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Bones and teeth isotopes as archives for palaeoclimatic, palaeoenvironmental and palaeoecological data

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ABSTRACT

This review paper explores the contribution of the stable isotope analysis of mammalian bones and teeth to the study of palaeoclimate, palaeoenvironment, and palaeoecology. These skeletal remains, composed of both organic and inorganic materials, preserve isotopic signals that reflect an organism's dietary habits and other behaviours, as well as environmental, and climatic conditions during an animal's lifetime. Here, we discuss how carbon, nitrogen, sulfur, oxygen, hydrogen, strontium, and zinc isotopes in bones and teeth have been used to reconstruct past changes in temperature, precipitation, aridity, permafrost, vegetation, seasonality, and animal diet and mobility. We identify areas where understanding is limited and suggest avenues for future research. Additionally, we highlight how information from different isotopes and tissues can be integrated with archaeological findings to assess the impact of environmental shifts on animal behaviour and ecosystems, offering a deeper understanding of human-animal interactions throughout (pre)history. Ultimately, stable isotopes in bones and teeth serve as more than just palaeo-proxies; they offer insights into human and non-anthropogenic impacts on ecosystems, and help establish baselines for contemporary conservation, ecosystem restoration and rewilding policies and practices.

1. Introduction

Mammal bones and teeth are skeletal hard tissues that are chemically resistant to decomposition. Under favourable conditions, they can preserve for long periods of time, often thousands (or even millions) of years. On a fundamental level, the suite of faunal species within the skeletal fossil record can provide broad environmental information. Species have different environmental tolerances; thus, the presence and absence of 'warm' or 'cold' adapted species in the fossil record can inform on the local conditions and past shifts in mammal biogeography (e.g. Schreve, 1998). However, the study of isotopes in faunal remains found in palaeontological contexts (isotope palaeontology) can provide us with more direct, empirical insights into the climates and environments of the past. This can yield information about the behaviours of those animals, and therefore illuminate their palaeoecology. With mammals often being central to human subsistence, the accumulated vertebrate fossil record at archaeological sites also represents the procurement strategies, decisions and behaviours of past human groups. Thus, the isotopic analysis of bones and teeth found at archaeological sites (isotope zooarchaeology) also represents a powerful means of accessing information about environmental conditions contemporary to the human activities that produced these remains and at a geographical scale relevant to the human experience - a rare trait for palaeoenvironmental archives. While bones and teeth rarely provide any kind of continuous record over time, data from these materials can be combined with additional chronological parameters from site stratigraphy or radiometric dating which can enable longer, integrated time sequences to be created. These local records, directly linked to the period of human activity, can be placed in the context of regional and global records.

Mammal bones and teeth, although complex materials, are well defined through metabolic processes, with their isotopic composition being directly determined by what the animal eats or drinks and the biological processes that occur within the mammal (Hedges et al., 2006). The link to climate is a broad one, with the isotopic composition of an animal's tissues influenced by both the animal's dietary choices and by the isotopic composition of the biosphere at the locality occupied

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by the animal (e.g., the 'baselines' of local plants or drinking water isotopic values). Compared to the plants and water sources, animal skeletal remains have the advantage of biologically averaging local and temporal variations during the period of tissue formation, providing a less noisy signal (Hedges et al., 2004). Isotope analysis of skeletal remains can focus on either the inorganic mineral (bioapatite) or organic (protein) components of palaeofaunas. Inorganic bioapatite makes up ~60 % of bone, ~95 % of enamel, ~70 % of dentine, and ~56 % of antler (Nanci and Ten Cate, 2008; Nowicka et al., 2006). Bioapatite differs from pure mineralogical apatite in that it contains many other substituted ions, such as carbonate which can exchange with the phosphate group, fluoride which can exchange with OH^-, or Sr^{2+} which can exchange with Ca^{2+} (Hedges et al., 2006). Enamel bioapatite has a well-developed crystalline lattice with extensive ionic substitutions, whereas bone and dentine bioapatites have fewer ionic substitutions, and their crystallites are smaller and more distorted (Driessens, 1980; Fernandes et al., 2023). Enamel bioapatite is generally considered to be more resistant to diagenesis than bone and dentine bioapatite due to its crystalline structure, the orientation and size of the crystallites, its density/lack of porosity and very low organic content (Lee-Thorp, 2008; Sponheimer and Lee-Thorp, 2006). Organics (primarily collagen type I) make up ~20–30 % of bone and dentine, and ~44 % of antler (Ambrose, 1990; Kendall et al., 2018; Nanci and Ten Cate, 2008; Nowicka et al., 2006; Trotter and Hixon, 1974; van Klinken, 1999). Collagen molecules are made from a triple helix—three strings of amino acid chains twisting around each other. The molecules are organised into structured microfibres, which serve as a matrix for the deposition of bioapatite. Preservation of collagen is dependent on a combination of burial environment conditions (temperature, soil moisture, pH, etc) and time, with cooler temperate conditions generally resulting in better preservation than hot and arid conditions. The collagen is largely protected from microbial and chemical attack so long as the matrix remains unaltered (Collins et al., 2002). Isotope analysis of collagen has been undertaken on specimens >300,000 years old (Jones et al., 2001; Kuitems et al., 2015). However, the material extracted from archaeological bone or dentine is rarely unaltered and so some authors use the term 'collagen' when referring to diagenetically altered extracted degraded archaeological material (Brock et al., 2013; DeNiro and Weiner, 1988). Indeed, although commonly used extraction protocols normally result in the inclusion of other minor protein components in extracts, even from modern bones, the term 'collagen' is widely used to refer to extracts from bulk protein from modern or archaeological bones.

While some isotopes can be analysed in both the organic and inorganic components of skeletal remains, their isotopic compositions are often not equivalent due to different processes involved in the formation of the different materials, different tissue structures, and their differential resistance to diagenesis. Furthermore, different skeletal tissues form over different periods in an animal's time-of-life, with some remodelling continuously after initial formation while others remain largely biologically inert after growth and mineralisation. Bone grows relatively slowly and continues to remodel throughout an individual's life. As a result, the isotopic composition of bone likely reflects a long-term average of the body's isotopic pool. However, certain bones, such as ribs, have faster turnover rates and may, therefore represent a more recent period before death (<5 years). In contrast, bones with a slow turnover rate, like femurs, may represent a significantly longer period before death (>10 years) (Cox and Sealy, 1997; Fahy et al., 2017; Hedges et al., 2007). Different teeth develop at different ages of life and grow over a finite time frame. Tooth development advances from the crown to the root and dental tissues do not remodel after formation. Thus, teeth record and preserve time series of isotopic variations in the mammal over the period of the tooth formation. Bulk samples of enamel or dentine spanning the entire length of the tooth growth axis provide an averaged representation of isotopic inputs throughout the formation period (Fricke and O'Neil, 1996; Reade et al., 2015; Sharp and Cerling, 1998), minus any portions of the tooth lost to wear, which can be common in ungulates in particular. Serial sampling enables time series of isotopic variations to be constructed, providing high resolution information potentially at a subannual scale over multiple years (depending on the formation time of the tooth in question). Tooth enamel formation occurs in two main stages: initial formation of a more organic-rich tissue matrix, and subsequent full mineralisation in the maturation stage. During the process of enamel maturation, the organic matrix is gradually replaced with inorganic minerals, with 75 % of the total mineral content added during this stage (Passey and Cerling, 2002; Tafforeau et al., 2007). Once the enamel is fully mineralised, it does not remodel (Dean, 1987). The progressive and extended process of mineralisation can result in a time-averaging of temporal signals, which serves to dampen the isotopic variation seen in the tooth compared to known values of ingested food and/or water (Passey and Cerling, 2002). This is especially the case because enamel maturation does not necessarily follow the same geometry or match the discrete increments of initial deposition, making it impossible to sample true biological increments corresponding to particular times of enamel formation (Balasse, 2002; Green et al., 2017; Zazzo et al., 2005). Like enamel, dentine forms incrementally, with a collagenous organic matrix being deposited then mineralised, but mineralisation is generally more instantaneous than in enamel (Kahle et al., 2018; Nanci, 2003). Primary dentine does not remodel, thus, as for enamel, a time series of isotopic variations is recorded in its increments across the period of tooth formation and mineralisation. For the purposes of palaeoenvironmental reconstruction and in palaeoecological studies, research tends to focus on mammals with high-crowned teeth such as horses and bovids (e.g. Balasse et al., 2012; Reade et al., 2015; Britton et al., 2019; Pederzani et al., 2024b; 2021a). Although their crowns are elongated, maximising time-series information, the dentine in high-crowned teeth grows at an angle to the vertical axis (Díez-Canseco and Tornero, 2024; Hillson, 2005). This presents challenges when trying to isolate dentine increments during a sequential sampling, however, certain sampling methodologies can reduce, but not eliminate, the damping and time-averaging of the temporal isotope signal from dentine (Díez-Canseco and Tornero, 2024). Depending on the species, tooth selected and periodicity of tooth growth, single teeth from high-crowned taxa may be sufficient to provide isotopic data spanning a year or several years. However, isotopic data from low-crowned species may represent a more restricted period of growth and several teeth may be required from the same specimen to reconstruct an annual isotopic input profile (e.g. with red deer and reindeer/caribou, Britton et al., 2009; Stevens et al., 2011). Antlers, such as those found on red deer and reindeer, grow very rapidly over a few months, do not remodel and are shed annually. Thus their isotopic composition reflects the body's isotopic pool over a short time period and will be seasonally biased (Royer and Somerville, 2023; Schwartz-Narbonne et al., 2021; Stevens and O'Connell, 2016). As with teeth, serial sampling of antler enables a time series of isotopic variations to be constructed, potentially providing information about the animal's movement, diet and water intake and ontogenetic variation in metabolism (Armaroli et al., 2024; Stevens and O'Connell, 2016). The timing of bone and tooth development may differ slightly between biological sexes for some species, but behavioural differences are more likely to result in greater isotopic differences between males and females. Sexual dimorphism is much greater for some species when it comes to the timing of antler growth, e.g. reindeer (Espmark, 1971; Høymork and Reimers, 1999), which will result in a different seasonal bias in their isotope values.

