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Lebanese faunal legacy collections uncover 400,000 years of woodland resilience and distinct hominin ecological strategies

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The Levant is a key biogeographic corridor, yet historical instability has limited research creating a polarization toward its southern region. To address this geographical bias, we reassessed three legacy faunal collections from Lebanon: Naame, Nahr Ibrahim, and Ras el-Kelb. For the first time, we obtained direct dates for these assemblages and, through zooarchaeological methods, dental wear analysis, and landscape modeling, reconstructed aspects of ungulate and hominin ecology and behavior. The results establish chronological control, defining one of the longest paleoecological records in the region spanning from ~400,000 to ~100,000 years ago, and reveal that productive Mediterranean woodland ecosystems persisted along the central Levantine coast throughout much of the Middle and Late Pleistocene, supporting diverse ungulate communities and enabling hominins to practice seasonal, habitat-specific hunting along coastal ecotones. Integrating these findings into the broader Levantine context reveals marked ecological differentiation between central and southern regions, challenging assumptions of regional uniformity and highlighting the importance of spatial variability in reconstructing Pleistocene paleoecology, human behavior, and biodiversity across this major dispersal corridor.

The Levantine corridor occupies a critical position at the junction of Africa, Europe, and Asia, forming one of the most important biogeographic crossroads of the Pleistocene. Its environment served as a key setting for major events that shaped human evolutionary history. Amongst those are multiple hominin dispersals[1], including those of *Homo sapiens* with their potential encounters with Neanderthals, that predate similar events in Europe, e.g., [2,3]. Thus, the Levant forms a key context for understanding how environmental structure might have affected population succession and evolutionary trajectories.

Undeniably, the Levantine region shows a rich and continuous archeological record that documents pivotal cultural developments throughout the Pleistocene[4,5]. Yet, despite the importance of this region for paleoecology and human evolutionary studies, research across the Levant has historically been uneven. Extensive and continuous research in the southern part over the last century has significantly advanced our understanding of human evolution, e.g.[6–11]. This, however, left a marked geographical bias that resulted in a disproportionate focus on the southern part of the Levant compared to its central and northern territories, which are less

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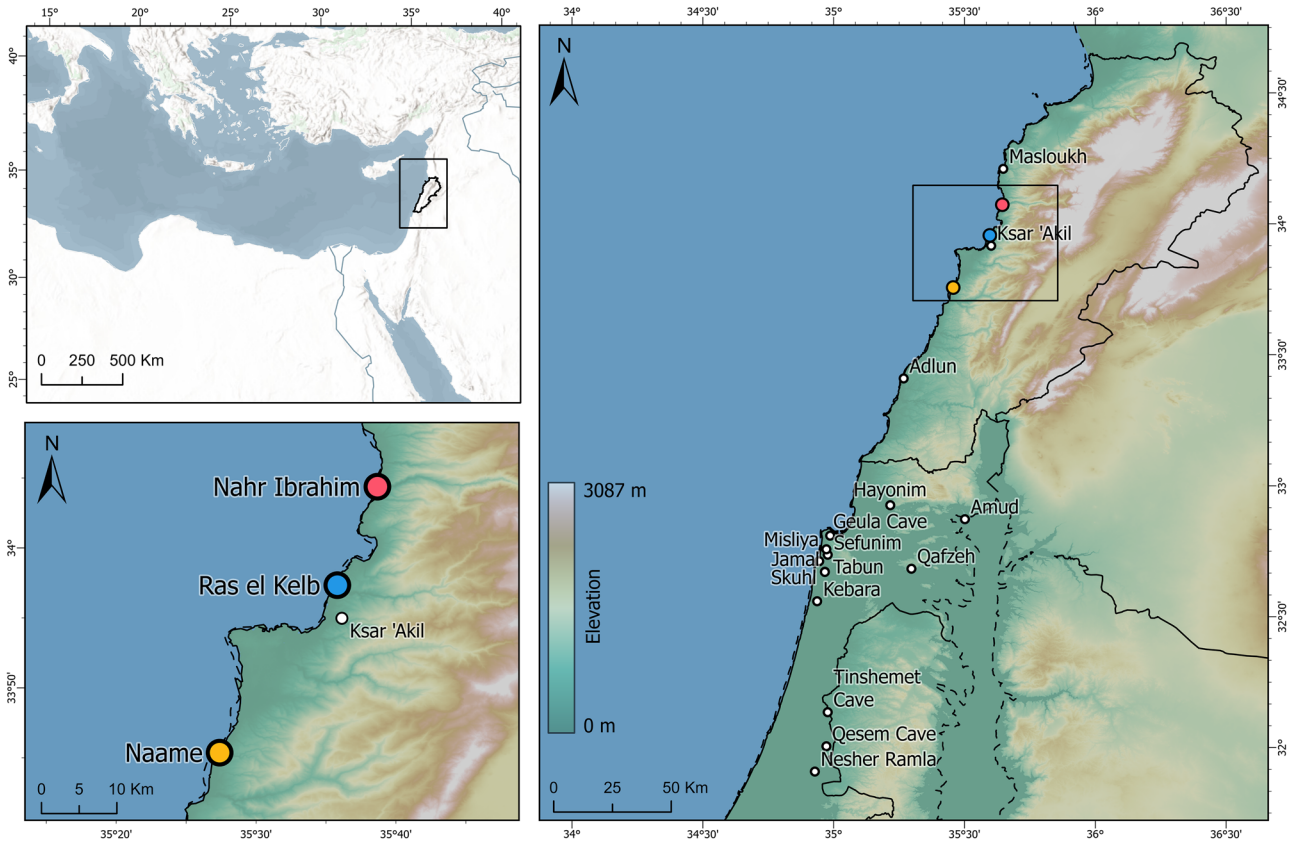

Fig. 1 | Map of the eastern Mediterranean and the central Levant. Location of the three Lebanese sites from which faunal material is analyzed in this study (Naame, Nahr Ibrahim, and Ras el-Kelb) and of other key Pleistocene sites mentioned in the text. The dashed line represents the reconstructed coastline under a −5 m relative sea-level scenario. The map was created with ArchGIS Pro version 3.0.5. and raster files were obtained from the Digital Elevation Model ALOS World 3D accessible via OpenTopography (https://portal.opentopography.org/raster?opentopoID=OTALOS.112016.4326.2).

studied. In the particular case of modern-day Lebanon, for example, the geopolitical instability since the 1970s has severely limited Pleistocene research there. Consequently, archeological evidence and environmental patterns documented in the southern Levant are often taken, explicitly or implicitly, to reflect patterns representative of the entire region, thus undermining possible effects of ecological and cultural variability across it. Meanwhile, botanical and geomorphological studies ([12,13], review in ref. 14) show a significant partition in physiogeographic and vegetation biomes across the modern Levant: while the south is marked by the Irano-Turanian steppe and Saharo-Arabian desert zones, both characterized by arid, sparsely vegetated environments, the central and northern coastal areas are part of the Mediterranean woodland zone, which is characterized by evergreen oak, *Pistacia*, and sclerophyllous vegetation, and which provides relatively stable and productive habitats year round.

Here, building on these ecologically and geographically diverse contexts, we aim to address some of the regional disparities that exist in the Levantine record. We thus examine faunal remains from Paleolithic sites on the underrepresented, ecologically rich Mediterranean coast of central Lebanon to reconstruct hominin subsistence strategies and habitat use during the Middle to Late Pleistocene. Ultimately, our goal is to see how the currently existing models arguing for uniformity in human ecological adaptation in the Levant, based largely on interpretations of southern regional datasets, would hold with the addition of the results of central Levantine study samples.

Although evidence of Paleolithic occupations in Lebanon has been recognized since the late 19th century[15,16], and surveys and excavations up to the 1970s revealed hundreds of sites—including caves—preserving lithics, faunal, and human remains[16–19], plans to further this research fell through as the political situation deteriorated at the outbreak of the civil war in 1975. Consequently, the available Paleolithic faunal and environmental studies from Lebanon remain limited in both scope and analytical resolution. While early faunal identifications (e.g., [20–22]) and pollen analyses (e.g., [23]) provided only sparse and cursory glimpses into Pleistocene ecosystems, they relied heavily on relative chronological inferences based on stone tool assemblages (e.g., [24]) and geomorphological investigations (e.g., [25]). The general lack of numerical age constraints has therefore significantly hindered interpretations of Paleolithic human ecology. As a result, modern interpretations of hominin-environment interactions and subsistence strategies during the Middle to Late Pleistocene in the central Levant remain largely speculative.

This study revisits understudied Pleistocene faunal legacy collections curated at the Museum of Lebanese Prehistory and originating from three key Paleolithic coastal sites in Lebanon, Nahr Ibrahim, Ras el-Kelb, and Naame, situated along the Mediterranean coast[16,26] (Fig. 1). Given the course chronological resolution and inherent palimpsestic nature of these legacy faunal assemblages, we situated our study within a time-perspectivist framework, which recognizes that archeological records characterized by temporal averaging and incomplete stratigraphic control are nonetheless well suited to addressing long-term questions about human behavioral ecology and human-environment interactions[27]. Thus, rather than reconstructing discrete events, this approach emphasizes aligning research questions with the temporal scale of the available data and treating time-averaging as an analytical feature rather than a limitation[27,28]. Using a multiproxy approach supported by new direct numerical age constraints, we integrate zooarchaeological, taphonomic, dental wear, and site catchment analyses to examine enduring patterns of habitat use, prey exploitation, and seasonal structuring of subsistence over long time spans. By situating these assemblages within a broader regional chrono-paleoenvironmental framework and comparing them to well-studied southern Levantine records, we

then assess spatial variability in human behavioral ecology and habitat structure and re-evaluate long-standing assumptions of ecological uniformity across the Levant. Through this integrative investigation, we aim to clarify the role of the central Levant in current discussions of human adaptation and ecosystem dynamics during the Pleistocene.

Results

Chronological framework

As a first step to our study, we obtained numerical ages for the assemblages in order to provide a chronological framework, which is essential for interpreting our results. This was necessary because existing dates for the deposits of Naame are scarce and do not meet modern reporting standards, while no stratigraphic information and age constraints were available for the collections of Ras el-Kelb and Nahr Ibrahim we studied. Importantly, the latter two assemblages were collected from early investigations in deposits that do not necessarily chronostratigraphically correspond to the later excavated and dated cave sequences. We thus selected five fossil teeth from the legacy collections available to us—3 from Naame (two from the top deposit *Niveau Supérieur*, and one from the lowermost breccia P^3III_0) and 1 each from Nahr Ibrahim and Ras el-Kelb for combined U-series/ Electron Spin Resonance (ESR) dating[29]. Importantly, all the teeth we selected had sediment attached in order to enable a proper dose rate evaluation. All dating sample procedures, analyses, and results are fully disclosed and extensively discussed in the Supplementary Material, which also includes comprehensive information on the archeological context of the collections.

For the Ras el-Kelb tooth (sample #861), the apparent U-series age obtained for the dentine provides a minimum age constraint of 135.8 ka, while the combined US-ESR age of 402 ± 46 ka for the enamel may be regarded as a reliable finite estimate for this tooth. For the Nahr Ibrahim tooth (sample #863), the dentine yields a minimum U-series age of 108.5 ka and a finite combined US-ESR age of 245 ± 23 ka. While we do acknowledge the existing uncertainty on the dose rate evaluation in relation to a possible spatial heterogeneity of the sedimentary environment, the long-term depth, and the long-term water content, our various sensitivity tests (Supplementary Notes S1) systematically return ages of between 200 and 300 ka for the Nahr Ibrahim tooth (sample #863) and 350−500 ka for the Ras el-Kelb tooth (sample #861), thus securing a Middle Pleistocene age for both samples. These ages indicate that the two fossil assemblages may significantly differ in age by about 150 ka. Additionally, the date obtained for Ras el-Kelb indicates that Zumoffen's collection is significantly older than the deposits of Ras el-Kelb Cave, which were later (in 1959) excavated and traditionally attributed to the MIS 5 (but see discussion in Supplementary Notes S4). Our date is, however, consistent with Zumoffen's noting the presence of Acheulean elements at the areas where he collected the faunal material (Supplementary Notes S1). The date obtained for Nahr Ibrahim broadly overlaps with the oldest age range usually estimated for the cave deposits, i.e., MIS 7-6 (see Supplementary Notes S1).

