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Barakat, S., Jimenez, E.-L., Heikkila, R. K., Royer, A., Hodgkins, J., Niven, L., Soulier, M.-C., Lagle, S., Dancette, C., Steele, T. E., Castel, J.-C., McPherron, S., Hublin, J.-J., Ruebens, K. ORCID: https://orcid.org/0000-0002-5621-5786, Discamps, E. and Britton, K. (2026) Sulfur isotopes evidence spatial ecology of Late Pleistocene ungulates in southwestern France. Quaternary Science Reviews, 374. 109744. ISSN 0277-3791 doi: 10.1016/j.quascirev.2025.109744 Available at https://centaur.reading.ac.uk/127835/

To link to this article DOI: http://dx.doi.org/10.1016/j.quascirev.2025.109744

Publisher: Elsevier

Quaternary Science Reviews 374 (2026) 109744

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Sulfur isotopes evidence spatial ecology of Late Pleistocene ungulates in southwestern France

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ARTICLE INFO

Handling Editor: Donatella Magri

Keywords:
Multi-isotope analysis
ZooMS
Palaeoecology
Biogeography
Neanderthal
Home range
Western Europe

ABSTRACT

Understanding prey species spatial behaviour is key to unravelling contemporary hunter-gatherer subsistence and movement patterns. Here, we use sulfur (δ^{34}S), carbon (δ ^{13}C) and nitrogen (δ ^{15}N) isotope compositions of bone collagen extracted from *Rangifer, Equus,* Bovinae, *Capreolus,* and *Cervus* ($n = 244$) to explore isotope spatial and dietary niches of several key hunter-gatherer prey species from three Late Pleistocene sites in southwestern France between MIS 5 and MIS 3. Alongside morphological identification, Zooarchaeology by Mass Spectrometry (ZooMS) was used to confirm deer taxa ($n = 125$) allowing for a better interpretation of the isotopic data. δ^{34}S analysis identifies differences in ranging sizes between ungulates with known large ranging sizes from those with small to medium size ranges. *Rangifer*, who, today, have large home ranges, have the largest range of δ^{34}S values and lowest δ^{34}S values with low to no overlap with other ungulate species through time. This indicates that *Rangifer* had a larger range size with a distinct isotopic area that is different to other ungulates, potentially farther inland and farther north. Bovines and *Equus* have largely overlapping δ^{34}S values that are similar to the modern local δ^{34}S value of the sites, and *Cervus* and *Capreolus* have δ^{34}S values that overlap but are slightly higher than the modern δ^{34}S values, potentially indicating a ranging area to the west of the sites. These results reveal that Neanderthals hunted three different groups of game who occupied different areas of the landscape.

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https://doi.org/10.1016/j.quascirev.2025.109744
Received 23 May 2025; Received in revised form 2 December 2025; Accepted 3 December 2025

1. Introduction

Pleistocene faunal remains are often the most abundant organic remains at archaeological and palaeontological sites and can provide a wealth of information on human-animal-environmental interactions in the past. These remains are often the focus of geochemical studies which aim to reconstruct human behavioural patterns based on animal resources, put archaeological layers in biochronological frameworks, and study past climates in the broadest sense (Craig et al., 2010; Drucker et al., 2003a, 2018a; Drucker and Bocherens, 2004; Drucker and Fontana, 2024; Hedges et al., 2004; Jones et al., 2021; Jones and Britton, 2019; Reade et al., 2020a, 2020b; Stevens et al., 2014; Stevens and Hedges, 2004). Isotope zooarchaeology has become increasingly useful in Pleistocene studies to provide a baseline for human dietary reconstruction (Bocherens and Drucker, 2021; Craig et al., 2010; Kuzmin et al., 2021), modelling dietary niches of extinct and extant species in ancient ecosystems using carbon and nitrogen isotope compositions (δ^{13}C and δ^{15}N) (Baumann et al., 2020; Britton et al., 2012; Richards et al., 2008), reconstruct local palaeoclimatic conditions using oxygen isotope compositions (Bernard et al., 2009; Britton et al., 2019; Fernández-García et al., 2022; Pederzani et al., 2021a, 2021b; Pryor et al., 2013; Royer et al., 2013; Tütken et al., 2007) as well as to explore past migratory behaviours of both humans and animals using strontium isotope analysis (^{87}Sr/^{86}Sr) (Barakat et al., 2023; Britton et al., 2011; Copeland et al., 2016; Hodgkins et al., 2024; Kowalik et al., 2020; Linscott et al., 2023; Richards et al., 2021; Sillen et al., 1995, 1998; Wooller et al., 2021), with recent approaches becoming increasingly focused on multi-isotopic analysis which allows us to understand various environmental and biological factors affecting past faunal behaviours (Britton et al., 2023a, 2023b; Heddell-Stevens et al., 2024; Jones et al., 2019).

In recent years, applications of sulfur isotope analyses (δ^{34}S) have increased in archaeological and palaeontological studies (Lamb et al., 2023; Madgwick et al., 2019a, 2019b; Nehlich, 2015; Nehlich et al., 2010; Nehlich and Richards, 2009; Rand and Nehlich, 2018; Reade et al., 2020a, 2020b; Richards, 2023; Stevens et al., 2021, 2023), facilitated in part by advances in mass spectrometry that allow analyses of several isotope elements with smaller sample sizes (1.2–1.5 mg) (Sayle et al., 2019). While useful in dietary reconstruction (Czere et al., 2021; Lamb et al., 2012; Nehlich et al., 2010, 2011, 2014; Oelze et al., 2012; Privat et al., 2007; Richards et al., 2001, 2003), and likely impacted by local climatic conditions, such as the extent of permafrost (Kemeny et al., 2023; Reade et al., 2020b; Stevens et al., 2023), sulfur isotopes vary across landscapes with underlying lithology and coastal proximity, making them especially useful in reconstructing past movement patterns (Bataille et al., 2021; Britton et al., 2023b; González-Rabanal et al., 2025; Linderholm et al., 2014; Nehlich et al., 2014; Richards, 2023; Richards et al., 2001).

Here, we present a large new sulfur isotope dataset ($n = 244$) from five different ungulate species identified via morphology and Zooarchaeology by Mass Spectrometry (ZooMS) across three Late Pleistocene archaeological sites in southwestern France (Roc de Marsal, Pech de l'Azé IV and Combe Grenal), and from archaeological layers covering the MIS 5 to 3 period. The aim of this work is to evaluate variations in δ^{34}S values between taxonomic groups (*Equus ferus* (horse), *Bos primigenius/Bison* sp. (bovines), *Rangifer tarandus* (reindeer), *Cervus elaphus* (red deer), *Capreolus capreolus* (roe deer)), in order to reconstruct the ecological behaviour of ungulate communities and to explore potential ecological variations throughout time during a period with large climatic variations. In the current study, δ^{34}S data are generated alongside, and compared to, δ^{13}C and δ^{15}N data as a means of further exploring relationships between landscape use and dietary niche.

2. Reconstructing faunal spatial and dietary palaeoecology through the carbon, nitrogen and sulfur analysis of bone collagen

Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope compositions from bone collagen have been used to reconstruct the feeding behaviours and dietary niches of both domestic and wild fauna for decades (Codron et al., 2016; Feranec, 2007; Hofman-Kamińska et al., 2018; Kristensen et al., 2011; Lee-Thorp et al., 1989, 2003; Schwarcz and Schoeninger, 2012; Schwartz-Narbonne et al., 2019; Stewart et al., 2003; Van Der Merwe, 1982; Vogel, 1978; Vogel and Van Der Merwe, 1977). Although most useful in differentiating between the use of marine and terrestrial resources (Schoeninger and DeNiro, 1984; Schwarcz and Schoeninger, 2012; Walker and Deniro, 1986); between C_3 and C_4 plant foods (Ambrose, 1986; Cerling and Harris, 1999; DeNiro, 1987; Jaramillo et al., 2022; Norman et al., 2009; Tipple and Pagani, 2007; Van Der Merwe, 1982; Vogel and Van Der Merwe, 1977); and identifying trophic level relationships (Ambrose, 1991; Bocherens and Drucker, 2003; Deniro and Epstein, 1981; Schoeller, 1999; Schoeninger and DeNiro, 1984), these approaches can also be useful in identifying dietary habits and niche feeding behaviours even amongst terrestrial herbivores (Britton et al., 2012, 2023b; Codron et al., 2016; Reiss et al., 2023; Tieszen, 1991). As bone collagen remodels during an individual's life, isotopic information from bone collagen provides an average of inputs that reflect dietary habits in the years prior to death (Britton, 2020; Goude and Fontugne, 2016; Richards, 2020; Schwarcz and Schoeninger, 2012). While sulfur isotope data (δ^{34}S) is also obtained from bone collagen, until recent years, applications have been severely limited due to analytical issues and needing large sample sizes. Recent mass spectrometry advancements allow for sequential measurements of δ^{13}C, δ^{15}N, δ^{34}S in a single sample, facilitating simultaneous analysis of dietary, ecological, and spatial studies, thus increasing the number of studies using δ^{34}S isotopic analysis (Nehlich, 2015; Richards, 2023; Sayle et al., 2019).

2.1. Carbon (δ^{13}C) and nitrogen (δ^{15}N)

Carbon isotope ratios between ^{13}C to ^{12}C (δ^{13}C, as compared to the international standard V-PDB) in herbivore bone collagen primarily reflect their diet and the types of plants consumed. For example, bone collagen δ^{13}C values can differentiate between grazers and browsers in mixed C_3-C_4 ecosystems (Codron et al., 2016; Tieszen, 1991; Vogel, 1978), where differences in photosynthetic pathways influence the values of these plants (Bender, 1968; Cerling, 1999; Cerling and Harris, 1999; DeNiro, 1987; Heaton, 1999; Kellogg, 1999; Tipple and Pagani, 2007; Van Der Merwe, 1982). In purely C_3- or in C_3- dominated ecosystems, as found in Pleistocene Northwest Europe, variations in collagen δ^{13}C values can reveal dietary habit and niche specialisation (Britton et al., 2023b), or reveal climatic conditions (Domingo et al., 2015; Drucker and Fontana, 2024).

Typical ungulates eating a primarily C_3, terrestrial, vascular plant-based diet should have δ^{13}C values around −26 ‰ (DeNiro, 1987; Van Der Merwe, 1982). If marine plants, such as seaweeds, are added to the diet, the δ^{13}C values will be more enriched (Blanz et al., 2019; Richards, 2020; Schoeninger and DeNiro, 1984; Schwarcz and Schoeninger, 1991). Another factor which can affect plant δ^{13}C, and thus bone collagen δ^{13}C, is densely covered forests, known as the canopy effect which causes depleted δ^{13}C values between −35 ‰ and −30 ‰ (Bonafini et al., 2013; Drucker et al., 2008; Van Der Merwe and Medina, 1991). Thus, if an animal is primarily foraging in woodlands, their δ^{13}C values should be depleted and archaeologists can infer both the presence of a more wooded landscape and faunal use of it. In comparison, if there are no signs of highly depleted δ^{13}C values, this could indicate a more open landscape, although these interpretations should be tested using other environmental proxies, such as pollen, charcoal, or small mammals. Finally, certain non-vascular plants such as mosses and lichen, typically have more enriched δ^{13}C values compared to vascular C_3 plants (Park and Epstein, 1960). Archaeological and palaeontological studies on reindeer, one of the only species which can consistently consume lichen, typically show δ^{13}C values ranging between −18 ‰ and −21 ‰ (Bocherens, 2003; Brenning et al., 2024; Britton et al., 2023a, 2023b; Drucker et al., 2001, 2011b; Fizet et al., 1995; Fjellström et al., 2023; Park and Epstein, 1960; Salmi et al., 2020, 2022).

In addition to dietary inputs, other factors can influence tissue δ^{13}C values in ungulates, even those consuming an isotopically homogenous diet. For example, due to the presence of symbiotic bacteria which produce methane, which has very negative δ^{13}C values, foregut feeders and ruminants, such as Bovinae and deer species, are expected to have slightly elevated δ^{13}C values in comparison to non-ruminants, such as horses.

