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Bone collagen hydrogen isotopes as tracers of local palaeoclimate: The Aurignacian from Isturitz cave (France) as a case study

M. Ibáñez-Herranz [a,*], L. Agudo-Pérez [a], M. Fernández-García [b,c], A. Cicero-Cabañas [a], M.C. Soulier [d], C. Normand Orieux [d,e], A.B. Marín-Arroyo [a,**]

[a] EvoAdapta Research Group (Evolución Humana y Adaptaciones durante la Prehistoria), Department of Historical Sciences, University of Cantabria, Santander, 39005, Spain
[b] Research Centre for Field Archaeology and Forensic Taphonomy, University of Lancashire, Preston, PR1 2HE, United Kingdom
[c] IPHES-CERCA (Institut Català de Paleoecologia Humana i Evolució Social), Tarragona, 43007, Spain
[d] Laboratoire TRACES, UMR 5608, CNRS, Université de Tolouse-Jean Jaurès, Cedex 9, Toulouse, F-31058, France
[e] Eusko Arkeologia - Groupe de Recherches Archéologiques du Pays Basque nord, Jauregiberria, Larceveau-Arros-Cibits, 64120, France

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ABSTRACT

Hydrogen stable isotopes (δ^2H) preserved in bone collagen have been proposed as a promising proxy for palaeoclimatic reconstruction, though empirical applications remain limited. We performed multi-isotopic analyses to evaluate the reliability and scope of this approach, integrating novel δ^2H data with recently published δ^{13}C, δ^{15}N and δ^{34}S, on 50 herbivore bone samples collected from three archaeostratigraphic layers spanning the Aurignacian sequence of Isturitz Cave (France). This archaeological, well-preserved, dated and studied site provides a robust framework for testing isotopic proxies across temporal and taxonomic gradients. Our results reveal a progressive δ^2H decline over ~3000-year interval, broadly consistent with regional paleoenvironmental records indicating cooling and a shift towards drier conditions, but in contrast with previously proposed local climate changes. We also identified species-specific δ^2H differences, underscoring the need for taxonomic resolution in future applications and general palaeoclimatic interpretations. While these samples reflect faunal remains accumulated through human activity—introducing potential ecological and sampling biases—they nonetheless provide valuable records of past local conditions at the time humans inhabited the site. Overall, our findings support the potential of bone collagen δ^2H as a sensitive indicator of past hydrological conditions and a complementary tool for reconstructing both climatic trends and human-environment dynamics.

1. Introduction

Over the past few decades, geochemical techniques such as stable-isotope analyses have transformed the study of past ecosystems, establishing themselves as a valuable tool for determining palaeoecological and palaeoenvironmental conditions (Stevens et al., 2025 and references therein). Among the array of available possibilities, the analysis of stable isotope ratios of oxygen (^{18}O/^{16}O, noted δ^{18}O) and carbon (^{13}C/^{12}C, noted δ^{13}C) in dental enamel emerged as the prevailing approach for studying past climates (e.g., Amiot et al., 2021; Lécuyer et al., 2021; Barakat et al., 2025). This method is of particular interest due to its ability to investigate seasonality in herbivores using transects of phosphate or carbonate of dental hydroxyapatite. However, it is worth noting that these analyses provide insights on a time scale corresponding to the tooth's mineralisation, which occurs during the first years of the animal's life (Balasse, 2002; Hoppe et al., 2004; Kohn, 2004). In an attempt to expand this timeframe, some studies have examined the possibility of measuring oxygen composition (δ^{18}O) in bone bioapatite, though it appears less reliable on bone tissues due to diagenetic alterations (Lee-Thorp, 2008; Pestle et al., 2014). Consequently, this creates an opportunity to explore alternative approaches to studying past climates directly on this kind of biological remains recovered from archaeological and palaeontological sites. Among all the analysable biological materials, bone collagen is attracting considerable attention for its relative abundance and preservation at archaeological sites and its capacity to provide insights into behavioural, dietary, and even climatic

* Corresponding author.
** Corresponding author.
E-mail addresses: ibanezhm@unican.es (M. Ibáñez-Herranz), marinab@unican.es (A.B. Marín-Arroyo).

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information over a presumably long-term period during the lifetime of an animal (Matsubayashi and Tayasu, 2019; Quinn, 2024).

The isotopic compositions most often studied in this context and material type are carbon ($\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, noted $\delta^{15}N$), which offer valuable information about an animal's diet and habitat, and in turn, its palaeoenvironmental setting. $\delta^{13}C$ values strongly depend on plant metabolism, which varies with habitat resources and environmental conditions, and differ between C_3 and C_4 photosynthetic pathways (Van der Merwe, 1982; Van Klinken et al., 1994). Thus, based on the principle of isotopic fractionation along the food chain, $\delta^{13}C$ values in animal collagen reflect, to a certain extent, the isotopic composition of the plants consumed, which is influenced by environmental conditions. For instance, lower $\delta^{13}C$ values are generally associated with colder and wetter conditions, as higher precipitation tends to decrease the $\delta^{13}C$ in C_3 plant biomass (Ehleringer and Monson, 1993; Kohn, 2010; Tieszen, 1991). Similarly, an analogous correlation has been observed between the nitrogen isotopic values of bone collagen and those of plants (Hartman, 2011; DeNiro and Epstein, 1981b). The latter depend on soil conditions and biological factors, such as mycorrhizal symbiosis, and are subsequently influenced by additional variables, including temperature and humidity (Craine et al., 2009). This results in more arid systems being categorised as having higher values of $\delta^{15}N$ (Craine et al., 2015; Heaton et al., 1986). Furthermore, another stable isotope system that has attracted attention in this field is sulfur ($^{34}S/^{32}S$, noted $\delta^{34}S$), which has also been utilised to deduce dietary and ecological information. In particular, $\delta^{34}S$ appears to be especially useful for evaluating habitat use in relation to mobility and migratory behaviours, given its strong reflection of geological influences and marine spray (Drucker et al., 2011; González-Rabanal et al., 2025; Jones et al., 2019; Privat et al., 2007).

However, two stable isotopes remain underutilised and that could be a direct reflection of climatic conditions, ^{1}H and ^{2}H. Also known as protium and deuterium, the relation between them ($\delta^{2}H$) has been considered a potential proxy for studying climates on organic tissues for decades (Cormie et al., 1994; Epstein et al., 1977; Estep and Dabrowski, 1980). In terrestrial ecosystems, the primary source of hydrogen in animals' tissues is meteoric water, either consumed directly through drinking or incorporated via the lower levels of the food chain (Cormie et al., 1994; Hobson et al., 1999; Topalov et al., 2019; Tuross et al., 2008). This makes hydrogen a potentially useful proxy for studying precipitation, offering a complementary perspective to other isotopes such as carbon or oxygen, which can also be influenced by respiration or other physiological processes in addition to ingestion (Tieszen, 1991; Passey et al., 2005; Cerling et al., 2021). Meteoric deuterium values are of particular interest due to their global variation, which is attributable to strong isotopic fractionation during condensation and precipitation processes inherent to the water cycle. Moreover, precipitation values depend on a series of geospatial characteristics, including altitude, latitude and distance from the sea; as well as on climatological or meteorological factors such as aridity, relative humidity or temperature; this results in a locally specific variation of $\delta^{2}H$ (Bowen et al., 2005; Bowen and West, 2019; Kendall and Doctor, 2003; Kern et al., 2020; Pfahl and Sodemann, 2014; Vystavna et al., 2021).

Indeed, several fields have exploited $\delta^{2}H$ on organic tissues to infer migration patterns, trophic levels, seasonal changes and even climatic conditions (Bearhop et al., 2003; Cryan et al., 2004; Dufour et al., 2025; Eerkens et al., 2020; Estep and Dabrowski, 1980; Hobson et al., 2012; Ruokonen et al., 2019; Sharp et al., 2003; White et al., 1994). Despite this potential, the main reason hydrogen isotopes have been overlooked in bone collagen research is the difficulty of obtaining direct and reliable values for isotopically labelled carbon-bonded hydrogens, as a fraction of them is exchangeable with environmental water or vapour (DeNiro and Epstein, 1981a). However, this problem has already been overcome analytically (Sauer et al., 2009; Soto et al., 2017; Wassenaar et al., 2023). Of the few studies that have analysed archaeological bone collagen, many have focused on palaeodietary or palaeoecology reconstructions (e.g., Arnay-de-la-Rosa et al., 2010; Gröcke et al., 2017; Reynard and Hedges, 2008; Topalov et al., 2013). From a climatological perspective, Leyden et al. (2006) and Reynard et al. (2020) found that $\delta^{2}H$ in bone collagen is consistent with precipitation, confirming its potential as a palaeoclimatic proxy (Fig. 1). Nevertheless, they were based on large-scale geographic regions such as North America and the Mediterranean region, where multiple factors can influence the interspecific and interpopulation values of the samples. Certainly, some studies have noted that non-exchangeable hydrogen values measured in mammalian tissues appear to vary between species (Reynard et al., 2020; Reynard and Hedges, 2008; Topalov et al., 2013), hypothesising that this is due to differences in body size and inherent differences in water intake requirements.

