos* plots closer to gouges (NG), possibly reflecting a harder diet relative to *U. spelaeus*. Although the sample size remains statistically insufficient, it reflects the constraints of the Pleistocene

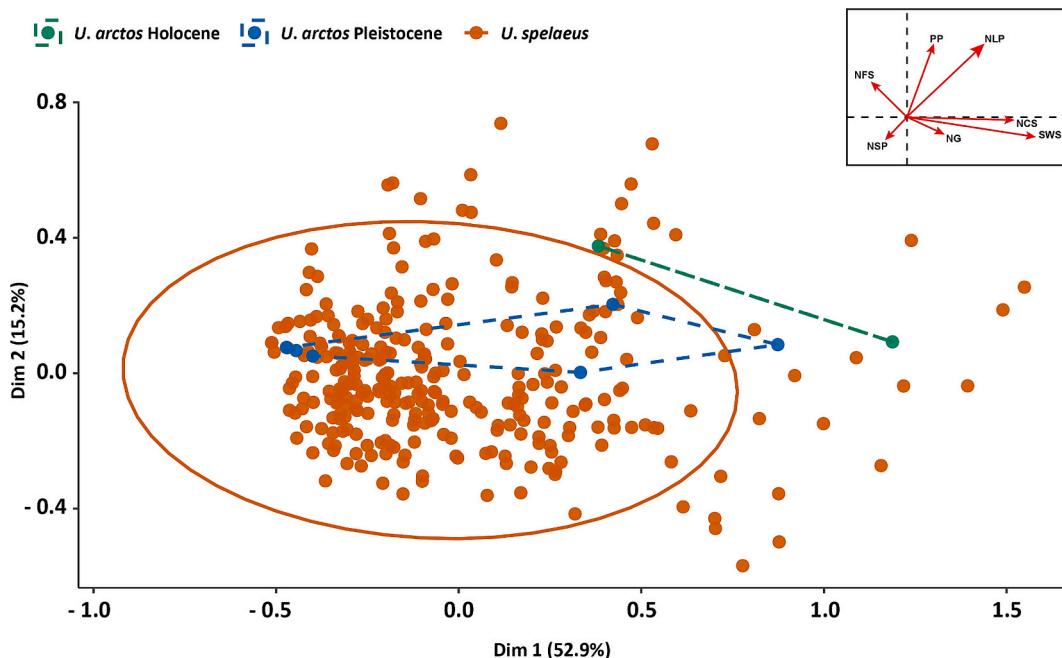


Fig. 10. Correspondence analysis (CA) at the species level comparing *U. spelaeus* (sensu lato) and *U. arctos* based on seven dental microwear variables: number of fine scratches (NFS), coarse scratches (NCS), small pits (NSP), large pits (NLP), gouges (NG), puncture pits (NPP), and scratch width score (SWS). Each point represents an individual specimen. *U. spelaeus* individuals (in orange) are enclosed by a 98 % confidence ellipse, illustrating the range of dietary microwear variation in this fossil taxon. *U. arctos* individuals are represented in two groups: Pleistocene populations (in blue) and Holocene populations (in green), each enclosed within convex hulls to highlight group spread. Auxiliary plot in the upper right illustrates variable loadings, with red vectors depicting the direction and relative contribution of each microwear variable to the first two CA dimensions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fossil record and includes individuals from several localities across South-Eastern Europe, offering limited yet potentially informative insights into regional dietary trends. Nonetheless, a larger and more balanced sample of Late Pleistocene *U. arctos* is required to robustly support these preliminary observations.

When correspondence analysis is performed at the individual level, the resulting distribution of all specimens (Fig. 10) suggests a potential niche overlap between *U. spelaeus* and *U. arctos* during MIS 3, where 5 out of 6 *U. arctos* specimens from MIS 3 (83.3 %) fall within the 98 % confidence ellipse of the *U. spelaeus* cluster (Fig. 10). Only one pre-LGM *U. arctos* individual (16.6 %) plots closer to the post-LGM *U. arctos*, though it still overlaps with the *U. spelaeus* distribution. In contrast, Holocene *U. arctos* individuals occupy the margins of the overall distribution, lying outside the 98 % confidence ellipses of both *U. spelaeus* and Pleistocene *U. arctos*, thereby indicating a distinct dietary niche (Fig. 10).