The ratio of ^{15}N–^{14}N (δ ^{15}N, in comparison to the international standard, AIR) in bone collagen has primarily been used to study food webs and trophic positions, as δ^{15}N increase by 3–5 ‰ with each trophic level shift (Ambrose and DeNiro, 1989; Bocherens and Drucker, 2003; Britton et al., 2012; Cerling and Harris, 1999; Clementz et al., 2009; Codron et al., 2018; Deniro and Epstein, 1981; Hedges, 2003; Palmqvist et al., 2008, 2003; Richards and Hedges, 2003; Schoeninger and DeNiro, 1984; Schulze et al., 1998; Thorp and Van Der Merwe, 1987). This normally means that, in comparison to omnivores or carnivores, herbivores should have low and very similar δ ^{15}N values to one another. However, in practice, baseline enrichment in soils due to local environmental conditions, or even due to deliberate modifications of soils (and thus to crops grown on them) through fertilising, for example, can serve to alter soil and plant values (Ambrose, 1986, 1991; Szpak, 2014), and potentially also affect herbivore δ ^{15}N values. Climatic conditions impact the productivity of nitrogen cycle in soil, with colder and wetter climates typically having less productive soil habitats, which leads to lower δ ^{15}N values available in plants and herbivore bone collagen (Ambrose, 1991; Craine et al., 2015; Drucker et al., 2011a; Hedges et al., 2004; Reade et al., 2023; Schwarcz et al., 1999; Stevens et al., 2008; Stevens and Hedges, 2004; Szpak, 2014; Van Klinken et al., 2002).

Herbivore feeding preferences can also affect δ^{15}N values. For example, certain plant species, such as N_2-fixing plants (e.g. legumes and certain lichens) who receive ^{15}N from the atmosphere will have distinct (lower) δ^{15}N values than non- N_2-fixing plants who absorb ^{15}N from the soil within the same area (Ambrose, 1991; Drucker et al., 2001; Shearer et al., 1983; Virginia and Delwiche, 1982; Yoneyama et al., 1986). Consequently, animals who consume N_2-fixing plants could have lower bone collagen δ^{15}N values (Palmqvist et al., 2008). Consumption of non-vascular plants can also affect nitrogen values of herbivore bone collagen. For example, lichens and mosses, which make up a large portion of reindeer winter diets (Drucker et al., 2010; Heggberget et al., 2002; Hiltunen et al., 2022; Russell et al., 1993; Webber et al., 2022), are poor in protein and typically have lower δ^{15}N values (Brenning et al., 2024; Drucker et al., 2001; Mcleman, 2006; Rioux et al., 2022). Comparatively, mushrooms and other fungi, which reindeer may eat in summers and autumns, are rich in nitrogen (Brenning et al., 2024; Drucker et al., 2010; Rioux et al., 2022).

Finally, metabolic changes and interspecies physiology can also affect herbivore δ^{15}N bone collagen (Sponheimer et al., 2003). For example, pregnancy, lactation, weaning, and malnutrition can all influence δ^{15}N values (Fuller et al., 2004, 2005, 2006; Gutierrez et al., 2024). Ruminants also will potentially have more elevated δ^{15}N values than non-ruminants (Coltrain et al., 2004; Sealy et al., 1987; van Klinken et al., 2002), however this is not seen at all Late Pleistocene sites (Britton et al., 2012) and a modern controlled-feeding study did not show a significant difference between ruminants and non-ruminants (Sponheimer et al., 2003).

2.2. Sulfur (δ ^{34}S)

Sulfur has four naturally occurring isotopes with the following abundances: ^{32}S (95.02 %), ^{33}S (0.75 %), ^{34}S (4.21 %), and ^{36}S (0.02 %) (Faure, 1986; Nehlich, 2015). The most popular ratio for analysis is between ^{32}S and ^{34}S due to their natural high abundances, and this ratio is reported as a δ^{34}S value in per mil (‰) against the international standard: Vienna Canyon Diablo Troilite (V-CDT) (Nehlich, 2015). The most common values found for δ^{34}S across terrestrial landscapes are between −20 and +20 ‰, whereas present-day oceans have a δ^{34}S value near +20.3 ‰ (Ault and Kulp, 1959; Krouse, 1980; Nehlich, 2015; Rees et al., 1978). Geological sulfur composition in aerobic soil environments is dominated largely by weathering bedrock so that lithologies made of sulfur-rich rocks (such as evaporites) have higher δ^{34}S compositions than areas with sulfur-poor rocks (i.e., sedimentary and igneous rocks) (Thode, 1991). During weathering, sulfur is released from the underlying bedrock and absorbed by nearby soils; plant roots can then absorb δ^{34}S directly from the soil. Typically, δ^{34}S values in plants largely reflect the soil δ^{34}S, although in cases where the bedrock has very low concentrations of sulfur, plants can absorb and reflect δ^{34}S from groundwater, atmospheric deposition (SO^2 and SO_4^{2-}) and aerosols, such as marine sea spray, volcanic sulfur compounds, biogenic emissions, and dry deposition, with atmospheric sulfur contributing <10 % of soil sulfur (Newman et al., 1991; Nielsen, 1974; Stevens et al., 2023; Tcherkez and Tea, 2013; Thode, 1991; Trust and Fry, 1992).

Marine sea spray can influence soil and plant δ^{34}S values via the ‘sea spray effect,’ which transfers high δ^{34}S values from marine ecosystems to otherwise terrestrial environments (Göhring et al., 2015; Nielsen, 1974; Richards et al., 2001). In areas within 30 km of the coastline, the sea spray effect can make up large portions of plant δ^{34}S content, although in certain environments, marine aerosols can travel up to 100 km or even more due to wind patterns and landscape (Szpak et al., 2019; Zazzo et al., 2011). This influence decreases at distances farther from the coast, and it can be assumed that areas greater than 150 km (or less depending on topography and wind patterns) from the coastline have little to no sea spray influence (Bataille et al., 2021; Nehlich, 2015; Tarrant and Richards, 2024).

In comparison to marine ecosystems, freshwater resources like rivers can have very large ranges of δ^{34}S values, which can be influenced via lithologies which the river runs through, rainwater, and the source of water sulfates (Nehlich, 2015; Robinson and Bottrell, 1997). Plants in riverine environments can be thus influenced by river water δ^{34}S values via plant absorption of river water; river flooding in floodplains and basins can also influence plants in these wider areas (Fry, 2002). The inhibition of bacteria in anoxic conditions, for example, due to waterlogging or permafrost, can lead to the development of sulfides, which have extensive fractionation and can cause very low values in local soils or plants which can affect δ^{34}S in mammals using resources from these environments (Guiry et al., 2022; Reade et al., 2020a, 2020b; Stevens et al., 2022; Thode, 1991). How plants uptake sulfur from the surrounding environment is still being investigated, but it is becoming clear that a range of factors beyond local lithology can affect sulfur values in plants including hydrology of the landscape (such as proximity to the coast or rivers) or local climatic conditions (such as the presence of permafrost (Cheung et al., 2021; Fry, 2002; Reade et al., 2020a, 2020b; Stevens et al., 2022; Tarrant and Richards, 2024). Furthermore, in contemporary environments, anthropogenic sources of sulfur through agricultural fertilisation, emissions from gas plants and mining may influence local soils and thus plants (Hinckley et al., 2020; Krouse et al., 1996; Krouse and Mayer, 2000; Rogers et al., 2017; Strauch et al., 2001; Winner et al., 1978); and isotopic analysis of sulfur in lichen (often focusing on arboreal types) is frequently used to identify anthropogenic pollution (Niepsch et al., 2023; Yun et al., 2010).

Mammalian bodies require sulfur to create crucial protein-building amino acids cysteine and methionine, which help the body metabolise food and protect cells from diseases; however, mammals cannot produce their own sulfur and are therefore reliant on dietary input (Nehlich, 2015; Nimni et al., 2007). Based on minimal sulfur fractionation rates in tissue uptake (less than 2.5 ‰ (Richards, 2023; Nehlich, 2015)), and mammals requiring sulfur from their diet, theoretically sulfur isotopes should be particularly useful in recreating diet and tracking provenance in both herbivores and terrestrial omnivores, as their bone collagen should reflect an average value of the localities they were sourcing their food (Nehlich, 2015; Richards, 2023; Richards et al., 2003; Stevens et al., 2023; Tcherkez and Tea, 2013). However, given the multiple potential ecosystem inputs of sulfur at any one location, and the equifinality that can be further introduced through different dietary sources (e.g., marine fish), the interpretation of sulfur isotope data remain complex (Richards, 2023).

Despite its complexities, δ^{34}S is becoming an increasingly useful tool for modern and past ecological investigations. Nonetheless, to fully characterise potential dietary inputs the combination of other isotope compositions (δ^{13}C and δ^{15}N) is needed to interpret δ^{34}S for potential mobility information. Although subsistence choices could complicate interpretation of omnivores and carnivores, for instance with freshwater fish consumption (Ebert et al., 2021; Hu et al., 2009; Irvine and Erdal, 2020; Nehlich et al., 2010, 2011; Privat et al., 2007; Rand et al., 2020; Richards, 2023; Tsutaya et al., 2019), it is assumed that due to their diet, herbivore δ^{34}S values should reflect only the geographical and environmental factors influencing plants. Therefore, this approach offers the opportunity to identify herbivorous mammals with local ranges and those with more expansive ranges whose δ^{34}S value should reflect the broader environmental inputs. In a food web study in Late Pleistocene Belgium, for example, δ^{34}S data was used to demonstrate residence differences between hominin groups and to highlight the migratory behaviour of some species (such as reindeer) and – conversely – the relatively local ranging behaviours of others (Wißing et al., 2019). This method thus has great potential, to explore differences in habitat use and total range size between different species, and to investigate variations through time (Bocherens et al., 2015a; Britton et al., 2023a, 2023b; Drucker et al., 2015; Reade et al., 2020b; Wißing et al., 2019).

To date, the majority of δ^{34}S studies have explored relative differences between species or through time, to investigate the potential impacts of climate change and the evolution of animal behaviour (Britton et al., 2023b; Reade et al., 2020a). Recent approaches focused on developing predicted landscape environmental δ^{34}S variability in soils and plants (i.e., isoscapes) offer new opportunities to move beyond identification of relative trends and to estimate areas of the landscape used. These isoscapes offer opportunities to be a baseline to reconstitute herbivorous mobilities within a spatial environment. It is important to note these reconstructed sulfur isoscapes are still in development, in particular for past periods, because of potential problems of modern pollution (i.e. anthropogenic contamination issues from agricultural practices and factory pollution) and past biotic and abiotic conditions (i.e. permafrost and wetlands), which could be prevalent in the Pleistocene (Aguraiuja-Lätti et al., 2022; Bataille et al., 2021; Brlík et al., 2024; Evans et al., 2023; Lamb et al., 2023; Stevens et al., 2022).

By analysing δ^{34}S in bone collagen we also aim to recreate long-term spatial palaeoecology of fauna using sulfur isotopes. As δ^{34}S values in plants typically vary by distance to the sea, changes in geology, and presence of permafrost, if certain fauna have a small δ^{34}S range it should suggest they are moving within a limited area of the landscape whereas fauna with larger δ^{34}S ranges are expected to move further around the landscape to incorporate more varying values. Thus, the goal of this study is to analyse multiple ungulate species from three Late Pleistocene sites ranging from MIS 5 to MIS 3 to identify any spatial partitioning between selected taxa that may be evident in the δ^{34}S data. The variation will allow us to evaluate fauna that likely had lower levels of mobility/smaller home ranges from those whose annual range was likely to be far larger. Along with interspecies differences, diachronic variation and relationship to (isotopic) dietary niche (as evidenced by δ^{13}C and δ^{15}N values) will also be explored.

3. Sites and species targeted

Renowned for its karstic landscape and subsequently rich Middle and Upper Palaeolithic archaeology, the abundant Late Pleistocene mammalian fossil record of the Dordogne allows archaeologists to understand changes in human and animal behaviour alongside environmental changes over thousands of years. Three Late Pleistocene sites in the Perigord region, Roc de Marsal, Combe Grenal, and Pech de l'Azé IV (Fig. 1), were chosen for this study, as they each contain an extensive record of ungulate remains (such as reindeer, bovines, horse, and red deer), are relatively close (~70 km^2) and have concurrent levels dating between MIS 5 to MIS 3. These sites thus offer an opportunity to examine the relative faunal home range size of these different ungulate species over a long period of time with distinct climate conditions, within a specific region of France. Furthermore, these sites have previously been investigated and compared to understand Neanderthal habits and changes through time such as hunting patterns, prey selection, prey mobility, and ability to produce fire (Dibble et al., 2018; Discamps and Royer, 2017; Hodgkins, 2012; Hodgkins et al., 2024; Sandgathe et al., 2011b; Sorensen, 2017). Prior to analysis, the δ^{34}S values of the landscape surrounding these sites was determined to be between 8 and 9 ‰ based on a Holocene δ^{34}S isoscape of Europe, with Roc de Marsal's δ^{34}S value equal to 9.0 ‰, Combe Grenal equal to 8.6 ‰, and Pech de l'Azé IV equal to 8.4 ‰ (Fig. 1) (Bataille et al., 2021).

