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Additive Partitioning of Shannon Diversity in Palaeolithic Zooarchaeology: A Case Study from Qesem Cave

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Abstract

Understanding how faunal diversity is internally organized remains a central but still underdeveloped issue in Palaeolithic zooarchaeology. This paper proposes additive partitioning of Shannon diversity to the published faunal datasets from Qesem Cave (Israel) to determine whether assemblage diversity is structured mainly by contrasts among pre-defined analytical groups or by heterogeneity retained within them. In practical terms, total Shannon diversity is separated into a between-group (interclass) component and a within-group (intraclass) component: the former describes how remains are distributed among analytical classes, whereas the latter describes the diversity preserved inside those classes. The results show that taxonomic **diversity** at Qesem is consistently dominated by the interclass component, indicating that contrasts among prey-size classes structure the assemblages more strongly than taxonomic heterogeneity within those classes. However, the intraclass contribution varies among horizons: SCW represents the most strongly interclass-structured assemblage, whereas SW Yab shows the highest intra-class contribution. This pattern is maintained under both NISP and MNI, although MNI makes intraclass taxonomic heterogeneity more visible and reduces the sharpness of some contrasts. Fragment integration increases total Shannon diversity unevenly across the sequence, showing that the fragmented but size-class-attributed fraction affects not only the magnitude of diversity but also its internal partitioning among prey-size classes. Anatomical diversity follows a different pattern: when each assemblage is considered a whole, anatomical profiles are comparatively homogeneous and slightly intraclass-dominated, while clearer contrasts emerge within size classes, especially among medium-sized prey, where diversity is strongly structured around proximal limb elements rather than evenly distributed across anatomical regions. Taken together, these results suggest that additive partitioning captures differences in how faunal assemblages were structured, accumulated, or segmented through time, rather than simply recording changes in prey spectrum. The approach is therefore best understood as a reproducible descriptive framework that formalizes assemblage structure and gains archaeological meaning when read alongside independent taphonomic, anatomical, and contextual evidence.

Keywords Shannon diversity · Additive partitioning · Zooarchaeology · Faunal assemblages · Qesem cave · Middle pleistocene

Introduction

Diversity indices are widely used in zooarchaeology, yet their archaeological meaning is often less straightforward than their mathematical form. Measures of richness, evenness, and dominance are routinely employed to compare faunal assemblages, characterize prey spectra, and describe patterns of taxonomic concentration or breadth, both in archaeology and in related ecological approaches (Faith & Du, 2018; Grayson, 1984; Lyman, 1994, 2008). In the classical ecological sense, diversity refers not simply to the number of taxa present, but to the combination of richness and the distribution of abundances among them (Magurran, 1988, 2004). However, the archaeological significance of diversity values is not self-evident. Diversity measures are sensitive not only to observed abundances, but also to classificatory choices, aggregation scale, counting procedures, and sampling conditions (Buchanan & Eren, 2022; Colwell & Chao, 2022; Cowgill, 1989; Lyman, 2008, 2022). In that sense, diversity must first be treated as a formal property of assemblage composition, structured by explicit classificatory and analytical choices, before it is used to support archaeological interpretation.

This issue is especially important in Palaeolithic zooarchaeology, where faunal assemblages are not simple reflections of prey communities, but are filtered by selective transport, carcass processing, fragmentation, burning, density-mediated survival, and other taphonomic processes (Binford, 1978, 1981; Faith & Gordon, 2007; Lyman, 1994, 2008). Archaeological diversity is therefore shaped not only by what was hunted or consumed, but also by how faunal remains were accumulated, modified, and recorded. A relatively low diversity value may reflect strong taxonomic concentration, functional specialization, restricted prey access, or highly focused procurement; a higher value may reflect broader prey use, longer or more cumulative accumulation, aggregation effects, or other forms of structural heterogeneity. Diversity measures are thus often informative, but never self-interpreting. Their archaeological relevance depends on the analytical units in which they are computed and on the independent contextual evidence against which they are read.

This paper focuses on Shannon's information entropy, used here as a measure of Shannon diversity, because it provides a formal way to describe not only how diverse an assemblage is, but also how that diversity is organized. Shannon's index is particularly relevant here because it combines richness and evenness in a single expression and can be partitioned analytically. Originally developed as an information-theoretical measure of uncertainty (Shannon, 1948), the same mathematical expression was subsequently adopted in ecology for the study of biological diversity (Good, 1953; Margalef, 1957), later extended to inequality analysis (Theil, 1967), where it was decomposed into two components, and used in other decomposition contexts, including seasonality analysis (Rosselló & Sansó, 2017).

In the present study, additive partitioning means that total Shannon diversity is separated into components whose sum reproduces the observed total. In the taxonomic analysis, the between-group, or interclass, component measures the part of diversity generated by the distribution of remains among prey-size classes, whereas the within-group, or intraclass, component measures the taxonomic diversity retained inside those size classes. In the anatomical analysis, the same logic is applied to skeletal-part categories: the interclass component describes contrasts among major anatomical groups, while the intraclass component describes diversity among skeletal elements within those groups. This distinction directly addresses a question that NISP or MNI alone cannot resolve: whether diversity is mainly structured by contrasts between analytical groups or by heterogeneity within them.

This use of Shannon's measure is consistent with broader traditions in ecology and palaeontology in which diversity has been examined not only as a total value but also as a structured quantity. SHE—species richness (S), Shannon diversity (H), and evenness (E)—analysis, for example, combines cumulative changes in richness, Shannon diversity, and evenness to identify ecological or stratigraphic discontinuities in abundance data (Buzas & Hayek, 1998; Hayek & Buzas, 1997, 2010). Buzas and Hayek (2005) further examined the behaviour of richness and evenness within and between communities, while Jost (2007) clarified the broader logic of diversity partitioning. Our approach differs from SHE analysis in aim and implementation: we do not use cumulative curves to identify biofacies boundaries, but we follow the same general principle that Shannon-derived measures can reveal how abundance structure is organized across predefined analytical units. Applied to zooarchaeological data, the contribution is therefore descriptive before it is interpretive. Additive partitioning does not assign behavioural meaning automatically; it provides a formal structure that must then be evaluated against independent taphonomic, anatomical, and contextual evidence.

Qesem Cave provides a particularly demanding and therefore informative case study for such an approach. Its faunal record is unusually well documented through previous work on taxonomic composition, taphonomic modification, skeletal representation, combustion, delayed consumption, marrow extraction, and bone-grease-related processing (Stiner et al., 2009, 2011; Blasco et al., 2014, 2016a, 2016b, 2019a, 2019b; 2024; Assaf et al., 2020). This independent zooarchaeological background makes Qesem suitable for evaluating whether the partitioning of Shannon diversity describes meaningful structure within the faunal record, rather than merely producing an isolated numerical result.

The interest of Qesem also lies in the combination of a stable taxonomic baseline and a heterogeneous occupational history. Fallow deer (*Dama cf. mesopotamica*) is the dominant species throughout the analysed horizons, while other ungulates, birds, and tortoises remain comparatively less abundant (Blasco et al., 2014, 2024; Rivals et al., 2021; Stiner et al., 2009, 2011). Precisely because one taxon remains strongly overrepresented, changes in diversity structure are less likely to reflect broad prey-base replacement than subtle variation in the internal organization of faunal assemblages. At the same time, seasonality analyses based on dental eruption, mesowear, and microwear indicate repeated cave use in different seasons, with important differences between horizons and, in some cases, between taxa (Rivals et al., 2021).

The Hearth horizon is compatible with recurrent seasonal use, probably through short-term events repeated more than once a year, whereas other horizons may reflect either repeated visits or longer episodes of occupation. Rivals et al. (2021) also note that, although fallow deer dominates the assemblages, less abundant taxa such as aurochs and horses still record behaviourally meaningful hunting events. In such a context, additive partitioning is not expected to measure occupation duration directly; rather, it provides a formal way of describing how faunal variability is organized within a cave repeatedly used under different functional and temporal regimes.

A further methodological reason for applying this framework at Qesem is the exceptional degree of fragmentation in the faunal record. Only a small proportion of specimens can be identified taxonomically, whereas a much larger part of the assemblage remains taxonomically indeterminate but still assignable to prey-size class or anatomical category (Blasco et al., 2024). This raises an important question for diversity analysis: whether such remains should remain excluded from taxonomic calculations or be integrated, at least at the level of grouped structure. In the present study, this problem is treated explicitly by comparing standard taxonomic counts with an extended framework that includes taxonomically indeterminate but size-class-attributed fragments. The aim is not to estimate hidden taxonomic richness, but to evaluate how these fragments modify the grouped partitioning of diversity across analytical classes. This issue is particularly relevant at Qesem, where fragmentation is not marginal but constitutive of the assemblage itself (Blasco et al., 2014, 2024).

Within this framework, our aim is twofold. First, we introduce additive partitioning of Shannon diversity into Palaeolithic zooarchaeology as a formal way to distinguish intra-class from inter-class components of diversity. Second, we apply this framework to several Qesem horizons to examine how taxonomic and anatomical diversity is organized across prey-size classes and skeletal groups. We compare taxonomic data quantified through NISP and MNI, and we also assess the effect of integrating taxonomically indeterminate but size-class-attributed fragments, not to privilege one counting procedure over another, but to evaluate how different quantification frameworks affect the partitioning of diversity in a highly fragmented assemblage. These procedures are not treated here as direct behavioural proxies, nor as alternatives to taphonomic analysis, but as structured analytical descriptions whose archaeological relevance depends on comparison with the independent evidence already available for Qesem Cave.

Site Presentation

Qesem Cave (Israel) is a late Lower Palaeolithic site near Tel Aviv excavated since the early 2000s (Barkai et al., 2017; Gopher et al., 2005; Stiner et al., 2009). The site contains a stratigraphic sequence of more than 11 m. Radiometric dating (U–Th, TL, ESR and ESR/U-series) places this sequence between ca. 420 and ca. 220–200 ka, spanning MIS 11 to MIS 7 (Falguères et al., 2022; Gopher et al., 2010; Mercier et al., 2013). ESR/U-series on teeth applied to two assemblages from the middle part

of the stratigraphy range c. 249–296 ka (mean $\approx$ 280 ka) and c. 279–382 ka (mean $\approx$ 313 ka) (Falguères et al., 2016). Thermoluminescence dates on burnt flints suggest that some areas in the upper part of the sequence may extend into early MIS 7 (Mercier et al., 2013).

The site preserves a rich archaeological record of faunal, lithic, and hearth remains, although the faunal assemblages themselves are highly fragmented and frequently thermoaltered. From a cultural point of view, the whole stratigraphic column corresponds to the Acheulo-Yabrudian Cultural Complex (AYCC), which chronologically postdates the Lower Palaeolithic Acheulean and predates the Middle Palaeolithic Mousterian. The AYCC is characterized by the coexistence of large stone implements (mainly hand-axes and spheroids), Quina and Demi-Quina side-scrapers, and blades. Generally, the lithics (technological and typological) of the AYCC show three expressions (industries): (1) Acheulo-Yabrudian, (2) Yabrudian, and (3) Amudian. The main differences between them are the relative frequencies and proportions of the main used tools: the Acheulo-Yabrudian shows high proportions of large implements, the Yabrudian shows more side-scrapers, and the Amudian more blades. Recent research, mainly based on Qesem Cave, indicates that the Amudian and Yabrudian expressions should be viewed as activity-related contexts of a single cultural entity, and not as independent cultural entities (Barkai et al., 2017; Gopher & Barkai, 2016). In the case of Qesem Cave, two of these technological expressions are dominant: the Amudian (assemblages HU, LSBS, DBS, SCW, SW Sph, Fig. 1), and the Yabrudian (assemblages Shelf Yab and SW Yab, Fig. 1). These assemblages are stratigraphically interfingered, reinforcing the idea of their non-diachronic relations.

The faunal record at Qesem allows for detailed taphonomic analysis and insights into carcass processing and resource exploitation (Blasco et al., 2024; Stiner et al., 2009). According to these studies, fallow deer (*Dama cf. mesopotamica*) was the dominant prey taxon, followed by other species, such as red deer (*Cervus elaphus*), aurochs (*Bos primigenius*), horse (*Equus ferus*), and occasionally, wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), European wild ass (*Equus hydruntinus*), and wild goat (*Capra aegagrus*). Faunal remains are characterized by a high degree of fragmentation and thermoalteration. The habitual use of fire is documented not only by the central combustion feature identified through micromorphology and FTIR microspectroscopy, but also by the widespread presence of wood ash, burnt flint, and burnt bone throughout the stratigraphic sequence (Barkai et al., 2017; Karakanas et al., 2007; Shahack-Gross et al., 2014).