This study aims to investigate whether $\delta^{2}H$ can serve as a proxy of local climatic evolution by leveraging the unique opportunities provided by archaeological deposits, where human groups accumulated faunal remains from the surrounding environment. To address this, we focus on the Aurignacian occupation of Isturitz (dated: to ca. 42,470 - 39,480 cal BP: Barshay-Szmidt et al., 2018) to test whether $\delta^{2}H$ values in bone collagen reflect local palaeoclimatic changes. We analysed three herbivore taxa that are well-represented in these deposits, including reindeer (*Rangifer tarandus*), bovids (*Bos primigenius/Bison priscus*) and horses (*Equus ferus*), to assess both climatic implications and potential species-specific differences in $\delta^{2}H$ signatures. To our knowledge, this is one of the first analyses of the temporal evolution of local $\delta^{2}H$ evolution in bone collagen from Palaeolithic faunal remains.

2. Archaeological site

Isturitz Cave (Western Pyrenees, France; Fig. 2A) is located at the confluence of Atlantic and continental climate influences. The site has a well-documented archaeological record, making it particularly suitable for exploring climate variability over a controlled period of around 3000 years at a regional scale. Two galleries within the Isturitz karstic cave system have been excavated since 1912 (De Saint-Périer, 1935; Normand, 2005; Passemard, 1913), revealing a stratigraphic sequence spanning from the Mousterian to the Bronze Age (Normand et al., 2007).

We will focus on the Aurignacian occupation phases within lithostratigraphic unit III, which has revealed well-preserved archaeological materials (Soulier, 2013; Tarriño and Normand, 2002; White and Normand, 2015, Fig. 2B). These Aurignacian levels are subdivided into three archaeostratigraphic phases—Proto-Aurignacian, 'Intermediate' Aurignacian (the designation "intermediate" is employed exclusively in a stratigraphy sense to describe a layer positioned between an assemblage securely assigned to the Proto-Aurignacian and another to the Early Aurignacian, it implies no cultural attribution; see Soulier, 2013), and Early Aurignacian—originally dated by Barshay-Szmidt et al. (2018) and recently recalibrated with IntCAL20 curve by Berlioz et al. (2025). The updated chronological framework places the Proto-Aurignacian between 42,470 and 41,460 cal BP, the 'Intermediate' Aurignacian between 42,090 and 40,790 cal BP and the Early Aurignacian between 41,450 and 39,480 cal BP (hereinafter also referred to as Proto, 'Intermediate' and Early). This corresponds to a temporal range of 42,470–39,480 cal BP.

3. Materials and methods

The carbon, nitrogen, and sulfur isotopic composition of the samples used in this study was previously reported by Berlioz et al. (2025). In order to complement the existing isotopic data, we conducted additional analysis on those previously analysed collagen samples, targeting hydrogen isotopes once the following quality indicators were set in order to ensure collagen integrity: ≥1% collagen (Ambrose, 1990; van Klinken, 1999), 2.9 – 3.6 C:N (Ambrose, 1990; M. DeNiro, 1985; Guiry and Szpak, 2021; van Klinken, 1999), 600 ± 300 C:S and 200 ± 100 N:S (Nehlich and Richards, 2009). We re-analysed a total of

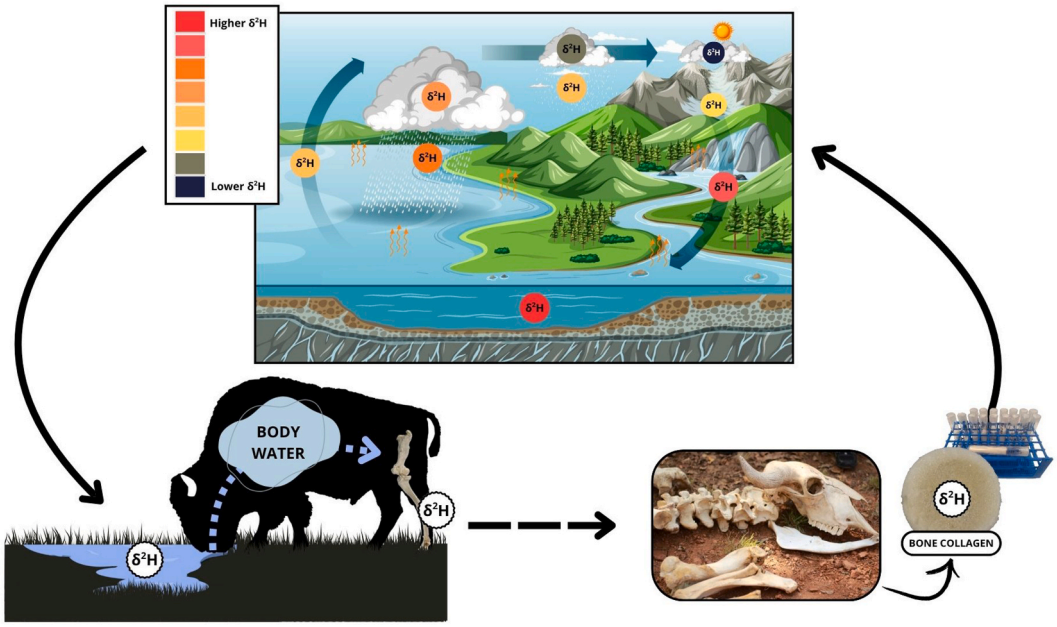

Fig. 1. General outline of the δ^2H analysis approach, from the description of how the hydrological cycle generates a characteristic δ^2H variation, to how this value is subsequently assimilated into different animal tissues, and how the analysis of bone collagen samples can be used to interpret the climatic isotopic variations.

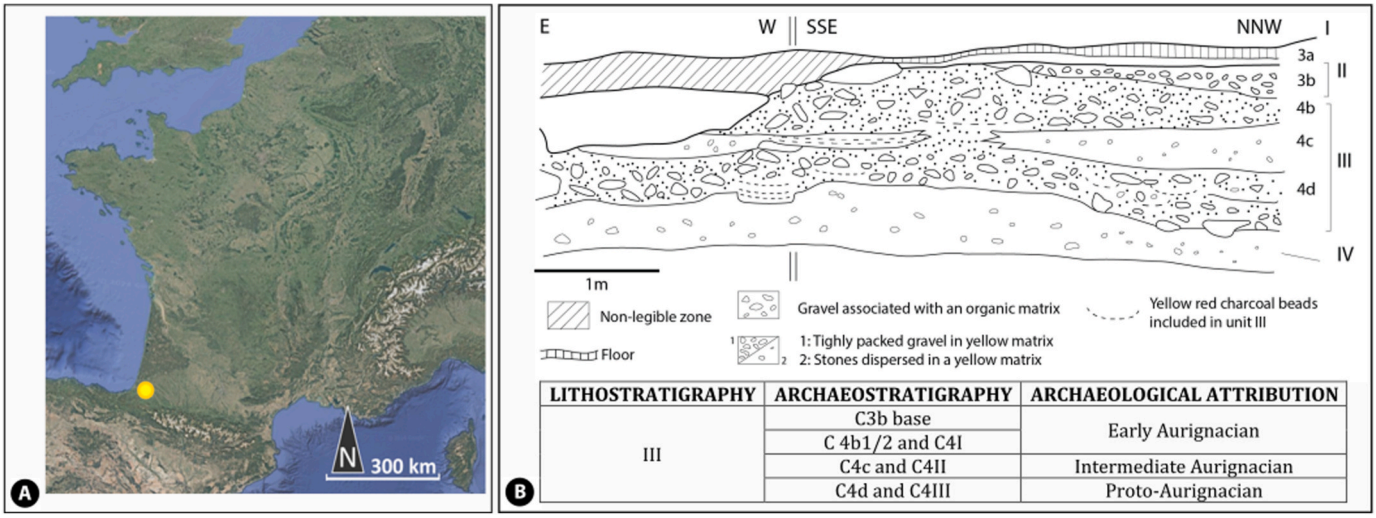

Fig. 2. A) Location of the Isturitz cave in the valley of the river L'Arberoue in France (Western Pyrenees). Modified from Berlioz et al. (2025). **B)** Synthetic stratigraphy of the excavated zone and correspondence between archaeostratigraphy and archaeological attribution of lithographic unit III, redrawn and modified from Normand et al. (2007).

50 bones from auroch/bison (*Bos primigenius/Bison priscus*, n = 20; hereafter referred to as bovine), horse (*Equus ferus*, n = 20), and reindeer (*Rangifer tarandus*, n = 10) based on initial morphological identification. Two specimens initially attributed to *Rangifer tarandus* exhibited isotopic values outside the taxons's expected range. To exclude potential taxonomic misidentification, we conducted ZooMS (Zooarchaeology by Mass Spectrometry, see Buckley et al., 2009) which reassigned both specimens to red deer (*Cervus elaphus*), resulting in a final count of eight reindeer and two additional red deer. Eleven additional bones were also analysed, including three red deer—bringing the total number of red deer specimens to five—, seven foxes (*Vulpes vulpes*) and one bear (*Ursus* sp.). These samples were excluded from further exploration because either species was present in only one cultural phase (*Cervus elaphus*) or to avoid dietary accumulation effects of carnivory and omnivory (Birchall et al., 2005; Pietsch et al., 2011). It is important to note that Berlioz et al. (2025) excluded samples with a carbon content (C%) below 30% as part of their criteria for collagen quality. However, this threshold may be excessively restrictive when considered in isolation, potentially leading to the rejection of reliable data (Ambrose, 1990; Harbeck and Grupe, 2009). In the present study, samples with a C% lower than 30% were kept for further statistical analysis only if all other key indicators confirmed collagen preservation (for more detailed samples information, refer to S1).