3.1. Roc de Marsal

Roc de Marsal (RDM, 44.895°N, 0.978°E) is a cave site located on a small tributary of the Vézère River, 80m above the tributary valley floor. The site was first excavated in the mid-1900s by Jean Lafille. Starting in 2004, the site was further excavated by Harold Dibble, Alain Turq and a large international team who identified 13 archaeological layers all related to the Middle Palaeolithic (Castel et al., 2017; Reeves et al., 2019; Sandgathe et al., 2011a; Turq et al., 2008). At the bottom of the stratigraphy, layers 7 through 5 are characterised by Levallois technology, with a higher proportion of denticulate in layer 7 and the number of scrapers increasing through layer 5 (Reeves et al., 2019; Turq et al., 2008). Zooarchaeologically, layer 7 has a high proportion of red and roe deer, followed by bovines and horse with a small proportion of reindeer. By layer 5, reindeer become the dominant species (70 % of NISP), suggesting a transition from a warmer to cooler climate conditions (SI Tables 1 and 2, Castel et al., 2017; Reeves et al., 2019). Luminescence dating puts layer 7 between 73 and 52 kya, likely deposited during MIS 4, and layer 5 between 65 and 49 kya. The transition from MIS 4 to MIS 3 likely occurred during, or around the time, that layers 5 and 6 were deposited according to absolute dates (Guérin et al., 2012, 2017), yet this chronology has been debated on the basis of other chronological arguments (Discamps and Royer, 2017). Layers 2 and 4 contain a relatively high level of large, retouched scrapers, which fit within the traditional Quina Mousterian lithic industry (Castel et al., 2017; Reeves et al., 2019; Turq et al., 2008). These two layers have a high frequency of reindeer remains (>70 % NISP), followed by horses, bovines, and red deer (Castel et al., 2017; Hodgkins et al., 2016; Lagle, 2021). Although the majority of Quina levels across southwestern France are attributed to MIS 4 or early MIS 3, indirect dating at RDM assigns the Quina material from layers 2 and 4 to around ~49kya (Discamps and Royer, 2017; Guérin et al., 2012, 2017).

3.2. Combe Grenal

Combe Grenal (44.806°N, 1.227°E) consists of a small cave and a large archaeological rich talus located south of the Dordogne River. The site was discovered in 1816, making it one of the earliest Palaeolithic sites studied in the region. Thus, it has been excavated several times in the past two centuries, the most famous of which are the François Bordes excavations from 1953 to 1965, although it has also been the focus of

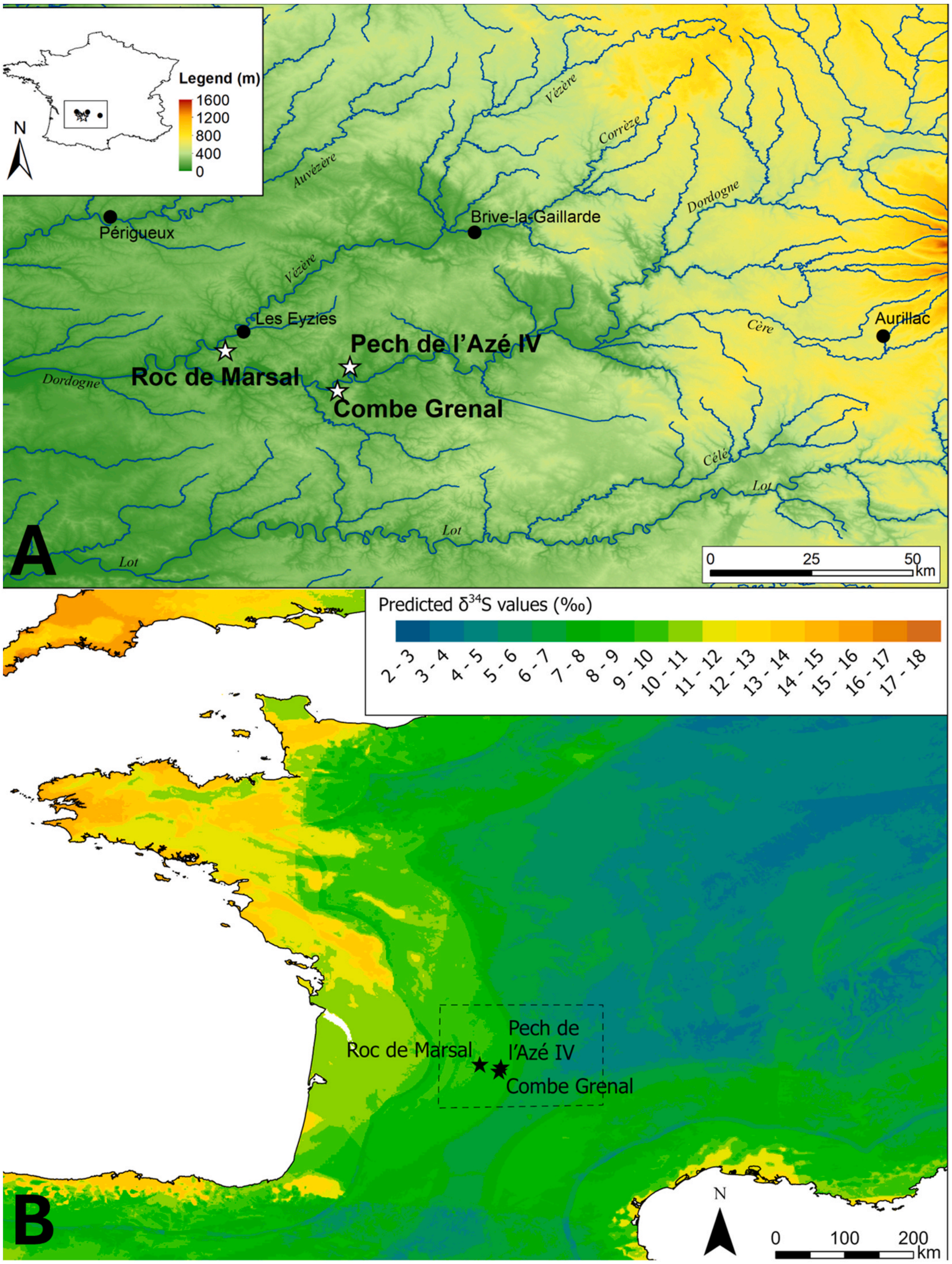

Fig. 1. A) Topographical map of region in study. Late Pleistocene sites in focus are highlighted by white stars while modern locations represented by black circles. B) Modern δ^{34}S isoscape based on Bataille et al. (2021) showing the bioavailability of δ^{34}S in the Holocene landscape. Dotted rectangle shows the expanse of map A. Maps were created in ArcMap 10.8 and ArcGIS Pro 3.1.2.

more recent investigations (Discamps and Faivre, 2017). At least 65 layers associated to the Middle Palaeolithic (lower 10 attributed to the Acheulian, upper 54 to the Middle Palaeolithic) have been identified and are rich in lithics, Neanderthal and faunal remains, bone tools, pigments, and ornamentation (latest studies of this material include Berlioz et al., 2023; Discamps and Faivre, 2017; Faivre et al., 2014; Morin and Laroulandie, 2012; Tartar et al., 2022, amongst many others). In layers 37 to 20, two main lithic technologies can be found. Layers 37 to 27 are dominated by Levallois tools with more retouch and resharpening found in 'Ferrassie Levallois' layers compared to 'Typical Levallois' layers. In layers 26 to 20 there is a change to Quina Mousterian tools with two major typologies found between the layers 'Classic Quina' in Layers 26 to 21 and 'Denticulate Quina' in layer 20 (Faivre et al., 2014). While recent reviews have highlighted potential bias in the Bordes faunal collections (Discamps and Faivre, 2017), over 12,000 specimens representing 27 different species have been identified (Chase, 1986; Delpech and Prat, 1995; Guadelli, 1987, 2012). Due to the importance of Combe Grenal and the abundance of faunal remains, many studies have used Combe Grenal as an example to study changes in palaeoclimate, palaeoecology and Neanderthal hunting patterns through time (Berlioz et al., 2023; Discamps et al., 2011; Discamps and Faivre, 2017; Discamps and Royer, 2017; Richards et al., 2017). Layers 37 to 33 typically have high amounts of temperate fauna such as bovines and red deer. Then, from layers 32 to 27 reindeer become more abundant while still having large amounts of red deer. Finally, reindeer become the dominant species in layers 26 to 20, followed by red deer, bison, and horses (SI Table 3, Guadelli, 1987, 2012). While Combe Grenal is an important site to understanding Middle Pleistocene palaeoecology, the sequence has not yet been firmly anchored to absolute dates. Ongoing analysis focused on obtaining new absolute dates and correlations with other archaeological sequences suggest layers 36–27 date to the Ante-Quina periods (~115-70 kya) but can be split into two periods (37-33 are temperate Ante-Quina, MIS 5, while layers 32- 27 correlate with the end of MIS 5 or start of MIS 4) and layers 26-17 correlate with Quina period, which date to the end of MIS 4 and Heinrich Stadial 6 (~70-60 kya) (Discamps and Royer, 2017).

3.3. *Pech de l'Azé IV*

Pech de l'Azé IV (44.806°N, 1.227°E) is a collapsed rock shelter on the foot of a cliff and is one of the four sites associated with Pech de l'Azé, located just north of the Dordogne River (Goldberg et al., 2018). The site was discovered in 1952 and excavated over the following decades by Bordes and Mortureux (Bordes, 1975; Sandgathe et al., 2018). The site was re-excavated in the 2000s by McPherron and Dibble, in which they identified eight Pleistocene layers spanning nearly 60,000 years from MIS 5d to MIS 3 (Jankowski, 2018; McPherron et al., 2012; McPherron and Dibble, 2000; Sandgathe et al., 2018; Turq et al., 2011).

The lowest layer, layer 8, dates to between ~99 and ~90 kya (based on OSL and TL dates) and corresponds to MIS 5d and MIS 5c (Jacobs et al., 2016; Jankowski, 2018; Richter et al., 2013). Archaeological finds in this layer include Typical Mousterian lithics (Turq et al., 2011), evidence of extensive use of fire (Goldberg et al., 2012), and a large number of red deer and roe deer remains, which suggests a more temperate, wooded environment (Niven, 2013). Above this, layer 6A dates from ~81 to ~73 kya using OSL dating (Hodgkins et al., 2016; Jacobs et al., 2016; Jankowski, 2018) which is associated with end of MIS 5a. This layer has an increasing amount of Levallois type lithics and has been assigned to the Asinipodian (Turq et al., 2011). The zooarchaeological record of 6A has an abundance of red deer, followed by roe deer and then horses (Niven, 2013; Niven and Martin, 2017). Finally, layer 4A dates between ~60 and ~54 kya using OSL dating and corresponds to the end of MIS 4 or beginning of MIS 3 (Jacobs et al., 2016; Jankowski, 2018). This layer has evidence of Quina technology (Jacobs et al., 2016; Turq et al., 2011) and has a significant change in zooarchaeological record with reindeer being the most abundant remains (SI Table 4, Hodgkins et al., 2016; Niven, 2013; Niven and Martin, 2017).