When conducting isotope analysis of mammal skeletal remains for palaeoclimatic, palaeoenvironmental, and palaeoecological reconstructions, it is important to carefully select the tissue type and material that will yield the necessary isotope information to address the research question. Whilst climatic and environmental parameters influence the isotope composition of herbivores, omnivores and carnivores, herbivores are most often favoured for palaeoclimatic and palaeoenvironmental reconstruction studies. The reasons for this are twofold. Firstly, herbivore isotopic composition more directly tracks either the impact of climatic and environmental changes via plants, or herbivore behavioural responses to these changes, while carnivore and omnivore isotopic composition tracks these influences on herbivores one step removed. Secondly, the additional, and potentially complicating factor of variations in trophic level enrichment in carnivore diets are avoided. For these reasons, we will focus our discussion largely on herbivores rather than carnivores and omnivores, and have not included details of trophic reconstruction in this review. However, we note that some have argued that carnivores may be better proxies than herbivores for palaeoenvironmental reconstruction as they integrate the isotopic variation seen at lower trophic levels (Luyt and Sealy, 2023). Furthermore, one should be aware that faunal isotope data provides information at different scales depending on the size of the animal, its typical home-range size (i.e. its spatial ecology), and its lifespan (although these factors may also, in themselves, become the focus of research efforts using isotopes). It is also imperative to consider the typical ecological niche and physiology of a taxon: for example, in studies that utilise oxygen or hydrogen, it is important to understand whether a species is likely to be an obligate drinker, or to gain all its water from its food. However, in order to infer differences in climatic and environmental conditions based on mammal isotope signatures, it is also necessary to consider not only the factors that influence their isotope values, but the extent to which these values vary within a specific taxon at a single location. Detecting small-scale climatic/environmental changes is only possible when the variances between samples are low (Ugan and Coltrain, 2011) or studies must take into account a large inter-individual variability. Additionally, one must consider the potential influence of diagenesis on the isotopic integrity of the material being analysed. Here we outline the contribution that isotope analyses of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), sulfur ($\delta^{34}S$), oxygen ($\delta^{18}O$), hydrogen ($\delta^{2}H$), strontium ($^{87}/^{86}Sr$), and zinc ($\delta^{66}Zn$) of faunal remains can make to palaeoclimate, palaeoenvironment and palaeoecology studies in the terrestrial biosphere.

2. Carbon isotopes

Carbon isotope analysis has been the backbone of isotope archaeology/palaeontology for nearly 50 years (van der Merwe and Vogel, 1978; Vogel, 1978; Vogel and Van Der Merwe, 1977). There are two stable isotopes of carbon (^{13}C and ^{12}C), and the ratio of ^{13}C to ^{12}C (commonly expressed as $\delta^{13}C$) has been extensively measured in skeletal remains. Carbon isotopes can be measured in the organic phase (bone or dentine collagen) and mineral phase (bone or enamel bioapatite) of mammal skeletal remains. Although collagen $\delta^{13}C$ can be preserved for many thousands of years (Britton et al., 2012; Flower et al., 2021; Jones et al., 2001; Stevens and Reade, 2021), it is necessary to ensure the isotopic compositions measured are representative of *in vivo* carbon isotope composition. The isotopic integrity of collagen is routinely assessed using the molar C:N ratios, collagen yield, and percentage of C and N as quality control criteria based on the elemental composition of modern mammalian collagen (Ambrose, 1990; DeNiro, 1985; Guiry and Szpak, 2021). The mineral phase of bone and enamel bioapatite also undergo diagenetic alteration, but the extent of this alteration varies significantly between these different tissues (and the moieties analysed) due to differences in the structure of the material and conditions of burial. For example, bone is highly susceptible to *post mortem* diagenetic alteration of its carbonate $\delta^{13}C$ composition, while enamel is more resistant (Kohn and Cerling, 2002; Lee-Thorp and van der Merwe, 1991; Wang and Cerling, 1994). As a result, enamel can potentially preserve the original carbonate $\delta^{13}C$ composition even after hundreds of millions of years (Lee-Thorp, 2002; Macfadden and Cerling, 1996). While a range of techniques have been suggested for assessing the extent of *post mortem* diagenetic alteration and the isotopic integrity of bone bioapatite $\delta^{13}C$ values, there are no agreed quality control criteria (see methodological discussions in Beasley et al., 2024; Chesson et al., 2021; Dal Sasso et al., 2018; Fernandes et al., 2023; Garvie-Lok et al., 2004; Person et al., 1995; Schoeninger, 1982; Shipman et al., 1984; Smith et al., 2007). Many researchers have therefore avoided working on bone bioapatite $\delta^{13}C$, favouring enamel instead, although some still argue valuable insights can be gained from bone bioapatite $\delta^{13}C$ (Clementz et al., 2009; Lee-Thorp, 2008; Lee-Thorp and Sponheimer, 2003).

Carbon isotopes in mammals analysed in either the mineral or organic phase reflect the $\delta^{13}C$ of the diet consumed, but isotopic fractionation occurs between diet and different tissues due to their formation processes, nutrient routing, and their different biochemical compositions. Thus bone collagen and bone/enamel carbon $\delta^{13}C$ values are not directly interchangeable (Ambrose and Norr, 1993; Codron et al., 2018; Krueger and Sullivan, 1984; Lee-Thorp et al., 1989). Due to protein routing within the mammalian body, collagen $\delta^{13}C$ primarily reflects the $\delta^{13}C$ of dietary protein (Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Fernandes et al., 2012), with dietary protein contributing at least three fifths of carbon atoms from intact amino acids (Froehle et al., 2010). However other dietary macronutrients may also affect collagen carbon, such as fats and carbohydrates (Froehle et al., 2010). The offset between diet and collagen $\delta^{13}C$ is around 5 ‰ (Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; van der Merwe and Vogel, 1978). Mammalian $\delta^{13}C$ values also show a small ~1–~2 ‰ increase with trophic level in tissue to tissue comparisons, but this can vary with species, tissue type, age, growth rate and food quality (Bocherens and Drucker, 2003; Caut et al., 2008, 2009; Krajcarz et al., 2018). Bone mineral and enamel $\delta^{13}C$ reflects the entire diet's $\delta^{13}C$ composition, which includes carbohydrates, lipids, and proteins. This is because it is precipitated in isotopic equilibrium with blood bicarbonate (Ambrose and Norr, 1993; Jim et al., 2006; Krueger and Sullivan, 1984; Passey et al., 2005b; Tieszen and Fagre, 1993; Tejada-Lara et al., 2018). The diet to carbonate $\delta^{13}C$ offset is thought to range between +10 ‰ and +14 ‰, with variation caused by body mass and dietary physiology (Ambrose and Norr, 1993; Cerling and Harris, 1999; Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Passey et al., 2005b).

Bone and tooth $\delta^{13}C$ values reflect climatic and environmental conditions as mammal $\delta^{13}C$ is determined by diet, which ultimately reflects the photosynthetic pathway of plants at the base of the food chain, along with the broader environmental and climatic parameters that influence photosynthesis and plant growth. The two main photosynthetic pathways result in substantially different plant $\delta^{13}C$ values. C3 plants (e.g. trees, shrubs, herbs, and temperate grasses) utilise the Calvin–Benson cycle directly for carbon dioxide fixation, and this process strongly discriminates against ^{13}C, resulting in plant $\delta^{13}C$ values of ~ −37 ‰ to −20 ‰ (Farquhar, 1983; Kohn, 2010; O'Leary, 1988). In C4 plants (including tropical grasses and many sedges), which fix carbon through the Hatch Slack cycle, there is less discrimination against ^{13}C, resulting in plant $\delta^{13}C$ values of ~ −16 ‰ to −10 ‰ (Farquhar, 1983; O'Leary, 1988). Variation in C4 plant $\delta^{13}C$ is partially linked to the leakiness of carbon from bundle sheath cells (Cernusak et al., 2013). Plants following the crassulacean acid metabolism (CAM), mostly succulents and bromeliads, occupy an intermediate position in carbon isotope space (Farquhar, 1983; Kohn, 2010; O'Leary, 1988). The C3 pathway, used by the majority of plants, is prevalent in relatively cooler and humid environments. The C4 plants pathway, used by a minority of plants, is prevalent in higher temperature and relatively arid environments, and evolved 24–35 million years ago million years ago (Sage, 2004). C4 plants commonly occur in warm tropical environments and were largely absent from Europe until the introduction of C4 crops such as millet during the Holocene. CAM plants are uncommon, and primarily found in arid and semi-arid regions.

As plants get their carbon from atmospheric CO_2 this exerts a substantial control on plant $\delta^{13}C$. Both the concentration of atmospheric CO_2 and its $\delta^{13}C$ have changed over time. For example, during the last glacial maximum (~20,000 years ago) the atmospheric CO_2 concentration was 160–200 ppm, rising to 275 ppm by the start of the Holocene (~10,000 years ago (Polley et al., 1993)). Along with lower CO_2

concentration during the last glacial period, atmospheric CO_2 $\delta^{13}C$ ranged between ~ −7 ‰ and −6.4 ‰ (Eggleston et al., 2016). Since the start of the industrial revolution, atmospheric CO_2 concentration has risen from ~280 ppm to ~425 ppm at the time of preparing this chapter (April 2024), and the $\delta^{13}C$ of the atmospheric CO_2 has shifted from ~ −6.5 ‰ to ~ −8.4 ‰ due to the release of ^{13}C depleted CO_2 into the atmosphere from organic sources (i.e., fossil fuel combustion, also referred to as the 'The Suess Effect') (Francey et al., 1999; Friedli et al., 1986; Graven et al., 2020; Keeling, 1979). As with the application of most methods that use proxies, the interpretation of bone and tooth $\delta^{13}C$ values are based on our understanding of the relationship between climatic and environmental parameters and faunal $\delta^{13}C$ today, and therefore many studies seek to compare archaeological or palaeontological faunal $\delta^{13}C$ values with those of modern populations. Therefore, where such comparisons are made it is necessary to apply a correction for the Suess Effect (Bump et al., 2007; Dombrosky, 2020; Long et al., 2005).

As well as having different $\delta^{13}C$ due to their distinct photosynthetic pathways, the tissue $\delta^{13}C$ of both C3 and C4 plants is influenced by environmental and climatic parameters. The wider range of plant $\delta^{13}C$ in C3 plants suggests that they are more susceptible to environmental influences than C4 plants (O'Leary, 1988). Water availability, latitude, altitude, light intensity and salinity have all been shown to influence C4 plant $\delta^{13}C$, although the relationship in not always simple or linear (An et al., 2015; Bowman et al., 1989; Buchmann et al., 1996; Ghannoum et al., 2002; Kromdijk et al., 2008; Lightfoot et al., 2020; Ubierna et al., 2013; Wang et al., 2008; Weiguo et al., 2005). For C3 plants, positive correlations have been observed between plant $\delta^{13}C$ and factors such as light availability, nutrient levels, salinity, and water use efficiency, while a negative correlation is typically seen with water availability (Dawson et al., 2002; Diefendorf et al., 2010; Heaton, 1999; Hill et al., 1996; Kohn, 2010; Marshall et al., 2007; O'leary, 1995; Sparks and Ehleringer, 1997; van Groenigen and van Kessel, 2002; Yakir and Israeli, 1995). While there are both positive and negative correlations with temperature, on a global scale, plant $\delta^{13}C$ tends to show a stronger dependence on mean annual precipitation (MAP), with a nonlinear increase in $\delta^{13}C$ values with decreasing MAP (Diefendorf et al., 2010; Kohn, 2010). Variations in $\delta^{13}C$ within and between plant species can be linked to genetic variation, which leads to different responses to the same environmental conditions (Handley et al., 1999; Schleser, 1995; Heaton, 1999).