In this study, we use five distinct Amudian assemblages (HU, LSBS, DBS, SCW, SW Sph) and two Yabrudian assemblages (Shelf Yab and SW Yab) from various parts of the stratigraphic column (from elevation 500 cm to elevation 1050 cm below datum that is a stratigraphic sequence of some 5 m in depth). This offers a robust framework for exploring variability between Amudian and Yabrudian at Qesem and, by extension, in the AYCC as a whole. Their respective locations are shown in Fig. 1.

HU (Hearth Unit) corresponds to a large central combustion zone ($\sim 4 \text{ m}^2$) showing multiple use cycles and superimposed occupation episodes (Shahack-Gross et al., 2014). This unit is rich in faunal remains and reflects intense domestic activity

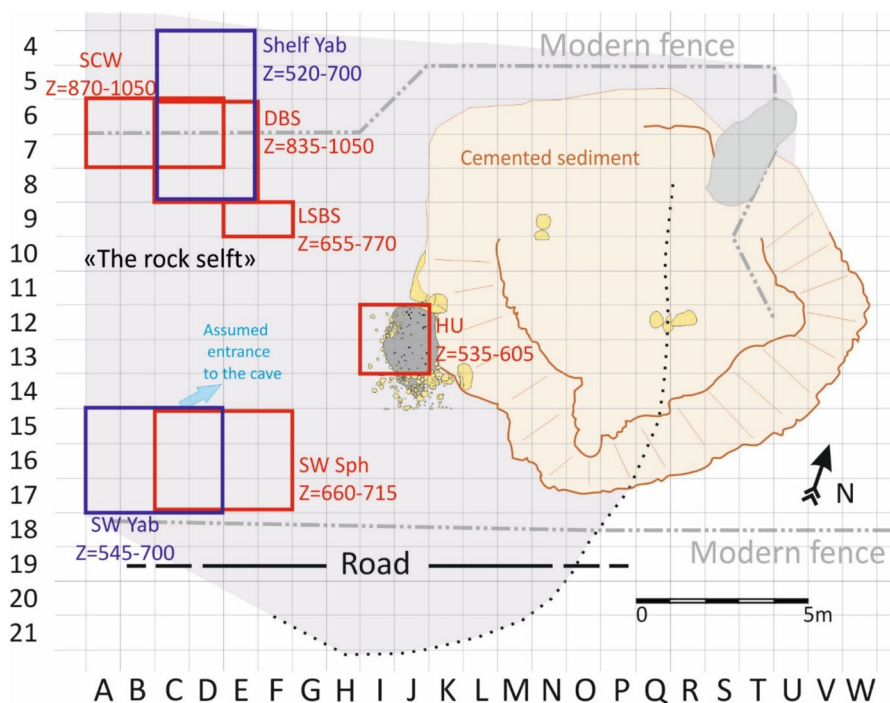


Fig. 1 Map of the site with the location of the different assemblages referred to in the text and their respective elevations (Z) in cm

(Blasco et al., 2024). Around the hearth, several archaeological facies have been identified, some consistent with shorter-term occupations and others with denser or more recurrent use, indicative of varied domestic functions. It is treated here as a single analytical unit, although Rivals et al. (2021) emphasized marked intra-unit variability in seasonality and procurement for this assemblage.

LSBS (Large Stone in Brown Sediment), a diffuse ashy horizon situated just above HU, has been interpreted as representing less intensive or secondary combustion events, possibly related to short-term occupations or cleaning activity (Blasco et al., 2024).

DBS (Dark Brown Sediment), lying beneath HU, is characterized by a dense accumulation of highly fragmented and burned faunal remains bearing abundant butchery traces, suggesting repeated processing activity in a space lacking formalized feature (Blasco et al., 2024).

SCW (Soft/Cemented sediments close to the Wall) and SW Sph (South West Spheroid) are localized assemblages situated in the southwestern part of the cave. They contain fewer faunal remains and possible smaller hearths, with SW Sph notably associated with the use of spheroid tools for bone grease extraction (Assaf et al., 2020).

Shelf Yab (Shelf Yabrudian) and SW Yab (South West Yabrudian) are both Yabrudian assemblages, differing from the Amudian in several aspects. Their lithic

assemblages are Quina scraper-dominated and show a low incidence of blade production and of larger heavy-duty tools, such as spheroids, handaxes, and limestone implements (Parush et al., 2016). However, the faunal spectrum remains broadly similar, with fallow deer (*Dama cf. mesopotamica*) predominating over the other taxa (Blasco et al., 2024).

The Whole unit, defined analytically for this study, aggregates all assemblages in order to provide a synthetic perspective from which to explore diachronic patterns in faunal exploitation across the sequence presented here.

Methodology

Analytical Rationale and Data Sources

The present study is designed to describe how faunal diversity is organized within and across archaeological horizons using Qesem Cave as example, rather than to treat diversity indices as direct behavioural proxies. The taxonomic and anatomical data analysed here derive from the published faunal datasets of Qesem Cave, especially those presented by Blasco et al. (2024), and are interpreted in conjunction with the independent zooarchaeological background already available for the site. The raw taxonomic counts used as the basis for the diversity calculations, including NISP and MNI values by taxon and horizon, are reported in Table 1, based on the published Qesem faunal dataset of Blasco et al. (2024). Because carnivores are extremely rare at Qesem, in terms of both remains and induced damage, these animals were excluded from the diversity analyses to avoid artificially inflating taxonomic richness in a predominantly anthropogenic assemblage.

The rows “Very large size,” “Large size,” “Medium size,” “Small size,” and “Very small size” refer to size-class-attributed specimens and are expressed as NSP, not taxonomic NISP. They include taxonomically indeterminate fragments assigned to body-size class.

The analytical workflow is organized around four related questions:

- (1) how taxonomic diversity is partitioned across prey-size classes;
- (2) how the integration of taxonomically indeterminate but size-class-attributed fragments affects that partition;
- (3) how dominance, evenness, and richness-sensitive indices behave under different counting frameworks; and
- (4) how anatomical diversity is distributed across major skeletal groups.

In addition to horizon-by-horizon analyses, a whole analytical unit is defined by pooling the seven horizons considered here to provide a site-wide comparative reference, following the logic already adopted in the original analytical tables of the study. The diversity measures included in the workflow and their interpretation are summarized in Table 2. To ensure transparency and reproducibility, all calculations were implemented in R using the diversityArch package, currently available on CRAN and developed by some of the authors, <https://cran.r-project.org/package=diversityArch>.

Table 1 Raw taxonomic counts by taxon and horizon used as the basis for the diversity calculations, based on Blasco et al. (2024)

Taxal/size body class	Amudian archaeological contexts					Yabrudian archaeological contexts										AMUDIAN					YABRUDIAN																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																												
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Table 1 (continued)

Taxa/size body class	Amudian archaeological contexts						Yabrudian archaeological contexts						AMUDIAN			YABRUDIAN				
	HU		LSBS		DBS		SCW		SW-Sph		Shelf-Yab		SW-Yab							
	Z = 535–605		Z = 655–770		Z = 835–1050		Z = 870–1050		Z = 660–715		Z = 500–700		Z = 545–635							
	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI		
<i>Cygnus</i> sp.			1	1	1	*									1	1	1	0	0	0
<i>Columba</i> sp.											1	1	1			0	0	0	1	1
Aves, unident			1	1	1		1	1	1						2	2	2	0	0	0
Very large size	2	1									13	2	5	1	2	1	0	18	3	0
Large size	948	21	362	15	311		304	7	1437		757	10	245	7	3362	43	0	1002	17	0
Medium size	3965	55	862	20	603		625	12	1475		1063	21	320	6	7530	87	0	1383	27	0
Small size	8742	166	5137	76	3024		3004	41	8860		8631	97	2672	35	28,767	283	0	11,303	132	0
Very small size	422		343		380		461		2137		583		306		3743	0	0	889	0	0
Total	15,464	592	46	7314	291	25	4795	190	15,223	348	51	12,266	541	33	47,666	2575	160	16,097	687	53

Quantification Units and Their Analytical Role

Several counting units are used in this study, but each serves a distinct analytical purpose. They are not treated as interchangeable, nor is any one of them assumed to provide a universally more accurate representation of assemblage structure than another. Instead, they are used as complementary descriptive frameworks that capture different aspects of the faunal record and remain subject to different inferential constraints, including aggregation effects and the procedures through which specimens are grouped and quantified (Domínguez-Rodrigo, 2012; Grayson, 1984; Lyman, 2008). More generally, diversity measures themselves remain sensitive to sample size, taxonomic structure, and the choice of index (Faith & Du, 2018), which is why the present study compares several quantification frameworks while keeping the additive partitioning of Shannon diversity as its main analytical focus.

NISP (Number of Identified Specimens) is used as the primary taxonomic count because it preserves the observed structure of the identified faunal assemblage at specimen level. It provides the baseline for taxonomic diversity analysis.

MNI (Minimum Number of Individuals) is used as a comparative individual-based count. Its purpose here is not to replace NISP, but to assess how the partitioning of taxonomic diversity changes when the faunal record is summarized at the level of minimum individual representation rather than specimen frequency. The NISP/MNI comparison is therefore treated as a structured sensitivity analysis, since the two measures summarize assemblage composition differently and entail distinct aggregation and inferential constraints (Domínguez-Rodrigo, 2012; Grayson, 1984; Lyman, 2008).

NSP (Number of Specimens) is used only where taxonomically indeterminate fragments can still be assigned to a prey-size class and therefore carry information relevant to the partitioning of taxonomic diversity among groups. At Qesem, fragmentation is intense, and a large number of specimens cannot be identified to taxon but can still be attributed to a size class. In such cases, excluding them altogether would remove a substantial part of the faunal signal from the interclass component of diversity (Blasco et al., 2024).

%MAU (Binford, 1984; Lyman, 2008) is used only for anatomical diversity. Here the objective is not to estimate taxonomic abundance, but to compare the relative representation of skeletal parts across major anatomical groups. %MAU therefore serves as a normalized skeletal-profile measure appropriate to this anatomical component of the study (Blasco et al., 2024).

Taxonomic Diversity and Additive Partitioning of Shannon Diversity

Shannon diversity is the central metric of the present study because it combines richness and evenness in a single formal measure and can be partitioned analytically. In this context, partitioning refers to the quantitative decomposition of a total magnitude into smaller components. A decomposition is additive when these components sum exactly to the original value: if a total quantity X is decomposed into two components Y and Z , then the decomposition is additive when $X = Y + Z$. Applied

Table 2 Diversity indices used in the analytical workflow, with formulas and interpretive roles. S indicates the number of species and p_i the proportion that species i represents; N is the total number of remains

Index	What it measures	Simplified formula	Primary interpretation	Scale/range
Shannon (H)	Richness + evenness	$H = -\sum_{i=1}^S p_i \log p_i$	Higher values indicate richer and more evenly distributed assemblages	0 to $\log(S)$; depends on number of taxa (S)
Pielou (J)	Evenness based on Shannon	$J = H/\log(S)$	Ranges from 0 (high dominance) to 1 (perfect evenness)	0 to 1 (unitless)
Simpson dominance (C)	Raw dominance of taxa	$C = \sum_{i=1}^S p_i^2$	Higher values indicate concentration in fewer taxa	1/ S to 1 (closer to 1 = high dominance)
Dominance corrected (Dc)	Corrected dominance (independent of S)	$Dc = (S \times C - 1)/(S - 1)$	Normalized measure of dominance	0 to 1 (adjusted for richness)
Simpson evenness (E_i)	Classical evenness from Simpson	$E_i = 1 - C$	Evaluates uniformity without correcting for taxon count	0 to 1 - 1/ S (closer to 1 = more even)
Simpson evenness corrected (VE)	Evenness derived from corrected dominance	$VE = 1 - Dc$	Evaluates regularity independently of taxon richness	0 to 1
Menhinick	Richness corrected for sample size	$R = S/\sqrt{N}$	Reduces bias in large assemblages	Varies; typically 0.1 to ~2 (unitless)
Margalef	Relative richness	$D = (S - 1)/\log(N)$	Sensitive to total number of remains	Varies; typically ≥ 0 , no upper bound

to Shannon diversity, this means that the observed total can be separated into a between-group (interclass) component and a within-group (intraclass) component whose sum reproduces the original value.

For each archaeological horizon, taxonomic diversity was first calculated from the relative frequencies of identified taxa. Taxa were then assigned to predefined prey-size classes to determine how much of the observed total diversity was associated with differences among these classes, and how much was retained as taxonomic heterogeneity within them.