Bone samples were originally collected at the Centre Départemental d'Archéologie of Hasparren (France), then collagen extraction was undertaken at the EvoAdapta clean lab at the University of Cantabria (Santander, Spain) following the methodology detailed in Brown et al. (1988) and Richard and Hedges (1999). All isotopic analyses were performed by the Iso-Analytical Laboratory (Crewe, UK) using a Europa Scientific 20-20 isotope ratio mass spectrometer, following the

procedure detailed in Jones et al. (2019) to measure $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, as stated in Berlioz et al. (2025). Subsequently, the remaining collagen was prepared for $\delta^{2}H$ analyses directly at Iso-Analytical facilities. As a precautionary measure, samples containing globules were freeze-dried before analysis to eliminate any residual water. Samples were then weighed (1.0 ± 0.1 mg) into open silver capsules, along with non-exchangeable hydrogen standards, and were comparatively equilibrated with moisture in laboratory air for 14 days prior to analysis. Once batch analysis had begun, the capsules were sealed and loaded into an autosampler, then dropped into a furnace at 1080 °C, where they thermally decomposed to H_2 and CO over glassy carbon. Any traces of water produced were removed by magnesium perchlorate. H_2 was resolved using a packed-column gas chromatograph maintained at 35 °C. The resultant chromatographic peak entered the ion source of the IRMS, where it was ionised and accelerated. Gas species of different masses were separated in a magnetic field and then simultaneously measured on a Faraday cup universal collector array. For H_2, masses 2 and 3 were monitored. Duplicate measurements were taken every five samples. Hydrogen isotopes quality measurements were checked using in-house standards IA-R002 (mineral oil: $\delta^{2}H_{V\text{-}SMOW} = -111.2‰$) and IA-R072 (mineral oil: $\delta^{2}H_{V\text{-}SMOW} = -148.61‰$) that were calibrated against the International Atomic Energy Agency (IAEA) standards NBS-22 (mineral oil: $\delta^{2}H_{V\text{-}SMOW} = -120‰$) and IAEA-CH-7 (polyethylene foil: $\delta^{2}H_{V\text{-}SMOW} = -100.2‰$). Deuterium non-exchangeable hydrogen measurements were comparatively equilibrated by a 3-point linear calibration and control checked by inter-laboratory United States Geological Survey (USGS) comparison standards: USGS42 (human hair: non-exchangeable $\delta^{2}H_{V\text{-}SMOW} = -72.9‰$), USGS43 (human hair: non-exchangeable $\delta^{2}H_{V\text{-}SMOW} = -44.4‰$), USGS CBS (caribou hoof: non-exchangeable $\delta^{2}H_{V\text{-}SMOW} = -157.0‰$) and USGS KHS (kudu horn: non-exchangeable $\delta^{2}H_{V\text{-}SMOW} = -35.3‰$). USGS43 was measured as a quality control check sample to verify the use of the 3-point linear calibration. As an additional control to ensure accuracy and replicability, six in-house standards prepared from a single archaeological ungulate sample at the EvoAdapta clean lab were sent to Iso-Analytical and analysed repeatedly alongside the samples, yielding a total of 15 measurements (STDC-3: $\delta^{2}H_{V\text{-}SMOW} = -29.6 \pm 0.75$). Average reproducibility of samples measured in duplicate was 1.30‰ for $\delta^{2}H$ and 1.51‰ for non-exchangeable $\delta^{2}H$. The $\delta^{2}H$, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values are reported relative to V-SMOW, V-PDB, AIR, and V-CDT standards.

Data were prepared and statistically analysed using R (R Core Team, 2024), RStudio v. 2024.12.1.563 (Posit team, 2025) and the packages "car" (Fox and Weisberg, 2019), "corrplot" (Wei and Simko, 2021), " dplyr " (Wickham et al., 2023), "effsize" (Torchiano, 2020), "FSA" (Ogle et al., 2023), "Hmisc" (Harrell Jr, 2025), "rstatix" (Kassambara, 2023), "tidyverse" (Wickham et al., 2019). For data groups with at least three stable isotopic values, the Kruskal-Wallis test was performed, followed by Dunn's post-hoc analyses with Bonferroni adjustment when statistically significant differences were detected. Effect size was estimated using epsilon-squared (ε^2) for the Kruskal-Wallis test and Cliff's δ for Dunn's analyses. Analyses were initially performed on the complete dataset to identify general trends in isotopic composition across cultural phases. Following this exploratory assessment, data were grouped by species, and interspecific analyses were conducted to evaluate differences among taxa. All raw data and the R code file of the analysis are provided as Supplementary Information (S1 and S2, respectively).

4. Results

4.1. Collagen preservation and sample selection

As noted above, of the 61 samples initially analysed, 48 met all our quality and methodological criteria. Therefore, all the samples that were further analysed had the expected terrestrial mammal values for preserved collagen, likely reflecting in vivo isotopic composition (Guiry and Szpak, 2021; Nehlich and Richards, 2009; van Klinken, 1999). The percentage of collagen for them ranged from 2.1 to 10.0%, with an average of 5.8%; for the C:N the range was 3.1 to 3.2; for the C:S ratio, the minimum value was 323.0 and the maximum 729.2; finally, for the N:S values, the minimum was 100.5 and the maximum 230.9.

4.2. $\delta^{2}H$, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotope data

The main isotopic results are shown in Table 1. Considering all herbivores species and cultural phases together, we found a mean value of −20.6 ± 0.8‰ for $\delta^{13}C$, of 7.2 ± 2.0‰ for $\delta^{15}N$, of 12.6 ± 1.4‰ for $\delta^{34}S$ and of −51.2 ± 11.5‰ for $\delta^{2}H_{non\text{-}exchangeable}$. As expected from previously reported result of this site, when evaluating the relationship between the different isotopes, we found a strong positive correlation between $\delta^{13}C$ and $\delta^{15}N$ (Pearson's r = 0.63, P= <0.001, Fig. 3). There was also a negative correlation between $\delta^{2}H_{non\text{-}exchangeable}$ and $\delta^{13}C$ (Pearson's r = - 0.36, P = 0.012) and between $\delta^{2}H_{non\text{-}exchangeable}$ and $\delta^{15}N$ (Pearson's r = − 0.53, P= <0.001).

Considering the data from all species together, it seems that the $\delta^{13}C$ evolution started with an increase from the Proto-Aurignacian to the 'Intermediate' Aurignacian phase ($\delta^{13}C_{Proto} = -21.3 \pm 0.3‰$, and $\delta^{13}C_{Intermediate} = -20.1 \pm 0.7‰$), followed by a small decrease in the Early Aurignacian ($\delta^{13}C_{Early} = -20.4 \pm 0.6‰$). However, even though the Kruskal-Wallis test revealed significant differences for this isotope ($\chi^2 = 24.3$, P= <0.001, $\varepsilon^2 = 0.5$), Dunn's post-hoc test showed that only the transition from the Proto-Aurignacian to the 'Intermediate' Aurignacian presents significant differences (z = 4.67, P= <0.001), with a large effect size (Cliff's δ = − 0.95; see Table 2 and Fig. 4), indicating that the 'Intermediate' Aurignacian had substantially higher values.

Conversely, $\delta^{15}N$ seemed to increase over time ($\delta^{15}N_{Proto} = 4.9 \pm 0.7‰$, $\delta^{15}N_{Intermediate} = 8.0 \pm 1.2‰$ and $\delta^{15}N_{Early} = 8.4 \pm 1.6‰$), but again, the only successive phase change that was significant was that from the Proto to the 'Intermediate' Aurignacian (Kruskal-Wallis test: ($\chi^2 = 26.32$, P= <0.001, $\varepsilon^2 = 0.54$; Dunn's test: z = 3.87, P= <0.001, Cliff's δ = − 0.96; Table 2), indicating also higher $\delta^{15}N$ for the 'Intermediate' Aurignacian. Hydrogen showed the opposite behaviour, apparently decreasing over time ($\delta^{2}H_{non\text{-}exchangeable \sim Proto} = -42.5 \pm 9.0‰$, $\delta^{2}H_{non\text{-}exchangeable \sim Intermediate} = -51.8 \pm 11.6‰$ and $\delta^{2}H_{non\text{-}exchangeable \sim Early} = 58.1 \pm 9.0‰$). In this case, the only significant difference takes place between the Proto-Aurignacian and the Early Aurignacian, with a large effect size indicating that the Proto-Aurignacian had markedly higher $\delta^{2}H_{non\text{-}exchangeable}$ values (Kruskal-Wallis test: $\chi^2 = 14.97$, P= <0.001, $\varepsilon^2 = 0.29$; Dunn's test: z = −3.86, P= <0.001, Cliff's δ = 0.79; Table 2, Fig. 4). Although $\delta^{34}S$ also appeared to decline across archaeological units ($\delta^{34}S_{Proto} = 13.3 \pm 1.4‰$, $\delta^{34}S_{Intermediate} = 12.4 \pm 1.0‰$ and $\delta^{34}S_{Early} = 12.2 \pm 1.6‰$), this difference was not statistically significant ($\chi^2 = 5.63$, P = 0.06, $\varepsilon^2 = 0.08$).