At Naame, the two teeth from the *Niveau Supérieur* return significantly different ages. First, U-series and combined U-series/ESR dating provide a minimum early MIS5 age (> 100 ka) for sample #860, while the age of 107 ± 13 ka may be regarded as a reliable finite estimate. In contrast, U-series and ESR data consistently support a much younger age for sample #862. Apparent U-series ages yield a minimum age of 6.9 ka for this sample, while the mean combined U-series/ESR age of 17.6 ± 2.7 ka may be regarded as the most reasonable finite age estimate for the tooth. Importantly, age sensitivity tests systematically place the age of this tooth within MIS 2 (Supplementary Notes S4). Consequently, there is little doubt that tooth #862 is significantly younger than #860, suggesting that the fossil assemblage from the *Niveau Supérieur* might include a proportion of much younger (post-MIS 5) material. Finally, the tooth sample (#859) from Naame's lowermost stratigraphic zone (P^3III_0) provides a minimum age of 60 ka based on the apparent U-series age from the enamel, while combined U-series/ESR age calculations return somewhat (methodologically) questionable results of around 100 ka (see Supplementary Notes S4 for further details). Our various sensitivity tests show that the ages for this tooth systematically fall within MIS 5. Consequently, a broad MIS 5 age may be tentatively proposed for #859 in the first instance, while the age of 107 ± 13 ka from #860 may be indirectly used as an additional minimum age constraint. Interestingly, the dating results from two of the Naame samples provide a solid confirmation of the previous chronological inferences attributing a MIS 5 age to this site[30].

Taxonomic composition of the faunal assemblages

The three faunal assemblages comprised a total number of remains (NR) of 721, the majority of which (559; 77.6 %) originated from Naame, whereas Nahr Ibrahim and Ras el-Kelb contributed 63 (8.7%) and 99 (13.7%) specimens respectively (Fig. 2A, Table 1, Supplementary Table S1). Out of the total sample, 203 (Number of Identified Specimens, NISP) were identified to taxon level, and an additional 16 (NISP) to size class, whereas 502 were too fragmented to be identified (Table 1, Fig. 2A).

The identified specimens correspond to a minimum number of individuals (MNI) of 54, belonging to 51 ungulates (with nine species represented), one rodent, one reptile, and one fish (Table 1). Overall, large and very large ungulates are well represented, particularly aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), and rhinoceros (*Stephanorhinus hemitoechus*), alongside medium-sized taxa such as Persian fallow deer (*Dama mesopotamica*) and wild goat (*Capra aegagrus*). Aurochs, fallow deer, and wild goat are the only taxa present at all three sites.

Sample completeness profiles were evaluated following the 4-step analysis of Chao et al.[31,32] for the ungulate species of the three legacy assemblages analyzed here, together with the Ras el-Kelb Cave ungulate assemblages from layers D-J and K-M[22], which represent the cave's most intensively occupied phases. The Ras el-Kelb Cave faunal assemblage was excavated and analyzed using more recent recovery protocols, and was included here as a comparative benchmark. Results of sample completeness profiles (Supplementary Fig. 1.a) indicate that all assemblages are incomplete with respect to rare taxa ($q = 0$), as expected for both legacy and excavated faunal assemblages, but approach high completeness for abundance-weighted components of diversity ($q \geq 1$). For most assemblages, completeness increases with q and reaches consistently high values at $q = 1$ and $q = 2$, indicating that dominant taxa and the bulk of recovered individuals are well represented despite differences in excavation history and assemblage size. Naame - $PIII_2$ completeness estimates for $q \geq 1$ are markedly lower and unstable, reflecting extreme dominance by a very small number of taxa, departing strongly from the general pattern. This behavior is consistent with the extremely small sample size of this assemblage (MNI = 3) and indicates limited effective information for abundance-weighted diversity estimation. Size-based rarefaction and extrapolation (Supplementary Fig. 1.b) show that diversity measures emphasizing common and dominant taxa ($q = 1$, $q = 2$) stabilize within or near observed sample sizes for all assemblages except Naame - $PIII_2$, whereas species richness ($q = 0$) continues to increase with extrapolation, indicating that richness estimates represent lower bounds. Accordingly, asymptotic diversity profiles (Supplementary Fig. 1.c) provide robust estimates for Shannon and Simpson diversity for most assemblages, but only minimum estimates for richness and abundance-weighted diversity in Naame - $PIII_2$. Coverage-based rarefaction (Supplementary Fig. 1.d) confirms that relative diversity rankings for $q \geq 1$ remain stable when assemblages are compared at equivalent completeness, demonstrating that differences driven by dominant taxa are robust to variation in sampling intensity and recovery. Evenness profiles (Supplementary Fig. 1.e) further indicate that assemblages are primarily differentiated by dominance structure among common taxa rather than by the representation of rare species, with Naame - $PIII_2$ emerging as a strongly dominance-driven outlier. Quantitative completeness and diversity estimates are summarized in Supplementary Table S2. Taken together, these results indicate that comparisons based on common and dominant taxa are robust for most assemblages, while interpretations of Naame - $PIII_2$ must be treated with caution due to its extremely limited sample size.

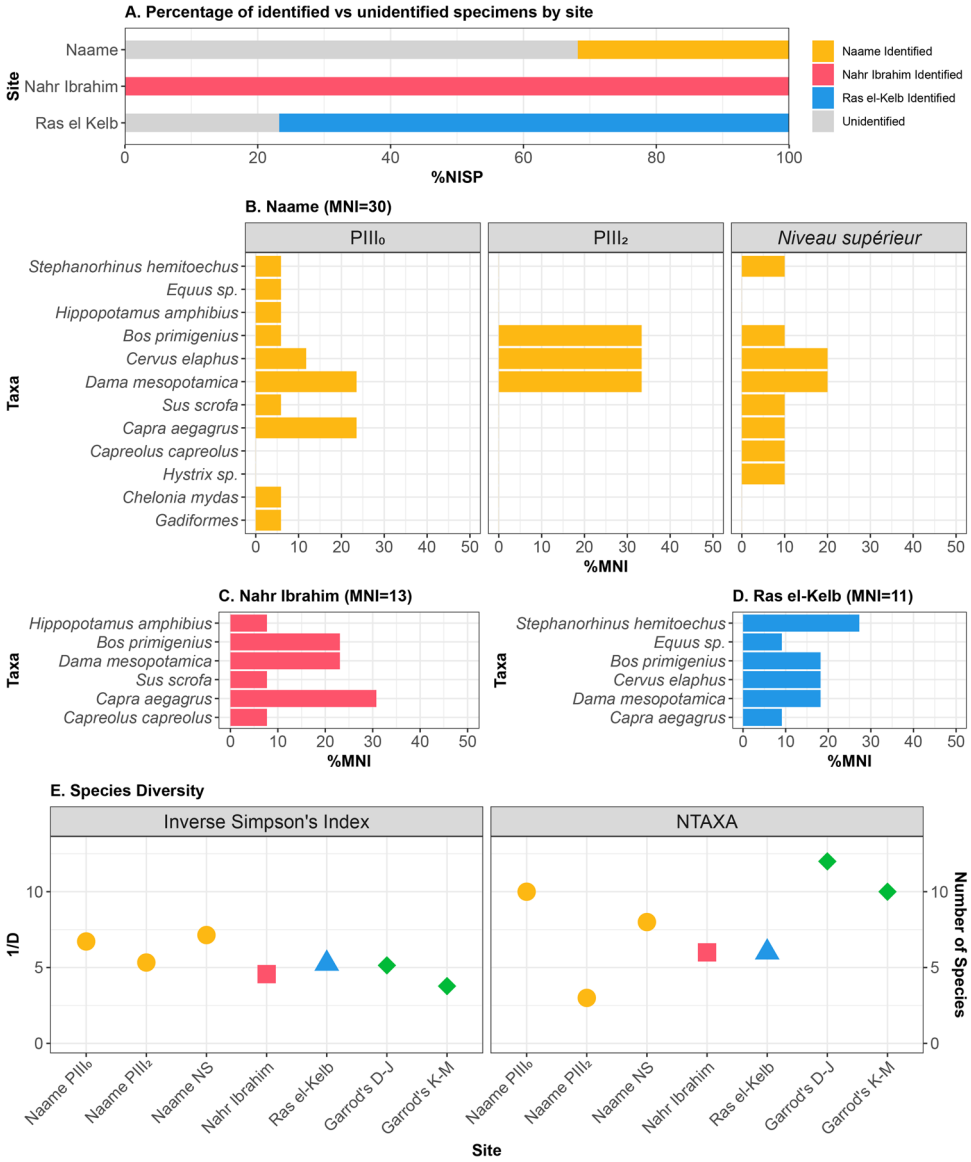

Fig. 2 | Species taxonomic composition and diversity at the different sites. A Percentages of identified and unidentified specimens (%NISP) per site. **B**–**D** Taxonomic composition (%MNI) for Naame, Nahr Ibrahim, and Ras el-Kelb. **E** Taxonomic richness (NTAXA) and species diversity (1/D) across individual layers of Naame and in comparative assemblages from Ras el-Kelb Cave[22].

Within this framework, overall at Naame, fallow deer and red deer emerge as the most abundant taxa, accounting for 23.3% and 16.7% of the overall MNI, respectively, followed by wild goat (16.7%) and aurochs (10%) (Fig. 2B). The assemblage from Naame - $PIII_0$ shows the highest taxonomic richness across the site's deposits (NTAXA = 10), with identified taxa also including green sea turtle (*Chelonia mydas*) and Gadiformes fish. Species diversity (as illustrated by the Inverse Simpson's Index, Fig. 2E), however, is greatest at Naame - *Niveau Supérieur* (1/D = 7.14), followed by $PIII_0$ (1/D = 6.72) and $PIII_2$ (1/D = 5.33). The low diversity recorded in $PIII_2$ is probably due to the small sample size. At Nahr Ibrahim, wild goat is the most common taxon (%MNI = 30.8%) (Fig. 2C), whereas at Ras el-Kelb, rhinoceros dominates, accounting for 27.3% of the assemblage (Fig. 2D). Ras el-Kelb and Nahr Ibrahim display similar diversity indices (1/D = 5.26 and 4.57, respectively).

Using Garrard's[22] faunal data from Ras el-Kelb Cave layers D-J and K-M, we assessed species diversity in these layers and compared the results with the collections we studied here. The Ras el-Kelb Cave assemblages show similarly high species diversity (1/D = 5.1 for layers D-J; 1/D = 3.8 for layers K-M), with no single taxon dominating. Overall, taxonomic richness at Ras el-Kelb Cave is high and most comparable to that of Naame - $PIII_0$ rather than to the other assemblages of our study (Fig. 2E).

Taphonomic signatures and anthropogenic modifications

The complex post-depositional taphonomic history of these assemblages was shaped first by the cementation of the sediments in which they were deposited into breccia, and later by the processes of their extraction from the breccia, which involved mechanical and chemical treatments. These interventions likely increased fragmentation, left visible marks on the bone surfaces, and introduced a bias toward bigger and more complete or diagnostic elements. Therefore, a detailed taphonomic analysis was conducted on all specimens from the three legacy collections to assess post-depositional alteration as well as the extent of human involvement in the accumulation of the faunal remains.