Formally, if p_i is the proportion of taxon i in a given horizon, total Shannon diversity is defined as:

$$H = - \sum_i p_i \ln(p_i)$$

Taxa are then partitioned into groups g . If P_g denotes the total proportion of group g , and H_g the internal Shannon diversity of that group, total diversity can be written as:

$$H = H_{between} + H_{within}$$

with

$$H_{between} = - \sum_g P_g \ln(P_g)$$

and

$$H_{within} = \sum_g P_g H_g$$

This is the formal additive decomposition underlying the partitioning approach used here: observed total Shannon diversity is divided into two components whose sum exactly reproduces the total value. The interclass component expresses the diversity associated with the distribution of the assemblage across the predefined groups, whereas the intraclass component expresses the weighted internal diversity of the taxa contained inside those groups.

For ease of interpretation, each component was also expressed as a proportion of the observed total:

$$Within(\%) = \left(\frac{H_{within}}{H} \right) \times 100$$

$$Between(\%) = \left(\frac{H_{between}}{H} \right) \times 100$$

These proportions provide a useful summary of the internal organization of diversity, although their interpretation remains dependent on counting framework, group definition, and sampling conditions.

For the partitioning of taxonomic diversity, taxa were assigned to four analytical prey-size classes following the organization of the reference Qesem datasets (Blasco et al., 2024) and the analytical tables used in the present study:

- **Group A**=very large and large-sized taxa: *Bos primigenius*, *Equus ferus*, *Stephanorhinus hemitoechus*
- **Group B**=medium-sized taxa: *Cervus elaphus*, *Equus hydruntinus*
- **Group C**=small-sized taxa: *Sus scrofa*, *Capra aegagrus*, cf. *Capreolus*, *Dama* cf. *mesopotamica*
- **Group D**=very small-sized taxa: *Cygnus* sp., *Columba* sp., *Testudo* sp., and a “large bird/Aves unident.” grouping

The “large bird/Aves unident.” category includes only avian specimens that could not be attributed to any of the identified bird taxa and was treated as mutually exclusive from them, so as not to introduce an artificial increase in taxonomic richness within a given horizon. Cervids not identified to species level were excluded from the partitioning of taxonomic diversity because they could overlap more than one size-class grouping. For simplicity, the combined very large+large category is referred to hereafter as large in the Results section and associated figures. These groups are used here as analytical body-size classes derived from the published Qesem dataset to assess whether taxonomic diversity is expressed primarily between prey-size classes or within them.

All taxonomic diversity calculations were performed separately for NISP and MNI. The aim is not to treat the two quantification units as interchangeable, nor to assume that one is inherently superior, but to evaluate whether the internal partitioning of diversity remains stable when assemblage structure is expressed in specimen-based versus individual-based form.

Integration of Taxonomically Indeterminate but Size-Class-Attributed Fragments

A distinctive aspect of the Qesem assemblages is the high number of fragmented remains that cannot be identified taxonomically but can still be assigned to a prey-size class. These fragments are not taxonomically identified in the usual sense of species- or genus-level attribution; they only contribute to the four analytical prey-size classes used in the partitioning procedure. To evaluate their effect on the organization of diversity, a second set of taxonomic partitioning analyses was run in which size-class-attributed indeterminate specimens were added to the group structure, while the internal taxonomic composition of each group remained based on the identified NISP counts.

The logic of this procedure is intentionally limited. Fragment integration modifies the relative weight of the prey-size classes and therefore the balance between interclass and intraclass components, but it does not create new taxonomic information within those classes. It is therefore treated as a test of how size-class-attributed indeterminate remains affect the partitioning of diversity, rather than as a way to estimate hidden taxonomic richness.

Whenever possible, fragments were assigned to prey-size class following the original criteria used in the published Qesem faunal datasets. In practice, this procedure extends the grouped structure of the assemblage while avoiding unsupported taxonomic redistribution within groups (Blasco et al., 2014, 2024).

Letting P_g^* denote the proportion of identified and size-class-attributed indeterminate specimens belonging to group g , the total diversity after integration is:

$$H^* = \sum_{g=1}^m P_g^* H_g + H(P_1^*, \dots, P_m^*)$$

where the internal group diversities H_g remain unchanged from the original taxonomically identified dataset. Size-class-attributed indeterminate fragments were incorporated only at the level of the four analytical size classes already defined for the partitioning of taxonomic diversity: Group A = very large and large; Group B = medium; Group C = small; Group D = very small.

Dominance, Evenness, and Richness-Sensitive Complementary Indices

Although additive partitioning of Shannon diversity is the main analytical focus of the paper, additional indices were calculated as complementary control measures. Their purpose is to determine whether observed patterns are associated mainly with dominance, evenness, or richness-sensitive structure, rather than to create a parallel interpretive framework.

Pielou's J was retained as the main Shannon-based evenness measure:

$J = \frac{H}{\log(S)}$ where S is the number of taxa. Pielou's index expresses how evenly taxa are distributed relative to the maximum entropy possible for a given richness.

Simpson dominance and its corrected form were also calculated. Because the raw Simpson index is influenced by the number of taxa present, the corrected dominance measure is emphasized in interpretation:

$D_c = \frac{S \times C - 1}{S - 1}$ Corrected Simpson evenness is then:

$VE = 1 - D_c$ Raw Simpson values are retained for transparency, but corrected dominance and corrected evenness are preferred for comparison across assemblages of differing richness (Faith & Du, 2018; Lyman, 2008).

Finally, Menhinick and Margalef were calculated as complementary richness-sensitive indices:

$Menhinick = \frac{S}{\sqrt{N}}$; $Margalef = \frac{S-1}{\ln N}$ where N is the total count in the relevant framework (NISP or MNI). These indices are not treated as substitutes for sample-standardization procedures such as rarefaction. Rather, they provide additional descriptive control on the richness component of diversity and help clarify whether variation in Shannon is accompanied by shifts in richness-sensitive structure as well as in evenness (Faith & Du, 2022; Grayson, 1984; Lyman, 2008).

Anatomical Diversity Partitioning

The same partitioning framework was also applied to anatomical representation. Here the aim is different from the taxonomic analysis: instead of describing how taxa are distributed across prey-size classes, the anatomical analysis describes how skeletal representation is distributed across broad anatomical groups.

The anatomical analysis was based on the Qesem skeletal data published by Blasco et al. (2024), using %MAU values (Table S1). Only three prey-size classes were retained for this part of the analysis—large, medium, and small—because very small, very large, and fully unidentified animals were not sufficiently informative for stable anatomical comparison.

Skeletal elements were grouped into four anatomical categories:

- **Group A = cranial:** cranium, maxilla, mandible
- **Group B = axial:** vertebrae, ribs, pelvis
- **Group C = proximal appendicular:** scapula, humerus, radius/ulna, femur, tibia
- **Group D = distal appendicular:** carpals/tarsals, metapodials, phalanges

Taxonomically indeterminate but anatomically identifiable fragments were incorporated into the anatomical analysis only when they could be reliably assigned to both a prey-size class and a skeletal element. In such cases, the observed %MAU profile of the identified fraction was used as a weighting structure to estimate the distribution of the broader NSP total. This procedure does not recalculate absolute MNE or MAU values. Instead, it preserves the proportional anatomical profile of the assemblage while allowing the fragmented record to be represented more fully.

Because this operation is a proportional rescaling, it does not alter the relative-frequency structure of the assemblage and therefore does not affect total Shannon diversity or its partitioning into interclass and intraclass components. For this reason, the anatomical analysis is centred on the partitioned Shannon diversity values rather than on the rescaled NSP totals themselves.

Reporting Strategy, Bootstrap Estimation, and Interpretive Limits

The main comparative output of the study is the additive partitioning of Shannon diversity into interclass and intraclass components, together with the proportional contribution of each component to the observed total. These values make the internal organization of diversity more explicit than total Shannon diversity values alone, while the complementary diversity indices are used as control measures to clarify whether the observed variation is associated mainly with concentration, distributional regularity, or richness-sensitive effects.

Because differences between horizons may still partly reflect counting framework, fragmentation, sample size, and preservation, bootstrap confidence intervals were also computed using the **diversityArch** package. For non-partitioned diversity indices, including total Shannon diversity and the complementary diversity indices,

these were obtained with the `bs()` function. For additive partitioning of Shannon diversity, the intraclass and interclass components were estimated with the `bs_dec()` routine, and for the fragment-integration procedure with the `bs_frag()` function. Unless otherwise stated, all bootstrap estimates were based on 1000 replicates and a 95% confidence level.

These intervals are treated here as descriptive margins of uncertainty. Their purpose is to assess the stability of the main ordering observed across assemblages, not to transform modest numerical differences into categorical separations. For this reason, the results are interpreted in conjunction with the independent taphonomic and seasonality evidence available for Qesem Cave, rather than as stand-alone behavioural measurements (Blasco et al., 2024; Rivals et al., 2021).

Bootstrap results are reported directly in the relevant Results subsections, where they are used to evaluate the robustness of the principal taxonomic, fragment-related, anatomical, and complementary-index patterns. In the main text, only the most informative intervals are summarized, whereas the full outputs are retained in the accompanying tables and supplementary computational workflow. Numerical values are presented at four decimal places to ensure reproducibility and direct comparability with the outputs of **diversityArch**. This precision supports a transparent analytical workflow, but interpretation does not rely on isolated decimal differences. Instead, the discussion focuses on recurrent and ordered patterns, their degree of overlap under resampling, and their consistency with the independent archaeological context.

Results

Taxonomic Diversity Partitioning Based on NISP

Taxonomic diversity based on NISP was first assessed through total Shannon diversity and then examined through its additive partitioning into intraclass and interclass components. The integrated structure of these results is shown in Fig. 2, in which observed total Shannon diversity is displayed together with its partitioned components and the corresponding bootstrap confidence intervals. The proportional balance between the two components is shown separately in Fig. 3. Full numerical values for total Shannon diversity, partitioned components, and bootstrap confidence intervals are provided in Supplementary Table S2.

Overall, NISP-based taxonomic diversity is dominated by the interclass component in all Qesem horizons. This indicates that most of the observed Shannon diversity derives from contrasts between prey-size classes rather than from taxonomic heterogeneity retained within those classes. At the same time, the relative contribution of the intraclass component varies in an ordered way across the sequence.

Observed total Shannon diversity ranges from 0.7414 in SCW to 1.1015 in SW Yab. The absolute intraclass component ranges from 0.0694 in SCW to 0.3248 in SW Yab, whereas the interclass component ranges from 0.6720 in SCW to 0.7767

in SW Yab. When expressed as proportions of total diversity, the intraclass contribution varies from 9.36% in SCW to 29.49% in SW Yab, while the interclass contribution ranges from 70.51% in SW Yab to 90.64% in SCW (Fig. 3; Supplementary Table S2).

Among the Amudian assemblages, SCW shows the strongest interclass structure and the lowest intraclass share. DBS and SW Sph also remain strongly interclass-dominated, with intraclass proportions of 16.72% and 17.58%, respectively. HU and LSBS occupy intermediate positions, with very similar intraclass values (19.44% and 19.00%, respectively). Within the Yabrudian horizons, Shelf Yab displays a higher intraclass proportion (21.02%) than most Amudian assemblages, whereas SW Yab stands out as the horizon with the highest relative intraclass contribution and the lowest relative interclass contribution in the sequence. Whole Qesem occupies an intermediate position ($H=0.8914$; H intraclass=0.1816; H interclass=0.7098; 20.38% intraclass; 79.62% interclass) and is retained here as a site-wide analytical baseline rather than as an archaeological horizon.

The bootstrap intervals shown in Fig. 2 and reported in Supplementary Table S2 broadly support this descriptive ordering. Several intermediate horizons overlap, but the overall separation between strongly interclass-dominated assemblages such as SCW and more internally heterogeneous assemblages such as SW Yab remains visible under resampling. The NISP-based partitioning of taxonomic diversity therefore reveals a gradient extending from highly interclass-structured assemblages to assemblages with greater intraclass taxonomic heterogeneity, even though all horizons remain dominated by the interclass component.

Taxonomic Diversity Partitioning Based on MNI

Taxonomic diversity was also calculated from MNI in order to evaluate whether the internal partitioning of diversity remains similar when assemblage structure is expressed through individual-based rather than specimen-based quantification. As for NISP, the integrated results are shown in Fig. 4, which combines observed total Shannon diversity, its intraclass and interclass components, and bootstrap confidence intervals. The relative balance between intraclass and interclass contributions is shown separately in Fig. 5. Full numerical values are provided in Supplementary Table S2.