However, conclusions regarding niche relationships between *U. spelaeus* and *U. arctos* must be interpreted with caution due to the substantial imbalance in sample sizes, particularly the limited representation of *U. arctos*. Additional specimens are needed to strengthen the analysis in future studies. The suggested regional niche overlap between Pleistocene *U. arctos* and *U. spelaeus* should be considered tentative. In contrast, Holocene *U. arctos* cannot be meaningfully evaluated, as the sample size ($n = 2$) is both minimal and geographically restricted to a single region.

5. Discussions

5.1. Romanian Carpathians

With the expansion of the sample set, including new site of Cioclovina, and new sampled individuals for the populations of Urşilor and Muierilor and taking into account the populations from previously published sites across a broader temporal and spatial range within the Romanian Carpathians, the results remain consistent with those previously reported at Duñó-Iglesias et al. (2024a). The new data confirm the initial observations of pronounced inter-population dietary flexibility in *U. spelaeus* during the pre-dormancy phase (Duñó-Iglesias et al., 2024a). While statistical analyses reveal that the Romanian Carpathians exhibited distinct, localized dietary adaptations. Each population likely relied on specific food resources available in its region, leading to clear differences in feeding patterns across sites. These dietary differences were locally structured, not mainly driven by variability among individuals within the same population, suggesting that local ecological factors shaped population-level dietary strategies during the Late Pleistocene. Therefore, the expanded dataset reinforces the interpretation that dietary diversity in Carpathian cave bears reflects a sustained local-adapted omnivorous feeding strategy linked to the ecological stability and persistent availability of plant-based resources in the region throughout the MIS 3 period (e.g., Richards et al., 2008; Robu et al., 2013, 2018; Duñó-Iglesias et al., 2024a).

However, an alternative explanation may lie in the inheritance of foraging behaviours through social learning in cave bears. A recent study by Meleg et al. (2024), which correlated isotopic signals from bone collagen with geographic location, sex, and genetic data (DNA) at the individual level, revealed that cave bears adapted their feeding strategies primarily through individual experience rather than being constrained by genetic or environmental factors.

Finally, the presence of puncture pits and gouges remained consistently observable across individuals from the Romanian Carpathians, even with an increased sample size, reinforcing the interpretation that hard-object consumption was a persistent dietary trait of cave bears in this region during MIS 3, potentially indicative of its role before dormancy in Romanian Carpathians glacial refugium (Duñó-Iglesias et al., 2024a).

5.2. Moldavian Plateau

The microwear analysis of *U. spelaeus* populations from Moldavian Plateau reveals notable dietary variability, indicating both specialized and more generalized feeding strategies. The Trinca population exhibits a highly specialized soft mast-dominated diet (Table 2; Fig. 5). Conversely, the Buzdujeni population demonstrates a more variable omnivorous diet, primarily incorporating soft mast and vertebrates (Fig. 5). The Duruitoarea Veche population also follows a diverse dietary pattern, including vertebrates as well as both soft and hard mast. Similarly, the Saharna population exhibits an omnivorous diet with a mix of hard and soft mast, without the possibility to discard the inclusion of vertebrates. The Buteşti population, though based on a small sample size ($n = 2$), presents a high density of pits, suggesting a diet dominated by hard mast. Overall, these *U. spelaeus* populations exhibit distinct dietary strategies, with Trinca showing a specialized reliance on soft mast, while Buzdujeni, Duruitoarea Veche, Saharna, and possibly Buteşti display greater dietary flexibility within predominantly soft-mast-based diets.