4.3. Interspecific isotope data

The results, categorised by species, are presented in Table 3. The three species *E. ferus*, *R. tarandus* and *B. primigenius/Bi. priscus* presented similar mean values for $\delta^{13}C$ (*R. tarandus* = −19.3 ± 0.3‰; *Bovines* = −20.5 ± 0.5‰; *E. ferus* = −21.0 ± 0.5‰), $\delta^{15}N$ (*R. tarandus* = 8.3 ± 0.5‰; *Bovines* = 7.4 ± 1.8‰; *E. ferus* = 6.8 ± 2.3‰) and $\delta^{34}S$ (*R. tarandus* = 11.5 ± 1.1‰; *Bovines* = 13.1 ± 1.2‰; *E. ferus* = 12.5 ± 1.5‰). Non-exchangeable hydrogen also showed similar values between species (*R. tarandus* = −52.7 ± 6.4‰; *Bovines* = −50.6 ± 14‰; *E. ferus* = −52. ± 13.9‰), although it was noticeable that the variability between samples is higher than for the rest of the isotopes analysed.

The results of the statistical analyses indicate that none of the species studied showed significant differences in any of the archaeological phases and general negligible effect sizes in terms of $\delta^{34}S$ ($\chi^2_{R.\ tarandus} = 0.33$, $P_{R.tarandus} = 0.56$, $\varepsilon^2_{R.tarandus} = 0.00$; $\chi^2_{Bovines} = 1.73$, $P_{Bovines} = 0.42$, $\varepsilon^2_{Bovines} = 0.00$; $\chi^2_{E.ferus} = 1.81$, $P_{E.ferus} = 0.56$, $\varepsilon^2_{E.}$

Table 1
Results of isotope data ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and $\delta^{2}H$non-exchangeable) by phases from bone collagen of Isturitz. Abbreviations: % Coll = mean percentage of extracted collagen; N = sample size; Min. = minimum value; Max. = maximal value; X^{-} = mean value; SD = Standard Deviation.

Aurignacian Phase	% Coll	N	$\delta^{2}H_{V\text{-}SMOW\ (non\text{-}exchangeable)}$ (‰)				$\delta^{15}N_{AIR}$ (‰)				$\delta^{13}C_{V\text{-}PDB}$ (‰)				$\delta^{34}S_{V\text{-}CDT}$ (‰)			
			Min	Max	$\overline{X}$	SD	Min	Max	$\overline{X}$	SD	Min	Max	$\overline{X}$	SD	Min	Max	$\overline{X}$	SD
All	5.8	48	−75.9	−24.2	−51.6	11.6	4.2	10.5	7.3	2.0	−21.7	−18.6	−20.6	0.8	9.9	15.5	12.6	1.4
Proto	5.1	14	−55.4	−24.2	−42.5	9.0	4.2	6.4	4.9	0.7	−21.7	−20.6	−21.3	0.3	10.3	15.5	13.3	1.4
Intermediate	6.7	15	−75.9	−31.8	−51.8	11.6	5.3	10.5	8.0	1.2	−21.1	−18.6	−20.1	0.7	10.7	13.8	12.4	1.0
Early	5.6	19	−74.9	−42.7	−58.1	9.0	4.7	10.4	8.4	1.6	−21.5	−19.4	−20.4	0.6	9.9	15.3	12.2	1.6

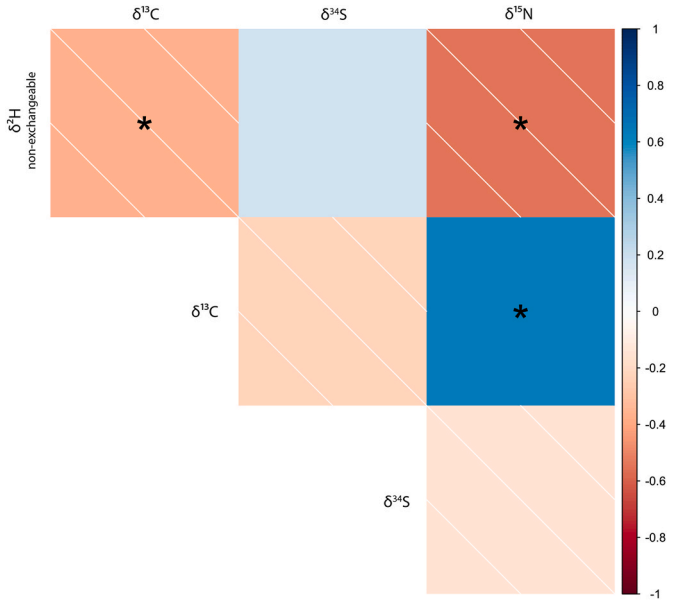

Fig. 3. Correlation matrix showing Pearson's r between the analysed stable isotope values (‰). Significant correlations ($p < 0.05$) are marked with asterisks (*).

ferus = 0.00; see Table 4). As previously reported by Berlioz et al. (2025), there were significant differences between the Proto-Aurignacian and both the 'Intermediate' and the Early Aurignacian for $\delta^{15}N$ in *B. primigenius/Bi. priscus* ($z_{Early\text{-}Proto}$ = 3.65, P= <0.001, Cliff's $\delta_{Early\text{-}Proto}$ = 1.00; $z_{Intermediate\text{-}Proto}$ = 2.62, P = 0.03, Cliff's $\delta_{Intermediate\text{-}Proto}$ = 1.00) and *E. ferus* ($z_{Early\text{-}Proto}$ = 3.17, P= < 0.01, Cliff's $\delta_{Early\text{-}Proto}$ = 0.90; $z_{Intermediate\text{-}Proto}$ = 2.45, P = 0.04, Cliff's $\delta_{Intermediate\text{-}Proto}$ = 1.00), where values appeared to increase over time (Fig. 5). Same pattern was also described for $\delta^{13}C$ levels, not only in bovines ($z_{Early\text{-}Proto}$ = 2.84, P = 0.01, Cliff's $\delta_{Early\text{-}Proto}$ = 1.00; $z_{Intermediate\text{-}Proto}$ = 3.34, P= <0.01, Cliff's $\delta_{Intermediate\text{-}Proto}$ = 1.00) and horses ($z_{Early\text{-}Proto}$ = 2.85, P = 0.01, Cliff's $\delta_{Early\text{-}Proto}$ = 0.84; $z_{Intermediate\text{-}Proto}$ = 2.64, P = 0.02, Cliff's $\delta_{Intermediate\text{-}Proto}$ = 1.00); but also, from the 'Intermediate' to the Early Aurignacian in reindeer, the only transition that could be studied for this species and therefore was only analysed by Kruskal-Wallis test (χ^2 = 5.33, P = 0.02, ε^2 = 0.72).

As for $\delta^{2}H$, we found fewer statistical differences. Only for bovids the values between the Proto-Aurignacian and the Early Aurignacian differed significantly, decreasing from the oldest to the most modern phase ($z_{Early\text{-}Proto}$ = −3.18, P = 0.004).

5. Discussion

The isotopic composition of biological tissues is, to some extent, a reflection of feeding behaviour, and hydrogen is no exception. While the degree to which $\delta^{2}H$ values originate from diet or drinking water is still debated, the most pronounced dietary effects are typically observed across trophic levels, where it is potentially valuable for differentiating between more herbivore or carnivore diets, even among omnivores (Birchall et al., 2005; Clauzel et al., 2022; Gröcke et al., 2017; Hobson et al., 1999; Newsome et al., 2020; Reynard et al., 2025). As our analysed dataset only considers herbivores, this possible trophic bias is minimised. Thus, the observed trend—from higher $\delta^{2}H$ values in the Proto-Aurignacian to lower values in the Early Aurignacian —is more likely a reflection of changes in drinking water sources. Hydrogen isotopes values in the water cycle depend on local factors such as distance to the sea, altitude and amount of precipitation, among others (Dansgaard, 1964; Dee et al., 2023; Kern et al., 2020; Pfahl and Sodemann, 2014). Hence, the change we observed from higher $\delta^{2}H$ values in the Proto-Aurignacian to lower values in the Early Aurignacian could be driven not only by climatic factors, but also by differences in the location from which the analysed species obtained their water. We analysed the $\delta^{34}S$ (Fig. 4) in order to address this duality, considered as a geographical proxy for its mainly dependence on geological composition and sea spray (Drucker et al., 2011; Guiry and Szpak, 2021). Although a slight downward trend is visible, the limited variation in sulfur over time suggests that the same landscape was exploited throughout the entire

Table 2
Kruskal-Wallis test and Dunn's post-hoc on the variability in all analysed isotopes for each archaeostratigraphic phase. The z-score correspond to the difference in the mean variability between the compared groups. ε^2 and Cliff's δ are reported as measures of effect size. When Kruskal-Wallis was not significant (p.value > 0.05), Dunn's post-hoc were not performed. Bold type indicates significant differences in mean variability between phases.