The MNI-based results differ markedly from the NISP-based ones in scale, because total Shannon diversity is systematically higher and the intraclass component contributes a much larger share of the total. Even so, all horizons remain at least slightly dominated by the interclass component. Observed total Shannon diversity ranges from 1.4172 in SW Sph to 2.0749 in LSBS. The intraclass component ranges from 0.4694 in SW Sph and SCW to 0.8074 in LSBS, whereas the interclass component ranges from 0.9478 in SW Sph to 1.2675 in LSBS. In proportional terms, the intraclass share ranges from 27.99% in SCW to 42.29% in SW Yab, while the interclass share ranges from 57.71% in SW Yab to 72.01% in SCW (Fig. 5; Supplementary Table S2).

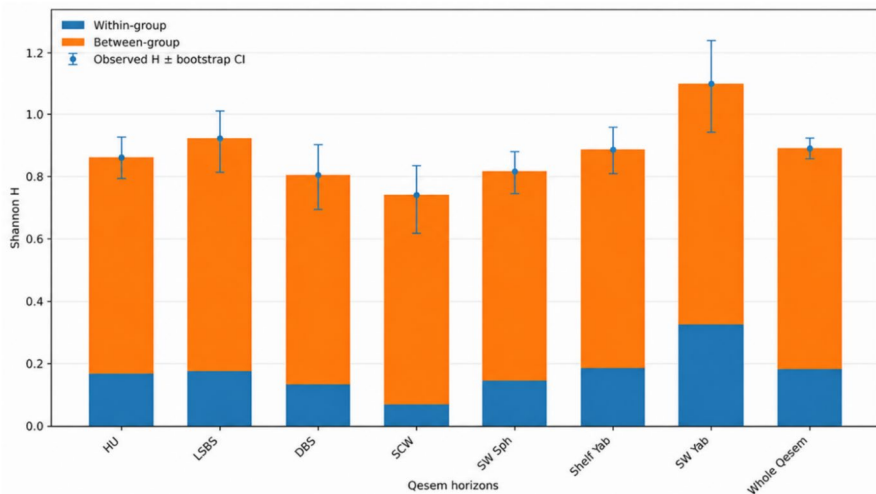


Fig. 2 Taxonomic Shannon diversity across Qesem horizons based on NISP, with additive partitioning and bootstrap confidence intervals. Stacked bars represent observed total Shannon diversity partitioned into intraclass and interclass components. Black points indicate observed total Shannon diversity, and vertical error bars show the bootstrap confidence intervals

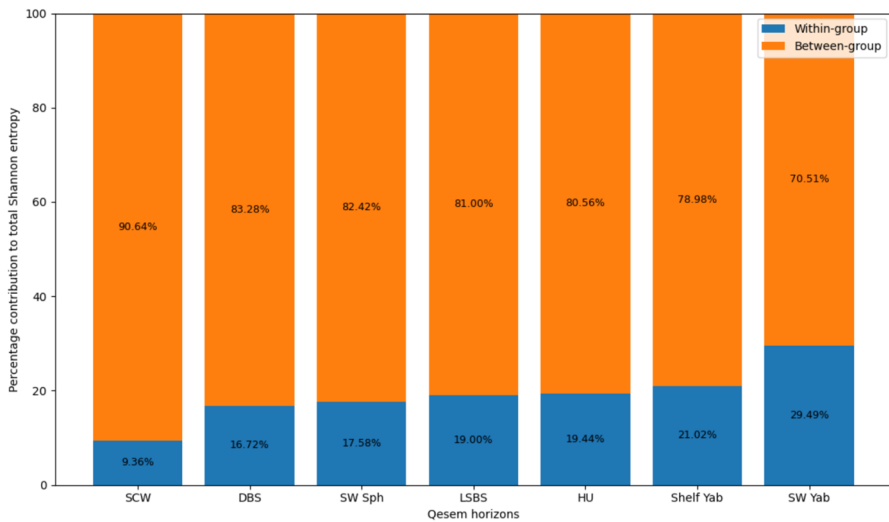


Fig. 3 Relative contribution of intraclass and interclass components to total taxonomic diversity across Qesem horizons based on NISP

The ordering of horizons also changes relative to NISP. LSBs yields the highest total Shannon diversity, followed by DBS, SW Yab, Whole Qesem, Shelf Yab, HU, SCW, and finally SW Sph. In contrast to the NISP-based results, the intraclass contribution is no longer weakest in absolute terms at SCW alone, since SW Sph yields

almost identical low intraclass values. At the other end of the sequence, LSBS and SW Yab show the strongest intraclass development, although their internal balance differs slightly: LSBS combines the highest total diversity and the highest interclass value with a strong intraclass component, whereas SW Yab shows the highest relative intraclass proportion.

The MNI-based partitioning therefore produces a less sharply hierarchical contrast than NISP, but it remains informative in a different way. The interclass component still dominates in all horizons, confirming that prey-size class structure remains the major source of diversity. However, the much stronger intraclass contribution indicates that, once assemblages are expressed in terms of individuals rather than specimens, taxonomic heterogeneity within prey-size classes becomes substantially more visible.

The bootstrap intervals shown in Fig. 4 and reported in Supplementary Table S2 suggest greater uncertainty than in the NISP-based analysis, especially for horizons with smaller effective counts. Several horizons overlap substantially under resampling, and caution is therefore required in treating intermediate assemblages as sharply distinct. Even so, the overall contrast between more strongly interclass-structured horizons such as SCW and assemblages with higher relative intraclass development such as SW Yab remains visible. In that sense, the MNI-based results do not overturn the taxonomic structure identified under NISP, but they show that the relative weight of intraclass diversity increases substantially when the assemblage is summarized through individual-based quantification.

Effect of Integrating Size-Class-Attributed Fragments on Taxonomic Diversity Partitioning

The integration of taxonomically indeterminate but size-class-attributed fragments produces strongly variable effects across the Qesem horizons (Figs. 6–7; Table S3). These added remains are not identified at species or genus level, but are assigned only to the four analytical prey-size classes used in the partitioning of taxonomic diversity. The procedure therefore affects the grouped structure of the assemblages rather than their internal taxonomic composition. However, the magnitude of this effect differs markedly from one horizon to another.

The strongest increases in total Shannon diversity are observed in SW Sph ($\Delta H = +0.3526$), SCW ($\Delta H = +0.2862$), HU ($\Delta H = +0.2527$), and DBS ($\Delta H = +0.2398$). Whole Qesem also shows a substantial increase ($\Delta H = +0.2289$). By contrast, the effect remains modest in Shelf Yab ($\Delta H = +0.0648$) and especially in LSBS ($\Delta H = +0.0283$), whereas SW Yab is the only assemblage to show a slight decrease in total Shannon diversity ($\Delta H = -0.0081$).

Fragment integration also modifies the relative ranking of the assemblages. Before integration, SW Yab yielded the highest total Shannon diversity, whereas after integration SW Sph becomes the most diverse horizon in total Shannon terms. Conversely, LSBS, which ranked among the more diverse assemblages before fragment addition, becomes one of the least affected contexts, while SCW and HU move

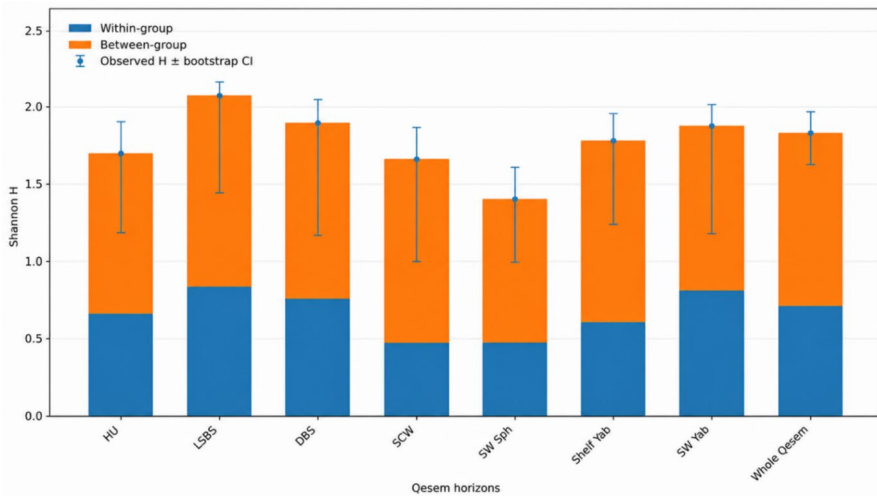


Fig. 4 Taxonomic Shannon diversity across Qesem horizons based on MNI, with additive partitioning and bootstrap confidence intervals. Stacked bars represent observed total Shannon diversity partitioned into intraclass and interclass components. Black points indicate observed total Shannon diversity, and vertical error bars show the bootstrap confidence intervals

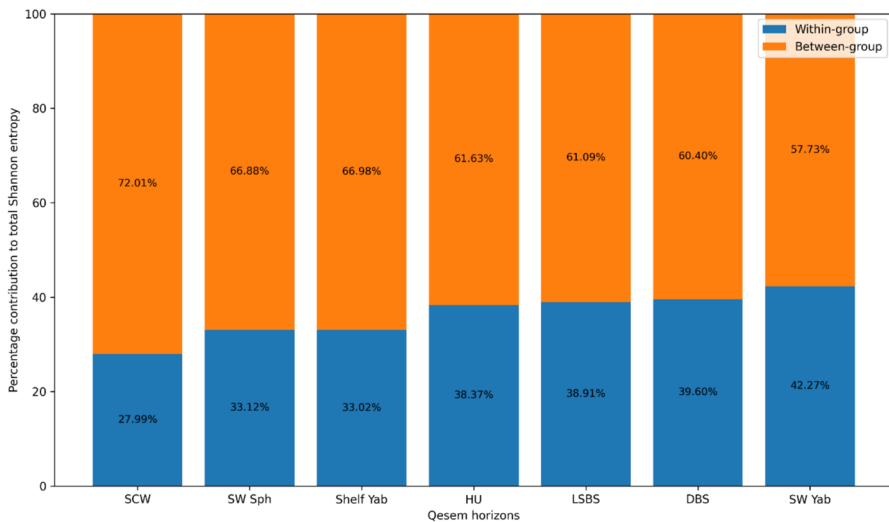


Fig. 5 Relative contribution of intra-class and inter-class components to total taxonomic diversity across Qesem horizons based on MNI

upward more markedly in the post-integration ordering. Whole Qesem rises from $H=0.8914$ to $H=1.1203$, confirming that the size-class-attributed fragmented fraction also exerts a strong effect at the scale of the pooled assemblage.

The effect of fragment integration is not limited to the magnitude of total Shannon diversity. It also modifies the internal balance between intraclass and interclass components (Fig. 7). In all horizons, the relative contribution of the interclass component increases after integration, whereas the relative contribution of the intraclass component decreases. This pattern follows directly from the logic of the procedure: because the added remains contribute only to the distribution of the prey-size classes and do not introduce new taxonomic information within them, their principal effect is to strengthen the interclass component of diversity. The contrast is particularly marked in SW Sph, HU, DBS, and Whole Qesem, whereas LSBS and Shelf Yab remain comparatively stable. SW Yab again stands out as a distinctive case, combining a slight decrease in total Shannon diversity with a clear reduction in the intra-class contribution.

Bootstrap estimates support this pattern (Table S3). After integration, the confidence intervals of the interclass and intraclass components remain non-overlapping in all horizons, indicating that the assemblages remain structurally dominated by interclass diversity. The bootstrap intervals for total Shannon diversity likewise show that the strongest post-integration values are observed in SW Sph, HU, Whole Qesem, and SW Yab, while LSBS and Shelf Yab remain among the least affected contexts.