At Naame, cut marks were observed on 5.5% of the total remains from the site. All these marks occurred on taxonomically indeterminate mammal diaphyseal fragments recovered from $PIII_0$ and *Bloc du 75*, many of which also showed traces of thermal alteration (Fig. 3A–C). Additionally, one diaphyseal fragment from a large herbivore from P^2III_0 had its edge intentionally retouched and was identified as an expedient bone tool (Fig. 3E). Other modifications are consistent with marrow extraction, for example, a longitudinally split of a fallow deer phalanx from $PIII_2$ (Fig. 3G) and an impact notch on a fallow deer metapodial from *Niveau Supérieur*. In terms of burning, we observed varied degrees of thermal damage primarily on indeterminate long bone fragments but also on a burned fallow deer

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Table 1 | Taxonomic abundance

	Naame													Nahr Ibrahim			Ras el-Kelb		
	$PIII_0$			$PIII_2$			*Niveau supérieur*			*Bloc du 75*	Total								
Taxon	**NISP**	**MNI**	**Biomass (Kg)**	**NISP**	**MNI**	**Biomass (Kg)**	**NISP**	**MNI**	**Biomass (Kg)**	**NISP**	**NISP**	**MNI**	**Biomass (Kg)**	**NISP**	**MNI**	**Biomass (Kg)**	**NISP**	**MNI**	**Biomass (Kg)**
Stephanorhinus hemitoechus	3	1	1250				1	1	1250		4	2	2500				19	3	3125
Equus sp.	1	1	150								1	1	150				1	1	150
Hippopotamus amphibius	1	1	1250								1	1	1250	1	1	1250			
Bos primigenius	7	1	400	1	1	400	2	1	400		10	3	1200	21	3	1200	23	2	800
Cervus elaphus	6	2	150	1	1	75	2	2	150		9	5	375				12	2	150
Dama mesopotamica	16	4	232	13	1	58	4	2	116		33	7	406	19	3	174	6	2	116
Sus scrofa	1	1	53				1	1	53		2	2	106	2	1	53			
Capra aegagrus	11	4	146				1	1	43		12	5	189	17	4	146	4	1	43
Capreolus capreolus							1	1	4.8		1	1	4.8	1	1	12			
Hystrix sp.							1	1	6		1	1	6						
Chelonia mydas	2	1	150								2	1	150						
Gadiformes	1	1									1	1							
Total taxon	49	17	3781	15	3	533	13	10	2022.8	0	77	30	6336.8	61	13	2835	65	11	4384
Size class																			
Very large ungulate	1										1						8		
Large ungulate														1			2		
Medium ungulate	1						1				2			1					
Small ungulate																	1		
Total size class	2	0	0	0	0	0	1	0	0	0	3	0	0	2	0	0	11	0	0
Indet.																			
Indet. mammal	200			10						269	479						23		
Grand Total	**251**	**17**	**3781**	**25**	**3**	**533**	**14**	**10**	**2022.8**	**269**	**559**	**30**	**6336.8**	**63**	**13**	**2835**	**99**	**11**	**4384**

Number of Identified Specimens (NISP), Minimum Number of Individuals (MNI), and estimated edible biomass (kg) for all identified taxa at Naame, Nahr Ibrahim, and Ras el-Kelb.

Fig. 3 | Taphonomic modifications and anthropogenic traces on faunal remains from the Lebanese legacy collections. **A**–**C** Cut marks on indeterminate mammal diaphyseal fragments from Naame ($PIII_0$ and *Bloc du 75*). Red arrows indicate cut marks; blue arrows highlight carnivore tooth marks in panel (**A**). Panel **C** also shows thermal alteration damage. **D** Butchery-related cut marks on an aurochs metapodial distal epiphysis from Nahr Ibrahim. **E** Very large herbivore diaphyseal fragment from Naame interpreted as an expedient bone tool, based on localized edge modification and retouch. Dashed lines indicate the active edge; white arrows in the close-up highlight deliberate changes in edge angle produced by flaking. **F** Wild goat frontal bone with horn cores from Nahr Ibrahim. **G** Longitudinally split fallow deer phalanx from Naame, consistent with marrow extraction. **H** Longitudinal spiral fracture fragment of a medium-sized ungulate long-bone diaphysis from Naame. **I** Charred indeterminate mammal diaphyseal fragments from Naame. **J** Hippopotamus lower second molar from Naame. **K** Red deer upper second molar from Naame. **L** Rhinoceros upper premolar from Ras el-Kelb showing post-depositional cracking and mineral staining.

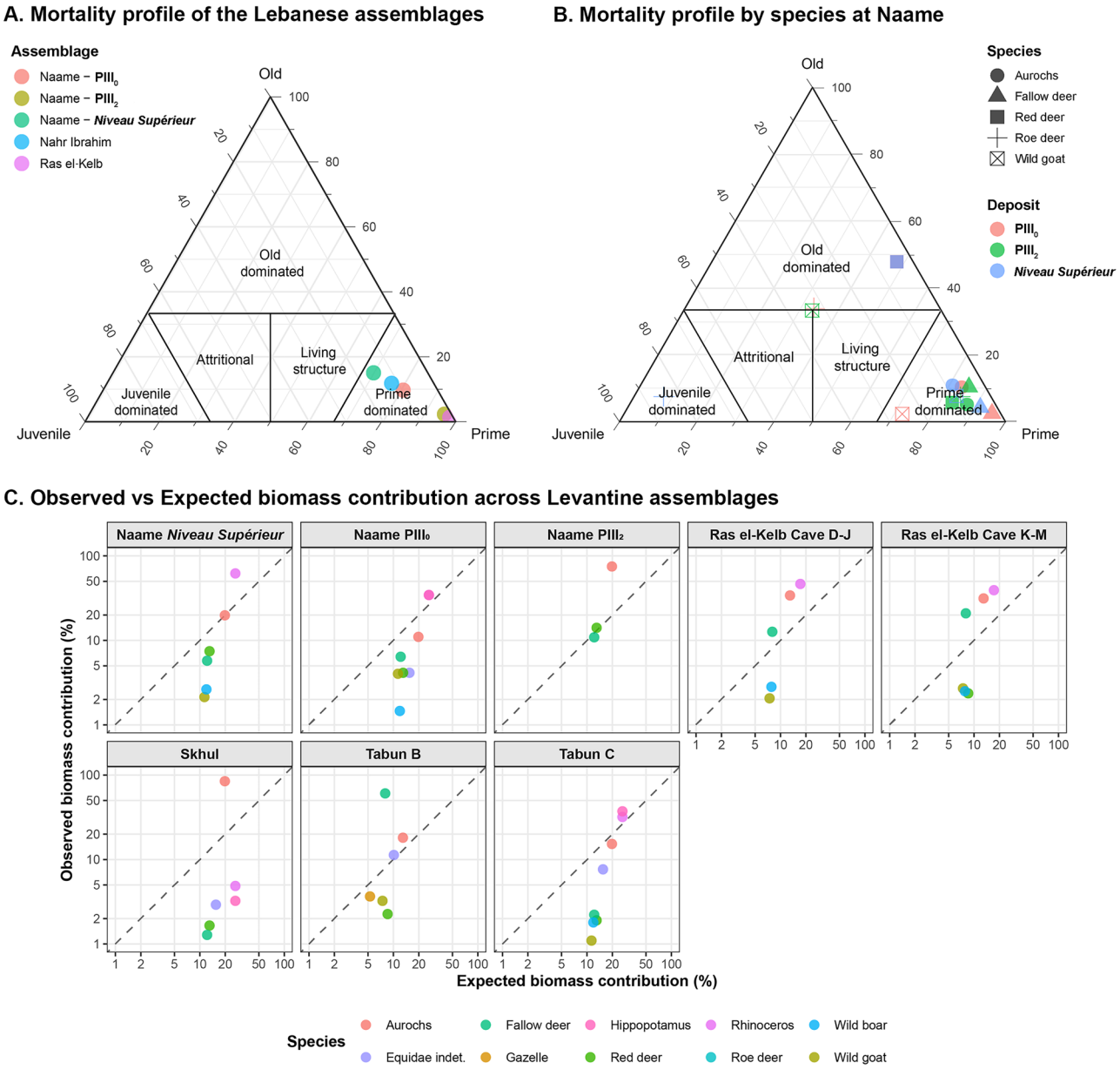

Fig. 4 | Prey selection and mortality profiles. A Mortality profile by age class of the studied collections, showing dominance of prime-age adults. **B** Mortality profile by species within Naame. **C** Comparison of observed versus expected biomass across taxa based on the minimum number of individuals (MNI) for Naame, Garrod's Ras el-Kelb Cave[22,33], Tabun, and Skhul[34]. Each point represents a species within an assemblage. The 1:1 dashed line indicates the null expectation (Damuth's law); taxa above the line are overrepresented relative to expectations, while taxa below are underrepresented. Axes are shown on a $\log_{10}$ scale to improve visualization.

tooth from $PIII_0$ (19.5% of the assemblage; e.g., Fig. 3C-I and Supplementary Fig. S2E-F; Supplementary Tables S3-S4), as well as on a fallow deer astragalus from layer $PIII_2$. Overall, even if bone modifications linked to human activity were not present at high frequency, biostratinomic alterations were almost non-existent. Only three specimens (0.5%) from the Naame deposits bore carnivore marks, in the form of pits and drag marks (Supplementary Fig. S2A–C); one of those also exhibited cut marks under the carnivore bite score, indicating prior human access to the bone(s) (Fig. 3A). Rodent gnawing was identified on three specimens (e.g., Supplementary Fig. S2D).

At Nahr Ibrahim, butchery-related cut marks were observed on an aurochs distal epiphysis (Fig. 3D), and fresh fractures were identified on another aurochs metapodial fragment. At Ras el-Kelb, although no cut marks were noted on the fauna, fresh fractures were observed on two specimens, and 11% of the remains showed early stages of thermoalteration. Even though anthropogenic modifications were rare on the remains from Nahr Ibrahim and Ras el-Kelb, carnivore tooth and digestion marks were completely absent.

To sum up, the analysis of all three assemblages suggests that large carnivores had a minimal role in the accumulation of the faunal remains. Instead, the evidence indicates that humans were the primary agents behind the deposition and modification of the Naame assemblages and were at least partly responsible for the accumulation of the Nahr Ibrahim and Ras el-Kelb assemblages.

Hominin subsistence strategies

Analysis of ungulate mortality patterns in the three Lebanese collections indicates that prime-age adults dominate all assemblages (Naame = 82%, Nahr Ibrahim = 70%, Ras el-Kelb = 100%), while older individuals and juveniles are much less common (Fig. 4A). However, we acknowledge that caution is needed when interpreting the results from Nahr Ibrahim and Ras el-Kelb, as unknown recovery criteria may have introduced sampling bias,

favoring larger or more complete specimens (see discussion below). At Naame, prime-age individuals consistently dominate the depositional sequence for both aurochs and fallow deer, while senile individuals are present only among red deer (in *Niveau Supérieur*), and the few juveniles are limited to smaller ungulates such as wild goats and roe deer (in $PIII_0$ and *Niveau Supérieur*, respectively) (Fig. 4B).

In terms of biomass, very large taxa, such as rhinoceros, hippopotamus, and aurochs, likely provided the greatest quantities of edible meat (Table 1). Out of these, only aurochs is represented in all assemblages, and with an estimated biomass of 1200 kg at Naame and Nahr Ibrahim and 800 kg at Ras el-Kelb, it would have formed an important component of the hominin subsistence. Medium-bodied ungulates followed in biomass contribution. Fallow deer and red deer (460 kg and 375 kg respectively) were next in significance at Naame, while at Nahr Ibrahim, it was fallow deer (174 kg) and wild goat (146 kg). At Ras el-Kelb, *Equus* sp. and red deer each contributed similar proportions of biomass (150 kg), whereas wild goat provided the least meat yield (43 kg) among the recorded taxa. Smaller ungulates, like roe deer, contributed minimally to the diet, with 16.8 kg at Naame and 12 kg at Nahr Ibrahim.