Stable isotope	Kruskal-Wallis				Dunn's post-hoc			
	χ^2	DF	p-value	ε^2	Aurignacian Phase	z-score	p-value	Cliff's δ
$\delta^{2}H_{(non\text{-}exchangeable)}$ (‰)	14.970	2	**<0.001**	0.288	Proto – Intermediate	−1.950	0.153	0.429
					Proto – Early	−3.864	**<0.001**	0.789
					Intermediate - Early	−1.842	0.196	0.375
$\delta^{15}N$ (‰)	26.326	2	**<0.001**	0.541	Proto – Intermediate	3.875	**<0.001**	−0.962
					Proto – Early	4.933	**<0.001**	−0.917
					Intermediate – Early	0.861	1.000	−0.263
$\delta^{13}C$ (‰)	24.300	2	**<0.001**	0.496	Proto – Intermediate	4.673	**<0.001**	−0.952
					Proto – Early	3.866	**<0.001**	−0.842
					Intermediate - Early	−1.085	0.834	0.263
$\delta^{34}S$ (‰)	5.633	2	0.059	0.081	-			
					-			
					-			

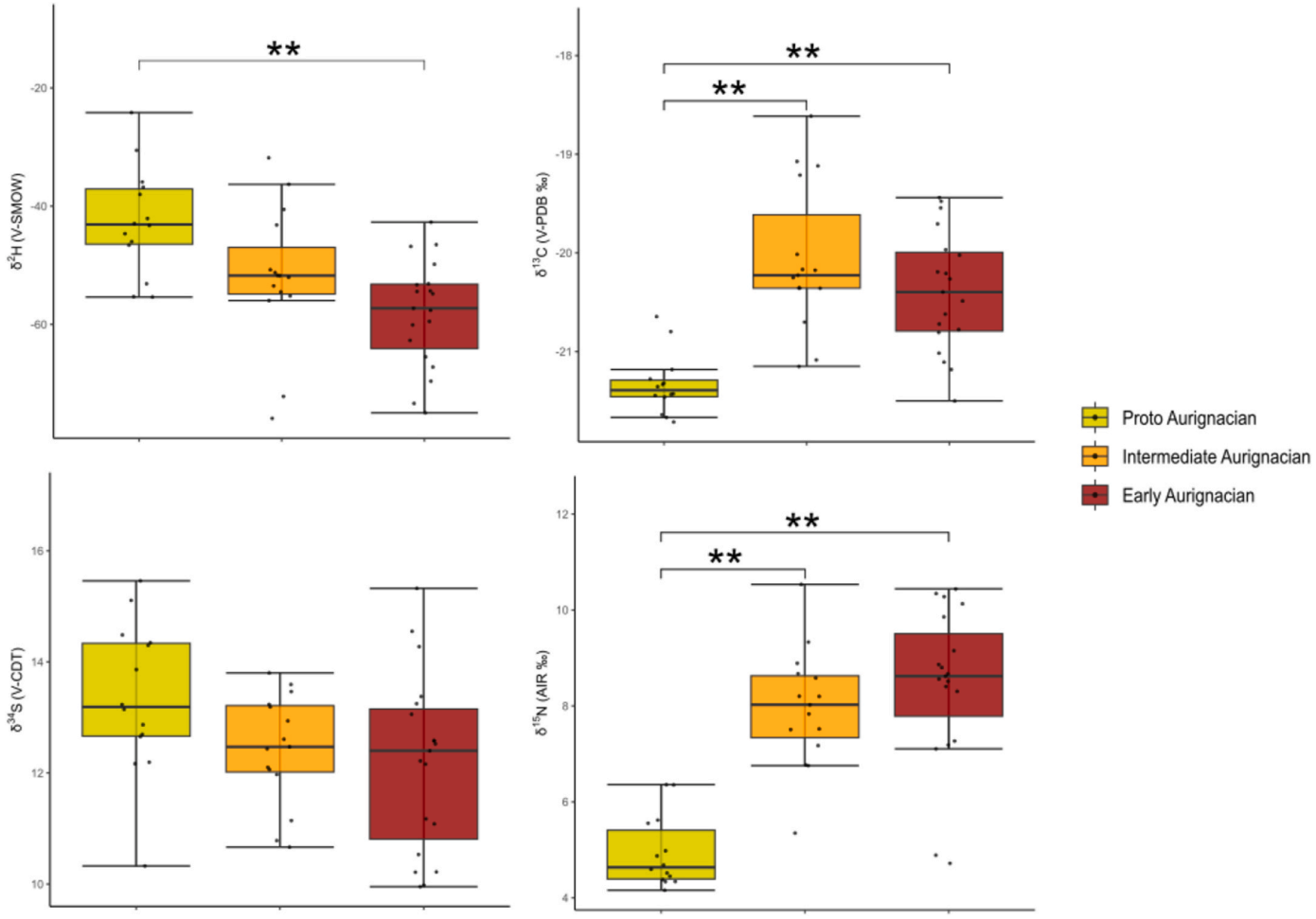

Fig. 4. $\delta^{13}C$, $\delta^{2}H$, $\delta^{34}S$ and $\delta^{15}N$ values from the bone collagen of Isturitz (mean ± SD). Significant differences ($p < 0.05$) are marked with asterisks (** refers to p-values <0.001).

sequence. This supports the interpretation that the observed hydrogen isotopes variations are a reflection of evolving local climatic conditions, such as rainfall regimes or temperature variations. Indeed, similar correlations between precipitation, temperature and collagen $\delta^{2}H$ have been reported in modern and archaeological herbivores, where increasing aridity and decreasing rainfalls were associated with higher values of $\delta^{2}H$ in precipitation and bone collagen (Cormie et al., 1994; Leyden et al., 2006; Reynard et al., 2020; Topalov et al., 2013).

Previous studies on hydrogen isotope ratios are grounded in environmental contexts that postdate the Last Glacial Maximum (LGM) and are associated with comparatively warmer and more stable climatic conditions. In contrast, the situation at Isturitz during the cultural phases examined here reflects a markedly different context. At ~40 ka BP, the site was immersed in the late Marine Isotope Stage 3 (MIS3), characterised by colder baseline temperatures, pronounced climatic instability, and rapid fluctuations between warming and cooling phases known as Dansgaard-Oeschger (D-O) oscillations (Wolff et al., 2010; Rasmussen et al., 2014). In addition, contemporaneous relative sea-level lowering displaced the coastline tens of kilometres seaward of its modern position, increasing the site's continentality and effective elevation, and thereby further shaping local environmental conditions (Siddall et al., 2008; Batchelor et al., 2019). Under such cold conditions, reduced evaporation from surface waters and enhanced equilibrium fractionation during condensation would have promoted Rayleigh distillation, leading to progressively ^{2}H-depleted precipitation (Dansgaard, 1964; Jouzel and Merlivat, 1984; Gat, 2000). Accordingly, the observed decrease in bone collagen $\delta^{2}H$ values at Isturitz is best explained by sustained cooling during the Aurignacian. However, a secondary, more tentative modulation of the isotopic signal may be occurring, related to a reduced contribution of local moisture, which could have limited secondary isotopic enrichment. This would allow precipitation and derived surface waters to more closely preserve their primary depleted signal. Although difficult to constrain with the available data, this effect is consistent with studies showing that isotopic variability in certain glacial or pre-glacial continental hydrological systems reflects the balance between precipitation input and evaporative modification, with cooler conditions reducing evapotranspiration and limiting local isotopic overprinting (Cluett and Thomas, 2020; Kjellman et al., 2024; Rozanski et al., 1993). Nevertheless, its influence is likely minor to the dominant effect of cooling.

While the progressive intensification of the aforementioned conditions accounts for the overall downward trend in $\delta^{2}H$ values throughout the Aurignacian sequence, they would not explain the absence of a clear isotopic shift between the Proto- and 'Intermediate' phases. Where such variation would be expected given the pronounced observed changes in both $\delta^{13}C$ and $\delta^{15}N$. This discrepancy is particularly notable in light of the multi-proxy palaeoclimatic reconstruction of Isturitz presented in Berlioz et al. (2025), which combines $\delta^{18}O$ and $\delta^{13}C$ from tooth enamel and $\delta^{13}C$ and $\delta^{15}N$ from bone collagen. The study documents an overall decrease in both humidity and temperature from the Proto-to the Early Aurignacian, punctuated by a phase of pronounced cooling during the 'Intermediate', for which a more marked $\delta^{2}H$ response would be expected. A possible explanation lies in the different nature of these isotopic proxies. $\delta^{13}C$ and $\delta^{15}N$ primarily reflect environmental conditions

Table 3
Results of isotope data ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and $\delta^{2}H_{non\text{-}exchangeable}$) by species from bone collagen of Isturitz. Abbreviations: % Coll = mean percentage of extracted collagen; N = sample size; Min. = minimum value; Max. = maximal value; $\bar{X}$ = mean value; SD = Standard deviation.