5.2.1. Palaeoenvironment of Moldavian Plateau during the late MIS 3: A mix of tundra-steppe and forest refugia

The dietary flexibility observed in some of these populations aligns with the environmental diversity of the Moldavian Plateau region during MIS 3, which supported a mosaic of landscapes ranging from tundra-steppe to forested environments (Gerasimenko, 2006). This period, preceding the LGM, was characterized by significant climatic fluctuations that shaped the regional faunal composition (e.g., David and Lungu, 1972; Markova, 2007; Puzachenko and Markova, 2019). The region generally featured a mix of steppe habitats supporting *Mammuthus* faunas; including *M. primigenius*, *Coelodonta antiquitatis*, *R. tarandus*, *Megaloceros giganteus* and *Ovibos moschatus*; alongside open-landscape taxa such as *Bison* sp. and *Equus* sp. Additionally, more temperate and forest-adapted species, including *Capreolus capreolus*, *S. scrofa*, and the ecologically flexible *C. elaphus*, indicate the persistence of wooded refugia (e.g., Croitor, 2008; Demay et al., 2019, 2024). The Moldavian Plateau region's proximity to the Carpathians has been linked to the existence of glacial refugia, which may have provided habitat stability for certain taxa during the climatic oscillations of MIS 3 (Sommer and Benecke, 2005; Sommer and Nadachowski, 2006; Sommer and Zachos, 2009; Stewart et al., 2010). This can be linked to the observed consumption of hard objects (such as nuts and hard-shelled fruits) for some population of the region (Xafis et al., 2017). Saharna (43–41 ka cal BP), Duruitoarea Veche (42.6–40 ka cal BP) and Buteşti (41.7–35 ka cal BP), dating to the MIS 3, representing late cave bear populations in the region and notably, both exhibit microwear patterns consistent with hard-mast consumption within a forested glacial refugium.

The faunal assemblage from Buzdujeni, dominated by *Equus* sp. and *Bison* sp., suggests an open tundra-steppe environment at the time of bone accumulation (Croitor and Burlacu, 2020), which is supported by the climatically-cold moment of accumulation, between 43.7 and 40.5 ka cal BP. However, the presence of *C. elaphus* (albeit in low numbers), might indicate patches of forested habitat, as its occurrence during cold phases of MIS 3 typically correlates with forest refugia (Croitor and Burlacu, 2020; Sommer, 2020). The *U. spelaeus* population from Duruitoarea Veche displays individual variation in microwear patterns, with some bears consuming hard objects and others relying more on soft mast. This variability likely reflects environmental conditions shaped by alternating cold and temperate phases, supporting a mosaic landscape of open and forested habitats, along with tundra-steppe biomes during colder periods, as inferred from the site's faunal assemblage (Robu et al., 2025).

Hence, the microwear analysis from Moldavian Plateau populations displays flexibility that can be linked to alternance of cold and temperate cycles during MIS 3, as well as reinforces the notion of the existence of

some vegetation and tree refugia in Moldavian Plateau before the faunal turnover that happened around ca. 20 ka BP, during the LGM (Willis and Vanandel, 2004; Stuart and Lister, 2011). These refugia likely provided suitable habitats for bear species such as *U. spelaeus* and *U. arctos*, which may have survived in isolated forested patches. From these refugia, brown bear populations are thought to have expanded post-LGM, facilitating the recolonization of northern Europe (Sommer and Bencke, 2005).

5.2.2. Local niche partitioning between *U. spelaeus* and *U. arctos* from Trinca

The *U. spelaeus* individuals from Trinca represent the only cave bears among Moldavian Plateau populations exhibiting a clearly specialized soft-mast diet. This dietary specialisation was likely driven by their coexistence with *U. arctos* at the same locality and the resulting necessity for niche differentiation within an eco-region marked by progressively limited vegetation resources and the total disappearance of temperate forest cover as the LGM approached (Willis and Vanandel, 2004). Moreover, the *U. arctos* from the Moldavian Plateau has a microwear pattern linked to hard object consumption, potentially including hard-shelled fruits or bone (Godfrey et al., 2004; Goillot et al., 2009). Niche partitioning between MIS 3 *U. spelaeus* and *U. arctos* has previously been inferred from microwear analyses in the Carpathians (Duñó-Iglesias et al., 2024a), and this may also apply to the site of Trinca. In contrast, the other Moldavian Plateau *U. spelaeus* populations from MIS 3 exhibit scratch-width patterns comparable to those of contemporary MIS 3 *U. arctos*, indicating a more flexible dietary strategy (see Supplementary Materials, section 3.2.). Such variability in microwear features underscores distinct ecological adaptations among cave bear populations within the same region, likely influenced by local environmental conditions, resource availability, and niche partitioning.