At a local scale other factors can be dominant. For example, CO_2 partial pressure and temperature collectively can lead to a positive correlation between plant $\delta^{13}C$ and altitude (e.g. Körner et al., 1991), although plant $\delta^{13}C$ does not appear to vary with atmospheric CO_2 concentrations over geological time periods (Arens et al., 2000). High salinity and the associated water stress can influence C3 plant $\delta^{13}C$ values with a positive correlation observed in both halophytic ('salt-loving') and non-halophytic plants (e.g. Guy et al., 1986a, 1986b, 1980; Poss et al., 2000; van Groenigen and van Kessel, 2002). In dense forests the 'canopy effect' can result in ground level plant $\delta^{13}C$ values 2–5‰ lower than those in open environment or leaves growing at the top of the canopy (e.g. Sonesson et al., 1992; van der Merwe and Medina, 1991, 1989; Vogel, 1978). This is the result of a combination of factors that come together under closed forest canopies. There is limited mixing between atmospheric and forest air CO_2 and the isotopically light CO_2 released by decomposing organic matter becomes trapped under the canopy, causing vertical stratification of the forest air $\delta^{13}C$ values. Limited light, nutrients, and water availability, combined with the intake of respired CO_2, further contribute to the depletion of ground-level plant $\delta^{13}C$ values (see discussions in Broadmeadow et al., 1992; Brooks et al., 1997; Buchmann et al., 1997; Schleser and Jayasekera, 1985). The canopy effect is most pronounced in dense forest areas and less significant in open canopy woodlands and at the forest edge, and has been observed in temperate, boreal and tropical forests (Bonafini et al., 2013; Drucker et al., 2008; van der Merwe and Medina, 1989). Low carbon isotope values in animals are commonly interpreted as evidence of them living in woodland settings (Drucker et al., 2008; Bonzani et al., 2024; Gillis et al., 2022; Guiry et al., 2021b; Makarewicz, 2023), however low carbon isotope values are not always observed for animals that are thought to have spent signficant amounts of time in woodlands (Bonafini et al., 2013; Stevens et al., 2006). This can be due to their feeding strategies and excursion of woodland animals onto cultivated land.

In addition to environmental variability, intra-species and intra-plant differences are apparent in $\delta^{13}C$ as well as predictable physiological differences between plant functional types. The $\delta^{13}C$ of different C3 plant organs (leaves, seeds, and branches) can vary by approximately 1–2 ‰ due to various factors. These include the difference in the $\delta^{13}C$ composition of the carbohydrates, lipids, and proteins from which they are formed, as well as physiological parameters such as leaf size, thickness, stomatal density, branch length, and growth rate. The time of year that they grow and the seasonal environmental conditions also play a role in these variations (see Heaton, 1999 for a review). Additionally, C3 plant $\delta^{13}C$ values have been found to increase with age (Donovan and Ehleringer, 1992). Typical natural intra-species $\delta^{13}C$ variability for C3 plants sampled at the same time and from the same area is approximately 0.8 ‰–1.5 ‰ (Heaton, 1999). In tundra and boreal environments, there is a predictable pattern of $\delta^{13}C$ values among different plant species in the same geographical area. Generally, shrub species have lower values compared to herbs (graminoids and forbs), however, there are instances where they overlap and do not differ significantly (Kristensen et al., 2011; Munizzi, 2017). Lichen consistently has higher $\delta^{13}C$ values than C3 plants in the same ecosystem (Ben-David et al., 2001; Maguas and Brugnoli, 1996; Park and Epstein, 1960).

Bone and tooth $\delta^{13}C$ values have been frequently used to investigate past palaeoenvironmental and palaeoclimatic conditions (Arppe et al., 2011; Bocherens et al., 1996; Ecker et al., 2018; Forbes et al., 2010; Lee-Thorp et al., 2007; Lee-Thorp and Beaumont, 1995; Prideaux et al., 2007; Quade et al., 1992; Sealy et al., 2020; Stevens et al., 2014; Stevens and Hedges, 2004; Szabó et al., 2022; Wang et al., 1994), and faunal palaeobaselines may be useful for present day conservation efforts (e.g. Bocherens et al., 2015; Shaikh et al., 2025). The $\delta^{13}C$ values of grazers and mixed feeders (that both graze and browse) have been employed to explore the past distribution of C3 and C4 plants (Lee Thorp and Merwe, 1987; Quade et al., 1992). The former provides information on the distribution of C3 and C4 grasses, while the latter acts as a proxy for the proportion of C3 and C4 plants in the overall flora. Consequently, these palaeoenvironmental reconstructions offer valuable insights into past climatic conditions, as the distribution of C3 and C4 plants is primarily influenced by temperature and summer rainfall, but also atmospheric CO_2 concentration (Cerling et al., 1997; Connin et al., 1998; Smith et al., 2002). For browsers (and grazers in C3 ecosystems) bone and tooth $\delta^{13}C$ reflect the degree of vegetation openness and water stress, with species specific variations linked to individual dietary selection (where $\delta^{13}C$ values differ between plant communities within an ecosystem) (Passey et al., 2005b).

A study on Southeast Asian mammals that spans the Quaternary period nicely exemplifies how mammal $\delta^{13}C$ can be used to reconstruct past environmental change (Louys and Roberts, 2020). The mammal $\delta^{13}C$ results indicate that the forests of the Early Pleistocene gave way to savannahs by the Middle Pleistocene, which then retreated by the Late Pleistocene and had completely disappeared by the Holocene, during which time the savannah was replaced by highly stratified closed-canopy rainforest (Fig. 1). These paleoenvironmental reconstructions also provide critical information about palaeoclimate in the region as past changes in the vegetation patterns are linked to temperature and precipitation which are governed by the position of the intertropical convergence zone and its impact on the East Asian and the Australian–Indonesian monsoons. Thus the palaeoenvironmental and palaeoclimate reconstructions provide critical context for understanding hominin and mammalian migrations and extinctions.

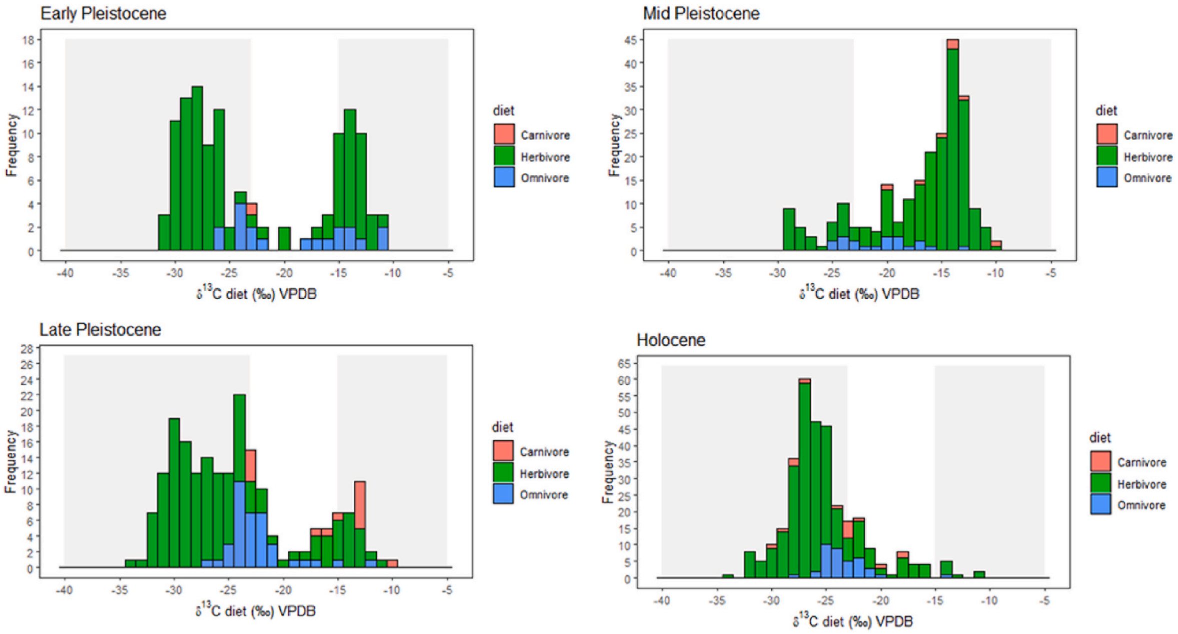

Fig. 1. **(**Data plotted from Louys and Roberts, 2020, SI). Distribution of δ^{13}C values across geological sub-epochs and epochs. Green bars, herbivores; blue bars, omnivores; red bars, carnivores. Shaded boxes represent the division between forests (consumers of 100 % C3 resources) and grasslands (consumers of 100 % C4 resources). All large-herbivore δ^{13}C values from enamel ($\delta^{13}C_{enamel}$) were adjusted by −14 ‰; omnivores, rodents, pigs and primates were adjusted by −11 ‰; Carnivora by −9 ‰; δ^{13}C values from hair or horn ($\delta^{13}C_{hair/horn}$) were adjusted by −3.1 ‰; samples from after AD 1930 were adjusted by 1.6 ‰. VPDB, Vienna PeeDee Belemnite.

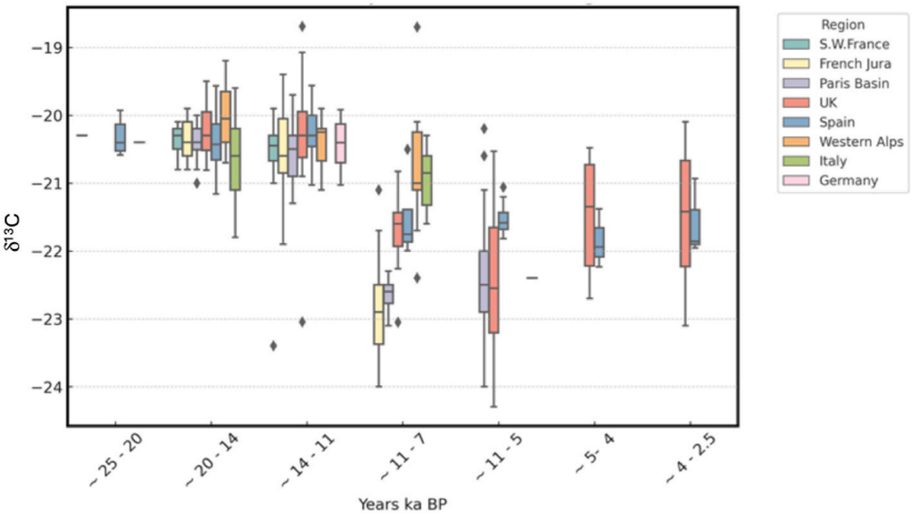

Fig. 2. (Replotted from Stevens et al., 2014, SI). Box plots of 426 red deer δ^{13}C results from El Miron Spain and collated from other areas of Europe divided into time units that are contemporary with the cultural units seen at El Mirón, Northern Spain.