Overall, fragment integration does not function as a uniform correction applied evenly across the sequence. Instead, it reveals strong differences in the degree to which the Qesem assemblages are affected by fragmented but size-class-attributed material, with some horizons showing substantial sensitivity to this fraction and others remaining comparatively stable. More importantly, it shows that fragmentation

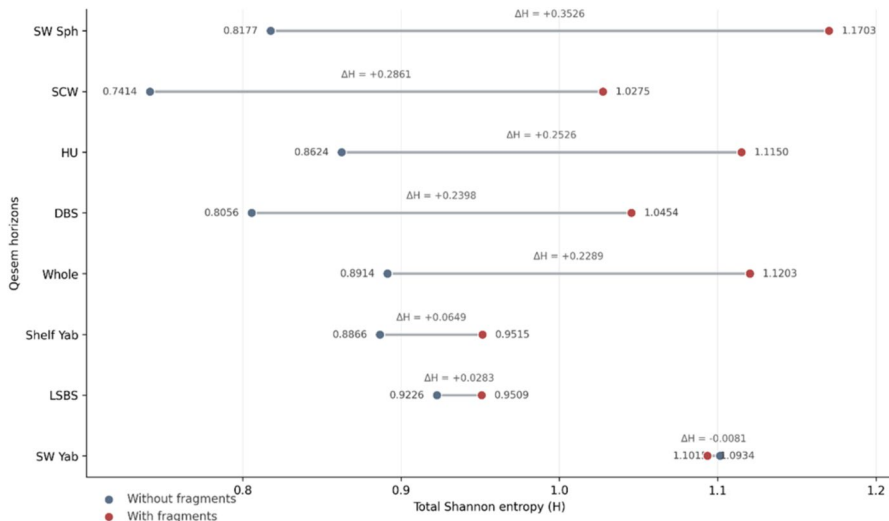


Fig. 6 Total Shannon diversity (H) calculated before and after integration of taxonomically indeterminate but size-class-attributed fragments across the Qesem horizons. Horizons are ordered according to the magnitude of change in total Shannon diversity (ΔH)

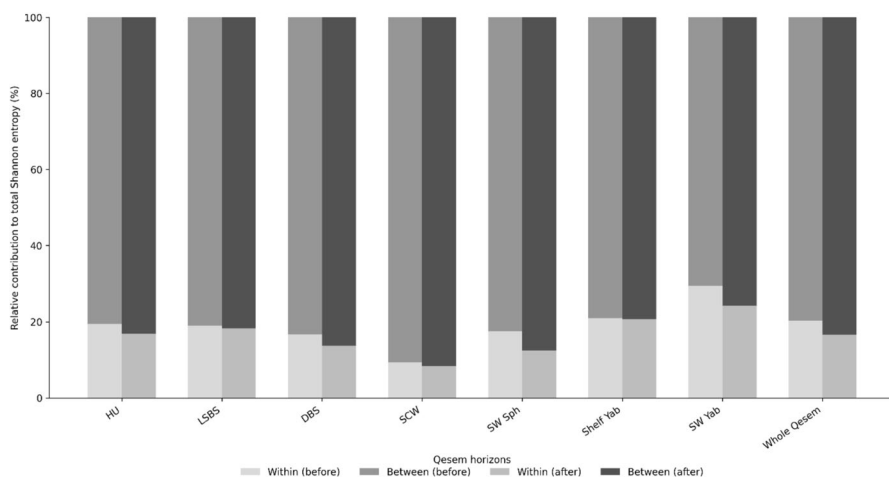


Fig. 7 Relative contribution of intraclass and interclass components to total taxonomic diversity across Qesem horizons before and after integration of taxonomically indeterminate but size-class-attributed fragments

at Qesem affects not only the magnitude of diversity, but also the way diversity is partitioned between prey-size classes and within them.

Complementary Diversity Indices

Complementary diversity indices were used as control measures to assess whether the partitioned Shannon diversity patterns observed across horizons were associated mainly with taxonomic concentration, distributional regularity, or richness-sensitive variation. Particular attention was given to corrected Simpson measures, because the raw Simpson index is partly conditioned by the number of taxa present, whereas the corrected forms are more appropriate for comparison across assemblages of differing richness. In the visual comparison below (Fig. 8), corrected evenness (VE) is emphasized rather than corrected dominance, since the two are mathematically complementary. Pielou's J is shown alongside VE in order to compare Shannon- and Simpson-based expressions of evenness, while corrected dominance remains reported in Table 3. Richness-sensitive variation is considered separately through Menhinick and Margalef, whose values and bootstrap confidence intervals are likewise summarized in Table 3.

The evenness profiles broadly reinforce the ordering already observed in the partitioning of Shannon diversity (Fig. 8). In the NISP-based results, SW Yab consistently occupies the high-evenness end of the spectrum, whether assessed through corrected evenness ($VE=0.5196$) or Pielou's J (0.5013), whereas SCW remains the least even assemblage under both measures ($VE=0.3864$; $J=0.3565$). DBS and SW Sph also remain relatively low, while HU, LSBS, and Shelf Yab occupy

intermediate positions. The most informative divergence between the two evenness measures concerns assemblages such as LSBS, HU, Shelf Yab, and Whole Qesem, for which VE is noticeably higher than Pielou's J . In these cases, the assemblages appear somewhat more even when examined through the corrected Simpson framework than when evaluated through Shannon-based normalization. The overall ordering is therefore stable, but the degree of evenness is not expressed identically by the two formalisms. The bootstrap intervals reported in Table 3 broadly support this pattern, while also showing overlap among several intermediate horizons.

In the MNI-based results, the same broad structure is preserved, although the contrasts between assemblages become less pronounced (Fig. 8; Table 3). LSBS, DBS, and SW Yab remain among the most even assemblages, whereas SCW and especially SW Sph remain comparatively less even. Here too, the comparison between VE and Pielou's J is informative rather than contradictory. SW Yab and DBS show close convergence between the two indices, which strengthens the robustness of their high-evenness signal. By contrast, HU, Shelf Yab, and especially Whole Qesem display wider gaps, indicating that their position is somewhat more sensitive to the evenness metric used. More generally, the shift from NISP to MNI tends to raise evenness values across the sequence and to compress some of the contrasts between horizons, even though the main ordering remains broadly stable. As in the NISP-based results, bootstrap confidence intervals do not overturn the descriptive pattern but suggest caution in treating the intermediate assemblages as sharply separated.

The richness-sensitive indices introduce a related but not identical picture (Fig. 9; Table 3). In NISP, SW Yab and LSBS show the strongest richness-sensitive profiles, while SW Sph remains the least rich assemblage under both Menhinick and Margalef. In MNI, LSBS becomes the clearest richness pole, followed by DBS and SW Yab, whereas SW Sph again occupies the lower end of the range. The most informative divergence between Menhinick and Margalef concerns large or aggregated assemblages, especially Whole Qesem, but also some intermediate contexts. Because Menhinick penalizes sample size more strongly than Margalef, abundant assemblages appear relatively poorer under Menhinick than under Margalef. This effect does not alter the main richness poles of the sequence, but it nuances the ranking of several intermediate horizons and shows that richness is not entirely independent from the correction formula adopted. The comparison between NISP and MNI also shows that the relative position of some intermediate assemblages remains sensitive to the quantification framework, even where the main richness poles themselves are preserved.

These additional measures refine rather than overturn the Shannon diversity partitioning results. The evenness indices confirm the contrast between less regular assemblages, such as SCW, and more evenly distributed ones, such as SW Yab and, under MNI, LSBS and DBS. The richness-sensitive indices add a further nuance by showing that strong intraclass representation does not always coincide with the highest richness values under all quantification frameworks. This is particularly clear in SW Sph, which remains comparatively low in richness-sensitive terms despite its strong response to fragment integration in the previous subsection. The complementary indices therefore support the main partitioning results while clarifying whether

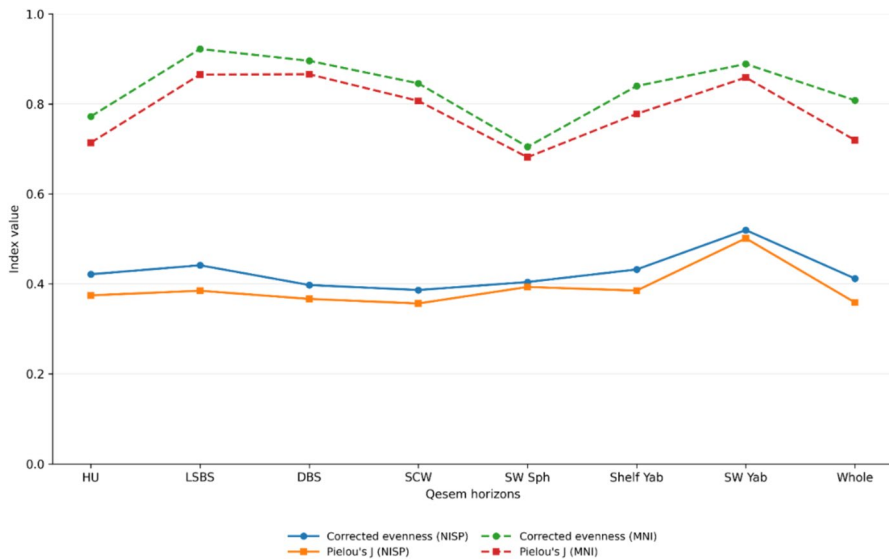


Fig. 8 Shannon- and Simpson-based evenness profiles across Qesem horizons based on NISP and MNI

the observed differences are associated primarily with distributional regularity or with richness-sensitive variation.

Anatomical Diversity Partitioning

Anatomical diversity was assessed through total Shannon diversity and its additive partitioning into intraclass and interclass components, using the %MAU-based anatomical datasets grouped into cranial, axial, proximal appendicular, and distal appendicular categories. In contrast to the partitioning of taxonomic diversity, the anatomical results reveal a much more stable overall structure across the Qesem assemblages, with the intraclass component remaining slightly dominant in most cases. The relative balance between intraclass and interclass components in the whole assemblages is shown in Fig. 10, while the corresponding numerical values and bootstrap confidence intervals are reported in Table 4. More detailed size-class variation is shown in Fig. 11. Complementary anatomical diversity indices, together with their bootstrap confidence intervals, are provided separately in Table S4.

When each assemblage is considered without subdivision by prey-size class, total Shannon diversity values remain relatively close, ranging from 2.2161 in SW Sph-whole to 2.3414 in Shelf Yab-whole. Across these whole assemblages, the intra-class contribution varies only between 53.37% (SW Sph-whole) and 55.60% (SCW-whole), while the interclass contribution ranges from 44.40% to 46.63%. Whole Qesem occupies a similarly intermediate position ($H = 2.3053$; H intraclass = 1.2557; H interclass = 1.0496; 54.47% intraclass; 45.53% interclass). Anatomical diversity partitioning at the whole-assemblage scale therefore appears markedly less uneven

Table 3 Complementary diversity indices across Qesem horizons based on NISP and MNI, with bootstrap confidence intervals in parentheses