5.3. Western Balkan Mountains and Western Rhodopes

The sites of Lakatnik and Borikovska lack a well-defined stratigraphic context. Lakatnik exhibits a soft mast diet with some possible variation towards vertebrate consumption. Borikovska, in contrast, exhibited a predominantly vertebrate-based diet, overlapping with *U. maritimus* along the y-axis of the bivariate plot. Borikovska exhibits a high number of pits, a feature associated with elevated plant intake in bear microwear analyses (Münzel et al., 2014), likely reflecting occupation of more vegetated habitats relative to Arctic environments. The correspondence analysis further differentiates this population from typical omnivores, with some individuals clustering near *A. melanoleuca* and others near *U. maritimus*. Although hypercoarse scratches are uncommon in herbivorous diets, they have been documented in omnivorous carnivores from temperate environments, where they are linked to bone processing (Goillot et al., 2009; Semprebon et al., 2011). Their presence in Borikovska supports dietary flexibility, including potential consumption of animal matter.

5.3.1. Refugia mosaic environments in mountain ranges from Western Balkan Mountains and Western Rhodopes during the MIS 3

Among the sites where paleoenvironmental data is available, Magura provides evidence of a mosaic environment. In particular, stable isotope analyses on herbivore taxa from Magura, as well as pollen extracted from hyenas' coprolites (Ivanova et al., 2016; Frémondeau et al., 2020), indicate the presence of steppe vegetation interspersed with patches of taiga and more humid aquatic environments. Isotopic analysis of cave bear remains reveals long-term dietary homogeneity, with all individuals exhibiting low nitrogen ($\delta^{15}\text{N}$) values, and thus herbivory (Frémondeau et al., 2020). While the co-occurrence of *U. arctos* alongside cave bears in some layers suggests niche partitioning based on the same stable isotope analysis (Frémondeau et al., 2020). Notably, the isotopic results match with microwear results in some aspects, the Magura cave bear population exhibits a preference for soft mast foods, although certain

individuals show a dietary shift towards harder objects consumption (Fig. 6; for a detailed explanation Supplementary Materials, section 3.3.2.). The diversification towards harder resources, which could be linked to hard-shelled fruits, roots, or animal matter (Goillot et al., 2009; Xafis et al., 2017) might have responded to the necessity to fulfil the energetic requirements of hibernation (Farley and Robbins, 1995; López-Alfaro et al., 2013; Coogan et al., 2014).

Bacho Kiro also reflects a mosaic environment, evidenced by the co-occurrence of steppe-adapted and woodland fauna, and a cold, continental climate inferred from $\delta^{18}\text{O}$ stable isotope analysis indicating marked seasonal temperature variation (Pederzani et al., 2021). The dietary pattern of *U. spelaeus* suggests a predominantly herbivorous diet with notable hard-object consumption. This inference is consistent with the presence of forested environments in the region that would have supported hard-shelled and seeded plant resources. This diversification towards hard-object consumption may reflect the targeting of carbohydrate-rich resources prior to hibernation, a behaviour typical of ursids (Bojarska and Selva, 2012; Coogan et al., 2018) and previously documented in MIS 3 cave bear populations from the Carpathians (Duñó-Iglesias et al., 2024a).