3.4. *Species targeted*

Bovinae (*Bos/Bison*) and horse (*Equus ferus*) were targeted as these species are generally anticipated to be non-migratory with moderately sized annual home ranges. In modern studies, they have been shown to vary substantially from <10 km^2 to >1500 km^2 in extreme environments (Glassburn et al., 2018; Krasińska and Krasiński, 2013) but are typically between 0.6 km^2 to ~200 km^2, (Kaczensky et al., 2008; Linklater et al., 2000; Lugauer, 2010; Schoenecker et al., 2023). Few studies exploring the mobility of these species have been conducted on Late Pleistocene material, but those undertaken to date do not suggest long distance movements in the European Pleistocene (Britton et al., 2011, 2023a; Pederzani et al., 2021b; Pellegrini et al., 2008). Thus, it is likely that these species will help to identify the potential 'baseline' for our sites and the immediate surrounding area with these species (Britton et al., 2011, 2023a; Feranec et al., 2009; Julien et al., 2012; Pellegrini et al., 2008). *Bos* and *Bison* are both identified within several layers at Combe Grenal (Guadelli, 2012). However, distinguishing these species among highly fragmented bones (as those sampled for isotopic analyses) is currently not possible using morphology or ZooMS. We will thus refer to both taxa as bovines. These two species have different evolutionary histories, physiologies, and behaviours which could lead to differences in isotopic signatures (Rosengren and Magnell, 2024; Terlato et al., 2019); however, Pleistocene isotopic studies on *Bos* and *Bison* have shown overlapping patterns in diets and habitat use (Bocherens et al., 2015b).

Modern roe deer and red deer, as well as Late Pleistocene red deer (Barakat et al., 2023; Pilaar Birch et al., 2016), are known to have short-distance seasonal (or partial) migrations (Mysterud, 1999; Mysterud et al., 2011, 2012, 2016, 2017; Peters et al., 2017; Ramanzin et al., 2007; Wahlström and Liberg, 1995). These taxa, while having small seasonal home ranges (roe deer <5 km^2 (Ramanzin et al., 2007; Saïd and Servanty, 2005) and red deer up to ~200 km^2 (Jarnemo et al., 2023)) largely based on availability of vegetation, should provide evidence for short-distance ranging (albeit potentially seasonally migratory) fauna with home ranges that are relatively small.

Modern *Rangifer* have both migratory and sedentary ecotypes, both with considerable ranging needs. Sedentary or woodland caribou can have range sizes typically between ~10 km^2 (Tyler and Øritsland, 1989) when in a contained area, such as Svalbard, to nearly 10,000 km^2 (Wilson et al., 2019) whereas migratory caribou such as those found in Alaska or Canada can have ranges between 80,000 and 900,000 km^2 or more (Nicholson et al., 2016; Schmelzer and Otto, 2003). Studies on Late Pleistocene European reindeer have shown that they, like modern *Rangifer*, had both migratory and non-migratory ecotypes (Britton et al., 2011, 2023a; Price et al., 2017). Although seasonal migrations have been confirmed in MIS 4 reindeer in the Charente-Maritime at the site of Jonzac (~70 kya (Britton et al., 2011);); recent strontium isotope research in the region, including at the sites of Pech IV and RDM (Hodgkins et al., 2024), has highlighted that such movements were probably restricted to the sedimentary basins of France (i.e., the Aquitaine, and/or Paris Basins) and that they are not likely to have crossed the Massif Central. However, the similarities between bioavailable strontium in the Aquitaine and Paris Basin make assigning a distance to those movements difficult. Other species, such as bovines and roe deer may have had more restricted home ranges or, in the case of red deer and horses included more upland areas in their annual ranges (Hodgkins et al., 2024) despite likely having smaller range sizes. Where horses, bovines and the different deer species are anticipated to have differences in both their movement behaviours and total range size of the different taxa, differences should be apparent in the sulfur isotope ratios of their bone collagen.

4. Material and methods

Ungulate bones from Roc de Marsal ($n = 119$), Pech de l'Azé IV ($n = 59$), and Combe Grenal ($n = 66$) were sampled for isotopic analysis, with five different taxonomic groups being selected based on morphological identifications that had been previously undertaken or were undertaken at the point of sampling. The primary ungulates collected at all three sites were *Bos/Bison* (bovines) ($n = 38$), *Equus ferus* (horse) ($n = 54$), *Cervus elaphus* (red deer) ($n = 63$), and *Rangifer tarandus* (reindeer) ($n = 73$), while *Capreolus capreolus* (roe deer) ($n = 16$) were also collected at Pech de l'Azé IV due to availability of a large number of samples. In total 244 bones were selected for collagen extraction and analysis across the three sites.

Bone collagen was extracted following the steps as described in Britton et al. (2012). This process uses a modification of the Longin (1971) method following the recommendations of Collins and Galley (1998) and includes an ultrafiltration step (Brown et al., 1988) to the >30 kDa fraction to maximise the yield of collagen of good preservation and remove any non-organic sulfur (Richards, 2023). Extracted collagen was weighed out in tin capsules (1.2–1.5 mg) and analysis for δ^{13}C, δ^{15}N, and δ^{34}S was undertaken at the Scottish Universities Environmental

Research Center (SUERC), with 20 % of samples ($n = 41$) being submitted for duplicate analysis. The three isotope ratios were co-analysed using the protocols outlined in Sayle et al. (2019). This method uses advancements in the EA IsoLink IRMS system (Thermo Fischer Scientific, Bremen, Germany) to co-measure δ^{13}C, δ^{15}N, and δ^{34}S at once using a single sample (Sayle et al., 2019). International Atomic Energy Agency (IAEA) reference materials USGS40 and USGS41a were used to normalise δ^{13}C and δ^{15}N values, while an in-house standard (F-SAAG) which is calibrated to the IAEA reference material IAEA-S-2, IAEA-S-3, and USG88 was used to normalise δ^{34}S values. Based on repeat measurements of the well characterised Elemental Microanalysis IRMS fish gelatin standard B2215, precision was determined to be ±0.15 ‰ (δ^{13}C), ±0.2 ‰ (δ^{15}N), and ±0.4 ‰ (δ^{34}S). After isotopic analysis, the data were assessed for quality indicators, with samples with C:N ratios outside of 2.9–3.6, C:S ratios outside of 600 ± 300, and N:S ratios outside of 200 ± 100 then being removed from the data set (Ambrose, 1990; Nehlich and Richards, 2009).

Although all samples were initially selected on the basis of morphological identifications, due to the general difficulties in identifying fragmentary deer bones (Discamps et al., 2024; Morin et al., 2023), the presence of multiple deer species at all sites, and the initial isotopic results obtained in this study, the extracted collagen from all Cervidae bones ($n = 125$) was further analysed using peptide mass fingerprinting (Zooarchaeology by Mass Spectrometry, ZooMS) to confirm species identifications (Buckley et al., 2009). This was undertaken at the Collège de France, Paris, following standard protocols (Buckley et al., 2009; Welker et al., 2016) with modifications allowing for the analysis of lyophilised collagen extracts from isotope analysis (Charlton et al., 2016; Presslee et al., 2021). Full details are presented in the Supplementary Information. All further data analysis, statistical tests, and data interpretation are based on these updated taxonomic assignments via molecular techniques.

δ^{34}S values were analysed using linear models to test for 1) the effect of the species and 2) effect of species based on time-period (Ante-Quina, Late Ante-Quina, and Quina) as defined by Discamps and Royer (2017) by combining absolute dates (where available) with other chronological indicators (including local environmental proxies, archaeostratigraphy, techno-cultural tradition and the faunal record within the region). Ante-Quina samples (~128-70 kya) relate to temperate climates in MIS 5 and include archaeological levels with a high proportion of red and roe deer and Levallois industries. Late Ante-Quina samples mostly relate to end of MIS 5 to early MIS 4 when climate becomes cooler and reindeer become more prevalent but red deer are still present in larger numbers, RDM layers 7-5 date to MIS 4 - early MIS 3, but are assigned to this period based on the lithic and zooarchaeological record. The majority of Quina samples (~70-60 kya) correlate to MIS 4 or the beginning of MIS 3, with the exception of RDM layers 4 and 2 which date to ~50 kya and relate to late MIS 4 or early MIS 3 but are still assigned to the Quina time period based on stone tools, and reindeer dominated assemblages (Discamps and Royer, 2017). As sample numbers were low when divided by time period and the isotopic results by species violated homogeneity of variance (δ^{34}S) or were not normally distributed (δ^{13}C), a Kruskal-Wallis test and *post-hoc* Dunn Test were used to compare species and species by time-period. Finally, we statistically analysed for the point-estimate overlap between δ^{13}C - δ^{34}S core isotope area of species in time-periods based on the maximum likelihood estimated SEA_c using SIBER in R (Jackson et al., 2011). The total area of isotope overlap between species was calculated by transforming convex hulls from SIBER into spatial objects and computing minimum convex polygons before calculating the intersection area and proportion of overlap. All data were analysed in R software using R versions 4.3.0 (R Core Team, 2024).

5. Results

5.1. ZooMS results and isotopic quality control

Out of 244 samples selected for collagen extraction, 51 samples failed to produce any or sufficient collagen for isotopic and/or ZooMS analysis and 12 did not pass isotopic quality control indicators (DeNiro, 1985; Nehlich and Richards, 2009). Of the 125 cervid bones analysed for ZooMS, 18 (14.4 %) returned differences between morphological and ZooMS identifications, and one sample proved inconclusive. ZooMS can identify *Rangifer tarandus* and *Capreolus capreolus* to species level, however can currently not distinguish *Cervus/Megaloceros/Dama/Alces/Saiga*. Considering the assemblages analysed, the abundance of *Cervus elaphus* remains, the absence of *Dama/Alces/Saiga* at the sites studied, the extreme scarcity of *Megaloceros* remains in the zooarchaeological assemblages from sites selected, along with the cortical size of bones (which is more compatible with *Cervus* than with *Megaloceros*), we hereafter refer to those samples assigned to *Cervus/Megaloceros/Dama/Alces/Saiga* via ZooMS as *Cervus elaphus* (which in the majority of cases, 78 %, had been previously assigned red deer on the basis of their morphology). Bone collagen δ^{13}C, δ^{15}N, and δ^{34}S results and ZooMS identifications can be found in Supplementary Tables 5a, 5b, and 6. The final count of samples post ZooMS and quality control is found in Table 1.

5.2. Isotope results by species

δ^{34}S isotope values range from 0.6 to 16.4 ‰, with taxonomic means of 10.2 ± 1.7 ‰ (bovines), 15.3 ± 1.1 ‰ (roe deer), 13.2 ± 1.1 ‰ (red deer), 10.7 ± 2.0 ‰ (horse), and 5.7 ± 3.0 ‰ (reindeer). Bovines and horse have the most similar δ^{34}S values and ranges and are not significantly different from each other (Table 2). Red deer are consistently significantly higher in δ^{34}S than all species except for roe deer, which are only present at Pech de l'Azé IV. Roe deer have the lowest δ^{34}S range (3.1 ‰) and have significantly higher δ^{34}S values than all species, except for red deer. Finally, reindeer have significantly lower δ^{34}S values compared to all other species and have the widest δ^{34}S range (11.1 ‰) across time (Fig. 2).

Reindeer have the most significantly elevated δ^{13}C values (−19.6 ± 0.4 ‰) with a range between −20.4 ‰ and −18.7 ‰, compared with all other taxa (SI Table 7). Roe deer have the lowest δ^{13}C values (−21.3 ± 0.7) and are significantly lower than red deer (−20.2 ± 0.3 ‰). Red deer δ^{13}C values are also significantly higher than horses (−20.8 ± 0.5 ‰). Bovine δ^{13}C values (−20.4 ± 0.3 ‰) are not significantly different than any species except reindeer.

δ^{15}N values range between 3.1 ‰ and 10.8 ‰ with majority clustering between 5 ‰ and 9 ‰ (SI Fig. 1). Bovines (7.1 ± 1.4 ‰) have significantly higher δ^{15}N values than roe deer (5.1 ± 0.6 ‰) and horses

Table 1

Table with successful samples per time period as described in Discamps and Royer (2017). Ante-Quina layers include Pech IV layers 6A and 8 and CG layers 35,36, and 37. Late Ante-Quina layers include RDM layers 5 and 7 and CG layer 27. Finally, Quina layers include Pech IV 4A, CG 20, 22, and 23, and RDM 2 and 4 (which date to MIS 3). The single sample which did not produce a ZooMS identification is not included in this table.

Species	Ante-Quina (MIS 5)	Late Ante-Quina (late MIS 5 - MIS 4)	Quina (MIS 4*)
Bovine	5	4	14
Capreolus capreolus	8		
Cervus elaphus	14	8	15
Equus sp.	7	3	28
Rangifer tarandus	7	14	54
Total count	41	29	111

Table 2
Pairwise comparison of δ^{34}S estimates from linear models testing the difference in δ^{34}S between species considering all time periods (δ^{34}S ~ species) using a Kruskal-Wallis test followed by the post-hoc Dunn Test. Significant value shown in bold. The effect size (r) is shown in the final column to show the magnitude of observed differences following Cohen (1992) and Wolverton et al. (2016). Strong effects (>0.6) are denoted by ***, medium (0.3–0.6) by **, small (0.1-0.3) by *, and no effect with no asterisks.