Horizon	Simpson dominance (NISP)	Corr. dominance (NISP)	Corr. evenness (NISP)	Pielou J (NISP)	Menhinick (NISP)	Margalef (NISP)	Simpson dominance (MNI)	Corr. dominance (MNI)	Corr. evenness (MNI)	Pielou J (MNI)	Menhinick (MNI)	Margalef (MNI)
HU	0.6207 (0.5895– 0.6498)	0.5785 (0.5399– 0.6081)	0.4215 (0.3913– 0.4618)	0.3745 (0.3526– 0.4234)	0.2705 (0.2164– 0.2705)	1.2465 (0.9695– 1.2465)	0.2980 (0.1995– 0.4754)	0.2278 (0.1068– 0.3733)	0.7722 (0.6254– 0.8918)	0.7139 (0.6104– 0.8408)	1.6775 (0.9150– 1.6775)	2.6587 (1.3294– 2.6587)
LSBS	0.5987 (0.5527– 0.6502)	0.5586 (0.5061– 0.6054)	0.4414 (0.3921– 0.4962)	0.3848 (0.3536– 0.4412)	0.4454 (0.3239– 0.4454)	1.5592 (1.0915– 1.5592)	0.1616 (0.1296– 0.2865)	0.0778 (0.0293– 0.1720)	0.9222 (0.8361– 0.9707)	0.8653 (0.7877– 0.9477)	2.2000 (1.2000– 2.2000)	3.1067 (1.5533– 3.1067)
DBS	0.6467 (0.6021– 0.7016)	0.6025 (0.5440– 0.6520)	0.3975 (0.3419– 0.4561)	0.3666 (0.3249– 0.4166)	0.3838 (0.2985– 0.3838)	1.2678 (0.9509– 1.2678)	0.2037 (0.1481– 0.4136)	0.1042 (0.0265– 0.2889)	0.8958 (0.7111– 0.9735)	0.8659 (0.7089– 0.9627)	2.1213 (1.1785– 2.1213)	2.7678 (1.3839– 2.7678)
SCW	0.6619 (0.6061– 0.7193)	0.6136 (0.5412– 0.6686)	0.3864 (0.3311– 0.4537)	0.3565 (0.3191– 0.4399)	0.3995 (0.2497– 0.3995)	1.1678 (0.6673– 1.1678)	0.2600 (0.1800– 0.4750)	0.1543 (0.0400– 0.3460)	0.8457 (0.6475– 0.9563)	0.8067 (0.6532– 0.9456)	1.7889 (0.8944– 1.7889)	2.3367 (1.0014– 2.3367)
SW Sph	0.6464 (0.6123– 0.6782)	0.5959 (0.5581– 0.6331)	0.4041 (0.3697– 0.4396)	0.3932 (0.3596– 0.4266)	0.2221 (0.1943– 0.2221)	0.9765 (0.8370– 0.9765)	0.3834 (0.2684– 0.5504)	0.2954 (0.1528– 0.4740)	0.7046 (0.5182– 0.8547)	0.6815 (0.5332– 0.8123)	1.1669 (0.8752– 1.1669)	1.8181 (1.2987– 1.8181)
Shelf Yab	0.6111 (0.5797– 0.6422)	0.5679 (0.5276– 0.6040)	0.4321 (0.3962– 0.4714)	0.3851 (0.3572– 0.4254)	0.2876 (0.2301– 0.2876)	1.2680 (0.9863– 1.2680)	0.2441 (0.1758– 0.3965)	0.1602 (0.0618– 0.2994)	0.8398 (0.6897– 0.9434)	0.7779 (0.6684– 0.9072)	1.7678 (1.0607– 1.7678)	2.5969 (1.4427– 2.5969)
SW Yab	0.5381 (0.4700– 0.6112)	0.4804 (0.3928– 0.5585)	0.5196 (0.4402– 0.5988)	0.5013 (0.4371– 0.5796)	0.5350 (0.4756– 0.5350)	1.4171 (1.2399– 1.4171)	0.2100 (0.1550– 0.4150)	0.1113 (0.0280– 0.2883)	0.8888 (0.7117– 0.9714)	0.8587 (0.7021– 0.9559)	2.0125 (1.1180– 2.0125)	2.6705 (1.3552– 2.6705)
Whole Qesem	0.6225 (0.6072– 0.6379)	0.5881 (0.5685– 0.6022)	0.4119 (0.3964– 0.4314)	0.3587 (0.3491– 0.3901)	0.1587 (0.1323– 0.1587)	1.2716 (1.0404– 1.2716)	0.2541 (0.2094– 0.3170)	0.1920 (0.1345– 0.2517)	0.8080 (0.7451– 0.8645)	0.7195 (0.6640– 0.7888)	0.9080 (0.6984– 0.9080)	2.2544 (1.6908– 2.2544)

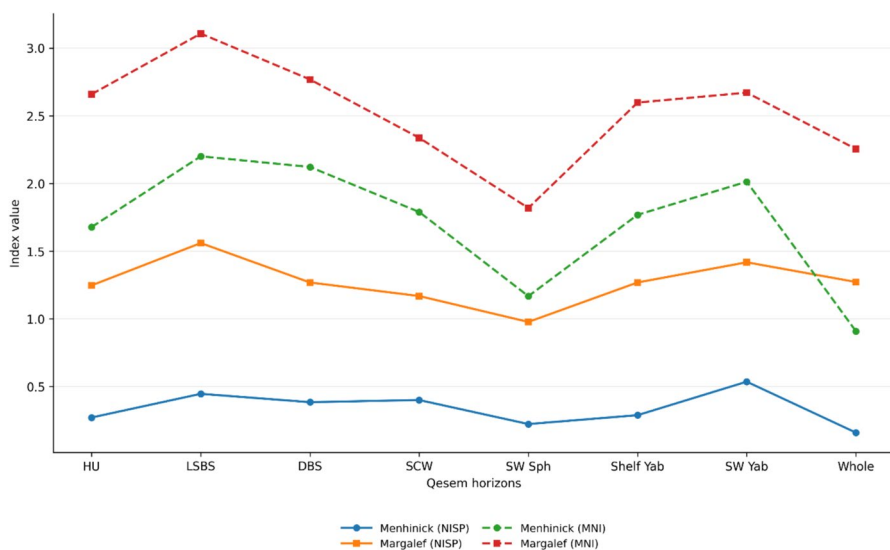


Fig. 9 Richness-sensitive indices across Qesem horizons based on NISP and MNI

than taxonomic diversity partitioning: all horizons remain close to a shared configuration in which internal anatomical diversity contributes slightly more than differentiation among major anatomical groups (Fig. 10; Table 4).

Bootstrap confidence intervals reinforce this impression of stability. For the whole assemblages, total Shannon diversity intervals are particularly narrow, for example in HU-whole (2.2525–2.2714), SW Sph-whole (2.2058–2.2255), and Whole Qesem (2.3001–2.3103). The bootstrap intervals for the partitioned components likewise confirm that, in all whole assemblages, the intraclass component remains higher than the interclass component, with no overlap between the two confidence intervals. This indicates that the shared intraclass-dominated anatomical structure is not a fragile numerical effect, but a stable feature of the anatomical organization of the assemblages.

More visible contrasts emerge when anatomical diversity partitioning is examined by size class (Fig. 11; Table 4). In the large-size category, most assemblages remain clearly intraclass-dominated, often above 60%, and reaching 63.20% in SW Yab-large. SCW-large is the main exception, and the only case in which the interclass component slightly exceeds the intraclass one (50.39% interclass vs. 49.61% intraclass). In the medium-size category, the intraclass contribution is generally even stronger, culminating in DBS-medium (69.10%) and remaining high in SCW-medium (62.28%), LSBS-medium (61.38%), and SW Yab-medium (59.23%). By contrast, the small-size category is much more balanced, with intraclass proportions generally close to parity, ranging from 51.99% in SW Sph-small to 54.96% in HU-small. The strongest internal anatomical structuring is therefore concentrated mainly in the large and especially medium size classes, whereas the small category remains more stable and more evenly split between intraclass and interclass components.

The bootstrap results clarify these contrasts further. Several medium-size assemblages show strongly separated intraclass and interclass intervals, especially DBS-medium, SCW-medium, LSBS-medium, and SW Yab-medium, confirming that the most pronounced internal anatomical structuring occurs in this size class. By contrast, SCW-large remains the clearest ambiguous case, as its interclass confidence interval (0.7542–0.8719) overlaps broadly with its intraclass interval (0.7082–0.8838). This result is consistent with the observed partitioning and indicates that SCW-large is the anatomical context in which the balance between the two components remains least stable under resampling.

The anatomical group proportions help clarify this pattern (Fig. 12). In most horizons and size classes, the proximal appendicular group is the dominant anatomical component, commonly representing around half or more of the assemblage and reaching particularly high values in several medium-size contexts, such as DBS-medium (81.01%) and SCW-medium (75.61%). By contrast, the axial group remains consistently weak and, in some cases, nearly absent, especially in several large- and medium-size assemblages. The cranial group is more variable, reaching comparatively high values in several large-size contexts, while the distal appendicular group generally remains secondary but increases more visibly in some small-size assemblages, particularly Shelf Yab-small (19.58%) and SW Sph-small (16.45%).

Anatomical diversity partitioning thus differs from taxonomic diversity partitioning in two important respects. First, the whole assemblages remain much more homogeneous across horizons, with only modest variation in the balance between intraclass and interclass components. Second, the most informative differences emerge less from overall horizon-to-horizon separation than from the way anatomical diversity is structured within the different size classes, especially in the medium-size category. In this sense, the anatomical results point to a relatively stable general

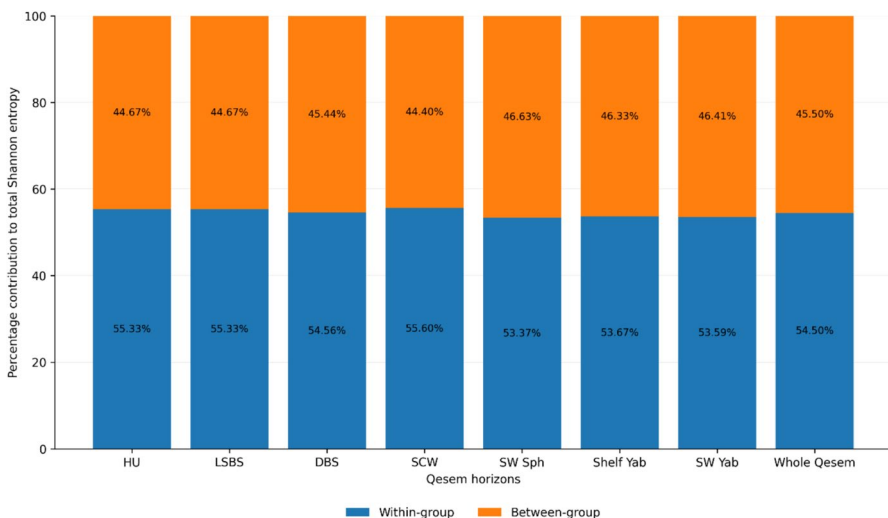


Fig. 10 Relative partitioning of total anatomical Shannon diversity across whole Qesem assemblages

Table 4 Anatomical Shannon diversity and bootstrap confidence intervals across Qesem horizons and size classes

Assemblage	Observed Shannon <i>H</i>	<i>H</i> low	<i>H</i> up	<i>H</i> interclass (between)	Between low	Between up	<i>H</i> intraclass (within)	Within low	Within up
HU-large	2.0552	2.0084	2.0908	0.7992	0.7657	0.8291	1.2560	1.2198	1.2838
HU-medium	2.1572	2.1400	2.1723	0.9508	0.9327	0.9679	1.2064	1.1868	1.2261
HU-small	2.2829	2.2719	2.2932	1.0282	1.0133	1.0427	1.2547	1.2417	1.2660
HU-whole	2.2623	2.2525	2.2714	1.0105	0.9977	1.0208	1.2518	1.2417	1.2627
LSBS-large	1.6698	1.6092	1.7102	0.6270	0.5734	0.6713	1.0428	0.9588	1.1147
LSBS-medium	2.0397	2.0040	2.0628	0.7877	0.7281	0.8348	1.2520	1.2085	1.2901
LSBS-small	2.3271	2.3109	2.3409	1.0651	1.0463	1.0841	1.2620	1.2455	1.2765
LSBS-whole	2.2878	2.2721	2.3008	1.0220	1.0021	1.0411	1.2658	1.2507	1.2805
DBS-large	1.9193	1.8575	1.9617	0.7412	0.6850	0.7893	1.1781	1.1028	1.2326
DBS-medium	1.8885	1.8469	1.9158	0.5836	0.5214	0.6434	1.3049	1.2519	1.3489
DBS-small	2.3006	2.2803	2.3178	1.0891	1.0669	1.1103	1.2115	1.1881	1.2327
DBS-whole	2.2712	2.2508	2.2877	1.0320	1.0100	1.0542	1.2392	1.2182	1.2561
SCW-large	1.6242	1.5180	1.7060	0.8184	0.7542	0.8719	0.8058	0.7082	0.8838
SCW-medium	1.9489	1.9095	1.9727	0.7351	0.6658	0.7980	1.2138	1.1538	1.2694
SCW-small	2.3012	2.2806	2.3194	1.0521	1.0279	1.0726	1.2491	1.2285	1.2653
SCW-whole	2.2723	2.2536	2.2873	1.0090	0.9890	1.0287	1.2633	1.2448	1.2790
SW Sph-large	2.1563	2.1186	2.1882	0.8950	0.8610	0.9286	1.2613	1.2336	1.2825
SW Sph-medium	2.2304	2.2006	2.2507	0.9852	0.9585	1.0088	1.2452	1.2150	1.2686
SW Sph-small	2.1868	2.1746	2.1972	1.0497	1.0382	1.0590	1.1371	1.1239	1.1494
SW Sph-whole	2.2161	2.2058	2.2255	1.0334	1.0236	1.0420	1.1826	1.1717	1.1942
Shelf Yab-large	1.7415	1.6797	1.7907	0.7766	0.7366	0.8122	0.9649	0.9067	1.0138
Shelf Yab-medium	2.2285	2.1910	2.2553	0.9901	0.9463	1.0340	1.2384	1.1946	1.2715
Shelf Yab-small	2.3601	2.3481	2.3716	1.0986	1.0866	1.1113	1.2614	1.2493	1.2720
Shelf Yab-whole	2.3414	2.3294	2.3512	1.0848	1.0731	1.0962	1.2566	1.2448	1.2680

Table 4 (continued)