A further example is that of reindeer collagen δ^{13}C during the Late Pleistocene and early Holocene. The δ^{13}C results indicate reindeer consumption of lichen changed over time and this is inferred to reflect changes in lichen availability linked to changing climates and/or humidity levels both during the Late Pleistocene (Britton et al., 2023b) and between the late Pleistocene and early Holocene (Drucker et al., 2011b). When making palaeoenvironmental/palaeoclimatic inferences from mammal δ^{13}C values it is, however, important to remember that multiple parameters could individually or collectively result in the observed δ^{13}C variation, and not to assume a single climatic parameter is the driving variable. Interpretation of temporal trends in δ^{13}C of western European mammal bone collagen during the late Pleistocene/Holocene transition exemplifies this issue. A shift of c. two or three ‰ lower δ^{13}C values has been observed in western European horse, roe deer, red deer, and aurochs/cattle (Drucker et al., 2003a,b, 2008, 2011b; Drucker and Célérier, 2001; Hedges et al., 2004, 2006; Hofman-Kamińska et al., 2018; McCormack et al., 2021; Richards and Hedges, 2003; Rosengren and Magnell, 2024; Stevens, 2004; Stevens and Hedges, 2004). The canopy effect is most frequently cited as the driving parameter behind the δ^{13}C trends in western Europe (Drucker et al., 2003a,b; Noe-Nygaard et al., 2005) as in modern European contexts the percentage of forest cover has been shown to correlate with faunal δ^{13}C (Drucker et al., 2008; Sykut et al., 2021) (although this is not always the case: see Bonafini et al., 2013). However, early investigations favoured a global factor, such as a change in atmospheric CO_2 partial pressure and atmospheric δ^{13}C as the driving parameter, as the temporal trends observed in early data sets were similar across species and regions (Richards and Hedges, 2003; Stevens, 2004; Stevens and Hedges, 2004). Other studies have argued that increased water availability is also a possible driving parameter (Hedges et al., 2006). As more data sets have become available, it is now evident that temporal $\delta^{13}C$ trends can vary between species (Lynch et al., 2008; Noe-Nygaard et al., 2005) and within a species across different regions (Drucker et al., 2011b; Stevens et al., 2014). A study of red deer bone collagen $\delta^{13}C$ from the Late Pleistocene and early Holocene compares data from El Mirón in Spain with published data from other European regions and provides some clarity on this issue (Stevens et al., 2014) (see Fig. 2). With the transition to the Holocene, a shift to lower deer $\delta^{13}C$ values is seen across Western Europe, from the UK in the north to Spain in the south. This supports the view that changes in $\delta^{13}C$ are linked to variations in atmospheric CO_2 levels and increased water availability. However, the magnitude of the shift in deer $\delta^{13}C$ varies between regions. Regions suspected of experiencing forest development exhibit lower $\delta^{13}C$ values, which suggests the influence of the canopy effect. Consequently, the shift in red deer $\delta^{13}C$ during the last deglaciation is the cumulative result of both global (see Hare et al., 2018) and local factors (the canopy effect, see Drucker et al., 2011b) playing a role. Studies can be bolstered by ensuring multiple species (e.g., of ungulates) are analysed from the same levels at the same sites, ensuring that diachronic 'baseline' trends can be differentiated from ecological 'behavioural' trends, where species may vary their niche feeding habits in response to climatic change in different ways, leading to variable inter-species trends (Britton et al., 2023b). A final point to remember is that there is no single faunal $\delta^{13}C$ value that demarcates an animal living in an open habitat from a forest environment. While a preindustrial collagen $\delta^{13}C$ value of −22.5 ‰ has been suggested as a landmark for suspecting a habitat in dense forest (Drucker et al., 2003a), it cannot always be universally applied. Factors such as location (e.g., altitude) and time-specific conditions (e.g., atmospheric CO_2) need to be considered when determining what faunal $\delta^{13}C$ value would indicate a forest dweller in each scenario.

3. Nitrogen isotopes

The vast majority of studies measure nitrogen isotopes in the organic phase (collagen) of bones, dentine and antler. Only a handful of studies have targeted nitrogen isotopes in fossil enamel (Leichliter et al., 2023) due to the limited amount of nitrogen in enamel, the complexities of extracting it for analysis, and the difficulty in confirming whether isotope ratios are representative of *in vivo* values and that the material has not been contaminated in the burial environment or during the extraction process. Nitrogen isotope values in bone and dentine collagen are almost entirely derived from dietary protein, and have a relatively simple relationship with its $\delta^{15}N$, with consumers' $\delta^{15}N$ values typically being elevated c. 3–4 ‰ over diet, although some studies suggest the enrichment can be from +1.5 ‰ to 6 ‰ (Ambrose, 2002; Caut et al., 2009; Deniro and Epstein, 1981; Minagawa and Wada, 1984; Schoeninger and DeNiro, 1984; Bocherens and Drucker, 2003). Thus "trophic level enrichment" between diet and body results in an overall increase in nitrogen isotopic values as the food chain is ascended (O'Connell et al., 2012). Despite decades of research in this area and its clear success as a dietary indicator, the mechanism resulting in $\delta^{15}N$ trophic enrichment remains poorly characterised (O'Connell et al., 2012). Tissue-to-tissue trophic level enrichment is thought to be largely the result of the differential loss of the lighter isotope (^{14}N) during excretion within an organism, however a variety of factors are known to influence the extent of this enrichment. For example, the amount of dietary protein consumed is a determining factor in the ^{15}N-enrichment from diet to tissue. Lower levels of dietary protein can result in decreased diet-tissue offsets and potentially lower tissue $\delta^{15}N$ values (Sponheimer et al., 2003a,b). Conversely, calorie restriction can lead to elevated tissue $\delta^{15}N$ values through utilisation of endogenous proteins during periods of reduced caloric intake (Fuller et al., 2005; Gutierrez et al., 2024; Mekota et al., 2006). Other physiological factors such as pregnancy, lactation, growth, and digestive physiology have also been found to impact ^{15}N-enrichment (e.g. Fuller et al., 2005, 2004; Mekota et al., 2006). Tissues formed during nursing may also have a higher $\delta^{15}N$ than that of the mother due to the trophic level effect (Fogel, 1989; Fuller et al., 2006). Differences in dietary selection and mobility behaviours among different animal species, populations, and individuals contribute to additional variations in the faunal $\delta^{15}N$ data (Reade et al., 2023), which can also simply reflect seasonal 'baseline' variations at any one location (e.g. Zazzo et al., 2015).

Beyond seasonal variations, and concerning the relationship between mammal nitrogen isotopes and climate, there are clinal patterns that can be observed at a global scale. Animals from hot and dry environments tend to have higher nitrogen isotope values compared to those at the same trophic level in cooler and wetter environments (Ambrose, 1991; Gröcke et al., 1997; Hartman, 2011; Heaton et al., 1986; Murphy and Bowman, 2006; Pate and Anson, 2008; Sealy et al., 1987). Many studies have suggested that these patterns are a result of the physiological response of animals to heat, water, and/or nutritional stress (Ambrose, 2002; Ambrose and DeNiro, 1986; Bada et al., 1989; Cormie and Schwarcz, 1996; Del Rio and Wolf, 2005; Hobson et al., 1993; Schoeninger et al., 1997; Sealy, 1986; Sponheimer et al., 2003a,b; Steele and Daniel, 1978; Vanderklift and Ponsard, 2003). Others, however, argue that higher faunal $\delta^{15}N$ values in arid environments are due to elevated plant $\delta^{15}N$ values being passed on to animals (Heaton, 1987; Pate et al., 1998; Schwarcz et al., 1999). A study specifically examining this issue confirmed that the isotopic composition of the diet is the primary factor determining mammal $\delta^{15}N$ values (Hartman, 2011). Therefore, the relationship between faunal $\delta^{15}N$ and environmental conditions is mediated by the climate's influence on the nitrogen isotope signatures of soil and plants, which are subsequently transferred up the food chain.

Plant $\delta^{15}N$ values range from at least ~ −15 ‰ to ~ +33 ‰ (Craine et al., 2009, 2015; Santana-Sagredo et al., 2021) and are influenced by various factors (see Craine et al., 2015 for recent review). Leguminous plants have a symbiotic relationship with bacteria that attach to their roots, enabling them to directly acquire nitrogen (N_2) from the atmosphere. In contrast, non-leguminous plants, which make up the majority of plants, cannot utilise atmospheric nitrogen directly. Instead, they primarily rely on soil inorganic nitrogen sources such as ammonium (NH_4^+) and nitrate (NO_3^-). When inorganic nitrogen is limited, plants may turn to organic nitrogen as an alternative. The nitrogen isotopic composition of a plant is determined by the type of nitrogen it obtains, whether it is taken up directly from the soil or through symbiotic microbes, and whether the nitrogen is assimilated in the roots or shoots (Craine et al., 2015; Szpak, 2014). Furthermore, the allocation of nitrogen to different plant parts, such as leaves, stems, or fruit, also affects the plant's nitrogen isotopic composition. While nitrogen cycling is very complex, broad isotopic patterns linked to climate are seen in soil and plant $\delta^{15}N$ values. On a global and continental scale, there are strong relationships between plant $\delta^{15}N$ and temperature and precipitation. Foliar $\delta^{15}N$ increases as mean annual precipitation (MAP) decreases and mean annual temperature (MAT) increases, but this latter pattern only holds true for ecosystems with MAT > -0.5 °C (Amundson et al., 2003; Craine et al., 2009, 2015; Handley et al., 1999). These relationships are also evident at smaller spatial scales, where there are significant variations in altitude and local topography (Liu et al., 2010; Männel et al., 2007). In addition, salinity impacts plant $\delta^{15}N$ with higher values observed where plants grow in high salinity soils (Heaton, 1987; van Groenigen and van Kessel, 2002; Virginia and Delwiche, 1982) due to increased ammonia volatilisation and plants taking up more ^{15}N-enriched ammonium (van Groenigen and van Kessel, 2002). It has been argued that the relationships between climate and plant $\delta^{15}N$ are linked to the openness of the nitrogen cycle (however see Craine et al., 2015 for further discussion). In hot and arid environments, the nitrogen cycle is generally open, with more extensive mineral leaching, denitrification, and ammonia volatilisation. These processes have large fractionations resulting in ^{15}N enrichment of soils and elevated plants δ^{15}N (Austin and Vitousek, 1998; Handley et al., 1999). In cold, wet environments the soil nitrogen cycle is more closed with fewer losses from the system and the soil contains relatively limited mineral nitrogen because most of the nitrogen is bound within dead organic matter (Read, 1991). As a result, plants primarily obtain nitrogen directly from dead organic matter, leading to the cycling of nitrogen between live and dead organic pools. Consequently, plant and soil organic matter's δ^{15}N values are lower because less ^{14}N is lost from the cycle through leaching, denitrification, and ammonia volatilisation (Austin and Vitousek, 1998; Handley et al., 1999; Peñuelas et al., 1999). In environments with limited nitrogen availability, plant species can coexist by competitively partitioning the nitrogen pool and utilising different nitrogen sources in the soil. As a result, plants exhibit different δ^{15}N values (Nadelhoffer et al., 1996). Additionally, in cold ecosystems, a higher number of plants have symbiotic mycorrhizae due to limited nitrogen availability (Michelsen et al., 1998). These mycorrhizal associations lead to lower plant δ^{15}N values, with certain types of mycorrhizal associations having a greater impact than others (Craine et al., 2009). Graminoids that do not have symbionts usually have higher δ^{15}N values compared to co-existing shrubs and trees which rely on mycorrhizae for nitrogen acquisition (Drucker, 2022).

It is important to note that the relationship between climatic/environmental parameters and plant δ^{15}N may often be decoupled from its natural state due to anthropogenic activity. A wide range of agricultural practices, such as the use of animal fertilisers, burning of vegetation or shifting cultivation, tillage, grazing intensity/stocking rate, and irrigation have been shown to impact soil and plant δ^{15}N and these effects are passed on to the animals (see Bogaard et al., 2007; Szpak, 2014). Such anthropogenic signals can be useful markers of human activities and their effects on past ecosystems.