For the Naame assemblages, we also examined species abundances using biplots of %MNI and %biomass as well as PCA to explore patterns in prey selection and meat exploitation in comparison to other contemporaneous faunal assemblages from the broader Levant. Comparable data were available from the sites of Ras el-Kelb Cave (from layers K-M and D-J)[22,33], Tabun (layers B, C), and Skhul[34].

In the %MNI PCA, where Dim1 (36.6%) and Dim2 (24.7%) together explain ~61% of the variance (Supplementary Fig. S3A), the Naame assemblages plot in different regions, indicating high variability across them. The frequency of roe deer and other medium-sized taxa aligns the *Niveau Supérieur* assemblage with that of Ras el-Kelb Cave layers D-J. Naame - $PIII_0$ groups with Tabun C, reflecting similar frequencies of large-bodied ungulates such as equids, hippopotamus, and rhinoceros. Naame - $PIII_2$ plots together with Skhul due to the contribution of species such as aurochs and red deer. For the %biomass PCA (Supplementary Fig. S3B), where Dim1 (34.5%) and Dim2 (30.3%) explain ~65% of the variance, the clustering of assemblages is largely consistent with the previous %MNI PCA: the assemblage from *Niveau Supérieur* at Naame clusters with that of Ras el-Kelb Cave layers D-J through the contributions of rhinoceros and wild boar, that from Naame $PIII_0$ clusters with Tabun C, as is driven by large-bodied taxa, and that from Naame - $PIII_2$ is closest to Skhul as they are both dominated by aurochs and red deer meat yield. Overall, the PCA shows that Naame's *Niveau Supérieur* and $PIII_0$ provide more reliable signals of prey choice and meat exploitation as they cluster with Ras el-Kelb Cave and Tabun C, respectively, potentially illustrating the diverse hunting strategies employed across the region. Naame - $PIII_2$ is most likely an outlier. Its small sample size inflates the relative values of aurochs compared to other species, associating it with Skhul, whose assemblage also shows an overabundance of aurochs compared to other Levantine sites, presenting it as an outlier in the region[34]. The biplots of %biomass vs %MNI, as well as observed versus expected %biomass contributions by assemblage, show that in the majority of the assemblages, rhinoceros and hippopotamus provide the highest meat yields per individual (Supplementary Fig. S3C; Supplementary Table S6), and they also show elevated contributions relative to their expected biomass (Supplementary Table S6). Aurochs consistently combines relatively high representation with substantial biomass returns; it is generally over-represented, plotting above the null expectation (Fig. 4C). Fallow deer is consistently among the most frequently represented taxa by individual counts, yet its contribution to overall meat return is modest compared to larger game (Supplementary Fig. S3C). Generally, medium-sized ungulates, including fallow deer, wild goat, and wild boar, typically fall below the 1:1 line, indicating underrepresentation relative to mass-abundance scaling (Fig. 4C). At Ras el-Kelb Cave, however, they plot just above the line, plotting together with aurochs and rhinoceros. Exceptions to these patterns are observed in Tabun B, Skhul, and Naame $PIII_2$. The latter two are outliers due to the overrepresentations of aurochs as mentioned above. Tabun B emerges as an outlier due to the exceptionally high frequency of fallow deer, which, based on mass-abundance scaling, greatly exceed its ecological expectations. Previous taphonomic assessments explain this over-representation by a complex accumulation process combining natural mortality, carnivore activity, with a limited human contribution rather than a sustained or selective human targeting[34,35]. Overall, the observed patterns from these biplots suggest a recurrent emphasis on large-bodied taxa, particularly aurochs, despite their low expected abundance in natural communities.

Paleoecology and ungulate seasonality

Overall, the mesowear patterns of ungulates from Naame, Ras el-Kelb, and Nahr Ibrahim classify all taxa as either browsers or mixed feeders, indicating a consistent general preference for leaf-based diets (Fig. 5A). Intra-species variability across the three sites revealed no significant differences in mesowear patterns, despite the chronological span across the sites (Kruskal-Wallis $\chi^2 = 2.16$, df = 2, $p = 0.339$). However, some trends were visible. At Naame, red deer, aurochs, and fallow deer (MWS = 0, 1.5, and 0.5, respectively) show less abrasive diets compared to their counterparts from Ras el-Kelb (1.5, 2.3, and 0, respectively). A similar pattern is observed in fallow deer between Naame and Nahr Ibrahim (0.5 and 1.0, respectively). These trends suggest that habitats around Naame may have supported more abundant leafy vegetation, resulting in reduced dental abrasion, compared to Nahr Ibrahim and Ras el-Kelb.

To assess broader environmental trends across sites and through time, we combined the mesowear data for all ungulate species per site and compared them among our Lebanese sites and against comparable data available from the southern Levantine deposits (Fig. 5B) of Amud Cave (sub-units B1-B4, 55–70 ka[36]), Nesher Ramla (Units I-IIb, 80–140 ka[37]), and Qesem Cave (Heart, Shelf Yabrudian, and SWY, ca. 300 ka; SWS, LSBS, and SCW, >300 ka; DBS, >400 ka[38]). With average ungulate species-combined MWS falling below 2 and statistically indistinguishable from one another (Naame = 1.05; Nahr Ibrahim = 1.5; Ras el-Kelb = 1.57; pairwise comparisons always returned a value for $p_{adj} > 0.05$, Supplementary Table S7), the ungulates from the different Lebanese sites are generally best described as mixed feeders with a browsing tendency. This suggests that wooded environments were constantly present in the central Levantine region throughout the chronological span of the fossil assemblages. By contrast, combined ungulate species average MWS from the southern Levantine sites show greater variability, potentially reflecting local ecological or chronological factors. At Nesher Ramla (MWS = 2.62) and also -albeit to a lesser extent- at Amud (MWS = 1.97), these values are elevated, exceeding or approaching 2, indicating increased grazing diets, and thus an association with more open habitats, compared to the other southern as well as central Levantine sites that we examined. These differences are also supported statistically, with Nesher Ramla being significantly different from Amud, and both differing significantly from Naame (Supplementary Table S7), which is chronologically positioned between them. On the other hand, Qesem Cave ungulates display consistently low and statistically indistinguishable average combined MWS values across its sequence (Qesem >300 ka = 1.67; Qesem >400 ka = 1.77; Qesem ca. 300 ka = 1.76), reinforcing the interpretation of open woodland habitats near this site[38]. Such an environmental reconstruction aligns closely with that made for the central Levant and is supported by the lack of significant difference in combined average MWS between the Qasem cave ungulates and those of the broadly contemporaneous collections of Nahr Ibrahim and Ras el-Kelb (Supplementary Table S7).

For the microwear analysis, the patterns observed on the specimens we analyzed from our three collections, Naame, Ras el-Kelb, and Nahr Ibrahim, are characterized by relatively low feature counts (Table 2; Fig. 6B). In terms of numbers of scratches and pits, all specimens fall within the established ranges for these values for browsers rather than grazers, with the exception of rhinoceros and hippopotamus from Naame whose scratch count values (Nscr = 17 and 21, respectively) are consistent with a mixed-feeding dietary signal. Aurochs from Naame and wild goat from Nahr Ibrahim exhibited the lowest number of scratches (Nscr = 5 and 4, respectively). Cervids

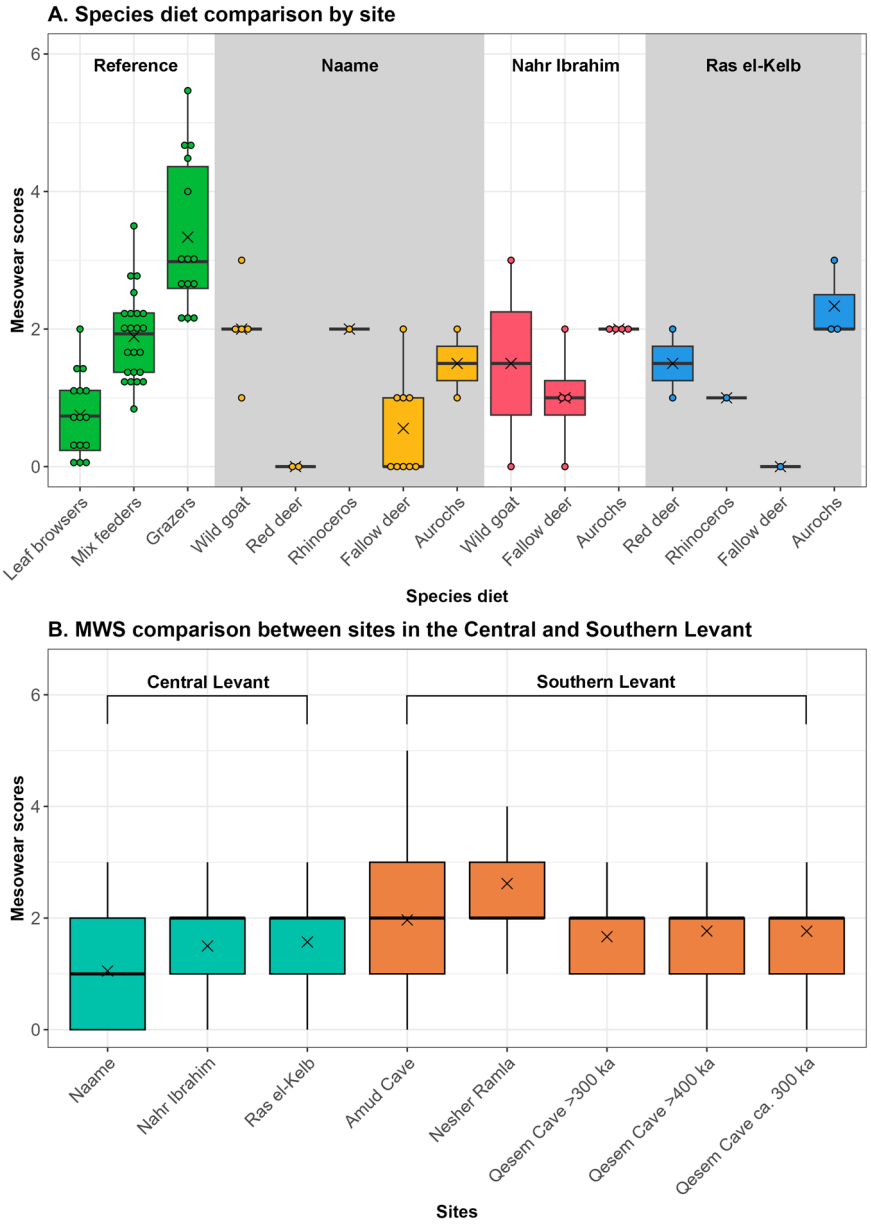

Fig. 5 | Mesowear results. A Mesowear scores (MWS) of ungulate species from Naame, Nahr Ibrahim, and Ras el-Kelb. **B** Comparative MWS data from Southern and Central Levantine sites (Amud[36], Nesher Ramla[37], and Qesem Cave[38]).

presented microwear features typical of extant browsing ungulates. This pattern was also consistent across all ungulate specimens from Ras el-Kelb. Additionally, two fallow deer specimens from Nahr Ibrahim displayed plucked enamel prisms (Fig. 6A), a feature commonly associated with strong browsing behavior[39,40]. Notably, one wild goat from Ras el-Kelb and one fallow deer from Nahr Ibrahim exhibited relatively high pit frequencies (Table 2), suggesting the ingestion of dust or grit during feeding, likely from low-lying vegetation[41]. Large pits were frequently observed (on 59.1% of the analyzed specimens). These, along with gouges, were also common among fallow deer, porcupine, hippopotamus, and rhinoceros from Naame. One rhinoceros from Ras el-Kelb showed gouges, large pits, and also a low frequency of hypercoarse scratches. All these features are commonly associated with the occasional consumption of bark, possibly as a result of feeding on twigs or small branches[42].