Species Contrast for δ^{34}S	Number of species 1	Number of species 2	Adjusted p-value	r (effect size)
Bovine - Capreolus	**23**	**8**	**0.004**	**0.63*** **
Bovine – Cervus	**23**	**37**	**0.002**	**0.48** **
Bovine - Equus	23	38	1.000	0.08
Bovine – Rangifer	**23**	**75**	**<0.001**	**−0.43** **
Capreolus – Cervus	8	37	1.000	−0.17*
Capreolus – Equus	**8**	**38**	**0.011**	**−0.48** **
Capreolus - Rangifer	**8**	**75**	**<0.001**	**−0.73*** **
Cervus - Equus	**37**	**38**	**0.004**	**−0.41** **
Cervus - Rangifer	**37**	**75**	**<0.001**	**−0.95*** **
Equus - Rangifer	**38**	**75**	**<0.001**	**−0.57** **

(6.0 ± 1.4 ‰) while reindeer (6.6 ± 1.4 ‰) have significantly higher δ^{15}N values than roe deer (SI Table 7). Red deer δ^{15}N values (6.0 ± 1.3 ‰) are not significantly different to any other taxa.

5.3. *Diachronic trends*

Reindeer have the largest δ^{34}S ranges (Quina = 10.9 ‰, Late Ante-Quina = 9.6 ‰ and Ante-Quina = 7.3 ‰) in all three periods while roe deer have the lowest range in the Ante-Quina (3.1 ‰), horses in the Late Ante-Quina (0.3 ‰), and red deer in the Quina (2.5 ‰). When comparing the species, reindeer have the lowest mean, median, and individual values across all time periods. Further, while reindeer maximum δ^{34}S values remain constant through time (11.4 ‰–11.7 ‰), the minimum values decrease through time and are significantly lower in the Quina period compared to the Late Ante-Quina (SI Table 8). Red deer have the highest δ^{34}S values across time except for in the Ante-Quina when roe deer have the highest δ^{34}S values (Fig. 3). Bovine δ^{34}S values remain consistent through time and have mean and median values between red deer and reindeer. Finally, horses have a gradual decline in δ^{34}S values with significantly lower δ^{34}S values in the Quina compared to the Ante-Quina (SI Table 8).

Bovine δ^{13}C values remain constant throughout time (SI Table 8) while δ^{15}N values steadily decrease from the Ante-Quina to Quina (SI Table 8), although not significantly. Red deer δ^{13}C decreases from the Ante-Quina to Quina period, but neither the δ^{13}C not the δ^{15}N values significantly change. Horse δ^{13}C values are significantly lower in the Ante-Quina compared to later periods, while δ^{15}N values are only

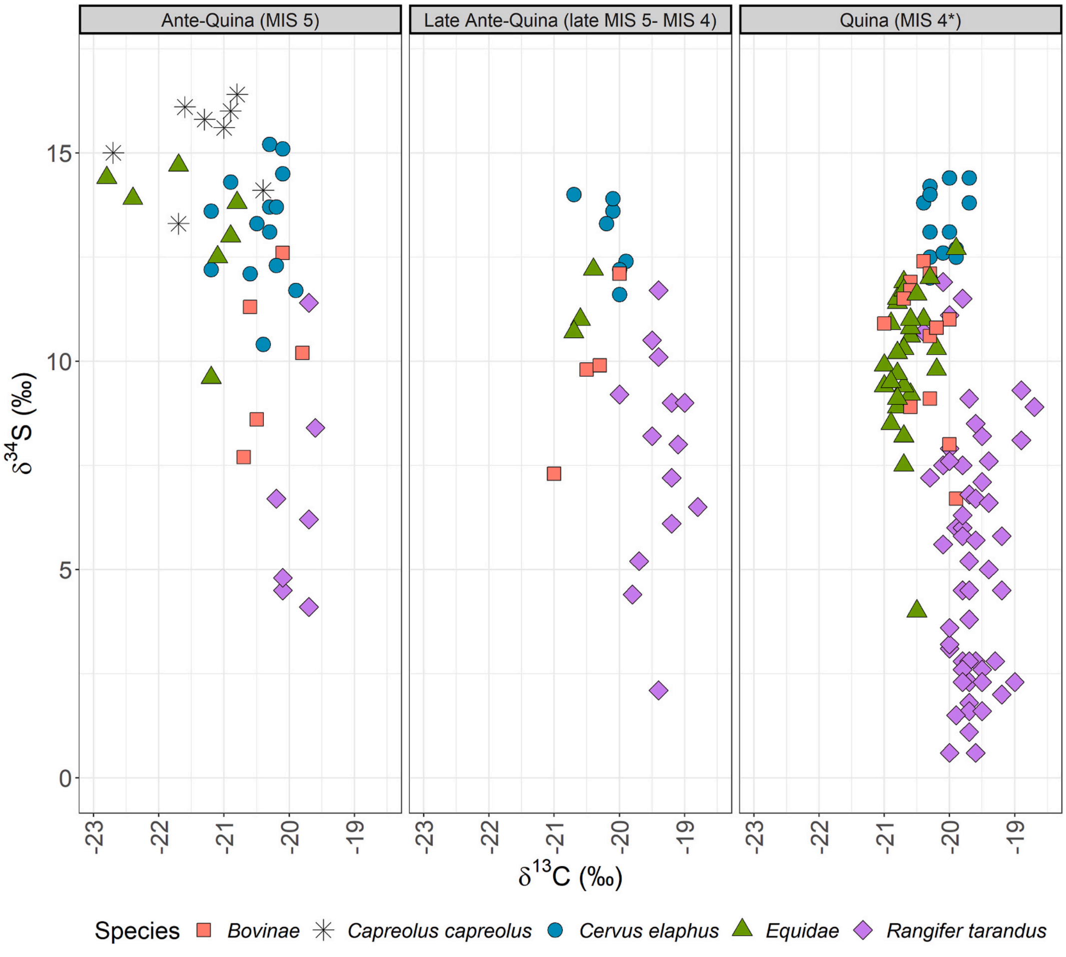

Fig. 2. Scatter plot with δ^{13}C along the x-axis and δ^{34}S along the y-axis. Red squares represent bovines, green triangles are horses, light blue circles are red deer, purple diamonds are reindeer, and black asterisks are roe deer. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

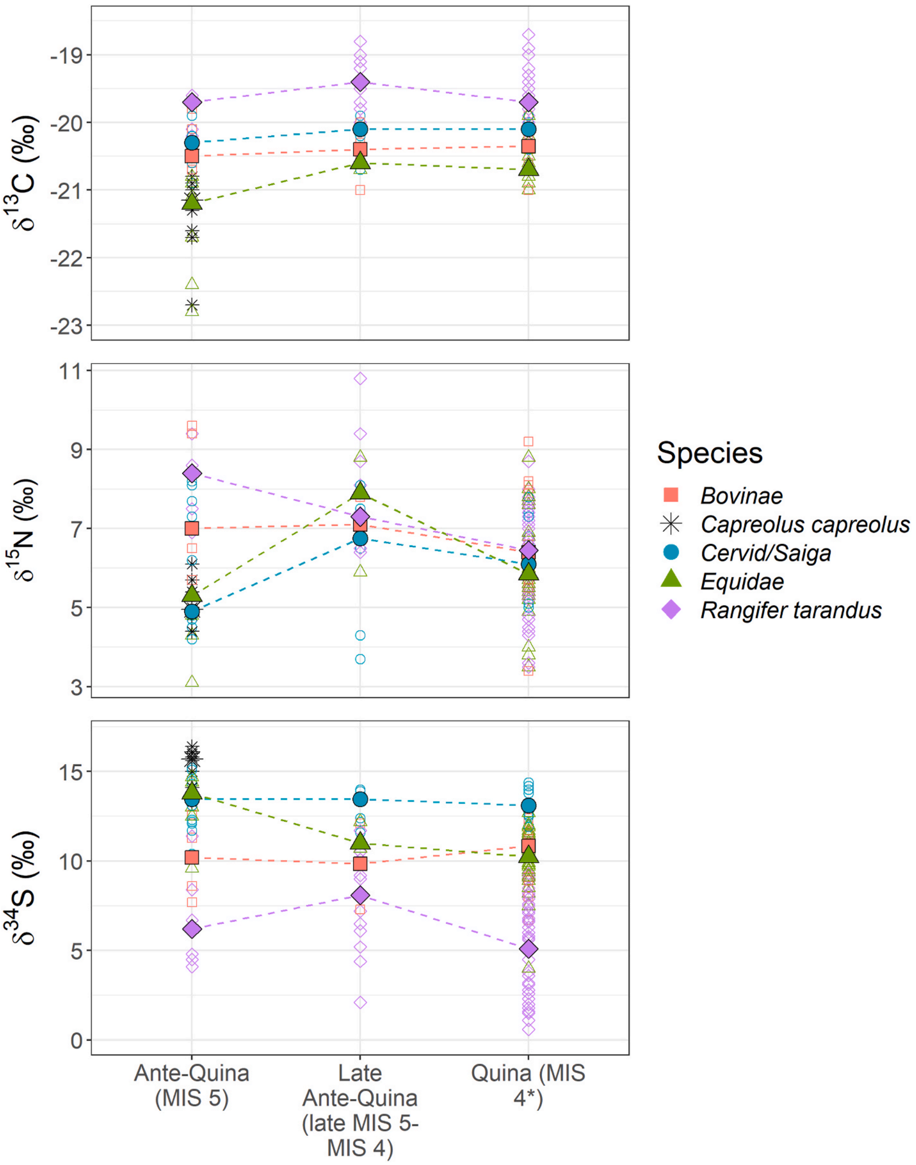

Fig. 3. Scatter plot showing $\delta\,^{13}$C, $\delta\,^{15}$N, and $\delta\,^{34}$S variation over time. The coloured symbol represents the median isotope value for each period and the dotted line connects the median values between periods to see how isotope values shift through time. The hollow symbols represent the individual data points. Quina (MIS 4) has an asterixis as it contains data from RDM level 2 and 4, which dates to MIS 3.

significantly higher in the Late Ante-Quina compared to the Quina period. Finally, reindeer δ^{13}C values are significantly higher in the Late Ante-Quina compared to both the Ante-Quina and Quina, while δ^{15}N values decrease through time with significantly lower values in the Quina period compared to both other periods.

5.4. Isotope niche space partitioning

Isotope niche space partitioning between species was evaluated by analysing the δ^{13}C-δ^{34}S isotopic space via SIBER (Jackson et al., 2011). The isotope niche partitioning plots (Fig. 4a–d) are based on data in SI Table 9. The plots show all data points with colour representing different species, the convex hull (light dotted line) which outlines the total area (TA) of isotopic space taken by each species, and the core area (thicker dashed line) of each fauna is represented by the standard ellipse area (SEAc, to correct for small samples sizes) which contains roughly 40 % of the data per species.

Across all time periods, the results show a clear separation in core area (SEAc) between reindeer and all other fauna (SI Table 9). Reindeer also have the largest core area when comparing all the data together. Bovine and horse core areas had a moderate (30–60 %) proportion of core area overlap and high (>60 %) proportion of total area overlap, which is highest in the Quina period. This is the only pairing which had a moderate proportion of core area overlap between species and there are no groupings which had a high proportion of core area overlap throughout time. In the Quina period, bovine total area has a moderate overlap with reindeer while reindeer-horses, bovines-red deer, and horse-red deer all have low proportions of total area overlap. Bovines and red deer are the only species combination that has total area overlap (<30 %) in the Late Ante-Quina period. In the Ante-Quina period, there is low overlap in core area between bovines-red deer, horse-red deer, and horse-roe deer, a moderate overlap between bovine and red deer total area, and a low overlap between reindeer-bovine, horse-red deer, horse-roe deer, and red-roe deer.