Significant temporal variations in faunal δ^{15}N values have been observed on long timescales (10^3–10^5 years) (Bocherens et al., 2014; Britton et al., 2023b; Drucker et al., 2003a,b, 2011a; Fox-Dobbs et al., 2008; Hedges et al., 2004, 2006; Mann et al., 2013; Rabanus-Wallace et al., 2017; Reade et al., 2020b, 2021, 2023, 2021; Richards et al., 2017; Richards and Hedges, 2003; Stevens, 2004; Stevens et al., 2008, 2009a, 2009b, 2014, 2021; Stevens and Hedges, 2004). It has been argued that variations in faunal δ^{15}N reflect changes in baseline (soil and plant) δ^{15}N values due to climatic and environmental factors. Some temporal changes in δ^{15}N have been noted in specific regions (to date, but future studies may show these patterns to be more widespread). For example the δ^{15}N of herbivores and carnivores in southwest France shift to higher values at around ~42,000 cal BP, then return to lower δ^{15}N values ~35,000 cal BP), and are thought to reflect increasing followed by decreasing aridity (Bocherens et al., 2014). Other temporal changes have been observed in different species across mid and high latitude environments. These include regional responses to broad-scale climatic excursions, such as Heinrich Events (Britton et al., 2023b). The most notable of these is the large decrease toward the end of the last glacial to very low values around 17,000 to 14,000 years BP followed by a rapid increase in δ^{15}N during the Late Glacial period. In recent years this trend has been referred to as the Late Glacial Nitrogen Excursion (LGNE) (Drucker et al., 2003a,b, 2011a; Mann et al., 2013; Rabanus-Wallace et al., 2017; Reade et al., 2020b, 2021, 2023; Richards and Hedges, 2003; Stevens et al., 2008; Stevens and Hedges, 2004; Stevens, 2004) (Fig. 3). As more data on the δ^{15}N of late Pleistocene herbivores has been collected, it has become increasingly clear that there are spatial and temporal asynchronicities in the LGNE (Rabanus-Wallace et al., 2017; Reade et al., 2023; Schwartz-Narbonne et al., 2019). Additionally, there are significant differences in species specific trends in δ^{15}N (Drucker, 2022; Reade et al., 2023; Schwartz-Narbonne et al., 2019; Stevens, 2004). Recent studies have applied an isoscape approach to model changes in spatial gradients of δ^{15}N in late Pleistocene Europe and explore how this relates to climate (Fig. 4) (Reade et al., 2023). Whilst a range of parameters have been suggested as the drivers of the LGNE excursion, the general consensus is that the observed trends (lowest δ^{15}N values seen in northern latitudes after, rather than during, the Last Glacial Maximum) are most likely related to changes in landscape moisture (particularly from increased input of meltwater from ice sheets and thawing permafrost) and soil activity linked to changes in permafrost intensity that occurred after the Last Glacial Maximum (Drucker et al., 2011b, 2012; Reade et al., 2020b, 2023; Stevens, 2004; Stevens et al., 2008).

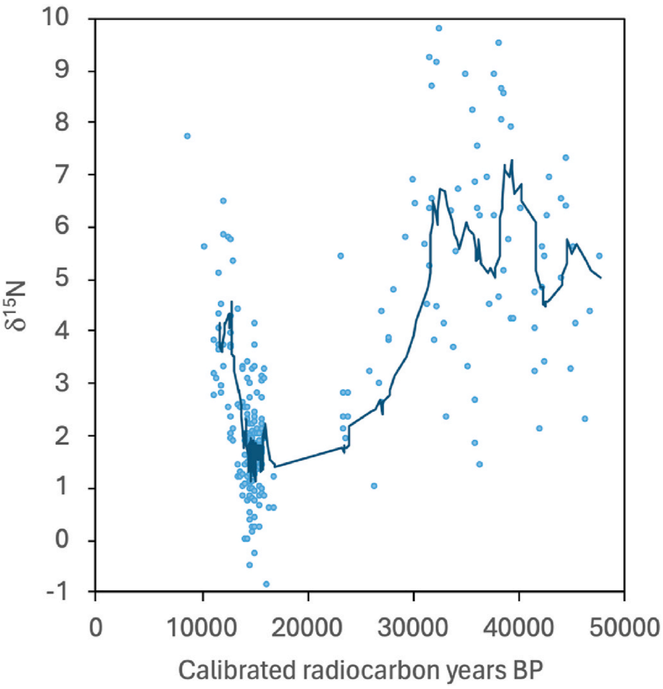

Fig. 3. δ^{15}N of 252 radiocarbon dated horse bone and tooth collagen from late Pleistocene Europe. (Data plotted from Reade et al., 2023). Circles are individual data points, line is 10 point running mean of data. Trend shows the LGNE after the Last Glacial Maximum.

As with carbon, interpretations of archaeological/palaeontological animal δ^{15}N values are potentially flawed as researchers too often assume a single climate or anthropogenic parameter is the driving variable, neglecting other possible parameters that could be contributing to the observed trend. With such a range of climatic (temperature, precipitation), environmental (topography, geology, salinity, permafrost conditions, soil hydrology, forest development) and anthropogenic (manuring, burning) parameters potentially influencing faunal δ^{15}N and the complexities of the relationship between climate and the nitrogen cycle it is very tricky to move climatic interpretations of faunal δ^{15}N values beyond qualitative statements of cooler, warmer, wetter, more arid to more quantitative interpretations. More extensive meta-analyses of modern faunal δ^{15}N values may help further understanding in this area, and provide information on deconvoluting climate linked δ^{15}N changes. When it comes to the past, trends in faunal δ^{15}N values may be the result of multiple factors impacting the nitrogen cycling. Furthermore, archaeological and palaeontological faunal δ^{15}N values are best interpreted alongside other climate proxies (including other isotopic proxies), which may help elucidate the driving parameter and assist with the interpretation, although there is always the danger of circularity with this approach. As with other isotopic or proxy approaches, the need and importance of sound chronological frameworks is at the fore when trying to relate variations in palaeo- or archaeo-faunal isotopes to environmental drivers.

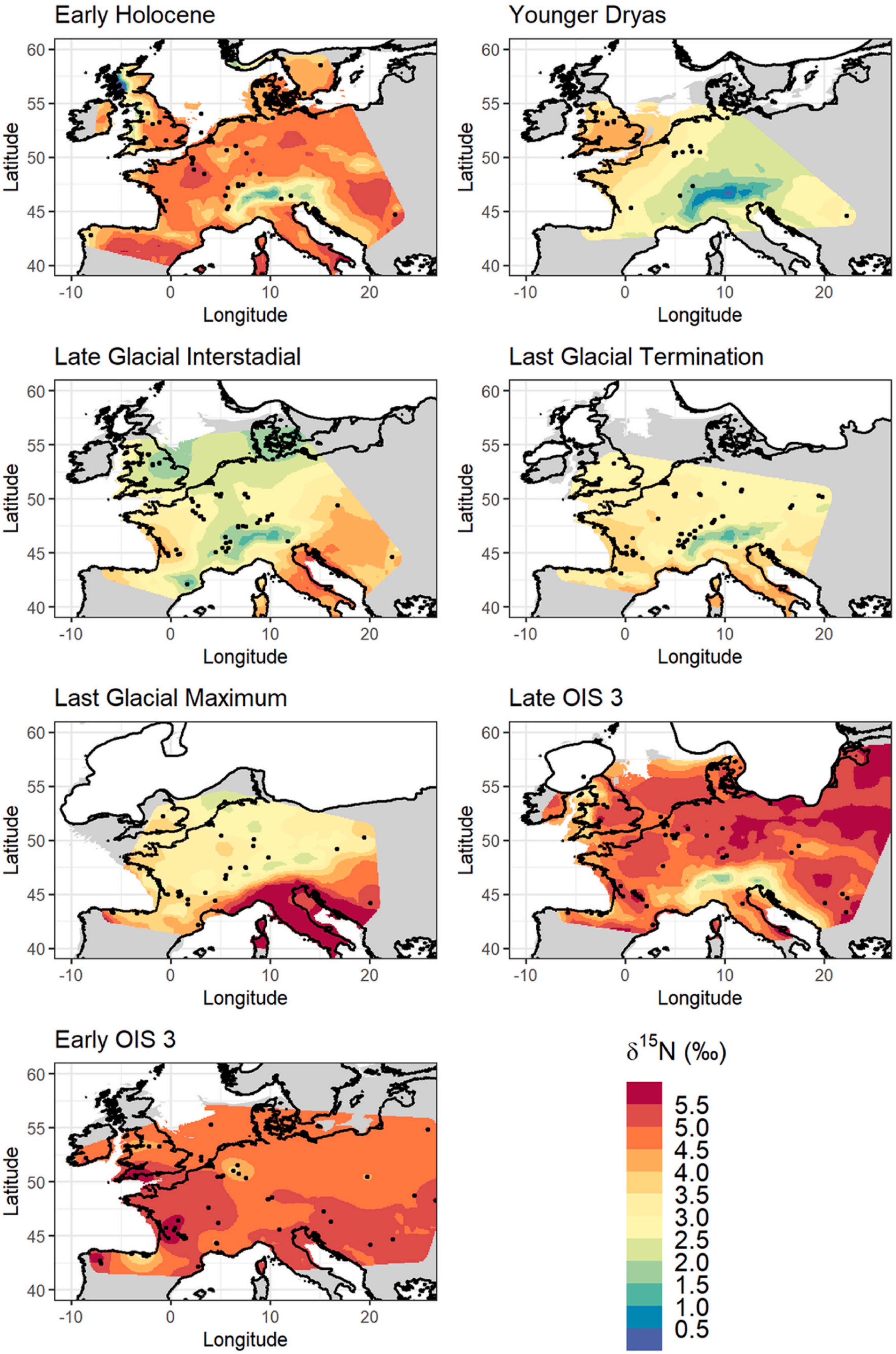

Fig. 4. (From Reade et al., 2023) $\delta^{15}N$ isoscape prediction surfaces for Europe based on herbivore collagen $\delta^{15}N$ values *(Alces, Bos/Bison, Capra, Capreolus, Cervus elaphus, Coelodonta, Equus, Megaloceros, Rangifer, Rupicapra, Saiga)*. Isoscapes model changes in spatial gradients of $\delta^{15}N$ in late Pleistocene Europe and explore how this relates to climate. Best performing model incorporating climatic fixed effect(s) is shown for each time bin.

4. Sulfur isotopes

Sulfur isotope analysis of skeletal remains focuses on the ratios of ^{32}S to ^{32}S (expressed as δ^{34}S) in organic phase sulfur, typically measured on extracted collagen from bones, dentine and antlers. The collagen in these materials is predominantly type 1 collagen, in which sulfur is only present in organic form in the amino acid methionine. Sulfur is also present in the mineral phase (bioapatite) in the form of sulfate (SO_4^{2-}) substituting for the phosphate group (PO_4^{3-}) (McArthur, 1978; Michener and Lajtha, 2007). However, very few studies have focused on the mineral phase due to the technical complexities of measuring the isotopes (Doubleday et al., 2018; Goedert et al., 2016).