To sum up, the dental wear results of the Lebanese taxa converge in supporting a browsing diet for most of the species in all three collections, except for hippopotamus at Naame. However, for aurochs, wild goat, and rhinoceroses, mesowear indicates a more abrasive mixed-feeder longer-term diet, whereas the microwear suggests a potential short-term, perhaps seasonal, shift toward increased browsing in the immediate period before their death.

Microwear scratch variability was also used to assess the duration of mortality events by species and by site (Fig. 6C, Supplementary Tables S8). Each collection was analyzed as a single depositional unit. Specimens from Naame—*Niveau Supérieur* were excluded to avoid potential chronological biases. The Naame assemblage ($n = 5$) lies at the boundary of the yellow uncertainty zone ($p > 0.05$) in Zone B of the classification plot (Fig. 6C), whereas the Nahr Ibrahim assemblage ($n = 6$) falls clearly within Zone B, suggesting a multi-seasonal or year-round exploitation. Ras el-Kelb ($n = 9$) plots in Zone A, consistent with shorter-duration accumulation, although close to the uncertainty margin. To explore whether these patterns were driven by particular prey taxa, microwear variability was further assessed for species with sufficient sample sizes. Fallow deer from Naame ($n = 2$) and Nahr Ibrahim ($n = 4$) show low variability and plot in Zone A, consistent with short-duration, potentially single-season mortality events. At Ras el-Kelb, aurochs ($n = 2$) exhibit very low variability characteristic of Zone A, while rhinoceros ($n = 5$) also plots in Zone A but near the uncertainty threshold ($p > 0.05$). Given the very small sample sizes, these interpretations should be treated with caution and are best considered preliminary until larger samples are available. Nonetheless, the results suggest that Naame and Nahr Ibrahim were likely occupied or visited throughout the year, whereas

Table 2 | Mean mesowear scores (MWS) and microwear counts by taxon and site

Site	Species	*N*	Mean MWS	Npit	Nscr	%LP	%G	%HC	%Plucked Prism	%PP
Nahr Ibrahim	Aurochs	4	0.75	16.25	12.75	50	0	0	0	0
Nahr Ibrahim	Fallow deer	7	0.67	23.5	10	75	25	0	50	0
Nahr Ibrahim	Wild goat	2	2	10	4	0	0	0	0	0
Naame	Aurochs	2	0.5	21	5	0	0	0	0	0
Naame	Fallow deer	9	0.38	13.25	13	100	50	0	0	0
Naame	Hippopotamus	1	–	20.5	21	100	100	0	0	0
Naame	Porcupine	1	–	29	12	100	100	0	0	0
Naame	Red deer	2	0	11	13	100	0	0	0	0
Naame	Rhinoceros	1	2	15	17	100	100	0	0	0
Naame	Wild goat	5	2	–	–	–	–	–	–	–
Ras el-Kelb	Aurochs	3	1.33	20.5	9.25	50	0	0	0	0
Ras el-Kelb	Fallow deer	3	0	–	–	–	–	–	–	–
Ras el-Kelb	Red deer	2	1	20	11	0	0	0	0	0
Ras el-Kelb	Rhinoceros	7	1	13.58	11.50	60	60	20	0	0
Ras el-Kelb	Wild goat	1	–	34.5	13.5	0	0	0	0	0

fallow deer exploitation may have been seasonal. At Ras el-Kelb, the apparent seasonality signal among large mammals such as aurochs and rhinoceros may indicate that the estuary served as a specialized hunting area during specific times of year.

Catchment area modeling and mobility patterns

Catchment area models for Neandertals and *Homo sapiens* resulted in similar proportions of terrain coverage above and below the 30% slope threshold for 1.2- and 2.5-hour radii even if *Homo sapiens* would have had access to an overall slightly larger area compared to Neandertals within the same time period (approximately 6.5–8.3% and 6.6–10.1% larger within 1.2- and 2.15-h periods respectively), thus justifying the use of either of models for our sites (Table 3).

All three sites studied here, Naame, Ras el-Kelb, and Nahr Ibrahim, are situated along the Lebanese coastal plain, a gently sloping and narrow zone well suited for forest-dwelling ungulates, which dominate the faunal assemblages. While Pleistocene sea-level change may have affected coastal morphology, available regional and analog reconstructions indicate that during interglacial periods relevant to the studied assemblages (MIS 5, MIS 7, and likely MIS 11), relative sea levels along the eastern Mediterranean coast were broadly comparable to modern conditions[43–47]. In our site catchment analysis, sea-level variation was explicitly incorporated by applying a conservative −5 m relative sea-level scenario to the digital elevation model. This adjustment results in only minor expansion of the coastal plain within the modeled foraging territories. Accordingly, the key factor structuring site catchments is not horizontal expansion of the coastal plain (e.g., Fig. 1), but the rapid transition from lowland coastal environments to elevated interior terrain. The steeply ascending geomorphology of the Lebanese interior brings elevated terrain within reach, even within a relatively limited 1.2-hour walking radius (Fig. 7). This is exemplified particularly at Nahr Ibrahim, where, within a 1.2-hour walking radius, 17% of the terrain exceeds a 30% slope. This proximity may have facilitated hominin access to montane animal species such as wild goat, which at Nahr Ibrahim is relatively highly represented (%MNI = 30%). Thus, Middle to Late Pleistocene foragers in the central Levant could have easily exploited both lowland and montane zones within a short distance from the site near the coast.

Discussion

Chronological placement of the Lebanese faunal assemblages

Our reassessment of the three legacy faunal collections from Lebanon offers new insights into Pleistocene hominin ecology and their environmental context in the central Levant, while situating them within the broader regional and chronological framework. Zumoffen's collections from Ras el-Kelb and Nahr Ibrahim, excavated over 130 years ago, are now dated to the second half of the Middle Pleistocene. The chronology of Nahr Ibrahim, at approximately 250 ka, coincides with the time of the transition from the Lower to the Middle Paleolithic in the Levant and is chronologically contemporary with the Acheulo-Yabrudian cultural complex, a phase marked by significant technological and behavioral innovations[48]. Additionally, the new age constraints on the collection from Ras el-Kelb provide a rare window into subsistence and environmental adaptations during the late Lower Paleolithic, around 400 ka, a critical phase in the early evolution of subsistence strategies, technological innovation, and social organization in the Levant as exemplified by the well-documented record from Qesem Cave[49].

On the other hand, more than fifty years after its initial discovery, our reassessment of the faunal assemblage from Naame firmly places the site's formation within MIS 5, making it broadly contemporaneous with key Middle Paleolithic sites in the southern Levant, including Tabun, Skhul, Qafzeh, Nesher Ramla, Hayonim, and Tinshemet Cave[50–54]. This pivotal period corresponds to the well-documented appearance of anatomically modern human populations at Qafzeh, Skhul, Geula Cave, and possibly Tinshemet Cave, representing one of the earliest major dispersals of our species outside Africa[11,55]. Our results reveal the anthropogenic nature of the Naame assemblage and provide new insights into prey selection, habitat use, and hunting strategies.

Assemblage formation, recovery bias, and implications for prey choice

The Ras el-Kelb and Nahr Ibrahim assemblages were recovered through hand collection prior to the establishment of systematic excavation and recovery protocols. Consequently, little detailed information is available regarding sampling strategies, selection criteria, or subsequent curation practices. The Ras el-Kelb material was collected in an open-air context from cemented osseous breccia, most likely in the vicinity of the Ras el-Kelb Cave, whereas the Nahr Ibrahim assemblage derives from softer sediments within the main gallery of the cave[16]. Although Zumoffen was a trained natural science scholar, and his collections reflect a deliberate effort to document Lebanese prehistoric sites rather than opportunistic or unsystematic gathering, we do acknowledge that clear recovery biases in these collections may be present. For example, at Ras el-Kelb and Nahr Ibrahim, rhinoceros and hippopotamus are represented exclusively by dental remains, suggesting preferential collection of large and conspicuous elements rather than

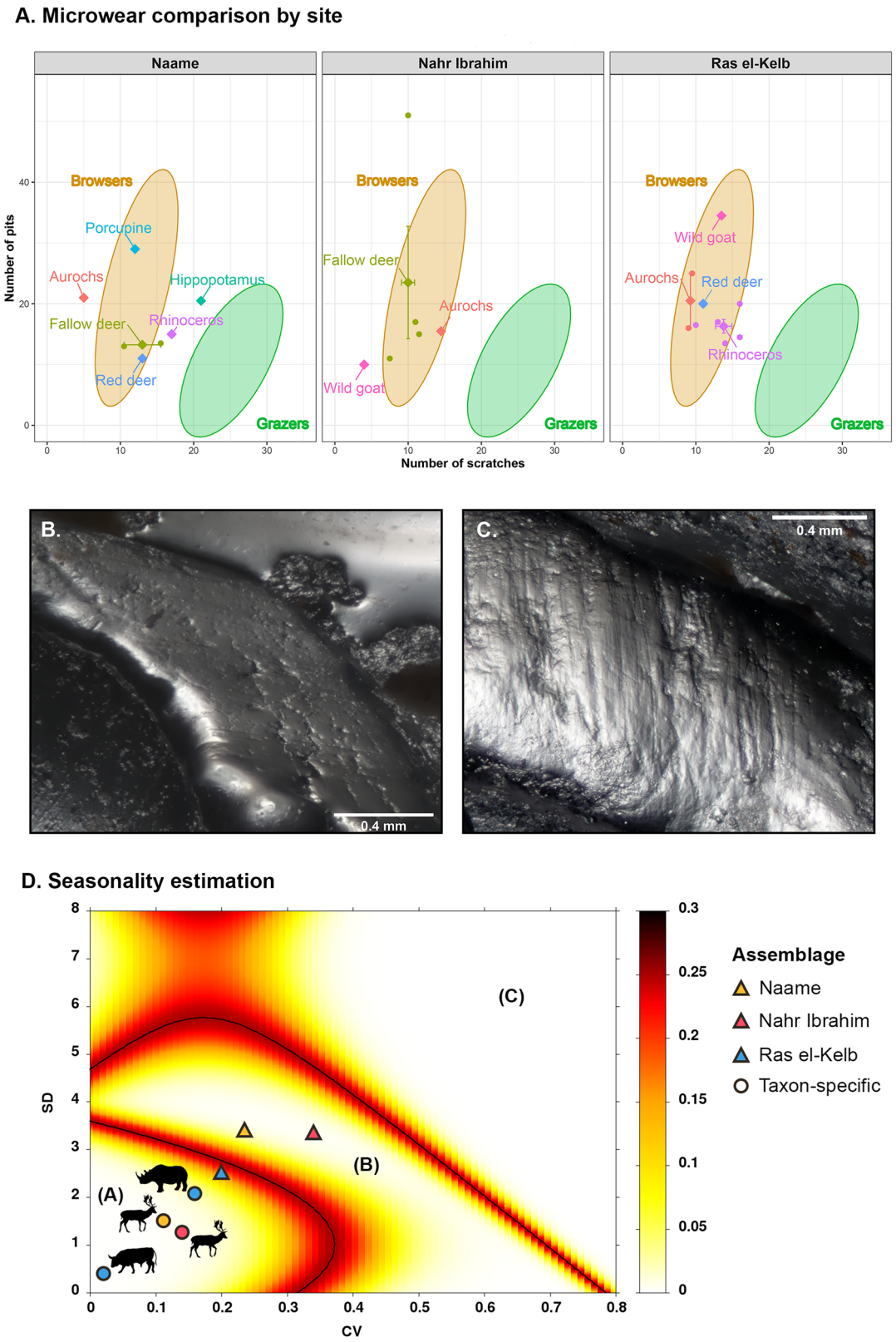

Fig. 6 | Short-term dietary signatures and mortality timing from dental Microwear. A Means of the number of scratches and pits by species at the different sites studied; **B** high-magnification image showing enamel prism plucking on fallow deer from Nahr Ibrahim. **C** Example of a well-preserved dental surface showing microwear features. **D** Heat map with error probability from coefficient of variation (CV) and standard deviation (SD) of microwear scratch counts for selected taxa, used to infer short-term duration in zone A, long-term events in zone B, and two non-consecutive mortality events in zone C.