Isotope niche partitioning between δ^{13}C-δ^{15}N, reveals larger areas of overlap (SI Fig, 2). Over all periods, bovine core areas moderately overlap with horses and red deer, roe deer core area moderately overlaps with horses, and total area overlap shows a high proportion of overlap

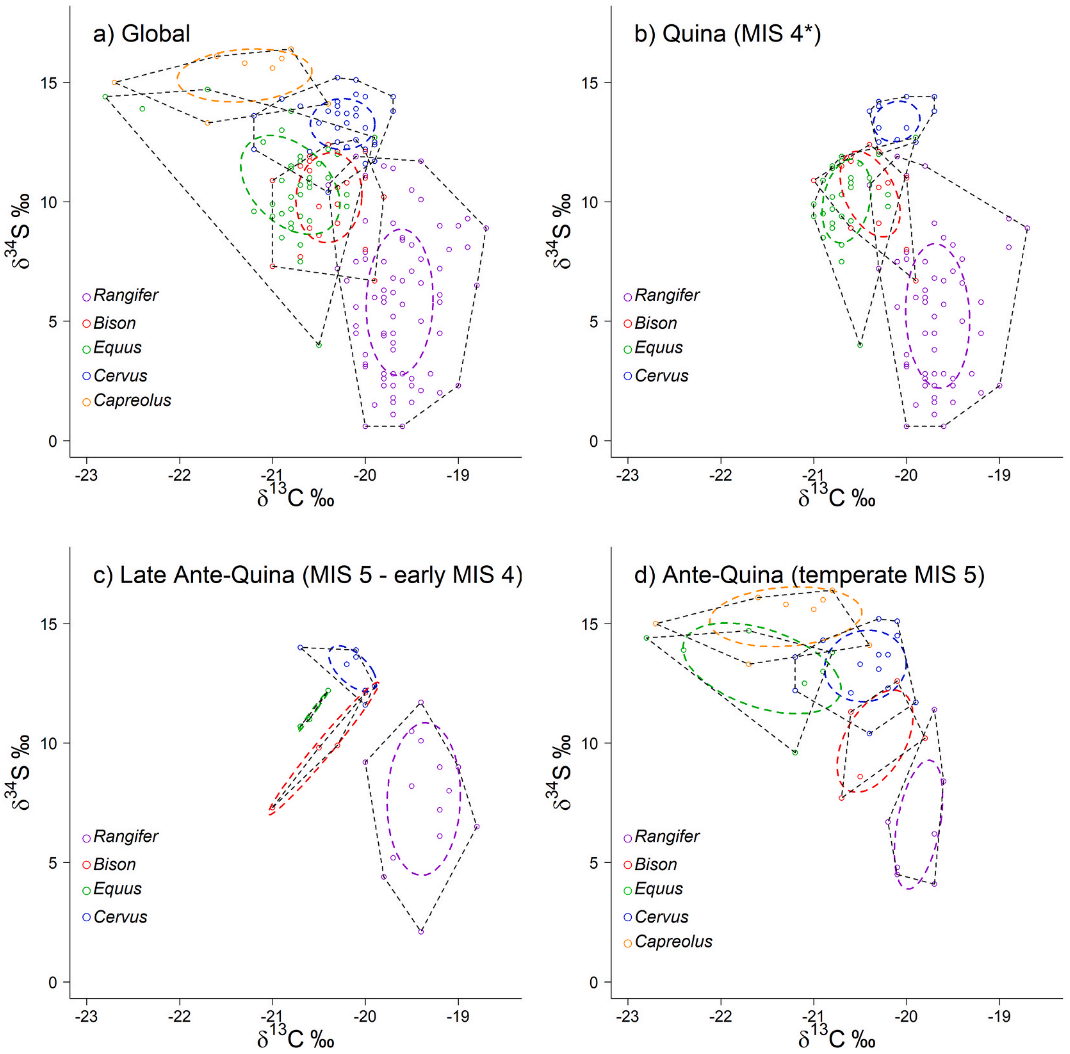

Fig. 4. Spatial niche partitioning between Rangifer, bovines, Equus, Cervus, and Capreolus based on the different time periods. (A) represents all data and all time periods together, (B) Quina data including data from RDM which dates to HS 5 in MIS 3, (C) Late Ante-Quina samples, and (D) Ante-Quina samples. The convex hull which encompasses the total isotope area (TA) is represented by light grey dashed lines, the core niche area is shown in the standard ellipse area (darker dashed lines, denoted by species colour), and individual samples are shown by single circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between bovines-horses, bovines-red deer, horse-red deer and horse-roe deer (SI Table 10). In the Quina period, bovines and horses have a moderate core aera, and high total area overlap. Red deer total area also has a high proportion of overlap with reindeer. The Late Ante-Quina period has moderate proportion of overlap between bovine and red deer core area, and a high proportion of total area overlap. Horses also have a moderate proportion of overlap with red deer in this period. Finally, in the Ante-Quina period, roe deer have a high proportion of overlap with horses in core and total area, while there is a moderate overlap between bovine and red deer core area. Bovines-red deer and red-roe deer all have a moderate overlap in total area in the Ante-Quina. Throughout all periods, reindeer have the lowest, or no, amount of overlap with all other species.

6. Discussion

6.1. Inter-species trends

The δ^{34}S results of this study show that horses, bovines, and red and roe deer have smaller intra-species ranges of δ^{34}S values, and generally higher δ^{34}S values, than reindeer. The small ranges of δ^{34}S values (and similar values) exhibited by the majority of the taxa compared to the reindeer is consistent with the total home range size of these species being smaller than that of reindeer throughout the periods covered in this study. The overlapping values of bovines and horses suggests that their physical ranges were similar and that the sulfur isotope values exhibited in these species may be representative of the more regional environmental values. This interpretation is consistent with other (strontium) isotopic evidence for Late Pleistocene bovine and horse movement ecology, which indicate that these faunas were likely non-migratory (Britton et al., 2011, 2023a; Julien et al., 2012; Pellegrini et al., 2008). While demonstrating a tight 'clustering' of values, red and roe deer are generally enriched in δ^{34}S relative to bovines and equids, and much more so relative to reindeer. This may suggest a distinct regional spatial partitioning of these species in Late Pleistocene Dordogne. Finally, reindeer have the lowest δ^{34}S values throughout time and the largest variation in δ^{34}S values (11.3 ‰). Reindeer also show the lowest overlap with other ungulates of isotope niche space suggesting they may be occupying a spatial area with different (and significantly lower) δ^{34}S values available. The wide range in δ^{34}S values could imply that reindeer, who today are known to have the largest home range compared to other fauna in this study, may have also had a very large home range which covers landscape areas with large δ^{34}S variations (including much lower values) in Late Pleistocene France.

To ensure patterns in δ^{34}S values represent ranging ecology rather than dietary niche, δ^{13}C and δ^{15}N can be analysed. Reindeer δ^{13}C values are significantly higher than all other species with values between 20.5 and 18.5 ‰, which is indicative of lichen in the diet, while δ^{15}N values reflect a typical herbivore diet. Lichen receives most of its δ^{34}S from the atmosphere (SO_2, H_2S, or sulfate ions from wet and dry deposition). Atmospheric δ^{34}S can rapidly change when near geothermal energy, an erupting volcano, or anthropogenic contamination sources (Case and Krouse, 1980; Gries et al., 1994; Krouse, 1977; Wadleigh, 2003), although these are unlikely to have been factors influencing *Rangifer* isotopic data in Late Pleistocene France. Still, the potential influence of lichen consumption on bone collagen δ^{34}S values must be examined.

There is currently a lack of studies identifying the direct effects of lichen consumption on δ^{34}S values in reindeer bone collagen, unlike the numerous studies on δ^{13}C (Ben-David et al., 2001; Brenning et al., 2024; Britton, 2010; Britton et al., 2023a, 2023b; Drucker et al., 2001, 2010, 2011b; Fizet et al., 1995; Rivals et al., 2020). Published studies highlight lithology and distance to coastline as the main influence on δ^{34}S values in archaeological samples (Bataille et al., 2021; Britton, 2010). Moreover, other isotopic work on European Late Pleistocene reindeer, which indicate lichen consumption, have demonstrated distinct δ^{34}S values in reindeer compared to other fauna which are not always depleted in the heavier isotope as observed in this study. For example, at Goyet cave, reindeer with elevated δ^{13}C values which indicate lichen consumption, have higher δ^{34}S values than all other ungulates, and are almost the same as Neanderthals (Wiβing et al., 2019). This pattern is also seen at Yudinovo, where reindeer have higher δ^{34}S than all other herbivores except muskox and an arctic fox (Drucker et al., 2018a). There are also several examples where reindeer δ^{34}S values largely overlap with other ungulate's δ^{34}S values, such as Abri du Maras, layer 4.1 (Britton et al., 2023a), Geißenklösterle (Drucker et al., 2015), and Kastelhöhle-Nord (Reade et al., 2020b). The ^{34}S-enrichment seen in some cases, the ^{34}S-depletion observed in our own study and sometimes overlapping values seen in others is therefore not consistent with a universal cause for δ^{34}S values related to either lichen consumption or otherwise unique to reindeer. In light of this, we can be more confident that the wide range of δ^{34}S values seen in reindeer across time in this study can be interpreted as reflecting movement across the landscape to areas with diverse and low δ^{34}S values and is not due to some hitherto undocumented innate species difference.

As most of the reindeer in this study have δ^{34}S values ranging between 0 ‰ and 10 ‰, it is unlikely these reindeer were travelling close to the coastline during their annual ranging and/or consumed a large proportion of plant material from within 30 km of the coastline, otherwise the δ^{34}S range would have more of a marine signal (expected δ^{34}S values would be above 10 ‰ and closer to 15 ‰ according to the modern δ^{34}S isoscape (Fig. 1) (Bataille et al., 2021)). As reindeer δ^{34}S values are much lower than those of the other ungulates across all Late Pleistocene sites, δ^{34}S values could reveal that reindeer are moving to areas with lower δ^{34}S values, such as areas farther inland or areas with permafrost coverage including potentially moving through the French river basins to the northeast or to areas with higher elevation and thus colder climates, such as going east to the Massif Central (Reade et al., 2020a, 2020b; Stevens et al., 2022; Thode, 1991).

When combined with previously-published ^{87}Sr/^{86}Sr data, it seems reindeer from Combe Grenal and Roc de Marsal were not going to the higher elevations of the Massif Central but were likely staying within river basins (Hodgkins et al., 2024), which is also consistent with data from the reindeer of Jonzac (Britton et al., 2011). δ^{34}S studies on early Holocene fauna from near the Seine River have identified widely varying but consistently low δ^{34}S values (2.2 ± 2.1 ‰) amongst terrestrial herbivores (Bocherens et al., 2011; Cheung et al., 2021, 2022; Drucker et al., 2018b). If reindeer travelled to the Paris Basin or ranged near the Seine River, this could potentially cause their bone collagen δ^{34}S to be lower. However, a contemporary δ^{34}S isoscape is necessary to confirm this as the modern isoscape may be different due to anthropogenic contamination and the effects of permafrost in the Pleistocene could significantly lower naturally available values.

Besides reindeer, who have the lowest overlap of δ^{13}C and δ^{15}N isotope niche space with other ungulates, bovine δ^{13}C and δ^{15}N isotope niche spaces overlap moderately with horses and red deer, while red deer have a moderate amount of overlap with roe deer as well. Bovines and red deer have the most similar δ^{13}C values throughout time and consistently have more elevated δ^{13}C values than horses, as is seen in other isotope studies on ruminants (Britton et al., 2012; Cerling and Harris, 1999; Codron et al., 2018; Hedges, 2003; Palmqvist et al., 2008, 2003; Richards and Hedges, 2003; Thorp and Van Der Merwe, 1987). While the δ^{13}C values in ruminants (except roe deer who have lower δ^{13}C and δ^{15}N values) are higher than horses, this does not translate to δ^{34}S values. Both red and roe deer have significantly higher δ^{34}S values than all other fauna with low ranges of values, while horse and bovine δ^{34}S values plot between the deer species and can have moderate changes in δ^{34}S values.

Bovine and horse δ^{34}S values fit between the three cervid species and have a moderate variation in δ^{34}S values. In modern studies, these taxa typically have range sizes up to 200 km^2, although this can change in extreme environments (Glassburn et al., 2018; Kaczensky et al., 2008; Krasińska and Krasiński, 2013; Linklater et al., 2000; Lugauer, 2010; Schoenecker et al., 2023). This change in modern home ranges may explain the moderate variation seen in δ^{34}S values in Late Pleistocene bovines and horses.