The Balkan Mountains are recognized, through genetic, pollen and mammal fossil analyses, as a refuge from which temperate species expanded throughout Eastern Europe after the Last Glacial Maximum (e.g., Hewitt, 2000; Tzedakis et al., 2002; Sommer and Zachos, 2009; Sadori et al., 2016; Lang et al., 2023). Recent palynological analyses of sediments and coprolites, combined with vegetation reconstructions from Pešturnica in the Central Balkans of Serbia (integrated with other paleoenvironmental data of the area, such as northern Balkan slopes and south-west of Southern Carpathians), have suggested a mosaic landscape characterized by dense patches of temperate woodland with high botanical diversity (Carrión et al., 2024; Ochando et al., 2024). Specifically, these studies reported a diverse assemblage of woody taxa persisting continuously throughout the Late Pleistocene, particularly during the final phases of MIS 3 (Ochando et al., 2024). This assemblage includes *Pinus*, *Juniperus*, deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Tilia*, *Ulmus*, *Buxus*, *Genisteae*, and *Cistus*, confirming that the Central Balkans served as a refugial area for meso-thermophilic vegetation during MIS 3, with a mosaic landscape encompassing open habitats in high altitude with densely forested patches in the valleys (Jarión et al., 2024). The microwear results, which highly diverge from one population to the other, support the presence of mosaic environments in the Western Balkan Mountains and Western Rhodopes territory during MIS 3, particularly in the northern slopes of the Western Balkan Mountains ranges and the Western Rhodope Mountains.

Finally, the Borikovska population, dwelling high altitude environments (ca. 1250 m a.s.l.) might have had to rely on other resources, specifically to a higher component of vertebrates and soft mast vegetation, moved by scarcity of plant resources in the alpine areas (Ochando et al., 2024). This dietary adaptation might reflect limited plant-based resource availability resulting from increased snowfall at higher altitudes, as documented for extant *U. arctos* populations (Bojarska and Selva, 2012).

The diversity of dietary signals among cave bear populations reflects occupation of ecologically heterogeneous landscapes, where steppe, boreal taiga, and temperate refugia coexisted. This environmental mosaic likely supported varied pre-hibernation foraging strategies. Such flexibility suggests cave bears adapted their diets to distinct biomes within dynamic environments.

5.4. Central Balkans

The microwear analysis of *U. spelaeus* populations from Central Balkans reveals some degree of dietary homogeneity (soft-mast dominated) for Hadži Prodanova and Risovača, while Ušačka population differentiates from the former two.

5.4.1. Soft mast diets with evidence of diversification

Hadži Prodanova cave individuals exhibit a general tendency towards a soft-mast-dominated diet, however, three individuals overlap with omnivorous bear populations from northern latitudes, suggesting room for dietary flexibility. Therefore, while the primary diet of this population appears to have been based on soft mast and abrasive plants items, some individuals might have diversified towards a diet that included the consumption of hard objects. The Hadži Prodanova faunal assemblage suggest that Late Pleistocene layers formed during a humid and relatively warm period within MIS 3, characterized by dense forest cover (Bogićević et al., 2017), conditions that are consistent with dietary diversification towards the foraging of hard-shelled and seeded fruits, and underground plant resources such as roots.

The presence of *U. arctos* suggests niche partitioning with *U. spelaeus* (Bogićević et al., 2017), as supported by isotopic (Bocherens et al., 2011) and dental microwear evidence through other sites (Duñó-Iglesias et al., 2024a), wherein *U. spelaeus* maintained a largely plant-based diet, while *U. arctos* exhibited more carnivorous tendencies. At Hadži Prodanova, microwear data for *U. arctos* are needed to further substantiate this dietary partitioning; however, *U. spelaeus* also consumed hard foods, likely reflecting pre-hibernation energetic requirements, as observed for MIS 3 Carpathian populations (Duñó-Iglesias et al., 2024a).

The cave bear population from Risovača predominantly exhibits a diet similar to northern latitude omnivorous bears, soft-mast-dominated, albeit with occasional hard-object consumption. Moreover, the occasional (although scarce) presence of hypercoarse scratches within the Risovača population ($n = 3$: 30 %) further supports a casual inclusion of hard items in their diet; although with a low frequency, the presence of hypercoarse scratches may suggest occasional consumption of vertebrate prey, as such features are otherwise only documented in reference bears for *U. maritimus* (Pappa et al., 2019). Hypercoarse scratches have also been documented in bone-consuming carnivores such as *Crocuta* spp. (Rivals et al., 2022), in omnivorous carnivores from temperate regions, where they are linked to enamel contact with bone during feeding (Goillot et al., 2009; Semprebon et al., 2011), and in carnivorous and piscivorous mammals inhabiting forested environments (Goillot et al., 2009; Xafis et al., 2017). The herbivore faunal assemblage of Risovača present a dominance of open-landscape species (i.e., *E. ferus*, *E. hydruntinus*, *Bos primigenius*, *Bison* sp.) (Forsten and Dimitrijević, 1995), this landscape matches with a diet based on abrasive items for cave bear populations, while some individuals might have diversified towards hard-object consumption, in order to diversify the resources to survive hibernation as observed in extant bears from northern latitudes (e.g., Bojarska and Selva, 2012).