deliberate Pleistocene hominin selection. Such patterns of recovery bias are well documented in early Near Eastern excavations[34]. Importantly, however, a relatively high representation of rhinoceros at the Ras el-Kelb promontory has been independently noted in earlier explorations[16,56] and the zooarchaeological analyses of the assemblages from the Ras el-Kelb Cave[33], suggesting that rhinoceros was indeed commonly present in this estuarine landscape during the Paleolithic and not solely an artifact of selective recovery. By contrast, the Naame assemblage derives from a later and more systematic investigation with more detailed descriptions of excavation procedures (see Supplementary Notes S1[26,57]). Although the work consisted largely of soundings and required mechanical and chemical extraction from cemented breccia (processes that likely increased fragmentation), the recovery effort was extensive. Very small bone fragments, low-density elements, teeth, and even fish remains were recovered, indicating that collection bias toward large or dense elements was substantially reduced at this site. For Naame, recovery-related loss of small or fragile remains is therefore unlikely to be the dominant driver of observed taxonomic patterns.

These faunal collections nevertheless represent filtered samples shaped first by hominin accumulation, then by taphonomic processes, and subsequently by recovery and curation efforts. Our assessment of sample completeness and diversity-based comparisons indicates that rare taxa are likely underrepresented – as expected in legacy collections and zooarchaeological assemblages more broadly[58]. However, the dominant taxa and overall abundance structure remained sufficiently robust to support their use for long-term paleoecological and behavioral inference.

During the Middle and Late Pleistocene, several medium and large carnivore species inhabited the central Levant, including golden jackal (*Canis aureus*), Arabian wolf (*Canis lupus arabs*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and brown bear (*Ursus arctos syriacus*), as remains of these taxa have been documented from Lebanese sites[22]. Carnivore remains are notably absent from the legacy collections that we studied (Naame, Ras el-Kelb, and Nahr Ibrahim), despite Zumoffen[16] reporting a bear tooth and indeterminate large carnivore teeth at Ras el-Kelb. While this absence may partly reflect recovery or curation bias, the overall scarcity of traces of carnivore activity on the bone surfaces suggests that non-human predators played only a limited role in the accumulation of these assemblages. Additionally, the documentation at Naame of one carnivore bite mark superimposed on anthropogenic cut marks underscores hominins' primary access to and control over carcass processing at the site.

Evidence for the anthropogenic involvement in the faunal accumulations was detected in all three collections we studied. Cut marks, impact notches, and split long bones from Naame and Nahr Ibrahim demonstrate a full range of butchery activities, including skinning, disarticulation, filleting, and marrow extraction[59,60] providing direct evidence for a significant

Table 3 | Catchment area statistics by site and hominin group

Naame							
Species	**Time**	**Km² flat**		**Km² steep**		**Km² total**	**% Difference**
H. sapiens	1.2 h	17.61	91%	1.84	9%	19.45	+8.29
	2.15 h	46.14	89%	5.66	11%	51.80	+6.55
Neanderthals	1.2 h	16.26	91%	1.64	9%	17.90	
	2.15 h	43.29	89%	5.21	11%	48.51	
Ras el-Kelb							
H. sapiens	1.2 h	15.01	90%	1.62	10%	16.64	+7.35
	2.15 h	35.79	86%	5.94	14%	41.73	+10.14
Neanderthals	1.2 h	14.00	91%	1.46	9%	15.46	
	2.15 h	32.44	86%	5.26	14%	37.70	
Nahr Ibrahim							
H. sapiens	1.2 h	7.96	71%	1.91	17%	11.15	+6.48
	2.15 h	22.59	71%	5.59	18%	31.74	+7.75
Neanderthals	1.2 h	7.46	71%	1.74	17%	10.45	
	2.15 h	20.95	71%	5.14	17%	29.37	

Quantitative summary of catchment area characteristics within 1.2- and 2.5-hour radii from each site, comparing terrain accessibility for Neanderthals and *Homo sapiens*.

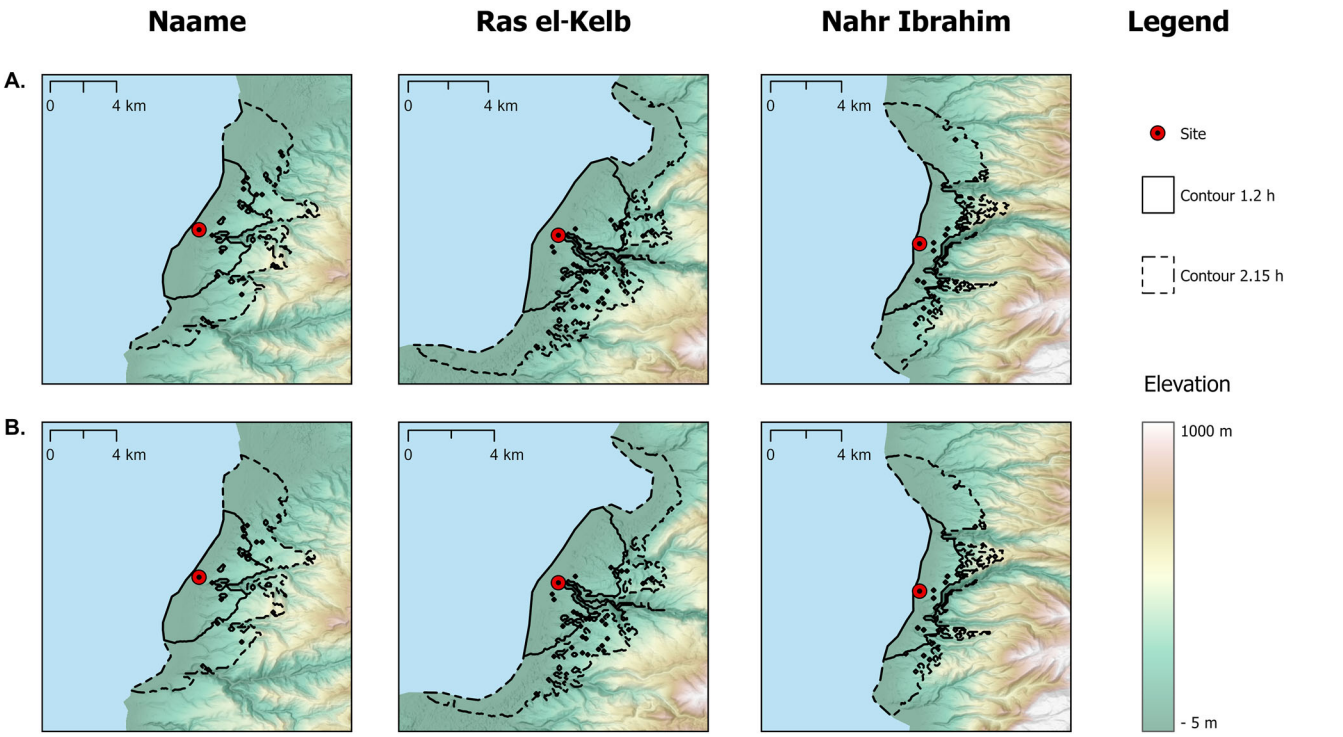

Fig. 7 | Catchment area modeling. Catchment area maps for Naame, Nahr Ibrahim, and Ras el-Kelb showing terrain within a 1.2-h walking radius, with slope thresholds above 30% indicated for (**A**) *Homo sapiens* and **B** Neanderthals.

hominin role in the accumulation of these assemblages. At Naame and Ras el-Kelb, bone surfaces show evidence of thermal exposure, though never to the extent of full calcination. This pattern may reflect exposure to domestic or cooking fires, or incidental burning, rather than deliberate use of bone as fuel[61,62]. Although no direct evidence of anthropogenic manipulation (e.g., cut marks) was identified in the Ras el-Kelb collection, the presence of burned bones in close association with lithic artifacts[16] points to hominin activity in the landscape during the deposition of the assemblage.

The overall species diversity, which can reflect the dietary breadth of prehistoric foragers, is comparable across the three collections, with no single taxon overwhelmingly dominating any assemblage. Nahr Ibrahim and Naame are similar in their prey species representation, with a primary focus on large game, particularly adult aurochs, fallow deer, red deer, and wild goats, with smaller ungulates such as roe deer hunted only occasionally. This pattern aligns with findings from Middle Paleolithic sites across the Levant, including, for example, Tabun, Kebara[63], Hayonim[64], and Qafzeh[65] from the south, Ras el-Kelb Cave[22,33] in the center, and Üçağızlı II[66], Dederiyeh[67] in the north.

Our assessment of prey choice patterns at Naame reveals that, despite the fallow deer abundance relative to other taxa in the assemblage, other more dangerous prey, such as aurochs and rhinoceros, were the preferred and selectively acquired targets, most likely due to the latter's higher meat return. Similar high frequencies of fallow deer have also been noted in southern Levantine Middle Paleolithic sites. Although this has been traditionally associated with hominin selective prey choice, they have more recently been associated with opportunistic acquisition rather than strategic targeting, reducing the importance of fallow deer for hominin subsistence[35]. In addition, wild goats seem to have also been actively selected at Naame, despite their lower meat yield compared to higher-ranked prey. Their selection might have been linked to their common occurrence in the steep or montane habitats in the vicinity of the site, which would have provided humans with continuous or seasonal access to them. Alternatively, wild goats may have been specifically targeted for reasons beyond subsistence, e.g., for particular uses of their hides or other body parts. Similar arguments for targeting specific ungulate taxa, e.g., gazelle, have also been made at other Levantine sites[68].

Paleoecology and landscape-scale foraging strategies

With most ungulate taxa classified as browsers or mixed feeders adapted to woody vegetation, the dental mesowear analysis of the herbivore species reveals a coherent signal of a Mediterranean woodland environment in all three central Levantine collections, spanning from approximately 400–100 ka. The interspecific differences visible from the mesowear scores speak for dietary niche partitioning among sympatric species, a key ecological mechanism that allowed multiple large herbivores to coexist within the same habitat[69,70].

Minor variations in the mesowear patterns, for example, reflecting a lower level of abrasives in the teeth of red and fallow deer at Naame compared to those from Ras el-Kelb and Nahr Ibrahim, respectively, may reflect subtle local (also possibly temporal) differences in vegetation structure across the Lebanese coast, possibly linked to denser tree cover in the region of Naame in the Middle Paleolithic.

A paleoenvironmental reconstruction indicating the prevalence of wooded conditions in coastal Lebanon during the Middle Paleolithic is also supported by the available palynological data from Naame as well as other broadly contemporaneous cave sites, i.e., Ras el-Kelb Cave, Nahr Ibrahim, and Adlun. Even though these studies are limited, they do indicated the presence of typical Mediterranean forest taxa, supporting the inference of a well-developed vegetation cover composed of a diverse mix of trees and shrubs, like fir (*Abies* spp.), wingnut (*Pterocarya* spp.), birch (*Betula* spp.), hazel (*Corylus* spp.), elm (*Ulmus* spp.), lime (*Tilia* spp.), hop hornbeam (*Ostrya* spp.), hornbeam (*Carpinus* spp.), and ivy (*Hedera* spp.), as well as members of the *Amaranthaceae* family, grasses (*Poaceae*, formerly *Gramineae*), thorny burnet (*Sarcopoterium spinosum*), and false gromwell (*Theligonum cynocrambe*)[23]. This woodland setting would have provided a mosaic of resources and habitats, including dense understory browse and seasonally productive clearings.