The low variation in red and roe deer, yet relatively high δ^{34}S values could suggest these deer species may have a slightly different range use. As red and roe deer can undertake short-distance, partial seasonal migrations (Albon and Langvatn, 1992; Barakat et al., 2023; Langvatn and Albon, 1986; Mysterud et al., 2016; Pellegrini et al., 2008; Qviller et al., 2013; White et al., 2010), this small range in δ^{34}S values could suggest that these cervids utilised modest home ranges in similar areas throughout time which would cause these taxa to have similar δ^{34}S values. These δ^{34}S values could also be due to red and roe deer living in areas closer to the coastline where the sea spray effect can serve to override (and generally enrich) any local geological δ^{34}S values. This could result in both higher, and more uniform δ^{34}S values in local fauna. The values seen in these cervid species roughly match with δ^{34}S values within 100 km of the sites based on Bataille et al. (2021).

Palaeolithic red deer are known to undertake short distance migrations (under 100 km) (Barakat et al., 2023; Pilaar Birch et al., 2016), which are either elevational (higher altitudes in summer, lower in winter) or coastal (living inland in summer and along coastlines in winter) (Albon and Langvatn, 1992; Langvatn and Albon, 1986; Mysterud et al., 2011; Qviller et al., 2013). Modern red deer living on coastlines are also known to eat seaweed which could cause δ^{34}S values to be much higher than in other fauna, although the δ^{13}C and δ^{15}N does not support this here (Ceacero et al., 2014; Conradt, 2000; Stevens et al., 2006). Thus, δ^{34}S values in red deer suggest that these populations could be spending some or most of their time to the west of the sites in areas nearer to the coastal plains, which have terrestrial vegetation that is enriched in δ^{34}S due to the marine sea spray. While this may be the most parsimonious interpretation of the data, a further possibility is that both deer species had ranges that compromised lithologies (and thus soils and plants) with naturally occurring high δ^{34}S values which have not yet been identified in the current isoscape due to the low sampling resolution in the current working model.

The Ante-Quina is the only period with roe deer, which have the highest δ^{34}S values of any fauna (ranging from 13.3 ‰ to 16.4 ‰). The high δ^{34}S values in roe deer could suggest that the range of this species was likely predominantly to the west of the sites in areas influenced by marine sulfur due to the sea spray effect. It is unlikely, however, that roe deer were directly eating sea plants as both the δ^{13}C and δ^{15}N values are not enriched compared to other fauna. Modern roe deer have the smallest home range size of the ungulates studied here and can have short-distance (<20 km) or no seasonal migrations; although there are rare cases of roe deer migrating more than 120 km (Cagnacci et al., 2011; Mysterud, 1999; Mysterud et al., 2012; Wahlstrom and Liberg, 1995). Given that the sea spray affect in sulfur can be visible up to 100 km inland, long distance migrations would not be required for a more westerly 'coastal' signature to be seen in the bones of these animals. Today, Pech de l'Azé IV is approximately 120 km away from the coastline which is at the maximum distance of known roe deer migration. Because there is a low range of δ^{34}S values, roe deer likely were not spread over landscape with varying δ^{34}S values, instead their range was likely restricted as a group to areas of relatively enriched δ^{34}S, such as those found in the coastal plains to the west or in lithological areas with enriched δ^{34}S that are not yet identified in the isoscape, like the red deer. Based on these results, roe (and red) deer could have had a range that incorporated regions at, or near, the sites where they were eventually found but likely incorporated areas closer to the coastal plains to the west. Changes in sea level from MIS 5 to MIS 4 and thus increase in the distance to coastline from the sites, might also explain part of the enriched δ^{34}S signal of roe and red deer. Alternatively, these species may have been hunted in areas closer to the coastline and transported back to sites by Neanderthal hunters.

6.2. *Diachronic trends*

Isotopic values for bovine and red deer are the most stable through time, with only δ^{13}C values being slightly higher in the Quina compared to Ante-Quina in red deer. This could suggest a stable ecological and dietary range through time (as previously argued on the basis of dental microwear texture analyses by Berlioz et al., 2023), however as the temperature decreases from MIS 5 to MIS 4 (or early MIS 3 at RDM) and the faunal and archaeological records change through time (Discamps and Royer, 2017), this stability in isotopic values could also be indicative of the adaptability of these fauna as mixed feeders, as seen at Les Cottés (Britton et al., 2023b), or the capacity of Neanderthal hunters to pursue similar hunting grounds in the landscape surrounding the sites (cf. Berlioz et al., 2023). The limited isotopic variation in bovines through time, further supports the grouping of *Bos* and *Bison* in isotopic Late Pleistocene southwestern France, although further studies which can identify highly fragmented bones to species level using aDNA or SPIN may be able to tease out dietary and habitat differences between the two species (Rüther et al., 2022; Smith et al., 2024a).

We observe more significant changes in isotopic values in horses, who are grazers with less dietary flexibility. In the Ante-Quina, horse δ^{34}S values are significantly higher than in the Quina, δ^{15}N values are lower compared to the Late-Ante Quina, and δ^{13}C values are significantly lower than in later periods. As horses have fewer adaptive traits than bovines and red deer, they may be a more accurate representative of the local environment (Britton et al., 2019, 2023a; Pederzani et al., 2021a). More research is needed before using horses as the local baseline for bone collagen isotopes as these variations could be due to a change in ranging ecology rather than dietary ecology, or Neanderthals changing their hunting patterns. However, as δ^{34}S values between horses (range: 4–12.7 ‰) and bovines (range: 6.7–12.4 ‰), two non-migratory taxa, moderately overlap in the Quina period, this could suggest that these taxa could be representative of local conditions in later periods, especially when a fractionation rate of up to 2.5 ‰ can occur between diet and consumer (Nehlich, 2015). For a better representation of the local baseline for all periods, small mammals from the same levels in the archaeological record should be analysed for δ^{34}S, which could then be used to generate time-sliced isoscapes.

Reindeer isotopic values also change significantly through time. δ^{13}C values are the most enriched in the Late Ante-Quina suggesting more lichen consumption. δ^{15}N values decline through time from the Ante-Quina and are significantly lower in the Quina than both other periods potentially indicating movement to colder and drier climates. Finally, δ^{34}S values are also significantly lower in the Quina compared to the Late Ante-Quina, which could be the result of reindeer moving to areas with lower δ^{34}S values due to a drop in temperature, and potentially even moving to areas with permafrost. As reindeer are the only species with δ^{34}S values below 4 ‰ in the Quina, it is unlikely that this is indicative of local δ^{34}S values significantly dropping but rather changing spatial ecology or a change in δ^{34}S values in the areas which reindeer range. ^{87}Sr/^{86}Sr isotope analysis between the different sites and periods could help to identify whether the difference is due to ranging ecology.

6.3. *Integrating ZooMS data*

In light of the isotopic results, it appears that throughout the three periods studied, Neanderthals hunted three different groups of game who occupied different spatial isotope niches. These include red and roe deer who potentially lived to the west of the sites or in areas with enriched δ^{34}S; horses and bovids who may have lived in the landscape surrounding the sites (which potentially overlapped in the Quina periods); and reindeer who have the largest isotopic niche throughout time, suggesting they are moving across the landscape and have large variation in their individual movements, similar to modern herds. These three groups have been identified using a combination of approaches including zooarchaeological identification, ZooMS, and isotopic analysis.

It is important to note that here, without the use of ZooMS to confirm species identifications assigned through morphological analysis, the species-specific isotopic differences – particularly amongst the cervids – would not be as distinct. This in turn could have led to significantly different interpretations of the overall data, i.e. that deer behaviour was more plastic and that isotope niche partitioning between species (in terms of their spatial ecology) was not as pronounced (Figs. 5 and 6). This highlights the strengths of isotope analyses in ungulate behavioural ecology, and the ability of these approaches in niche space analysis. The findings also highlight the importance of using multiple complementary tools in palaeoecology and advocates for their use in an iterative way, where a set of results may lead to the need for further analyses *post-hoc*. The strength of zooarchaeological analyses was vital to both designing the isotopic sampling strategy and to data interpretation. The integration of biomolecular methods, such as ZooMS, may be particularly important at sites/in specific periods where certain taxa may be morphologically distinct from contemporary reference examples (e.g., the large roe deer found in Late Pleistocene France); where faunal remains endured intense fracturing for marrow extraction (e.g., as in the case of most Mousterian assemblages); where unusual faunal suites are suggested from morphological analyses; or, conversely, to ensure wider representation of taxa in what otherwise might appear to be mono-specific assemblages (e.g., to help overcome 'reindeer blindness' at cold-phase sites) (Smith et al., 2024b). Future studies which want to further distinguish *Bos/Bison* and *Cervus/Megaloceros/Dama/Alces/Saiga* may benefit from higher resolution identification techniques, such as aDNA or shotgun proteomics (e.g. Jensen et al., 2020; Rüther et al., 2022; Smith et al., 2024a).

6.4. *Implications and future work*

The results from this study suggest that palaeofaunas with likely large ranging ecologies (and potentially long-distance migrations) may demonstrate distinct δ^{34}S values from fauna with smaller ranging ecology (and short distance, partial, or no migrations) but also demonstrate a greater range of δ^{34}S values. These differences are apparent in spatial partitioning modelling, suggesting that fauna with large home ranges will have a larger isotope core area and a wider range of δ^{34}S values than others.

Limited ^{87}Sr/^{86}Sr analysis on ungulates at some of the sites included in this study indicate the generally limited movement of bovines, roe deer and horses (albeit to some upland areas), but also that reindeer