Species	Aurignacian Phase	% Coll	N	$\delta^{2}H_{V\text{-}SMOW}$ (non-exchangeable) (‰)				$\delta^{15}N_{AIR}$ (‰)				$\delta^{13}C_{V\text{-}PDB}$ (‰)				$\delta^{34}S_{V\text{-}CDT}$ (‰)			
				Min	Max	$\bar{X}$	SD	Min	Max	$\bar{X}$	SD	Min	Max	$\bar{X}$	SD	Min	Max	$\bar{X}$	SD
Bos / Bison *sp.*	All	6.2	22	−80.4	−20.9	−50.6	14.0	4.2	10.4	7.4	1.8	−21.6	−19.7	−20.5	0.5	11.2	15.5	13.1	1.2
	Proto	5.8	8	−55.4	−20.9	−38.3	12.7	4.2	9.4	5.8	1.6	−21.6	−19.7	−21.0	0.6	12.2	15.5	13.6	1.2
	Intermediate	6.9	7	−56.0	−43.2	−51.8	4.2	6.8	9.3	7.9	0.9	−20.4	−20.0	−20.2	0.1	12.1	13.8	12.9	0.6
	Early	6.13	7	−80.4	−53.3	−63.3	9.4	7.2	10.4	8.9	1.3	−20.6	−20.0	−20.3	0.2	11.2	15.3	12.7	1.4
Equus ferus	All	4.9	20	−75.9	−31.8	−52.1	13.9	4.3	10.5	6.8	2.3	−21.7	−20.2	−21.0	0.5	9.9	14.5	12.5	1.5
	Proto	4.4	7	−55.3	−36.8	−44.1	6.2	4.3	5.0	4.6	0.3	−21.7	−21.3	−21.5	0.2	10.3	14.3	13.0	1.4
	Intermediate	5.9	4	−75.9	−31.8	−54.0	23.2	5.3	10.5	7.7	2.2	−21.1	−20.2	−20.8	0.4	12.0	13.4	12.6	0.7
	Early	4.8	9	−74.9	−42.7	−57.4	11.9	4.7	10.3	8.0	2.1	−21.5	−20.2	−20.8	0.4	9.9	14.5	12.0	1.8
Rangifer tarandus	Both	6.4	8	−62.7	−40.5	−52.7	6.4	7.3	8.9	8.3	0.5	−19.7	−18.6	−19.3	0.3	10.2	13.2	11.5	1.1
	Intermediate	7.2	4	−54.5	−40.5	−49.4	6.1	8.0	8.7	8.4	0.3	−19.2	−18.6	−19.0	0.3	10.7	13.2	11.5	1.2
	Early	5.6	4	−62.7	−49.8	−56.0	5.4	7.3	8.9	8.2	0.7	−19.7	−19.4	−19.5	0.1	10.2	12.6	11.5	1.3

and are more sensitive to changes in vegetation structure and dietary behaviour, making them particularly responsive to rapid ecological shifts. In contrast, $\delta^{2}H$ mainly reflects the isotopic composition of surface water used for drinking, which is strongly shaped by catchment hydrology. Hydrological systems integrate water over long residence times and often include stable components such as groundwater storage, lakes, longer flow paths and snow or glacial melt, which can preserve isotopic signatures over extended periods (Ala-aho et al., 2017; López-Moreno et al., 2023; Pederzani and Britton, 2019; Voss et al., 2020). Such factors can buffer or delay the isotopic response to climatic shifts, meaning that $\delta^{2}H$ may not reflect initial environmental changes until hydrological thresholds are exceeded and the system becomes dominated by new water inputs.

Beyond hydrological buffering, environmentally driven changes in plant community composition may also contribute to the observed discrepancy among isotopic proxies. The levels of $\delta^{13}C$ and $\delta^{15}N$ in plants vary due to multiple factors, including climatic conditions and the morphology and physiology of each species. Our carbon isotopic values, published in Berlioz et al. (2025), reflect the dominance of C_3 plants in open landscapes across the sequence. Therefore, changes in canopy effects due to different plant distribution (e.g., more forested vs more open areas) are unlikely to explain the observed shifts in $\delta^{13}C$ between levels, or the lack thereof in $\delta^{2}H$. Another possibility could be the plant species consumed by the analysed herbivores. Palynological analysis of Isturitz samples showed a change in the representation of plant biodiversity from *Pinus*, *Alnus*, *Asteraceae* and *Poaceae* during the 'Intermediate' Aurignacian, to an increase in the variety of represented taxa during the Early Aurignacian, including species such as *Betula*, *Corylus* and *Quercus*, as well as the already known *Pinus*, *Alnus*, *Asteraceae* and *Poaceae* (Normand et al., 2007). No pollen analysis has been conducted specifically on the Proto-Aurignacian of Isturitz, nor during the excavations of C. Normand or A. Leroi-Gourhan (Leroi-Gourhan, 1959; Normand et al., 2007). However, the results of marine core analysis in the Bay of Biscay pointed to the general abundance of Atlantic forests and semidesert steppes in the region during this period based on the presence of pollen from *Betula*, deciduous *Quercus*, *Pinus, Alnus*, *Corylus*, *Carpinus*, *Calluna*, *Ericaceae*, *Artemisia*, *Amaranthaceae*, *Cyperaceae*, and *Poaceae* (Fourcade et al., 2022; Sánchez Goñi et al., 2008). This pattern suggests that woody species temporarily retreated under colder and likely drier conditions, expanding again either with a slight climatic improvement, even in the absence of major increases in temperature and precipitation, or due to the stabilisation of better-adapted plant communities (Zhang et al., 2023). Such vegetation dynamics would be consistent with temperature-driven shifts and moderate aridification that may not be fully captured in collagen $\delta^{2}H$ values. Highlighting that biological systems can respond more rapidly and sensitively to climatic fluctuations than the slower, more buffered hydrological processes reflected in hydrogen isotope records.

Moreover, the significant increase in both $\delta^{13}C$ and $\delta^{15}N$ values between the Proto and 'Intermediate' Aurignacian may reflect not only a shift in biodiversity driven by progressive cooling but also specific adaptations in plant carbon and nitrogen fixation under increasing of both conditions. During the early stages of moderate but sustained cold and water stress, C_3 plants can enhance carbon assimilation and water-use efficiency through stomatal regulation and biochemical adjustments (Robertson et al., 2021; Wittmer et al., 2008; Xu et al., 2015). These responses can lead to slightly higher $\delta^{13}C$ values in plant tissues, which are then transmitted to the collagen of herbivores that consume them. A similar increase in $\delta^{15}N$ may also occur, though this signal is more often linked to shifts in nitrogen sources and uptake strategies under water limitation than to direct metabolic enhancement (Amundson et al., 2003; Hartman and Danin, 2010). As the abiotic limitations intensify, species with fibrous root systems and rapid stomatal regulation are likely to gain dominance, outcompeting less stress-tolerant taxa. Such ecological turnover could stabilize isotopic values despite ongoing environmental stress, thereby explaining the absence of significant

Table 4
Kruskal-Wallis test and Dunn's post-hoc on the variability of all analysed isotopes for each species and archaeostratigraphic phase. The z-score correspond to the difference in the mean variability between the compared groups. ε^2 and Cliff's δ are reported as measures of effect size. When Kruskal-Wallis is not significant (p. value > 0.05), Dunn's post-hoc are not reported. Bold type indicates significant differences in mean variability between phases; except for *Rangifer tarandus*, for which no such analysis was carried out.

Species	Stable isotope	Kruskal-Wallis				Dunn's post-hoc			
		χ^2	DF	p-value	ε^2	Aurignacian Phase	z-score	p-value	Cliff's δ
Bos/Bison *sp.*	**$\delta^2H_{(non\text{-}exchangeable)}$ (‰)**	10.170	2	**0.006**	0.480	Early - Intermediate	−1.881	0.180	−0.762
						Early - Proto	−3.183	**0.004**	−0.905
						Intermediate - Proto	−1.355	0.526	−0.551
	$\delta^{15}N$ (‰)	14.274	2	**0.003**	0.722	Early - Intermediate	1.129	0.777	0.571
						Early - Proto	3.646	**<0.001**	1.000
						Intermediate – Proto	2.620	**0.026**	1.000
	$\delta^{13}C$ (‰)	13.142	2	**0.001**	0.655	Early - Intermediate	−0.376	1.000	−0.190
						Early – Proto	2.836	**0.014**	1.000
						Intermediate – Proto	3.343	**0.003**	1.000
	$\delta^{34}S$ (‰)	1.727	2	0.422	0.000	-			
						-			
						-			
Equus ferus	**$\delta^2H_{(non\text{-}exchangeable)}$ (‰)**	3.669	2	0.160	0.098	-			
						-			
						-			
	$\delta^{15}N$ (‰)	11.354	2	**0.003**	0.550	Early – Intermediate	0.109	1.000	0.111
						Early – Proto	3.173	**0.005**	0.905
						Intermediate – Proto	2.446	**0.043**	1.000
	$\delta^{13}C$ (‰)	10.429	2	**0.005**	0.496	Early – Intermediate	−0.359	1.000	−0.111
						Early – Proto	2.854	**0.013**	0.841
						Intermediate – Proto	2.639	**0.025**	1.000
	$\delta^{34}S$ (‰)	1.807	2	0.564	0.000	-			
						-			
						-			
Rangifer tarandus	**$\delta^2H_{(non\text{-}exchangeable)}$ (‰)**	1.333	1	0.248	0.055	-			
	$\delta^{15}N$ (‰)	0.000	1	1.000	0.000	-			
	$\delta^{13}C$ (‰)	5.333	1	**0.021**	0.722	-			
	$\delta^{34}S$ (‰)	0.333	1	0.564	0.000	-			