Assemblage	Observed Shannon H	H low	H up	H interclass (between)	Between low	Between up	H intraclass (within)	Within low	Within up
SW Yab-large	1.8924	1.8166	1.9335	0.6972	0.6389	0.7426	1.1952	1.1153	1.2543
SW Yab-medium	2.0400	1.9665	2.0796	0.8317	0.7424	0.9044	1.2083	1.1332	1.2634
SW Yab-small	2.3413	2.3152	2.3617	1.1193	1.0958	1.1412	1.2220	1.2001	1.2411
SW Yab-whole	2.3215	2.2997	2.3395	1.0775	1.0557	1.0985	1.2440	1.2253	1.2607
Whole Qesem	2.3053	2.3001	2.3103	1.0496	1.0442	1.0551	1.2557	1.2506	1.2607

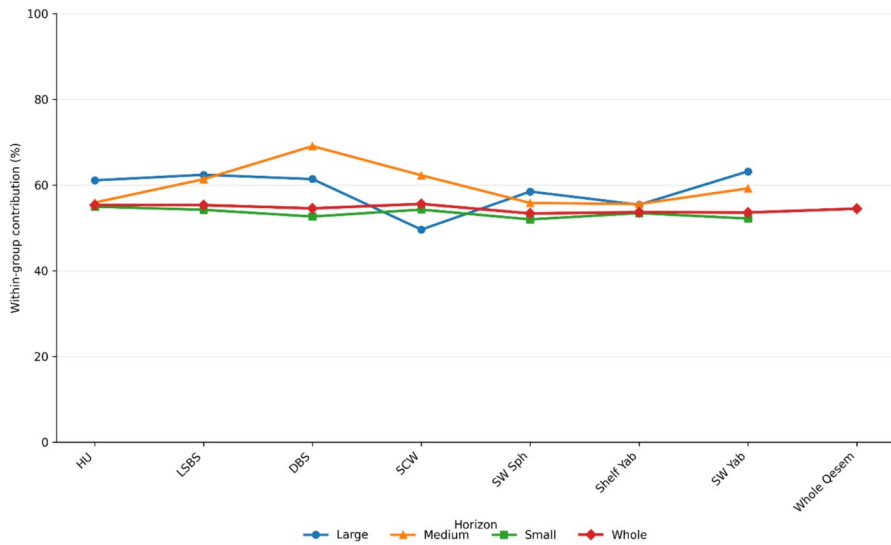


Fig. 11 Intra-class contribution to anatomical Shannon diversity across Qesem horizons and size classes

pattern combined with more localized contrasts in the internal organization of skeletal-part representation. The complementary anatomical indices reported in Table S4 are consistent with this reading: they refine the description of evenness- and richness-related variation, but do not alter the main conclusion that anatomical diversity at Qesem is globally more homogeneous and structurally more stable than taxonomic diversity.

Discussion

Intra-class diversity and occupation structure at Qesem

At Qesem, the interpretive value of Shannon diversity partitioning lies less in determining whether one horizon is globally more or less diverse than another than in describing how diversity is internally structured across and within prey-size classes. Because the faunal sequence remains taxonomically stable and strongly dominated by fallow deer, archaeologically meaningful variation is unlikely to appear only through major reversals in total Shannon diversity. What becomes informative instead is the balance between the interclass component, which reflects contrasts among prey-size classes, and the intra-class component, which reflects taxonomic heterogeneity retained within those classes.

This distinction becomes particularly relevant when the partitioning results are compared with the independent seasonality and event-structure framework proposed by Rivals et al. (2021), developed on the same Qesem horizons analysed here. Their study does not simply oppose short and long occupations, but distinguishes among short events, accumulations extending beyond one season, and separate short events

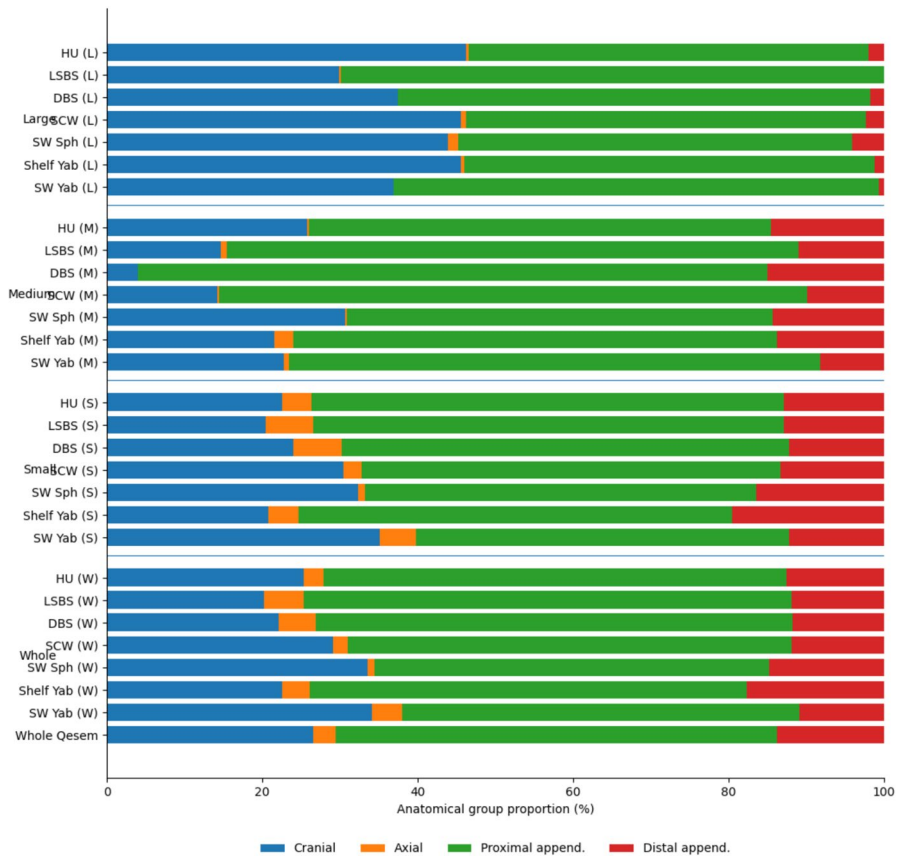


Fig. 12 Anatomical group proportions across Qesem horizons and size classes. Stacked horizontal bars show the relative contribution of cranial, axial, proximal appendicular, and distal appendicular groups to each assemblage, grouped by size class. Note: L=large; M=medium; S=small; W=whole

occurring in non-contiguous seasons. The intraclass component should therefore not be read as a direct proxy for occupation duration. Rather, it provides a formal descriptor of how taxonomic heterogeneity is distributed inside prey-size classes, which can then be compared with independent evidence for segmentation, recurrence, or cumulative occupation history.

In this light, the clearest correspondence is observed in SW Yab, which Rivals et al. (2021) associated with short events and which also shows the highest intraclass proportions in both NISP and MNI. At the other end of the pattern, SCW, interpreted as reflecting a longer seasonal signal, yields the weakest intraclass contribution and thus provides the clearest counterpoint to the short-event pole. LSBS tends toward the same short-event side of the pattern, though less strongly, while Shelf Yab remains intermediate and more clearly dominated by the interclass component. At Qesem, such modest but recurrent inflections are archaeologically meaningful precisely because the underlying taxonomic structure is otherwise highly stable.

This contrast is illustrated schematically in Fig. 13, which renders visible what the partitioning captures statistically by combining prey-size classes, the number of taxa within each class, and the relative amplitude of each taxon through circle size. The NISP-based contrast is particularly informative. SCW yields the lowest total Shannon diversity of the sequence ($H=0.7414$) and the lowest intraclass contribution (H intraclass=0.0694; 9.36%), whereas SW Yab yields the highest total Shannon diversity ($H=1.1015$) and the highest intraclass contribution (H intraclass=0.3248; 29.49%). This difference is not reducible to assemblage size: SCW contains more total NISP than SW Yab (401 vs. 283 specimens), yet its identified faunal structure remains markedly less internally distributed. The complementary indices support the same reading: corrected evenness is lower in SCW than in SW Yab (0.3864 vs. 0.5196), as is Pielou's J (0.3565 vs. 0.5013), while richness-sensitive indices are also lower in SCW (Menhinick=0.3995; Margalef=1.1678) than in SW Yab (Menhinick=0.5350; Margalef=1.4171). In visual terms, SCW is dominated by a narrower configuration centred on the small-size class and especially on fallow deer, whereas SW Yab retains a broader internal distribution. This broader structure reflects not only the additional representation of *Sus*, *Capra*, and cf. *Capreolus* within the small-size class, but also a more even distribution within the large-size class, where rhinoceros, horse, and bovine remains are more evenly represented than in SCW. Figure 13 should therefore be read as a heuristic rendering of the statistical result: its purpose is to show that assemblages with different internal organization cannot be reduced to total diversity alone.

The comparison becomes even more informative when examined within, rather than only between, the main techno-typological facies. Within the Yabrudian, the contrast between Shelf Yab and SW Yab is particularly instructive. Both belong to the same broad facies, yet they diverge in both the seasonality signal reported by Rivals et al. (2021) and their partitioned diversity structure: Shelf Yab remains more strongly dominated by the interclass component, whereas SW Yab shifts more clearly toward intraclass representation. A parallel contrast can be observed within the Amudian assemblages, where LSBS tends toward the short-event side of the pattern and SCW toward the longer or more cumulative side, while DBS and SW Sph occupy more equivocal positions. Such internal variability argues against a strictly cultural reading and instead supports the idea that the partitioned structure of diversity is sensitive to how occupations were organized within the cave.

These more ambiguous cases are essential to the argument. SW Sph is associated by Rivals et al. (2021) with short events, yet it does not display the highest intraclass values. Rather than a contradiction, this suggests that event duration or recurrence alone cannot determine the partitioned diversity structure of an assemblage. Functional specialization also matters, and SW Sph has been independently discussed in relation to marrow extraction and intensive bone reduction. DBS is similarly mixed and is best regarded as a composite case, while HU probably smooths a more differentiated internal reality, given the coexistence of distinct seasonal signals across its sub-contexts.

The richness-sensitive indices help clarify this point. Menhinick's index is useful not as an independent proxy for occupation duration, but as a control on whether relatively high intraclass values merely reproduce corrected richness. The Qesem

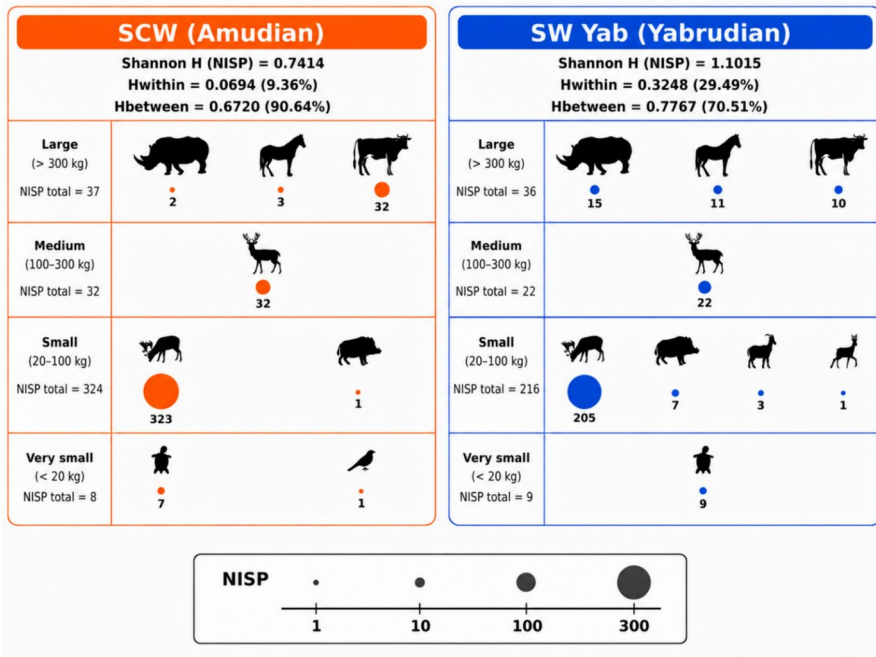


Fig. 13 Comparative schematic representation of SCW and SW Yab, the two extreme Qesem horizons in terms of NISP-based intraclass contribution. Silhouettes are organized by analytical prey-size class, and circle size is proportional to NISP

results do not support such a reduction. The intraclass signal cannot be reduced either to total Shannon diversity or to richness alone: it captures the extent to which heterogeneity is retained inside prey-size classes rather than expressed mainly through contrasts between them.

A cautious interpretive proposition nevertheless emerges. At Qesem, relatively stronger intraclass contributions are compatible with contexts independently reconstructed as short events or recurrently segmented occupations, whereas lower intraclass values are more consistent with cumulative or more strongly size-class-structured assemblages. This pattern should remain a contextual hypothesis rather than a general rule. Its value lies in its convergence with the independent framework of Rivals et al. (2021), its recurrence across both NISP- and MNI-based calculations, and its partial support under bootstrap resampling.