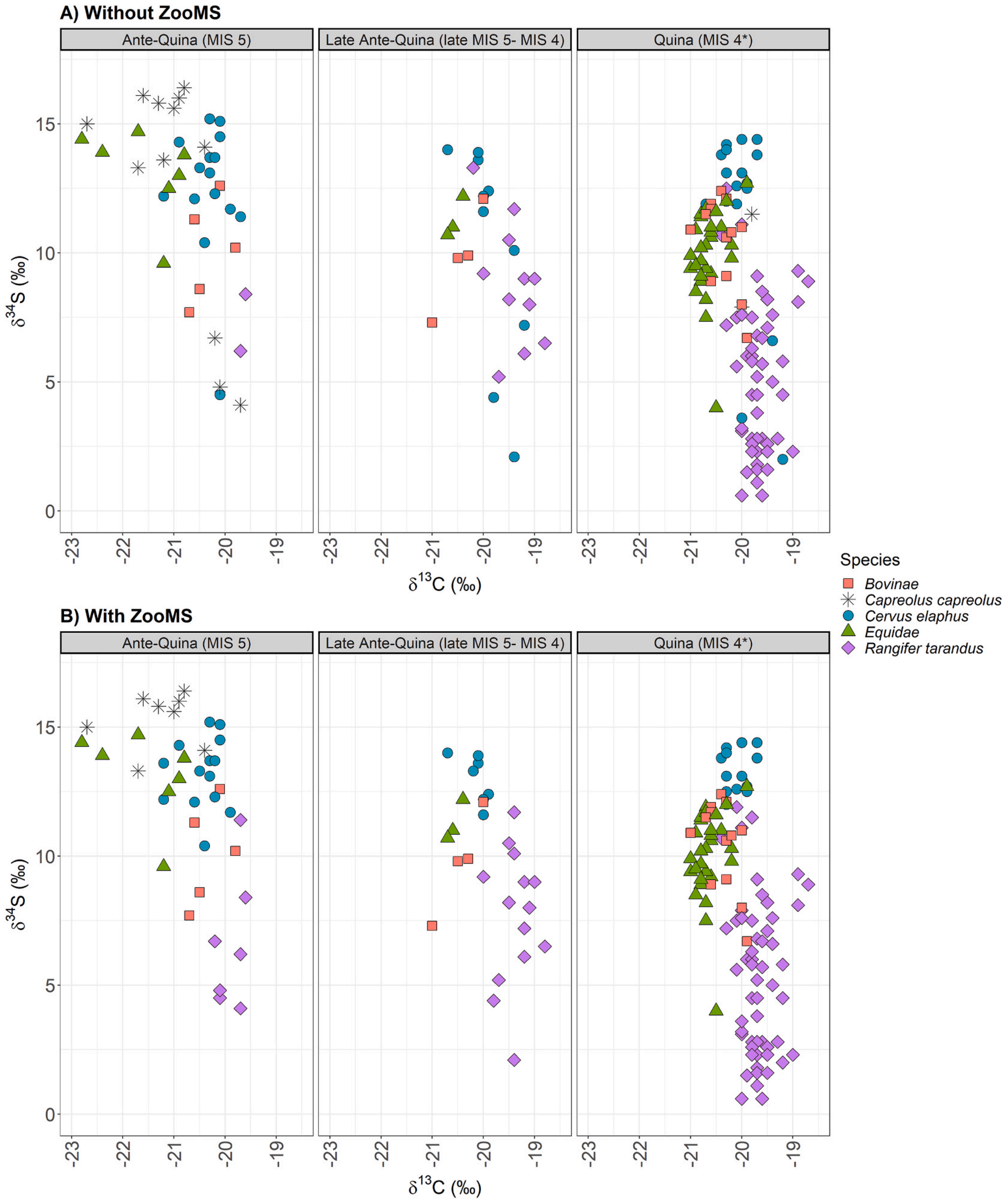

Fig. 5. Scatter plot with δ^{13}C along the x-axis and δ^{34}S along the y-axis before and after ZooMS analyses. A) represents the δ^{13}C-δ^{34}S isotopic results based on taxonomic identification of ungulates across three time periods. B) shows the same δ^{13}C-δ^{34}S isotope results after ZooMS analysis of all cervid bones. Red squares represent bovines, green triangles are horses, light blue circles are red deer, purple diamonds are reindeer, and black asterisks are roe deer. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mobility was restricted to areas of sedimentary lithology (Hodgkins et al., 2024). By integrating these results with the findings of the current study, we can perhaps tentatively suggest that the areas traversed by reindeer included not only the Aquitaine Basin but sedimentary basins to the north. Further, higher resolution ^{87}Sr/^{86}Sr analysis of *Rangifer* specimens from both Aquitaine and the Paris Basin will be important to understanding how these two isotopes can be used together to maximise insights into Late Pleistocene *Rangifer* ranging behaviours. Furthermore, by undertaking regional studies, rather than site by site studies, we can have a better overview of faunal ecology both spatially and temporally. This will be especially significant where specimens can be directly dated using radiocarbon dating (i.e. after ~46 ka), increasing the sample sizes that can be achieved at single sites and helping to discount site-specific human behaviours that may influence the makeup of specific assemblages.

In this study, there were also some indications of changing climate alongside potential dietary and spatial ecology adaptations to cope with that climate change in the faunal isotope dataset. To better understand if these variations in isotopes through time are due to changes in climate, dietary or spatial ecology, it would be beneficial to analyse further herbivores dating to period of extreme climate change such as the Late Glacial Maximum and Late Glacial, as has been highlighted by previously-published studies (Drucker et al., 2003a, 2003b, 2011a, 2011b; Drucker and Fontana, 2024; Reade et al., 2023; Richards and Hedges, 2003). Incorporating sulfur isotope analyses in such studies in the future will allow an examination of how δ^{34}S values vary between interglacial and extreme glacial environments (perhaps due to permafrost, see Reade et al. (2020a, 2020b) and Stevens et al. (2022)), and the

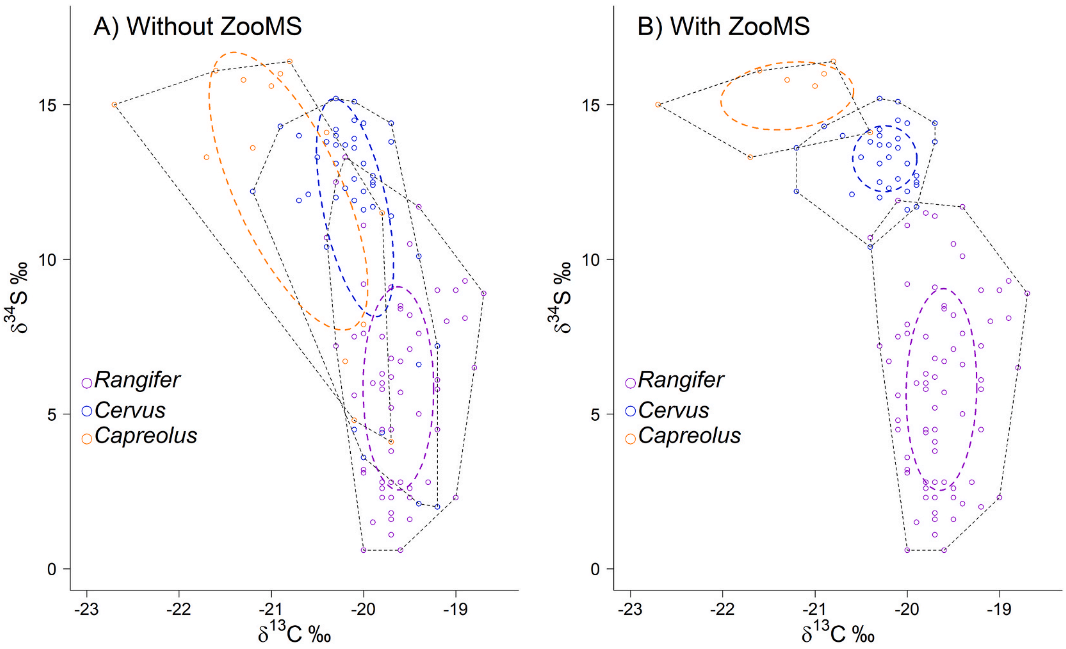

Fig. 6. Spatial niche partitioning of δ^{13}C-δ^{34}S for cervids through time before and after ZooMS analyses. The grey dashed lines represent the convex hull of each species, and the thicker dotted coloured line represents the core area (SEAc) which is approximately 40 % of each species. A) represents taxonomic identification of deer across three time periods. B) shows the same data after ZooMS analysis of all cervid bones.

interactions between climate change, and faunal dietary and ranging palaeoecology.

Analysing other species, such as carnivores and small fauna, throughout the Pleistocene will also provide us with better insights into food webs which will ultimately help us better understand early human behaviours and living landscapes. Such datasets, especially those including small animals (e.g., rodents, lagomorphs) with restricted home ranges, are integral to helping construct time-sliced maps of landscape-level variability in environmental δ^{34}S, which are essential for assigning spatial distributions to collagen δ^{34}S values of larger animals. Integration of faunal isotope datasets with other climatic and environmental proxy datasets will also help to disentangle isotopic variations due to 'baseline' changes (e.g., extent of permafrost, aridity, etc.), to faunal behaviours modifications (e.g., dietary changes, expansion of home ranges), or even to better understand the relationship between the two.

This research has also demonstrated the advantages of integrating complementary methods such as zooarchaeological studies, isotopic analysis, and ZooMS for palaeoecological interpretations. Here, we based our sampling strategy on robust zooarchaeological identification (85.6 % accuracy in cervids, as confirmed by molecular techniques). After initial isotope results there was a large overlap in deer isotopic spatial niche space, which was resolved through *post-hoc* ZooMS analysis. This shows the benefit of combining these three methods, whether during the sampling stage when there are difficulties in morphologically identifying multiple related species (e.g., cervids) or *post-hoc* for isotopic data interpretation. The triple-method, iterative approach employed in the current study has enhanced our ability to reconstruct Pleistocene living landscapes and better understand ungulate palaeoecology and is recommended for future studies.

7. Conclusion

As our understanding of sulfur isotopes further develops, and sulfur becomes more frequently analysed alongside carbon and nitrogen in bone collagen, we anticipate that sulfur will become increasingly useful in exploring spatial partitioning and the movements of past fauna and humans in both archaeology and palaeontology. The results of this study show that fauna with large home ranges, such as reindeer, may not only have distinct δ^{34}S values from other taxa but may also have larger δ^{34}S variation than taxa with small home ranges who are also likely non-migratory. In this study, we have shown evidence for this at three Late Pleistocene sites in southwest France, where reindeer have the largest range of δ^{34}S values and subsequently the largest plotted core areas on multi-isotope Bayesian ellipse plots (representative of isotopic niche partitioning) compared to other contemporary cervids, bovines, and horses. When analysed through time, δ^{34}S values did not change for majority of small-ranging taxa likely due to the lack of permafrost in this area of south-west France during the Late Pleistocene, while reindeer δ^{34}S values did decrease in colder periods potentially reflecting the incorporation of areas containing more extensive permafrost into their ranges at these times. In contrast to reindeer, red and roe deer have the smallest range of δ^{34}S values as well as the highest values suggesting the ranges of these animals may have included areas to further to the west/closer to the coast (and thus bearing elevated environmental δ^{34}S values due to a marine influence) or possibly ^{34}S-enriched areas of lithology in the broader region which have yet to be characterised. Finally, although δ^{34}S values measured in horses and bovines are typically similar to one another, demonstrate less intra-species variation than reindeer, and are assumed to represent more local values, determining what those local values should be remains difficult.

In addition to further studies on ungulates and other megafaunal taxa, studies focused on characterising past landscape variability in environmental δ^{34}S are required, for example, incorporating microfauna or other species with likely small home ranges (e.g., rodents, lagomorphs) to produce period-specific maps of baseline variability. Combining palaeoecological, paleoenvironmental, and palaeoclimate studies will further help illuminate the ranging behaviours and dietary palaeoecology of ungulates in the Late Pleistocene, how these species interacted with past climatic changes, and how these behaviours intersected with the socio-economical organisation of past human populations.

Author contribution

Sarah Barakat: Conceptualisation, data curation, formal analysis, investigation, methodology, visualisation, writing- original draft, writing-reviewing and editing **Elodie-Laure Jimenez**: Conceptualisation, data curation, investigation, methodology, writing-review and editing **Raija Katarina Heikkilä**: Data curation, investigation, methodology, writing-review and editing **Aurélien Royer**: Formal analysis, resources, writing-reviewing and editing **Jamie Hodgkins**: Resources, writing-reviewing and editing **Laura Niven**: Resources, writing-reviewing and editing **Marie-Cécile Soulier**: Resources, writing-reviewing and editing **Susan Lagle**: Resources, writing-reviewing and editing **Christelle Dancette**: Resources, writing-reviewing and editing **Teresa E. Steele**: Resources, writing-reviewing and editing **Jean-Christophe Castel**: Resources, writing-reviewing and editing **Shannon McPherron**: Resources, writing-reviewing and editing **Jean-Jacques Hublin**: Resources, writing-reviewing and editing **Karen Ruebens**: Investigation, methodology, supervision, writing – review and editing **Emmanuel Discamps**: Funding acquisition, investigation, supervision, resources, writing-review and editing **Kate Britton**: Conceptualisation, funding acquisition, investigation, methodology, project administration, supervision, writing- original draft, writing-review and editing.

Declaration of competing interest

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

Acknowledgements

Funding for isotopic and proteomic analysis was funded by PleistoHERD (ref: RPG-2017-410), Leverhulme Prize (ref: PLP-2019-284), DeerPal (ANR-18-CE03-0007), and the University of Aberdeen. Zooarchaeological morphological analysis at Pech de l'Azé IV was funded in by the Max Planck Society and the Archaeological Research Centre and Museum for Human Behavioural Evolution (Neuwied, Germany). Sampling permits were given to E.D. and E.L.J. by the Conseil Départemental de Dordogne (Roc de Marsal), and the Musée National de la Préhistoire des Eyzies (Roc de Marsal, Combe Grenal, Pech de l'Azé IV). We thank UKRI (NERC QUADRAT DTP studentship ref: NE/S007377/1 to SB; ERC-selected/EPSRC-funded project ref: EP/Y023641/1 to KB) for salary support during production of this manuscript. We would like to thank Pauline Raymond at the Collège de France for her help with ZooMS sample preparation, and Emmanuelle Demey-Thomas and Joelle Vinh at the ESPCI Paris for their assistance with the MALDI-TOF mass spectrometry, Orsolya Czére (Aberdeen) for assistance with collagen extractions, and the staff from the Musée National de la Préhistoire for their help during initial sampling of faunal collections. We would like to thank Mael Le Corre for his assistance with statistical analysis and model building. We would also like to thank Clément Bataille for his random forest R code to help rebuild a cropped version of the modern sulfur isoscape.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2025.109744.

Data availability

The isotopic and ZooMS data are available in Supplementary Tables 1 and 2. The ZooMS spectra are available in mzxml format on Zenodo: https://zenodo.org/records/17738202. Access to codes to build the figures can be made available upon request.

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