isotopic changes between the 'Intermediate' and the Early Aurignacian. Furthermore, such physiological responses are often species-specific. For example, *Pinus* species often show elevated $\delta^{13}C$ values under drought conditions, likely due to more conservative or controlled stomatal behaviour and a lower discrimination towards this isotope (Diefendorf et al., 2010; Martínez-Sancho et al., 2018). This physiological adaptation places *Pinus* among early-successional species during the initial stages of ecosystem recovery following disturbance. Therefore, its persistence not only throughout the entire Aurignacian period, but especially after the first stages of climate change during the 'Intermediate' Aurignacian, is not surprising (Beloiu Schwenke et al., 2024). The same applies to the genus *Alnus*, whose species are symbiotically associated with the actinobacterium *Frankia* and are typical nitrogen-fixing, non-leguminous trees. In general, both soil and plant $\delta^{15}N$ values increase systematically along drought intensification, but this would be even more noticeable across time in species like this, which under stress conditions change the main assimilation of nitrogen from their actinorhizal symbiosis to nitrogen from soil (Hartman and Danin, 2010; Kohls et al., 2003). Taken together, such physiological and ecological dynamics would be expected to influence the isotopic composition of herbivore bone collagen. Individuals with narrow dietary breadth may show stronger reflection of these plant-level adaptations, especially where plants like *Pinus* and *Alnus*, were prevalent during the 'Intermediate' Aurignacian, whereas animals with access to a more diverse plant community would exhibit more variable isotopic signatures. Beyond these species-specific examples, the broader implication is that plant physiology and animal dietary behaviour must be considered when interpreting isotopic data. The absence of a parallel shift in δ^2H supports a scenario in which ecological and physiological responses were decoupled from major hydrological changes, highlighting the differing sensitivities of isotopic proxies. Although hydrogen isotopes may partly reflect temperature-related processes affecting the isotopic composition of precipitation, their signal is primarily governed by integrated hydrological dynamics. As a result, δ^2H values may not respond in phase with the more rapid ecological and physiological adjustments captured by $\delta^{13}C$ and $\delta^{15}N$. Overall, this multi-isotopic approach underscores the complexity of ecosystem responses and the need for caution when interpreting climatic signals from proxies that integrate both environmental and biological processes.

Likewise, when interpreting isotopic data from bone collagen, it is essential to account for interspecific differences in feeding strategies and water use, as these directly influence the isotopic signals preserved in tissues. Based on these carbon and nitrogen isotope results, Berlioz et al. (2025) previously interpreted that horses, bovids, and reindeer generally exhibited grazing behaviour, consistent with dental microwear analyses. However, individual-level variability was also observed, indicative of opportunistic or flexible feeding strategies that may be associated with the utilisation of resources typically found in woodland habitats. This variation is particularly evident in carbon isotopes. Reindeer, for example, tend to exhibit elevated $\delta^{13}C$ values compared to other herbivores due to lichen consumption, which is also linked to seasonal grazing and aridification conditions at the intraspecific level (Takken Beijersbergen et al., 2021). Although our dataset for reindeer is limited, both in sample size and temporal representation, the fact that we not only observed such interspecific elevated values but also a significant change in the transition from the 'Intermediate' to the Early Aurignacian only for this isotope, would again suggest and highlight how this isotope is more reflective of the environmental exploitation performed by these animals. By the same token, under cooling conditions, when preferred forage became scarce, Bisons can also incorporate lichens and mosses into their diet as fallback resources (Hecker et al., 2021; Julien et al., 2012; Jung, 2015). This strategy would also have a significant impact on carbon isotope values and may help explain the pronounced increase in $\delta^{13}C$ observed in the species between the Proto- and 'Intermediate' Aurignacian, a pattern not equally mirrored in equids. Besides diet alone, species-specific behaviours -such as feeding

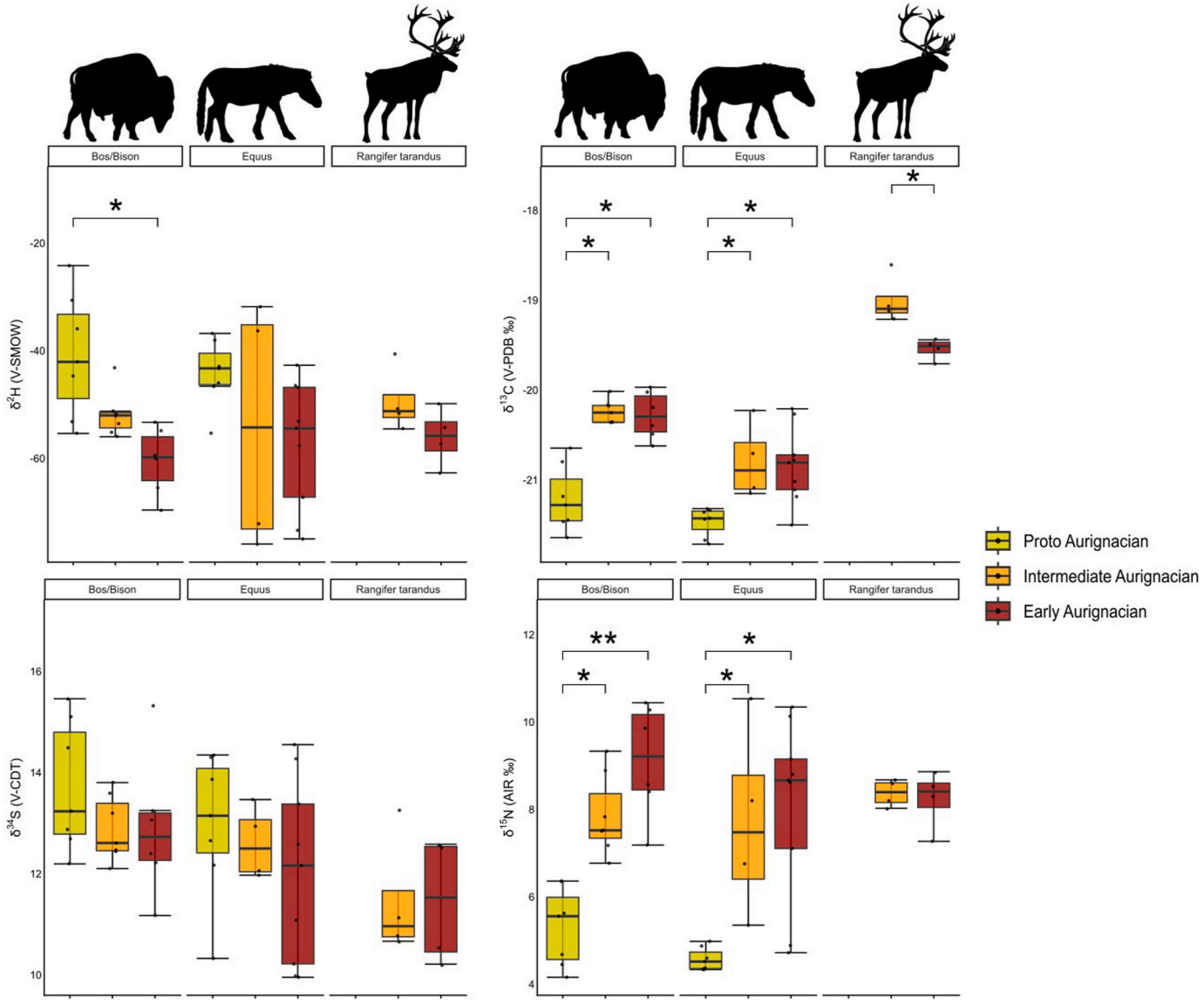

Fig. 5. $\delta^{13}C$, $\delta^{2}H$, $\delta^{34}S$ and $\delta^{15}N$ values from the bone collagen of Isturitz (mean ± SD) by species. Significant differences ($p < 0.05$) are marked with asterisks (* refers to p-values <0.05, while ** indicates values < 0.001).

selectivity, plant part preference, seasonal mobility, and even sex-related differences-can influence both $\delta^{13}C$ and $\delta^{15}N$ values (Berini and Badgley, 2017; Britton et al., 2023; Metcalfe, 2021). These behavioural and physiological variables likely contribute to the significant shifts in carbon and nitrogen isotopes we observed between the Proto- and the 'Intermediate' Aurignacian for bovids and horses. The consistency of the patterns across species suggests that niche partitioning or specialization is unlikely to explain the observed isotopic variability.