Anatomical Diversity Partitioning and Carcass Processing at Qesem

In contrast to the taxonomic results, anatomical diversity partitioning points to a comparatively stable structural regime across the Qesem sequence. At the scale of the whole assemblages, total anatomical Shannon diversity values remain tightly grouped, and the intraclass component consistently contributes slightly more than

the interclass component. Anatomical diversity at Qesem thus appears to be generated less by strong contrasts between cranial, axial, proximal appendicular, and distal appendicular groups than by recurrent internal variability within a broadly similar skeletal profile. The anatomical signal is therefore less horizon-specific than the taxonomic one and instead suggests a repeated organization of carcass processing across the cave.

This stability is consistent with previous zooarchaeological work at Qesem. Earlier studies had already shown that skeletal representation is not evenly distributed across the carcass but strongly biased toward nutritionally valuable limb elements. Blasco et al. (2024) sharpen this interpretation by arguing that the marked scarcity of appendicular epiphyses cannot be reduced either to carnivore ravaging or to fossil-diagenetic destruction alone, but is better explained by intensive anthropogenic processing, including the targeted destruction of grease-rich and highly porous articular ends. Read in that light, the weak inter-horizon variation in whole-assemblage Shannon diversity is not trivial: it indicates that the same broad anatomical regime was repeatedly reproduced through time.

The anatomical group proportions clarify how this regime was structured. In most horizons and size classes, proximal appendicular elements dominate, often accounting for around half or more of the assemblage and reaching particularly high values in several medium-size contexts. The slight predominance of the intraclass component should therefore not be mistaken for generalized carcass completeness. On the contrary, the assemblages remain strongly organized around limb-focused representation. What the partitioning adds is that much of the anatomical diversity is generated internally within this dominant appendicular signal, through the co-occurrence of several proximal limb elements rather than through a balanced distribution across all anatomical regions. In that sense, the partitioned anatomical pattern formalizes rather than weakens the skeletal-part bias already documented at the site.

This reading becomes more meaningful when compared with the broader evidence for intensive bone processing. Blasco et al. (2024) explicitly relate the disappearance of epiphyseal-rich portions to grease-oriented exploitation, while experimental and residue-based work has shown delayed use of marrow- and fat-rich resources, pointing to planned resource management rather than immediate undifferentiated consumption (Blasco et al., 2019b). The dominance of proximal appendicular representation in the present results is therefore compatible with grease-oriented processing: shafts and surviving limb portions remain archaeologically visible, whereas the greasiest articular ends were likely reduced, fragmented beyond recognition, or otherwise underrepresented in the identifiable record.

Prey size provides the clearest internal differentiation within this otherwise stable regime. The strongest intraclass structuring is concentrated in the large and especially medium-size categories, whereas the small-size class remains much closer to parity between intraclass and interclass components. Large and medium animals thus appear to have been subject to a more selective and more internally structured concentration on limb portions, whereas small-size assemblages preserve a somewhat broader anatomical spread. This does not amount to true whole-carcass representation for small prey, since proximal appendicular elements still dominate and axial values remain weak, but it does indicate that the degree of anatomical

polarization varied with prey size. The partitioning results therefore do more than restate that Qesem is limb-dominated: they show that the strength and internal organization of that dominance differ across size classes. This is broadly consistent with more general zooarchaeological models linking prey size to differential skeletal selectivity and transport constraints (Faith & Gordon, 2007).

This reading is also broadly consistent with the complementary indices. Evenness-related measures do not suggest anatomically even carcass representation across regions, but instead support the persistence of structured skeletal-part profiles, while richness-sensitive indices indicate that the observed variation cannot be reduced to simple differences in the number of represented anatomical categories alone. At the scale of the whole assemblages, for example, corrected evenness and Pielou remain high and relatively compressed (e.g., HU-whole: $VE=0.9539$, $J=0.8572$; Shelf Yab-whole: $VE=0.9584$, $J=0.8872$), whereas richness-sensitive values remain comparatively low (Menhinick= 0.1197 and 0.1301 , respectively). In that sense, anatomical diversity partitioning is not an isolated signal: the complementary indices act here as control measures, confirming that the main pattern identified at Qesem is one of recurrently structured carcass processing rather than anatomically balanced representation.

At the same time, the anatomical data do not support a strong Amudian/Yabrudian dichotomy at the scale of the whole assemblages. Whole-assemblage Shannon diversity values remain remarkably close across the sequence, arguing against sharply distinct carcass-processing regimes when viewed at a broad scale. Some local contrasts nevertheless persist and may plausibly be read against the techno-functional differences documented independently for the two facies at Qesem (e.g., Parush et al., 2016). In this respect, anatomical diversity partitioning complements rather than duplicates the taxonomic analysis: the latter is more sensitive to horizon-specific contrasts, whereas the former reveals the relative stability of the underlying carcass-processing regime and the more localized ways in which it varied by prey size.

Methodological Implications and Broader Applicability

Recent reassessments of occupation duration and site function have shown that taxonomic diversity remains a useful variable, but not a self-sufficient one. Lubrano et al. (2025), in their review of temporal indicators of Neanderthal occupations, note that taxonomic diversity has often been mobilized as a proxy for occupation duration or site function, with high diversity commonly associated with longer or more complex occupations and low diversity with shorter or more specialized ones. At the same time, their reassessment makes clear that this relationship is not stable. Depending on environmental availability, human behavioural choices, carnivore input, palimpsest formation, fragmentation, and the quality of faunal identification, both short- and long-term occupations, may display relatively high diversity. Their conclusion is therefore not that diversity should be abandoned, but that it must be contextualized and interpreted in relation to other archaeological variables.

A similar point emerges in predictive approaches. In Grégoire et al. (2021), Shannon diversity is explicitly introduced as a discriminant variable in a machine-learning framework designed to characterize occupation patterns. Yet the archaeological interpretation of that variable remains grounded in earlier discussions of specialization, subsistence breadth, and site function rather than in any intrinsic behavioural meaning of Shannon itself (Binford, 1981; Daujeard & Moncel, 2010; David & Enloe, 1993; Magniez, 2010). In other words, Shannon diversity already enters quantitative and predictive archaeology as a potentially informative feature, but one whose meaning remains partly equivocal when taken as a global value alone. From this perspective, additive partitioning is useful because it does not replace Shannon diversity; it refines its descriptive use by distinguishing the share of diversity generated between predefined groups from the share retained within them.

In the present study, those groups were taxonomic prey-size classes and anatomical categories, because these are archaeologically meaningful partitions for the questions addressed at Qesem. Yet the method is not restricted in principle to these specific groupings. It can be applied to any predefined and mutually exclusive system of classes, provided that the classificatory scheme is explicitly justified in relation to the archaeological problem under study. In zooarchaeology, such classes may include anatomical regions, ecological categories, body-size classes, taxonomic groupings, or other structured partitions of assemblage composition. More broadly, the same logic could be extended beyond zooarchaeology whenever archaeological data can be organized into interpretable grouped distributions.

The main methodological contribution of the approach is therefore not tied to a single classificatory solution, but to the possibility of formalizing how total diversity is internally distributed across and within analytically relevant groups. This is especially useful in cases where global diversity values remain difficult to interpret on their own. Additive partitioning does not remove that ambiguity by itself, nor does it transform Shannon diversity into a direct behavioural proxy. Rather, it specifies the internal architecture of the diversity signal and provides a more explicit descriptive basis for subsequent archaeological interpretation.

A further advantage is that the procedure can be implemented reproducibly. In the present study, the *diversityArch* package was used to calculate total Shannon diversity, additive partitioning, complementary indices, and bootstrap confidence intervals within a transparent workflow. Because partitioning is not evaluated in isolation, evenness-, dominance-, and richness-sensitive indices can also be computed as control measures, helping to assess whether an observed pattern reflects the internal organization of diversity itself or is driven more broadly by abundance structure or richness.

This framework matters not only for the present case study, but also for wider comparison across assemblages, sites, and analytical traditions. By making the partitioning of Shannon diversity operational and reproducible, it facilitates sensitivity tests and controlled comparisons between alternative grouping strategies. Such formalized variables may also prove useful in future quantitative workflows, including predictive and machine-learning applications, precisely because they remain both archaeologically interpretable and mathematically explicit. Their value, however, depends on the same principle defended throughout this study: diversity measures

are most informative when treated as structured descriptors and interpreted in relation to independent archaeological evidence.

Conclusion

This study examines not only how diverse the Qesem faunal assemblages are, but how that diversity is internally organized. By applying additive partitioning of Shannon diversity to both taxonomic and anatomical data, it distinguishes diversity generated by contrasts among predefined analytical groups from diversity retained within those groups. Diversity is therefore treated here not as a direct behavioural proxy, but as a formal property of assemblage structure whose archaeological meaning depends on contextual comparison.

At the taxonomic level, the results show a robust and recurrent pattern. Diversity is consistently dominated by the interclass component, indicating that contrasts among prey-size classes remain the main source of taxonomic structure at Qesem. However, the intraclass component varies between horizons, revealing differences in the distribution of taxa within size classes that are not visible from total Shannon diversity alone. SCW illustrates a more narrowly structured configuration centred on the small-size class and fallow deer, whereas SW Yab shows a broader internal distribution, both through additional small prey and through a more even representation within the large-size class. This is one of the main gains of the approach: it shows not only whether an assemblage is more or less diverse, but where that diversity is located.

The comparison between NISP and MNI further shows that quantification framework matters. NISP emphasizes specimen-level structure and remains more sensitive to abundance concentration and fragmentation, whereas MNI makes intraclass taxonomic heterogeneity more visible and reduces some of the sharper contrasts observed under NISP. The persistence of interclass dominance under both frameworks supports the stability of the broad taxonomic pattern, while their differences identify which aspects of the signal are quantification-dependent. Similarly, the integration of taxonomically indeterminate but size-class-attributed fragments shows that fragmentation affects not only the magnitude of Shannon diversity, but also its partitioning among and within prey-size classes.

The anatomical results provide an important counterpoint. When assemblages are considered a whole, anatomical diversity is comparatively homogeneous and slightly intraclass-dominated. Clearer contrasts emerge within size classes, especially among medium-sized prey. Read alongside the independent zooarchaeological evidence from Qesem, this pattern is compatible with a recurrent limb-focused processing regime, modulated by prey size and by localized techno-functional variation. The anatomical analysis therefore shows that additive partitioning is not restricted to taxonomic diversity but can also describe how skeletal-part representation is internally organized.

These results clarify both the value and the limits of the approach. Additive partitioning does not directly measure occupation duration, seasonality, transport decisions, or carcass-processing behaviour. Rather, it provides a reproducible descriptor

of assemblage structure that can be compared with independent taphonomic, anatomical, technological, and contextual evidence. In relation to the event-structure and seasonality framework proposed by Rivals et al. (2021), the Qesem patterns are archaeologically meaningful, but they should not be treated as direct measures of occupational duration.

Overall, this study shows that additive partitioning makes Shannon diversity more informative by reopening a global index into archaeologically interpretable components. Complementary richness-, evenness-, and dominance-sensitive indices remain useful as controls, but the main contribution of the procedure lies in formalizing the internal architecture of diversity. Its value is not to replace conventional zooarchaeological interpretation, but to clarify what kind of diversity is being observed, where it is located within the assemblage, and how stable it remains under alternative analytical frameworks. For this reason, the approach has potential beyond Qesem Cave, particularly in comparative, computational, and predictive workflows where reproducible and archaeologically interpretable variables are needed.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10816-026-09802-3>.

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Author Contribution A.B. curated the dataset; performed the analyses in R; generated tables and figures; and wrote the original draft of the manuscript. A.S. developed the R workflows and authored the R package used for diversity and entropy computations; wrote the methodological section; contributed to the analytical design; and reviewed the manuscript. J.R., R.B., M.A., G.C., D.V., R.L., E.A., R.B. and A.G. contributed to interpretation; provided critical revisions; and approved the final version. All authors read and approved the final manuscript. J.R. supervised the research.

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Data Availability Supplementary Tables S1–S2 are available as Online Resource 1. The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

Code Availability The R package diversityArch used in this study is publicly available from CRAN (<https://CRAN.R-project.org/package=diversityArch>; <https://doi.org/10.32614/CRAN.package.diversityArch>). The package reference manual and the recommended citation are provided on the CRAN package pages. Additional analysis scripts are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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