The Ušačka cave bear population displays a predominantly soft-mast diet, although vertebrate consumption cannot be ruled out due to overlap with northern latitude omnivorous bears. This soft-mast diet potentially reflects the high-altitude habitat (1200 m a.s.l.) they occupied. Such elevations likely imposed harsher conditions and favored access to more abrasive, open-habitat plant resources. The absence of hypercoarse scratches supports limited vertebrate consumption prior to death, consistent with an abrasive, predominantly herbivorous diet.

Dietary variability among the Hadži Prodanova, Risovača, and Ušačka cave bear populations reflects the ecological heterogeneity of the Central Balkans during MIS 3; a mosaic landscape of temperate woodlands and open steppe habitats (Argant and Dimitrijević, 2007; Jovanović et al., 2022; Carrión et al., 2024). Open areas offered abundant soft mast (e.g., sprouts, grasses, flowers, leaves), while woodland patches supported occasional hard-mast consumption (e.g., hard-shelled fruits and nuts), likely supplementing herbivorous diets during seasonal scarcity or pre-hibernation.

5.5. Regional niche overlap between *U. arctos* and *U. spelaeus* in SE Europe during MIS 3

Dental microwear data suggests a certain overlap in short-term

dietary niches between Late Pleistocene *U. arctos* and *U. spelaeus* populations from South-Eastern Europe (Figs. 9 and 10). The dietary preferences reconstructed from our limited sample of *U. arctos* suggest a regional scale overlap at a short-term scale (e.g., seasonally) with *U. spelaeus* (Fig. 10). However, we did not find this overlap at the locality of Trinca, where these species co-existed. Hence, more data on *U. arctos* are needed to confirm our hypothesis of a seasonal niche overlapping.

The isotopic signatures (i.e., $\delta^{15}\text{N}$) of pre-Last Glacial Maximum (LGM) brown bears have been interpreted as indicative of a predominantly carnivorous diet (Münzel et al., 2011; Bocherens, 2015; Bocherens et al., 2015; Ersmark et al., 2019), the reported elevated $\delta^{15}\text{N}$ isotopic values may reflect adaptations to carcass scavenging in colder, more open environments (Marciszak et al., 2019). Additionally, high $\delta^{15}\text{N}$ values could result from the consumption of nitrogen-fixing plants (Schwarcz et al., 1999; Hartman, 2011), such as grasses and sedges characteristic of the Mammoth Steppe, as observed in large herbivorous mammals of the Late Pleistocene, including *Mammuthus* sp. and *Megaloceros* sp. (e.g., Kuitems et al., 2015; Rey-Iglesia et al., 2021). Elevated nitrogen values may also be associated with physiological responses to water stress in particularly arid steppe environments (Bocherens, 2015). High $\delta^{15}\text{N}$ values were recorded in the steppe-adapted giant brown bear *U. arctos* "priscus," which likely relied heavily on scavenging in the northern latitudes of Europe during MIS 3–2 and may have consumed up to 50 kg of meat daily to sustain its body size (Mattson et al., 1991; Schwartz et al., 2014; Marciszak et al., 2019). In contrast, smaller-bodied brown bears inhabiting temperate refugia may have maintained a more omnivorous diet with a substantial intake of plant matter (Sommer and Benecke, 2005). Local-scale niche partitioning between the two species appears to have occurred at least seasonally. Therefore, dental microwear patterns suggest the hypothesis that *U. arctos* populations from South-Eastern European refugia competed with *U. spelaeus* during the pre-dormancy period; a critical time for accumulating energy reserves for hibernation.