Given this, it is also reasonable to consider that $\delta^{2}H$ values could be influenced by species-specific behaviour in water acquisition and metabolism. Indeed, in our dataset, a significant shift in $\delta^{2}H$ was recorded only for *Bos/Bison*. Among the species analysed, the absence of change in reindeer would be expected, as they possess highly efficient water conservation strategies -including moisture extraction from vegetation and snow, and reduce respiratory water loss-which enable them to survive and thrive in cold environments (Dryden, 2011; Nilssen et al., 1990). This ethological behaviour could mask the signal of precipitation-derived hydrogen isotopes in tissues. Conversely, if climatic conditions were not sufficiently extreme to enforce a strong reliance on vegetation-derived water, and instead allowed reindeer to increase their intake of free water, an opposing isotopic signal might also be expected. Additional mechanisms supporting reindeer survival in cold climates are closely tied to their thermoregulatory strategies -such as excellent insulation, selective brain cooling, and behavioural mechanisms that limit overheating and reduce evaporative water loss (Blix, 2016; Nilssen et al., 1994). These adaptations may minimise internal hydrogen isotopic fractionation during physiological processing. Under such conditions, reindeer collagen could therefore provide a relatively unmodified reflection of climatic $\delta^{2}H$ from their drinking sources. Given these factors, we cannot confidently evaluate either scenario at Isturitz, as the absence of Proto-Aurignacian individuals limits our ability to compare changes across the full sequence. It remains possible that the lack of isotopic differences between 'Intermediate' and Early Aurignacian reindeer reflects consistently similar water sources over the studied period—for example, a continued reliance on snowmelt or other isotopically stable reservoirs. If so, little isotopic change would be expected during this phase-shift, in contrast to what may be observed across the whole sequence, as is the case in bovids. Nonetheless, it is worth noting that the visual pattern of $\delta^{2}H$ decline in reindeer broadly resembles that observed in bovids, suggesting that both taxa may have experienced

similar overarching hydrological conditions.

Horses and bovids, by contrast, are more dependent on regular access to free water. Yet only bovids exhibited a clear δ^2H shift through the Aurignacian sequence. This discrepancy may be related not only to behavioural distinctions, but also to differences in physiology and water flux. Horses exhibit relatively high daily water requirements due to factors such as their monogastric system, which extracts less water from ingesta, making them more prone to migrate or move across their habitat to reach reliable water sources (Cao et al., 2023 and references there in; Vasantha et al., 2025). Based on this, horses might be expected to serve as good indicators of climatic δ^2H. However, contrary to this initial expectation, our results do not show such a straightforward pattern. This discrepancy may be related to the fact that horses rely heavily on sweating for thermoregulation, which increases evaporative loss and may influence the fractionation of body water isotopes in these animals, interfering on the climatic signal of δ^2H in collagen (Arnold et al., 2006; Scheibe et al., 1998). Nevertheless, while δ^2H values reported for Proto- and Early Aurignacian equids are broadly comparable, marked variability emerges during the 'Intermediate' Aurignacian. Among the four horses analysed from this cultural phase, two display higher values comparable to those presented in the preceding and subsequent phases, whereas the remaining two exhibit substantially lower values. This divergence may indicate intraspecific variability in resource-use strategies at the time. In particular, individuals with lower values may have responded to the changing conditions by relaying on alternative water sources, such as snowmelt, as a primary component of their drinking water. Notably, the other stable-isotope proxies analysed do not show corresponding differences, suggesting that this pattern does not reflect a clear separation of ecological niches, but rather a diversification in the exploitation of available water resources.

Bovids, on the other hand, retain water more efficiently, and their larger body sizes results in higher body water volume and greater water turnover, likely contributing to a more faithful integration of drinking water isotopic signals on their tissues (Magozzi et al., 2019). In modern bison from eastern Kansas (USA), Nippert et al. (2013) successfully traced drinking water sources using faecal water by analysing δ^{18}O and δ^2H, showing that isotopic fractionation of water isotopic fractionation varies only minimally during its passage through the body and associated physiological processes. Building on previous species-specific results regarding bone collagen hydrogen isotopes (Reynard et al., 2020), these findings suggest that bovids may serve as more reliable indicators of local hydrological conditions, while species such as horses and reindeer require more cautious interpretation. Furthermore, Nippert et al. (2013) observed that bison relied primarily on ephemeral water bodies formed by recent rainfall for most of the year, with increased reliance on stream water during seasonal transitions and the coldest winter periods. If a similar preference for stream water during cooling events was previously observed, our results may reflect the isotopic signature of more persistent water sources rather than that of short-lived ponds or ephemeral waters. Such a pattern would be consistent with a progressive reorganization of local hydrological catchment and associated ecosystem, where hydrogen isotopes integrate environmental information over longer temporal and spatial scales, recording broader climatological trends rather than short-term ecological adjustments.

Overall, our results reveal clear shifts in hydrogen isotopic values in bone collagen over a 3000-year period, thereby indicating the climatic changes that modern humans faced during their occupation of the Aurignacian at Isturitz. This finding highlights the potential of δ^2H in bone collagen as a proxy for reconstructing general local palaeoclimatic conditions, and attests to its usefulness in Palaeolithic contexts, particularly when applied to ungulates with evidence of human manipulation, such as butchering marks. While traditional isotopes such as δ^{13}C and δ^{15}N remain valuable indicators of environmental change, their values can respond relatively quickly to shifts in diet or vegetation their interpretation is often complicated by dietary and ecological variables. In contrast, δ^2H appears to primarily records hydrological conditions and reflects longer-term or larger-scale environmental changes, providing a signal that is less sensitive to short-term biological variability. The integration of δ^2H with established isotopic systems provides a more nuanced understanding of past climate-environment-faunal interactions. Importantly, the faunal remains analysed here derive from archaeological human occupation levels, which introduces an inherent selection bias related to past hunting strategies and site-occupation patterns. While this limits the representativeness of local faunal communities, it also provides a valuable lens for exploring how prehistoric humans interacted with and responded to changing environments. The integration of δ^2H with established isotopic systems thus not only refines palaeoclimatic reconstructions but also offers new opportunities to investigate the ecological context of human behaviour. Future studies incorporating broader taxonomic samples and higher temporal resolution will be essential to validate δ^2H as a robust palaeoclimatic proxy, reveal its isoscapes, and further unravel the complex interplay between climate, ecosystems, and human adaptation.

6. Conclusions

Reconstructing palaeoclimatic conditions remains a methodological challenge, often constrained by the nature of available materials and proxies. This study provides one of the first assessments of δ^2H in bone collagen from Palaeolithic faunal remains as a proxy for local climatic conditions during human occupation of the area. Our results reveal significant variation in δ^2H values across the Aurignacian at Isturitz, broadly consistent with predicted regional climatic trends, but contrast with previously proposed local climate scenarios that suggest more abrupt environmental shifts from the Proto to the Intermediate Aurignacian. This pattern suggests a progressive reorganization of the local hydrological system, broadly consistent with reconstructions based on other isotopic and palaeoenvironmental indicators, which may reflect early ecological or biological responses to changing conditions. The absence of significant shifts in δ^{34}S supports the inference that animals have long inhabited the area used as human hunting grounds, strengthening the interpretation that δ^2H changes reflect evolving local climate rather than geographic shifts in resource exploitation.

Species-specific responses highlight the influence of physiological and behavioural factors on isotope incorporation, particularly in relation to water intake and dietary preferences. Notably, δ^2H shifts were recorded only in bovids, supporting their utility as reliable indicators of climate. By contrast, more complex isotopic responses in δ^{13}C and δ^{15}N appear to be driven by changes in plant physiology under drought stress and by the dietary ecology of different herbivores.

As these faunal samples come from anthropogenic levels within an archaeological site, they inevitably reflect human hunting choices and seasonal occupation patterns. While this introduces potential biases in species representation, it also offers valuable insights into how Upper Palaeolithic first anatomically modern humans adapted to changing climatic and ecological local conditions. Integrating δ^2H with other isotopic and climatic proxies in archaeological contexts offers promising avenues for exploring past climates and human-environment interactions with increasing nuance.

Data availability

Supplementary 1 (S1): Raw sample information for bone collagen samples and Hydrogen, Nitrogen, Carbon and Sulfur results with quality indicators.

Supplementary 2 (S2): R code used for data processing and statistical analyses.

CRediT authorship contribution statement

M. Ibáñez-Herranz: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **L.**

Agudo-Pérez: Methodology, Project administration, Visualization, Writing – review & editing. **M. Fernández-García:** Investigation, Methodology, Writing – review & editing. **A. Cicero-Cabañas:** Methodology, Writing – review & editing. **M.C. Soulier:** Methodology, Writing – review & editing. **C. Normand Orieux:** Resources, Writing – review & editing. **A.B. Marín-Arroyo:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Ana B. Marín-Arroyo reports financial support was provided by Spanish Ministry of Science, Innovation and Universities. Miriam Ibáñez-Herranz reports financial support was provided by Spanish Ministry of Science, Innovation and Universities. Ana B. Marín-Arroyo reports financial support was provided by European Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2026.106644.

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