To date, sulfur isotopes in mammal bones and teeth have mainly been used for studying past diet and mobility. δ^{34}S has been employed to investigate the consumption of marine and freshwater resources (e.g. (Craig et al., 2006; Drucker et al., 2018; Guiry and Szpak, 2020; Nehlich et al., 2010; Privat et al., 2007; Richards et al., 2001; Szpak and Buckley, 2020), the movements of humans and animals (Ebert et al., 2021; Guiry et al., 2015; Madgwick et al., 2019a, 2023, 2019b; Richards, 2023), variations in range use by different species in the same region (Britton et al., 2023a; Reade et al., 2021; Wiβing et al., 2019), and potential changes in the hunting range used by humans and/or the spatial palaeoecology of prey species over time (Jones et al., 2019). Most studies have interpreted animal and human δ^{34}S values as reflecting one or more sources of bioavailable δ^{34}S, but assume the sources are isotopically static and not influenced by changing environmental parameters. Recent studies have, however, shown faunal sulfur isotopes in the same species can vary through time at the same location (e.g. Drucker et al., 2011a, 2012; Reade et al., 2021, 2020b) and therefore, provide useful information on palaeoclimate and palaeoenvironment because they are derived from plants or other animals and not only reflect bioavailable δ^{34}S baselines but also the processes which alter them (Lamb et al., 2023; Stevens et al., 2025).The primary source of terrestrial sulfur is geological, derived from mineral weathering of parent bedrock both as sulfate (SO_4^{2-}) and as the reduced form sulfide (S^{2-}) as well as elemental sulfur (S^0). Geological sulfur has a very wide range of δ^{34}S values reflecting the interplay of isotopic fractionation from microbial sulfur cycling in ocean sediments with fluctuations in sea level and other environmental factors over millennia (Nehlich, 2015). There are broadly two categories of geological sulfur deposits which feed the bioavailable sulfur pool for plants and animals to take up: those that reflect the δ^{34}S of ocean water sulfate at the time of deposition (marine evaporites, with δ^{34}S values c. 10 ‰ to 30 ‰ e.g. Claypool et al., 1980; Kampschulte and Strauss, 2004), and those that were formed from microbial sulfide production in marine and continental environments (geological pyrites with usually negative δ^{34}S values fractionating up to 72 ‰ e.g. Pasquier et al., 2021).

Sulfur carrying geological and/or palaeoenvironmental signals in δ^{34}S is incorporated into collagen via the uptake of sulfate by plants. A proportion of this sulfate is used by plants to make the amino acid methionine, a component of plant protein, with the rest incorporated into other amino acids including cysteine, used for metabolic processes, or stored in cell vacuoles. Methionine is an essential amino acid for mammals and has to be acquired through diet, thus herbivores can only acquire methionine by eating plants (Nimni et al., 2007). The majority of this methionine is used by herbivores to form protein in tissues including collagen and muscle, with a smaller proportion utilised to synthesise other amino acids and in metabolic processes. Methionine is the dominant form of sulfur incorporated into type 1 collagen, thus sulfur in collagen from bones, dentine and antlers largely reflects dietary intake rather than internal synthesis (Anné et al., 2019). Through the uptake pathway, bioavailable sulfur from the environment is fixed in plant protein within methionine, taken up by herbivores, and can be passed on to carnivores via ingestion of herbivore tissues. Where freshwater or marine fish and shellfish comprise a significant source of dietary protein, this can alter mammal collagen δ^{34}S. Therefore, palaeoenvironmental signals are best focused on herbivores. With respect to δ^{34}S, herbivore bone collagen δ^{34}S is expected to reflect the geological and palaeoenvironmental conditions in which food plants were growing. This is supported by: i) observations that bulk plant δ^{34}S reflects the δ^{34}S of bioavailable sulfate in the soil in which the plant grows (Nehlich, 2015; Tcherkez and Tea, 2013); ii) the fact that there is a zero to small trophic level effect associated with the uptake of sulfur in dietary protein (e.g. c. $\pm$ 0.5 $\pm$ 2.4 ‰, (Krajcarz et al., 2019; Nehlich, 2015; Raoult et al., 2024); and iii), the assumption that the δ^{34}S of plant methionine closely matches bulk plant material δ^{34}S. Controlled feeding studies broadly support this, indicating a small offset between plant-based feed δ^{34}S and collagen δ^{34}S (Tanz and Schmidt, 2010; Webb et al., 2017).

As is the case with archaeological/palaeontological bones and teeth for other stable isotope analyses, collagen samples for sulfur isotope analysis must be screened to rule out post-deposition diagenetic sulfur contamination, which may be caused by protein degradation and contamination with exogenous sulfur (Bocherens et al., 2011). This is carried out by examining carbon to sulfur and nitrogen to sulfur mass ratios (Nehlich and Richards, 2009), taking into account the possibility of variation in these ratios across species (Bocherens et al., 2011).

Although plant (and animal) δ^{34}S values reflect geological sulfur there is not always a direct correlation. This is because not all of the sulfur in bedrock is accessible to plants, and due to the fact that biogeochemical sulfur cycling in surface deposits can modify δ^{34}S values. Different geological units weather at different rates when exposed as a result of differences in their chemistry. This means that sulfur from one rock type may dominate the overlying soil even though another sulfur bearing rock is also present below the soil. Changes in the rates of bedrock mineral weathering due to variations in soil hydrology linked to changes in climate can influence bioavailable δ^{34}S. Enhanced geological weathering caused by ice-sheet or glacial flow in mountainous regions can also result in the transport of δ^{34}S from weathered mountain geology over long distances in meltwater drainage (Hindshaw et al., 2016). A further source of sulfur entering the soils (and passed on to plants) is the atmosphere (via dry or wet deposition of SO_4^{2-} aerosols and minor biogenic sources of gaseous sulfur in various forms). Sea spray can transport sulfur particles from the ocean to coastal areas, resulting in some coastal soil δ^{34}S values that closely resemble those found in the ocean (Wadleigh et al., 1994). This sea-spray effect most greatly influences terrestrial δ^{34}S values within c. 30 km of the coast (Guiry and Szpak, 2020; Nehlich, 2015), although this depends on prevailing weather patterns, and smaller amounts of marine sulfate can be deposited farther inland (Bataille et al., 2021; Zazzo et al., 2011). Saline intrusion, the process by which seawater replaces groundwater in aquifers in coastal regions, can increase the extent of the marine δ^{34}S influence, especially in deltaic regions and around larger estuaries (Eslami et al., 2021), and is affected by changing sea levels. Past sea level change has undoubtedly impacted terrestrial bioavailable δ^{34}S as regions became less or more coastal, changing the geography of the coastal δ^{34}S signal. For example, during the Last Glacial Maximum sea levels were about 130 m lower than today, which not only changed the location of palaeo-shorelines, but exposed land surfaces which became new potential sources of sulfate through weathering, aeolian sediment transportation and deposition (Lambeck et al., 2014; Stevens et al., 2025).

Bioavailable δ^{34}S can also be affected by volcanic eruptions that create sulfur bearing dust which travels long distances in the atmosphere to be deposited on soils, weathered, and taken up by plants and animals. Volcanic derived sulfur has δ^{34}S values linked to the eruption type and the material produced (e.g. 4.1 $\pm$ 0.5 ‰, Jongebloed et al., 2023). Past climate change has been linked to increased volcanic activity and inputs of volcanic sulfur to the atmosphere, which occurred when surface load pressure decreased due to the melting of glacial ice (Lin et al., 2022). Changes in global wind patterns also affected bioavailable δ^{34}S via deposition of loess which contained sulfur from volcanic dust as well as from geological weathering from wide geographical areas (Rousseau and Hatté, 2021; Ryskov et al., 2007; Schaffernicht et al., 2020). During glacial periods loess deposition was extensive across large areas of the world (Lehmkuhl et al., 2021), and thus it is an important potential driver of changes in bioavailable δ^{34}S over time.

A ubiquitous process that strongly affects the bioavailable δ^{34}S taken up by plants and animals is contemporaneous microbial sulfur cycling. Heterotrophic dissimilatory sulfate reduction to sulfide (DSR) is a pathway for the microbial oxidation (respiration) of organic carbon in anaerobic sediments and soils. DSR can cause large isotopic fractionation (average c. 28 ‰ (Canfield, 2001) which has been found to vary with the ratio of sulfate to organic carbon as well as differences in temperature and microbial strain (Canfield et al., 2006; Mitchell et al., 2009; Sim et al., 2023). Typically isotopic fractionation associated with DSR produces sulfide which is isotopically lighter than the sulfate substrate from which it is formed, while the residual sulfate substrate becomes isotopically heavier as it is used up by DSR. Most plants primarily take up sulfate and cannot access sulfide unless it is re-oxidised by a different microbial community back to form sulfate, when oxygen returns to the soil or sediment. Thus, it is the complete reduction-oxidation of inorganic sulfur by two distinct microbial communities requiring contrasting environmental parameters which forms bioavailable sulfate with lowered δ^{34}S values. For sulfate reduction to proceed, strongly reducing conditions must develop in soils and sediments which contain sufficient organic carbon as a bacterial substrate. These conditions usually occur after prolonged soil waterlogging, for example in wetlands, marshes, and bogs, and on inundated floodplains. In such environments this process has been shown to result in extremely low sedimentary δ^{34}S values typically −30 ‰ to −25 ‰ and occasionally as low as −70 ‰ (Fry et al., 1982; Krouse, 1989; Pasquier et al., 2021; Peterson and Fry, 1987). Some plants are adapted to indirect sulfide uptake via oxygen loss from roots which facilitates microbial sulfide oxidation to sulfate in otherwise anaerobic environments, and thus can incorporate highly ^{34}S-depleted sulfate in sediments where DSR is active, without the necessity for the sediment as a whole to switch to aerobic conditions (Carlson and Forrest, 1982; Guiry et al., 2022; Lamers et al., 2013). In addition, in saltmarsh environments, which are hotspots of DSR, low δ^{34}S values have been found in plants despite the fact that sediments are inundated twice daily with seawater with δ^{34}S c. 20 ‰ (e.g. Carlson and Forrest, 1982; Guiry et al., 2022; Lamers et al., 2013). Low archaeological/palaeontological δ^{34}S collagen values can potentially indicate wetlands, marshes, bogs, saltmarshes, or inundated floodplain landscapes in the palaeoenvironment through the transfer of the DSR-oxidation sulfur cycling signal to plants and animals (Guiry et al., 2021a, 2022; Lamb et al., 2023; Stevens et al., 2022; Carlson and Forrest, 1982; Lamers et al., 201). Past changes in climate affected the storage and distribution of freshwater across terrestrial hydrological reservoirs, sometimes raising groundwater levels and leading to the development of new rivers, lakes, saltmarshes and other wetland environments which potentially can be tracked through archaeological faunal δ^{34}S values.