In comparison to southern Levantine sites, ungulate mesowear data show that in the Middle Pleistocene woodland habitats analogous to those present at Ras el-Kelb and Nahr Ibrahim extended southward, as documented through the low abrasion mesowear pattern of ungulates of Qesem Cave. During the Late Pleistocene, however, woodland cover seems to have retreated northward, persisting in the central Levant as is evident by the mesowear patterns of ungulates at Naame, but disappearing from the southern Levantine regions of Nesher Ramla and Amud Cave as reflected by the more abrasive mesowear patterns of their ungulate taxa indicative of more open, grass-dominated environments[36,37]. This pattern establishes a persistent north-south ecological gradient during the Late Pleistocene, with the central Levant acting as a stable refugium for forest-adapted fauna, sustaining diverse ungulate communities and supporting hominin foraging strategies finely tuned to local ecological conditions.

The Late Pleistocene vegetation gradient that characterized the eastern Mediterranean coast is further supported by the evidence for the distribution of gazelle (*Gazella* spp.), notable from the Levantine sites. The sheer abundance of gazelle remains in archaeofaunal assemblages from the coastal southern Levantine sites, particularly during the Late Pleistocene[71–73], contrasts sharply with this taxon's representation in the broadly contemporaneous central Levantine assemblages, whether its complete absence from the collections we studied here or its low representation in other collections, for example from Ksar'Akil rockshelter, and Ras el-Kelb and Nahr Ibrahim caves[33,74,75]. Notable as well is the gazelle's documented absence from faunal assemblages from Late Pleistocene sites located further north along the Levantine coast[66,76], where the woodland-shrubland mosaic environment likely extended. Today, in the Near East, gazelles are typically associated with xeric, open landscapes and are primarily grazers, with some seasonal browsing[77,78]. Its high representation in the south would thus advocate the analogous presence of increasingly open environments. By contrast, the Pleistocene coastal woodlands of the central and northern Levant could have therefore represented the northern limit of gazelles' ecological tolerance.

Zooarchaeological data from Syria further indicate that this north-south gradient formed part of a broader mosaic of Levantine environments during the Late Pleistocene. Middle Paleolithic assemblages from interior sites such as Umm el Tlel and the El Kowm/Hummal complex are dominated by equids, camelids, and gazelles, indicating open, arid to semi-arid steppe landscapes structured around springs and wadi-bottom water sources, with little evidence for sustained woodland expansion[67,79,80]. Similarly, at Wadi Mushkuna rockshelter in the Anti-Lebanon foothills, equid-dominated faunal spectra have been interpreted as reflecting water-point-focused hunting strategies in open steppe settings[81,82]. These records show that Middle Paleolithic hunter-gatherer groups occupied ecologically distinct desert-steppe environments in the northern Levantine interior, demonstrating that hominins adapted to a diversity of paleoecological zones across the Levant.

The dental microwear analysis, although constrained by sample size, provides important complementary evidence overall supporting a wooded environmental reconstruction, as almost all analyzed specimens have microwear signatures expected of browsers. Ungulate taxa that are commonly mixed feeders, such as aurochs, wild goats, and also rhinoceros, here exhibit microwear indicative of episodic shifts toward more intensive browsing. Additional microwear features, including high pit frequencies detected in wild goats and hypercoarse scratches and gouges observed in rhinoceros and fallow deer, point to the occasional ingestion of dust-laden or gritty low-lying vegetation, as well as bark stripping, or small branches and twigs feeding. Such behaviors tend to occur during periods of resource scarcity or intensified interspecific competition, most plausibly at the end of the dry season (typically September to December)[83,84]. During this time, herbaceous vegetation would have been limited, and ungulates would have shifted their diets toward more fibrous, leaf-based resources. Documenting these behaviors in microwear patterns suggests that it is therefore likely that at least some of the analyzed individuals died during this time of the year.

The microwear signatures provide further evidence for the seasonal patterns of animal accumulation within the investigated collections. Analysis of scratch variability suggests that aurochs and rhinoceroses were accumulated over a restricted period of the year at Ras el-Kelb, thus supporting episodes of single-season hunting of this taxon at this site. A similar pattern of seasonal accumulation is observed for fallow deer at both Naame and Nahr Ibrahim, even if year-round occupations at these sites are generally evident from the microwear scratch variability of all taxa combined. These findings support a model in which hominins would have conducted seasonal hunting campaigns, likely during the end of the dry season. Our results for seasonal hunting behavior detected at Nahr Ibrahim and Ras el-Kelb, i.e., at the Lower to Middle Paleolithic transition, document the earliest zooarchaeological evidence for such behavior in Lebanon. This evidence complements previous findings from the southern Levant, where seasonal hunting behaviors have also been detected at the broadly contemporaneous deposits of Qesem Cave[38].

In the Middle Paleolithic, the better representation of sites and faunal assemblages allows for better reconstructions of hominin behavior. During this time, in the more open and dry southern regions of the Levant, hominins appear to have structured their foraging around temporary water sources and the cyclical availability of plant resources, timing their activities to coincide with productivity peaks at the onset or end of the rainy season[36,37,85,86]. By comparison, the central Levantine pattern is characterized by hominins targeting large-bodied browsers and mixed feeders in Mediterranean woodland settings during the late dry season, when prey vulnerability and predictability were heightened. Overall, by selectively targeting ecotones and microhabitats where prey tended to concentrate, hominins likely enhanced hunting efficiency. This is well exemplified by the differing faunal compositions at the studied sites in spite of their geographic proximity. At Nahr Ibrahim, for example, wild goat is represented at a higher frequency, likely related to the increased proximity of mountainous terrain compared to the other sites. At Ras el-Kelb's estuarine settings, the prevalence of rhinoceros in the faunal collection suggests deliberate movement of hominins between ecologically distinct habitats to maximize foraging success. Therefore, rather than responding passively to environmental conditions, hominin groups in the central Levant appear to have had a good knowledge of the landscapes and to have strategically navigated territories, returning seasonally to hunting grounds located within manageable distances from primary occupation sites, something also documented in the southern Levant[34,37,87]. Landscape-scale energetic models emphasize the role of terrain in structuring hominin land use, proposing that rugged Mediterranean woodland landscapes supported compressed exploitation territories that could offset the higher locomotor and energetic costs associated with Neanderthals, whereas broader and more environmentally variable landscapes were exploited more extensively by anatomically modern humans[88]. Although it is not currently possible to determine which hominin species was responsible for the accumulation of the assemblages examined here, our site catchment analyses are broadly consistent with this framework. The exploitation of woodland and ecotonal settings documented along the central Levantine coast therefore provides faunal-based support for the interpretation that Levantine coastal landscapes constituted favorable foraging contexts for Middle Paleolithic hominin populations, within which ecological niches likely overlapped even as strategies of landscape use and foraging organization may have varied.

Overall, these behaviors point to a resilient and flexible foraging system in the wooded central Levantine coastal strip during the Middle and Late Pleistocene, in which hominins repeatedly adjusted subsistence strategies to seasonal constraints while maintaining long-term engagement with complex, resource-rich landscapes.

Broader implications, limitations, and future directions

This study provides new evidence for complex and adaptive hominin foraging strategies in the central Levant. Our findings demonstrate that Mediterranean woodlands persisted in the central Levant, potentially providing refugia during the Middle and Late Pleistocene. These landscapes sustained diverse ungulate populations and enabled hominins to develop seasonally structured hunting practices. The paleoenvironmental contrasts between the central and southern coastal Levantine regions highlighted by our study carry significant implications for understanding regional variability in hominin adaptations. This divergence likely influenced not only prey selection, but also mobility patterns, technological organization, and potentially even social dynamics.

We acknowledge that limitations inherent in legacy collections, such as recovery bias and limited stratigraphic control, constrain the resolution of our interpretations. Yet, our research highlights the importance of revisiting long-forgotten historical collections. Overall, our findings challenge simplistic narratives of uniform hominin adaptation across the Levant, emphasizing instead the critical role of local environmental conditions in shaping the diversity of Paleolithic lifeways.

Future research integrating stable isotope analysis, the study of lithic material associated with these collections, and the systematic comparison with newly excavated or other overlooked collections from Lebanon and neighboring regions will be essential to refining paleoenvironmental reconstructions and understanding the full extent of hominin adaptability in the eastern Mediterranean corridor.

Materials and methods

The faunal material analyzed in this study originates from legacy collections curated at the Museum of Lebanese Prehistory (Saint Joseph University of Beirut), Beirut (Lebanon). The faunal remains from Nahr Ibrahim and Ras el-Kelb were collected in the late 19th century by the Jesuit Father Godefroy Zumoffen[16] from within or from the vicinity of the two respective cave sites, in which excavations were later conducted by other researchers (see Supplementary Notes S1 for further details). These later excavations at both caves yielded Middle Paleolithic lithic industries[18,89]. Since the material Zumoffen collected from Nahr Ibrahim came from within the cave, even if lacking stratigraphic control, we expect it to broadly fall within the chronological range of the later excavations carried out by Ralph Solecki. In the case of Ras el-Kelb, Zumoffen's collected material came not from the cave itself, but from a locality on the promontory higher than the cave. Zumoffen reported the presence of Acheulean alongside Mousterian lithic artifacts from the regions where he collected the fauna[16]. It is worth noting that a later report confirmed the presence of Acheulean industries in the same area[90]. Thus, here we expect Zumoffen's faunal collections to be older than the dates obtained from the later excavations of Ras el-Kelb Cave. The material from Naame was recovered during excavations of the site in 1967 by the Jesuit Father Henri Fleisch[26,57]. Specifically, our material comes from Fleisch's area three (PIII) from zones 2 and 0 ($PIII_2$ and $PIII_0$) within the brecciated deposits that he found in this area, as well as from one of the trenches (Trench A) which he dug in what he called the *Niveau Supérieur*, an area in grounds above these brecciated deposits. Additionally, we also analyzed material recovered from a breccia block (*Bloc du 75*), which was recovered by Fleisch during a later visit in 1975 to the site when it was being blasted for the construction of the coastal highway. Although there is no record of the specific profile zone from which this bloc originated, it most likely came from levels below the *Niveau Supérieur* and down to $PIII_0$ and was included in the analysis to maximize the dataset from Naame.

Overall, the Naame deposits all yielded a relatively homogeneous Middle Paleolithic technocomplex and a preliminary date placing this assemblage at the end of MIS 5 (see Supplementary Notes S1 for further details).

Given the substantial alteration or destruction of the original site contexts, the legacy faunal collections analyzed in the present study represent a unique and irreplaceable source of information for reconstructing the Pleistocene record of coastal Lebanon.

Chronology

Dating analyses of five selected fossil teeth (three from Naame and one each from Ras el-Kelb and Nahr Ibrahim, Supplementary Table S9) were carried

out at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Spain. ESR Dose evaluation utilized the multiple aliquot additive dose (MAAD) method, and the enamel powder was split into twelve aliquots and gamma irradiated at increasing doses. ESR measurements were carried out at room temperature with either an EMXmicro 6/1 Bruker or an ELEXSYS E500 Bruker X-band ESR spectrometers (Supplementary Table S10) coupled to a standard rectangular ER 4102ST cavity following the standard procedure employed at CENIEH. The ESR intensities were extracted from T1-B2 peak-to-peak amplitudes of the ESR signal[91]. D_E values were obtained by fitting a single saturating exponential (SSE) through the mean ESR intensities derived from the repeated measurements, with data weighted by the inverse of the squared ESR intensity ($1/I^2$)[92,93]. The ESR dose response curves (DRC) are displayed in Supplementary Fig. S4, while numerical fitting results are provided in Supplementary Table S10. Solution U-series analyses of powdered dental tissues were carried out using a NEPTUNE MC-ICP-MS, following chemical treatment procedures and MC-ICP-MS analytical protocols described elsewhere, e.g., [94,95]. Closed-system U-series ages were calculated following Pourmand et al.[94]. Analytical results are given in Supplementary Table S11.