5.5.1. Localized foraging behaviour in *U. spelaeus*

This study reveals seasonal ecological flexibility in South-Eastern European cave bears, challenging the notion of a uniform herbivorous diet tied to the Mammoth Steppe biome. Different microwear patterns indicate dietary plasticity, comparable to that of extant omnivorous bears like *U. arctos*, suggesting an ability to exploit a broad range of resources. Furthermore, the similarity of microwear patterns to those of extant omnivorous species with broad dietary repertoires supports the interpretation of a flexible and opportunistic diet adapted to local ecological conditions of the time.

Their seasonal diet appeared to be closely tied to the local ecological and competitive pressures, reflecting an adaptable foraging strategy. While some regional consistency is observed, dietary patterns are more reliably maintained at the population level, suggesting behavioural inheritance, likely the result of foraging strategies transmitted across generations (Meleg et al., 2024). The present findings extend this pattern beyond the Romanian Carpathians, indicating that such ecological learning may have been a species-wide trait in *U. spelaeus*. The foraging behaviour of cave bears, particularly during the hyperphagic pre-hibernation phase, a period of heightened vulnerability to natural selection, became closely tied to the surrounding landscape, most probably due to ecological pressures. As a result, during the MIS 3 foraging strategies were closely shaped to local environmental conditions, reinforcing a strong ecological link to the immediate landscape. This is supported by the highly localized microwear patterns observed among populations, contrasting with species-level dietary uniformity.

6. Conclusion

This study demonstrates that *U. spelaeus* populations from South-Eastern Europe exhibited marked local-scale dietary flexibility during the MIS 3 pre-hibernation period, as reflected in highly variable dental

microwear patterns. Rather than supporting a uniform herbivorous diet across its range, our results reveal population-level dietary adaptations shaped by local environment and ecological settings. Microwear evidence from the Romanian Carpathians, Moldavian Plateau, and from Western and Central Balkan ranges as well as Western Rhodopes indicates that cave bear populations responded to locally specific ecological pressures, including resource availability and interspecific competition with *U. arctos*, through the development of distinct seasonal foraging strategies. In some cases, local niche partitioning, especially at Trinca where both bear species coexisted, suggests that *U. arctos* may have imposed ecological constraints on *U. spelaeus* during critical hyperphagic periods. These findings refine our understanding of the ecological dynamics that shaped *U. spelaeus*'s adaptive strategies prior to its extinction. Importantly, they underscore the need to interpret cave bear paleoecology at different temporal scales and point to the value of further integrating microwear data with stable isotopic studies to explore the mechanisms behind megafaunal persistence and extinction during the Late-Quaternary.

Ethics approval/declarations

Not applicable.

CRediT authorship contribution statement

Paulo Duñó-Iglesias: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Iván Ramírez-Pedraza:** Writing – review & editing, Visualization, Supervision, Data curation, Conceptualization. **Florent Rivals:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Data curation, Conceptualization. **Ionuț-Cornel Mirea:** Writing – review & editing, Funding acquisition, Data curation. **Luchiana-Maria Faur:** Writing – review & editing, Data curation. **Marius Vlaicu:** Writing – review & editing, Data curation. **Theodor Obadă:** Writing – review & editing, Data curation. **Roman Croitor:** Writing – review & editing, Data curation. **Viorica Pascari:** Writing – review & editing, Data curation. **Elena Delinschi:** Writing – review & editing, Data curation. **Latinka Hristova:** Writing – review & editing, Data curation. **Nikolai Spassov:** Writing – review & editing, Data curation. **Marin Gospodinov:** Writing – review & editing, Data curation. **Vesna Dimitrijević:** Writing – review & editing, Data curation. **Sanja Alaburić:** Writing – review & editing, Data curation. **Katarina Bogićević:** Writing – review & editing, Data curation. **Ivan Stefanović:** Writing – review & editing, Data curation. **Marius Robu:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113200>.

Data availability

Datasets related to this article can be found at <https://doi.org/10.5281/zenodo.16793240>, an open-source online data repository hosted at Zenodo (Duñó-Iglesias, 2025).

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