Permafrost environments interact uniquely with the microbial sulfur cycle. These environments lock away moisture, sulfur and organic carbon, and limit microbial cycling in the soil. Sulfur is added to the permafrost surface from atmospheric deposition and aeolian dust. During seasonal thawing and freezing of the active layer, plants grow and die, and over time, organic matter accumulates due to the suppression of microbial decomposition in cold temperatures (Herndon et al., 2020). When the active layer thaws, a lack of vertical drainage caused by the frozen subsurface forces water laterally, such that minor differences in topography create a patchwork of aerobic-anaerobic gradients, supporting both DSR and sulfide oxidation (Herndon et al., 2020). Plants which flourish on the active layer during seasonal thawing may incorporate sulfate bearing this signal in δ^{34}S, and pass on the lower δ^{34}S values to animals (Stevens et al., 2025). Some of the sulfide produced by DSR is stored in frozen deposits as the permafrost aggrades. Past permafrost thaw due to warming global temperatures will have led to permafrost degradation and a deepening of the active layer, returning large quantities of sulfide with lowered δ^{34}S sequestered in surface sediments to microbially active organic carbon rich soil. When oxygenated conditions developed, this sulfide would have been oxidised to create high concentration bioavailable sulfate with lowered δ^{34}S (Herndon et al., 2020; Kemeny et al., 2023), to be taken up by plants and animals.

As is the case with nitrogen, significant temporal variations in faunal δ^{34}S values have been observed over long timescales. A high-magnitude excursion in faunal δ^{34}S, termed the Late Pleniglacial Sulfur Excursion (LPSE), has been observed in some areas of Eurasia between approximately 30 and 15 kyr BP (Stevens et al., 2025). This period corresponds to the latter part of the last ice age and covers much of Marine Isotope Stage 2 (MIS 2, c. 29–11.7 kyr BP), including the Last Glacial Maximum (LGM, c. 26.5–19 kyr BP). In some regions the magnitude of the LPSE is up to ~35 ‰. The LPSE is particularly pronounced in regions where there is good temporal coverage within a discrete geographic area, such as in Britain and Belgium, and is also evident in other regions, such as central Europe north of the Alps (Stevens et al., 2025)(Fig. 5). However, the limited temporal and spatial coverage of data currently make it impossible to determine whether the LPSE is time transgressive across the region in which it is observed. The LPSE occurs in multiple species with differing dietary niches and mobility behaviours. At present, the LPSE is argued to be primarily driven by changing permafrost conditions, especially permafrost thaw during the transition from Pleniglacial to Late Glacial ~15,000 year before present (yr BP), which would have liberated sequestered sedimentary sulfide for oxidation and plant uptake into the food chain, although loess transportation is also thought to have played a role. However further research is needed in this area to fully understand the mechanism driving and the temporal and spatial extent of the LPSE. Given that temporal variations are seen in faunal δ^{15}N and δ^{34}S in the late Pleistocene, further research would help us understand connections between climate, nitrogen and sulfur cycling at this time.

Extensive evidence that bioavailable δ^{34}S is dynamic and influenced by climatic and environmental parameters over a range of spatial scales, necessitates an incorporation of this knowledge into studies of human and animal past mobility and spatial ecology. In order for interpretation of δ^{34}S results to be optimised, there is a need for contemporaneous bioavailable δ^{34}S baselines maps to be developed. Critically, the sulfur isotopic composition of bones and teeth via plant uptake provides an archive of the environmental conditions in which the plants grew and animals lived, integrating signals from geology, the changing climate and environmental processes, as well as the biogeography of the individual animal. When used in conjunction with other palaeoenvironmental proxies, collagen δ^{34}S is a powerful, and, as yet, underexplored tool for investigating past environments.

5. Oxygen isotopes

Oxygen has three naturally occurring stable isotopes (^{18}O, ^{17}O, ^{16}O), of which ^{16}O is the most (99.755 %) and ^{17}O (0.039 %) the least abundant (Rundel et al., 1989). In stable isotope applications in earth and biological sciences, including archaeology, the ratio between ^{16}O and ^{18}O (expressed as δ^{18}O) is most commonly analysed (Pederzani and Britton, 2019). More recently, novel analyses of other isotope ratios including triple oxygen isotope analysis and clumped isotope analysis (Δ_{47}) have been increasing in prominence, but are still in the early stages of development and much less prevalent than δ^{18}O analyses (Bergmann et al., 2018; Feng et al., 2024).

Oxygen isotope analyses are usually conducted on the mineral bioapatite phase of skeletal remains, where oxygen is present in the phosphate (~65 %), carbonate (~4–5 %), and hydroxyl (<2 %) groups (Driessens, 1980; Klimuszko et al., 2018). Analyses of collagen oxygen δ^{18}O is also possible, but not common as collagen. Oxygen can exchange with reagent oxygen during sample processing and with atmospheric

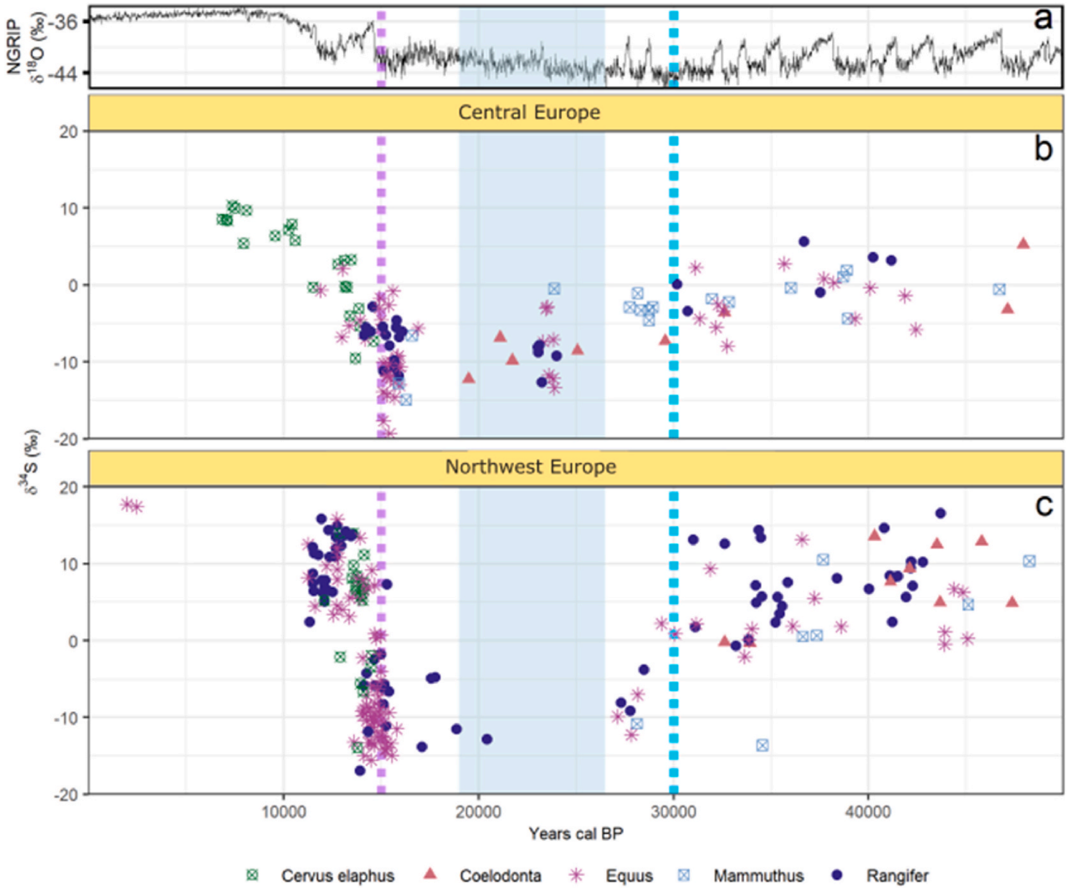

Fig. 5. (Adapted from Stevens et al., 2025): $\delta^{34}S$ values of radiocarbon dated herbivores from Central Europe (46.5N–54N, 6E to 21E) (Panel b) and Northwest Europe (50N–60N, 10E to 6W) (Panel c) for the five most abundant taxa in both regions (*Cervus elaphus*, Coelodonta antiquitatis, Equus sp., Mammuthus primigenius and *Rangifer tarandus*). Panel A shows the Greenland ice-core oxygen isotope record, a proxy for global temperature (Andersen et al., 2004). Shaded blue area indicates approximate duration of the Last Glacial Maximum. The dashed blue line indicates the approximate timing when continuous permafrost development began to develop (c. 30 kyr BP) and and the dashed purple line the timing of widespread thaw (c.15 kyr BP) in western Eurasia. The Late Pleniglacial Sulfur Excursion (LPSE) is seen as move to lower $\delta^{34}S$ values between c. 30 and 15 kyr BP followed by a return to higher $\delta^{34}S$ values.

oxygen during sample storage, and quantifying the amount of exchange is difficult (Kirsanow et al., 2008; von Holstein et al., 2018). Within the mineral phase, the phosphate moiety exhibits the highest resistance to post-depositional alteration of the isotopic signal, followed by the carbonate moiety, while the hydroxyl group is not normally analysed due to low abundance and preservation potential (Wang and Cerling, 1994; Zazzo et al., 2004). For both the phosphate and carbonate groups tooth enamel is generally the preferred analytical substrate due to its greater diagenetic resistance and bone bioapatite $\delta^{18}O$ measurements of the carbonate group are commonly considered to be potentially unreliable (Koch et al., 1997; Kohn et al., 1999). Bone and tooth dentine mineral $\delta^{18}O$ measurements of the phosphate group on the other hand have been shown to preserve biogenic ratios in some studies, usually on materials of Holocene age (Britton et al., 2015) or from exceptional preservation conditions such as permafrost (Fisher and Fox, 1998). Generally, $\delta^{18}O$ measurements of the carbonate moiety of tooth enamel is most commonly used due to lower analytical cost and ease of sample preparation compared to phosphate, although phosphate is most often preferred in deeper time applications or in applications where $\delta^{18}O$ data are being used for palaeoclimate reconstructions (Pederzani and Britton, 2019; Stevens and Reade, 2021).

Oxygen isotope applications using skeletal materials in the palaeosciences range across a wide variety of topics, chiefly among them studies of past temperatures and hydroclimatic changes, animal movement and spatial ecology, and terrestrial animal drinking behaviour. Bioapatite $\delta^{18}O$ in animal skeletal remains reflects $\delta^{18}O$ of body water, which is in turn driven by the isotopic composition and mass balance of oxygen-bearing inputs (drinking water, water in food, structural oxygen in food, inhaled oxygen) and outputs (exhaled carbon dioxide and water vapour, excreted water) (Bryant and Froelich, 1995; Kohn, 1996). Among these, consumed water through drinking or contained in food is the most important driver of animal body water $\delta^{18}O$ (Bryant and Froelich, 1995; Kohn, 1996). Bioapatite $\delta^{18}O$ values are in equilibrium with those of body water, and thus reflect these inputs as well (Daux et al., 2008; Iacumin et al., 1996; Luz et al., 1984). Metabolic processes and associated isotopic fractionation transform $\delta^{18}O$ values until their final expression in bioapatite, with strong influences of body (and therefore bioapatite precipitation), temperature, and metabolic rate. However, due to the constant body temperature of mammals, these metabolic processes are usually expressed as a constant species-specific offset (Kohn, 1996). In this way bioapatite $\delta^{18}O$ of terrestrial mammals reflects underlying oxygen isotope systematics of surface and plant water consumed by these animals, and changes therein. Depending on the drinking behaviour of the animal, inputs from drinking water or from water contained in food vary in importance for determining bioapatite $\delta^{18}O$, with drinking water being the dominant influence in large obligate-drinking animals consuming large quantities of liquid water via drinking (Bryant and Froelich, 1995; Kohn, 1996). Animals that drink little, irregularly, or not at all (non-obligates), more strongly reflect $\delta^{18}O$ patterns in water contained in their food such as that of plant water or the body water of prey animals (Levin et al., 2006; Pietsch et al., 2011).