The environmental dose rate from the sediment was evaluated from the samples collected during tooth preparation. The following parameters were used for the dose rate calculations: an alpha efficiency of 0.13 ± 0.02[96], Monte-Carlo beta attenuation factors from Marsh[97], dose-rate conversion factors from Adamiec and Aitken[98], and Guerin et al.[99], an estimated long-term water content of 0, 5 ± 3 wt.% and 20 ± 5 wt.% in enamel, dentine, and sediment, respectively. The long-term depth was roughly evaluated based on the information available in the literature. Combined U-series/ESR age calculations were performed with DATA[100] and USESR programs[101], using the US[102], AU[103], and CSUS uptake[104] models. Data inputs and outputs are given in Supplementary Table S12, while a complete description of the analytical procedure can be found in the Supplementary Notes S3. A series of sensitivity tests was carried out in order to properly evaluate the impact of the main sources of uncertainty on the age results (Tables S13 and S14).

Faunal and taphonomic analysis

The faunal assemblages analyzed here derive from legacy collections excavated using different recovery strategies and curated prior to modern standards. Due to the absence of formal cataloging, all specimens were recorded in a custom zooarchaeological database developed for this project and for the archives of the Museum of Lebanese Prehistory (Saint Joseph University of Beirut). Taxonomic identifications were made to the most specific level possible using as references the University of Tübingen's comparative skeletal material as well as digital resources, e.g., [105–107]. A subset of the material had taxonomic labels, but all specimens were reassessed to ensure consistency. Identifications were taxonomic and by skeletal element, portion, side, and preservation status. Unidentifiable fragments were classified by size categories[64].

Zooarchaeological quantification included the standard parameters: i.e., Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), and Minimum Number of Individuals (MNI)[108–110]. Taxonomic diversity was quantified using the Inverse Simpson's Index[111], which integrates species richness and evenness into a single metric of abundance structure. Simpson-based measures are considered relatively robust to variation in sampling effort and incomplete detection of rare taxa, particularly in uneven assemblages and small samples[58,112], making them well suited to legacy zooarchaeological collections.

Differences in recovery history among sites necessarily affect the representation of rare taxa and small-bodied animals[58,108,109]. To evaluate the robustness of diversity-based comparisons and the influence of sampling and recovery bias quantitatively, we applied a sample completeness and diversity comparison framework well known in ecology and increasingly adopted in reconstructing deep-time biodiversity patterns research[32,113–116]. Using MNI data, we implemented the four-step analysis of Chao et al.[32]: (1) estimation of sample completeness profiles across diversity orders (q = 0–2), (2) size-based rarefaction and extrapolation to evaluate asymptotic behavior, (3) coverage-based rarefaction and extrapolation to standardize diversity comparisons by sample completeness rather than sample size, and (4) assessment of evenness profiles. Analyses were conducted on the iNEXT.4steps Online software[31], with uncertainty estimated via bootstrap resampling (500 iterations). This framework allows diversity comparisons to be evaluated conservatively, distinguishing patterns driven by dominant taxa ($q \geq 1$) from those sensitive to rare taxa ($q = 0$), and provides an explicit means to assess whether observed diversity differences are robust to recovery and sampling biases.

For taxonomic abundance, the MNI was used as the primary unit, with biomass estimates calculated by multiplying MNI values by estimated meat yields for Levantine ungulates[22], adjusted for age. We then compared relative abundances of %MNI and %biomass by assemblage to assess the economic contribution of prey species to the hominin diet. To explore regional patterns in prey selection and meat exploitation, we conducted a principal component analysis (PCA) of %MNI and estimated %biomass using the data from the different Naame assemblages as well as comparable datasets available from the broadly contemporaneous (MIS 5) assemblages from Ras el-Kelb Cave (from the layers K-M and D-J[22,33]), and of the southern Levantine sites of Tabun (from layers B, C), and Skhul[34]. Unfortunately, no comparable datasets were available for our Nahr Ibrahim and Ras el-Kelb collections. Given the inverse relationship between body size and population density[117,118], we estimated the expected biomass of large species in natural communities and compared it to the zooarchaeological record to examine whether these taxa appear overrepresented, something which may indicate selective human emphasis on large-bodied game beyond ecological availability. We used Damuth's law as a null ecological hypothesis[119], calculating observed biomass as MNI × body mass and expected values from mass-abundance scaling (Expected MNI = Mass^(-0.75); Expected biomass = Mass^(0.25)). These relationships assume that species of greater body size occur at lower population densities but contribute proportionally to community biomass. We then plotted %Observed biomass against %Expected biomass, with a 1:1 dashed line indicating the null expectation. Taxa positioned above the line can be interpreted as overrepresented relative to their expected abundance, whereas those below the line are underrepresented. It should be noted that this comparison offers valuable insights into hominin prey choice, but they do not consider factors such as search time, handling time, or return rates, which also impact the overall costs of acquiring prey[120–122]

Age-at-death was assessed through dental eruption and wear, as well as epiphyseal fusion, and classified individuals as juveniles, prime or old adults[123–129]. Mortality profiles were plotted in ternary diagrams to assess hunting behavior[125].

Despite the challenging preservation conditions and breccia concretions, the taphonomic analysis of the bone surfaces was carried out to reconstruct the origin of the bone accumulations for all three collections. Taphonomic modifications were examined on all specimens >2 cm in length. Surface modifications, including cut marks, impact damage, burning, carnivore damage, and weathering, were assessed following established protocols[60,62,130–134]. Biostratinomic and diagenetic alterations such as rodent gnawing, root etching, and chemical erosion[135,136] were recorded in terms of presence/absence. Microscopes used included Leica S9D and Zeiss SteREO Discovery.V8; images were captured with integrated digital photomicrography.

Dental wear analysis

Mesowear analysis[137] was conducted following the "ruler method" developed by Mihlbachler et al.[138] on the well-preserved (i.e., complete and undamaged) buccal and lingual cusps of upper and lower molars of bovids and cervids, and on upper molars of rhinoceros. Only prime-aged adults were included to restrict possible ontogenetic wear variation[139]. Each cusp was assigned a mesowear score (MWS) from 0 to 6 based on macroscopic gradual changes in cusp shape and relief, from high and sharp to blunt and no relief[138,140]. Mesowear scores were calculated at the individual level by averaging cusp values when multiple teeth were available. To test whether

upper and lower molars could be combined, individual-level scores were compared between tooth classes within each site using Wilcoxon rank-sum tests. No statistically significant differences were detected (Naame: $W = 47.5$, $p = 0.79$; Nahr Ibrahim: $W = 12.5$, $p = 0.71$; Ras el-Kelb: $W = 1.0$, $p = 0.095$), and distributions were comparable. Upper and lower molars were therefore pooled, combining this data for all subsequent analyses – species-level and site-level averages. Differences in mesowear scores among species and sites were tested using Kruskal-Wallis rank-sum tests, followed by Dunn's post-hoc pairwise comparisons with Benjamini-Hochberg correction.

Microwear analysis was performed on high-resolution casts of the cleaned occlusal surfaces, which were made using polyvinylsiloxane molding (Coltene President Microsystem regular body) and clear epoxy resin (Epo-Tek 301). Only specimens that were well-preserved and free of taphonomic damage were included[141,142], thus reducing the original sample by 47.8% (i.e., from the 46 initially selected specimens to 22 on which this analysis could be performed). Using a Zeiss Stemi 2000C microscope at 35x magnification, microwear features within a standardized 0.16 mm^2 area were categorized as either scratches (elongated microfeatures) or pits (scars with circular or sub-circular outline), and counted[41,143]. A comparative and interpretive reference microwear database of extant and extinct ungulates with well-known dietary habits was used[41,144]. Bivariate plots of pits vs. scratches counts were produced using the R script *microwearbivaR*[145]. Since dental microwear patterns reflect short-term dietary signals and thus an individual's diet a short period before death, patterns of anthropogenically accumulated fauna can be used to infer death seasonality, and this can in turn provide an estimation of the duration of human occupation in the layer where the fauna was deposited[146,147]. We estimated seasonality of key prey ungulates in our samples and analyzed intra-group variability in microwear scratch frequency using the coefficient of variation (CV) and standard deviation (SD). These values were plotted on a classification graph dividing events into short-term, continuous, or non-consecutive mortality patterns[146]. Given our small sample size, we applied a joint bootstrapped estimate (with $n = 500$ times) of CV and SD to improve the statistical robustness[148].

One observer (GR) conducted both wear analyses to minimize inter-observer error.

Catchment area analysis

To model the potential foraging territory of prehistoric humans, we generated a digital elevation model (DEM) of Lebanon modified to reflect sea levels during MIS 5. We computed travel cost surfaces and walking speed contours using Tobler's Hiking Function, adjusted for different hominin locomotor profiles (Neanderthals and *Homo sapiens*). Catchment areas were reconstructed as travel-time polygons for each site. To infer ungulate habitat suitability, terrain slope was classified using a 30° threshold to distinguish plains vs. mountainous zones[149]. Slope categories were overlaid with catchment contours and corrected for submerged coastal areas. Wild goat habitat was restricted to steeper slopes, while grazing ungulates were associated with flatter terrain. All GIS and modeling steps were carried out in R (v.4.2.1; RStudio v.2022.2.3.492) using the raster and gdistance packages for cost-distance analysis, and in ArcGIS for slope classification and terrain composition statistics. The scripts and detailed workflow are provided in the Supplementary Notes S2.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data are available in the main text or the supplementary materials. The R script and datasets used for the zooarchaeological analyses are freely available at https://github.com/gabrieleru91-coder/Paleoecology-Lebanon, while the R script used for the site catchment analysis can be found at https://github.com/sdmclin/SET-PHMC.

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Author contributions

G.R. conceived the study, developed the methodology, conducted the zooarchaeological, taphonomic, dental wear, and interpretive analyses, contributed to investigation and visualization, supervised aspects of the

work, and wrote the original draft; F.R. contributed to the methodology, particularly the dental wear analytical framework, helped interpret the results, and contributed to reviewing and editing the manuscript; M.D. contributed to the methodology and investigation, particularly the combined U-series/ESR dating analyses, helped interpret the chronological results, and contributed to reviewing and editing the manuscript; S.D.M. contributed to visualization, including spatial and landscape-related analyses, and contributed to reviewing and editing the manuscript; M.A.A.F. contributed to reviewing and editing the manuscript; M.H.-B. contributed to the study through support related to the Lebanese legacy collections and contributed to reviewing and editing the manuscript; V.M.-P. contributed to the investigation, particularly the dating-related analyses, and contributed to reviewing and editing the manuscript; A.H. contributed to the investigation, particularly the dating-related analyses, and contributed to reviewing and editing the manuscript; A.G. contributed comparative zooarchaeological expertise and contributed to reviewing and editing the manuscript; F.B. contributed to supervision, helped interpret the faunal and paleoecological results, and contributed to reviewing and editing the manuscript; Y.H.H. contributed to the investigation and supervision of the work and contributed to reviewing and editing the manuscript; S.EIZ. conceived the study, supervised the work, helped interpret the results, and contributed to reviewing and editing the manuscript.

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