Underlying oxygen isotopic patterns that can thus be reflected in mammal bioapatite δ^{18}O are therefore tied to the large-scale systematics of the hydro- and biospheres. Important to consider are, in particular, surface water isotope systematics, plant water δ^{18}O, prey body water, and in the case of humans, culinary and cultural transformations of liquids and foods (Brettell et al., 2012; Royer et al., 2017; Tuross et al., 2008 Pederzani and Britton, 2019). Oxygen isotope systematics in the water cycle follow predictable effects related to moisture transport and climatic conditions, due to isotopic fractionation involved in evaporation and condensation processes (Dansgaard, 1964; Gat, 2010; Rozanski et al., 2013). Therefore, δ^{18}O values of precipitation ($\delta^{18}O_{precip}$) show both geospatial and climatic patterns with latitude, altitude, distance from the coast, rainfall amount, temperature, and aridity being important drivers (Craig, 1961; Dansgaard, 1964). Spatial effects are predominantly rooted in preferential rain-out of isotopically heavy (relatively ^{18}O enriched) water as water masses move away from the equator, traverse land, and ascend up orographic slopes, leading to progressively lower $\delta^{18}O_{precip}$ values at higher latitude, further away from the coast and at higher elevation (Dansgaard, 1964; Araguás-Araguás et al., 2000; Gonfiantini et al., 2001; Yurtsever, 1975). Within a single location $\delta^{18}O_{precip}$ further varies by climatic conditions during precipitation events and the source of moisture. In the tropics the dominant climatic effect on $\delta^{18}O_{precip}$ is rainfall amount (the 'amount effect'), while temperature most strongly drives $\delta^{18}O_{precip}$ in mid to high latitudes (Dansgaard, 1964; Gonfiantini et al., 2001; Yurtsever, 1975). Typically, high amounts of rainfall will cause lower $\delta^{18}O_{precip}$ values, while temperature-dominated oxygen isotope systems exhibit high $\delta^{18}O_{precip}$ values during high temperature conditions (Dansgaard, 1964; Rozanski et al., 2013; Bowen, 2008). These effects are expressed on both seasonal (sub-annual) and longer timescales (Müller et al., 2017; Streletskiy et al., 2015; Stumpp et al., 2014). Moisture source effects can strongly affect $\delta^{18}O_{precip}$ especially in locations where weather systems can originate from very distinct source areas and follow specific atmospheric circulation configurations, as is for instance the case in many subtropical rainfall regimes such as the Asia summer monsoon (e.g. Aggarwal, 2004). Many water bodies such as rivers, streams, lakes or groundwater broadly represent meteoric water inputs, but water transport, mixing, residence times, and evaporation can further modulate δ^{18}O of surface water bodies (Gat, 2010). Both climatic and geospatial δ^{18}O effects are commonly exploited to elucidate past climates and help assess animal spatial ecology.

For the study of past climates, oxygen isotope analyses of terrestrial mammal remains have several key advantages, despite not yielding the type of long-term continuous palaeoclimate data generated from proxies such as ice cores or marine cores. In contrast to these more dominant palaeoclimate archives, terrestrial mammal δ^{18}O data offers rare insights into terrestrial climatic conditions and can be used to generate climatic information in much closer connection with archaeological sites as faunal remains form a common part of the archaeological record (Pederzani et al., 2021a; Reade et al., 2020a). This is a crucial advantage for studying human-climate interactions and stable isotope analyses of animal teeth have played an important role in elucidating the role of climate in human evolutionary history. Especially in later human evolution in the Middle and Upper Palaeolithic (coinciding approximately with MIS 7-3, ~300-12 ka BP) the archaeological record includes a large number of anthropogenic faunal remain assemblages from well-stratified, in-situ hominin habitation sites. Mammal skeletal remains in these sites are often largely accumulated by human action and therefore exhibit a direct contextual connection with phases of human activity. At the same time, the temporal resolution of oxygen isotope data from mammal teeth is commonly annual or sub-annual and, on the level of the individual specimen, these data undergo significantly less time-averaging than most geologically accumulated palaeoenvironmental archives (although palimpsest effects on an assemblage level are important to consider). Faunal δ^{18}O data thus offer a unique window into climatic conditions that can be much more directly connected with evidence of human behaviour and ecology. This is especially important for studying Palaeolithic human evolution because chronometric dating uncertainty in these contexts is almost always prohibitively large - commonly at least double the length of stadial-interstadial cycles - for making robust correlations with distant palaeoclimate archives. Due to the connection with times of human activity and high temporal resolution, faunal δ^{18}O data can diverge substantially from palaeoclimatic inferences based on naturally accumulated and more highly time-averaged archives (Fig. 6) (Pederzani et al., 2021a; Pryor et al., 2013; Reade et al., 2016, 2020a).

For these reasons, zooarchaeological oxygen isotope studies can be of particular value and, indeed, have led to important novel insights into the climatic preferences and tolerances of Pleistocene hominins. For example, oxygen isotope data from anthropogenically accumulated horse teeth at some of the earliest occurrences of *Homo sapiens* in Europe have shown that these already occurred in very cold subarctic climates - contrary to established models of *H. sapiens* expansions being predicated on warm climate phases (Pederzani et al., 2024; 2021b) (Fig. 7A–C) In this way, oxygen isotope data from faunal remains could show that cold climate resilience appeared earlier in our evolutionary history than previously thought, with most previous data relying on lower-resolution comparisons between the absolute dates of archaeological deposits and spatially distant climate archives such as the NGRIP ice cores. In some cases, faunal δ^{18}O can also yield results that diverge from local but geologically derived environmental archives due to the different accumulation and time-averaging characteristics. Examples of this can be found with faunal isotope data indicating both colder (e.g. Reiss et al., 2024), or warmer climatic conditions during hominin presence than previously inferred from more time-averaged geologically-derived archives (e.g. Pederzani et al., 2021a). In the case of the late Neanderthal site of La Ferrassie, France, a divergence between warm-climate evidence in faunal stable isotope data with naturally accumulated sedimentary indicators of cold climatic conditions has been used to argue that Neanderthal occupations of the site predominantly took place in punctuated interstadial warm phases of MIS 4 and 3 (Pederzani et al., 2021a). Indeed, faunal oxygen isotope data from late Neanderthal sites often seem to indicate occupations predominantly coinciding with ameliorated and stable environmental conditions (Britton et al., 2019, 2023a; Carvalho et al., 2022; Pederzani et al., 2021a, 2023). The number of sites examined this way remains small, so overarching conclusions about hominin climatic niches should be regarded as preliminary. However, these examples illustrate the unique utility of oxygen isotope palaeoclimatology applied to zooarchaeological assemblages.

To be able to robustly capitalise on these unique palaeoclimatic archives it is, however, paramount to consider and account for the challenges in interpreting oxygen isotope variation in mammalian skeletal remains, particularly in a quantitative way. As with other isotopic systems discussed above, oxygen isotope variation is influenced by multiple and sometimes interconnected effects that are both climatic and non-climatic in nature (Pederzani and Britton, 2019). Isolating a single effect of interest - i.e. temperature change - from this complex multicausal web of effects can be extremely challenging and full isolation is usually impossible. Acknowledging this, certain design choices can be made and checks conducted with independent lines of evidence to minimise potential pitfalls stemming from equifinality. For palaeoclimatic interpretations, geographical setting of the study area is the first important aspect to consider as this will dictate both the dominant climatic effect on $\delta^{18}O_{precip}$ (rainfall amount vs temperature) and the complexity of the hydroclimatic setting in terms of atmospheric circulation. For palaeotemperature estimations from faunal δ^{18}O, studies should be set in mid to high latitude areas and regions where moisture transport systems are as stable through the time of interest as possible. For example, these prerequisites are arguably sufficiently well fulfilled for studies of Pleistocene Europe and northern Asia (see Pederzani et al., 2024). In tropical or subtropical regions atmospheric circulation systems can be much more variable, and $\delta^{18}O_{precip}$ values - and therefore faunal oxygen

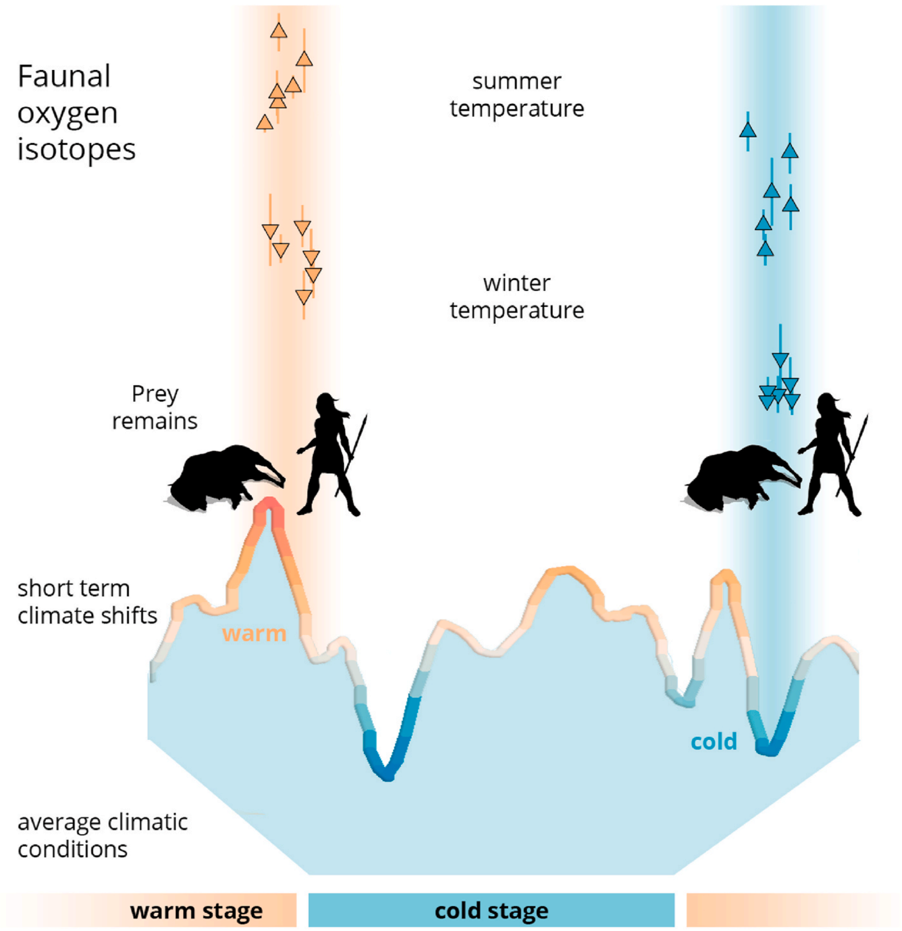

Fig. 6. (From Pederzani, 2020): Schematic of how oxygen isotopes of archaeological faunal material provide direct, minimally time averaged evidence of climatic conditions during site use. Due to strong short-term climatic shifts, these can differ substantially from the broad climatic average that can be assigned to an assemblage based on correlating chronometric dates with more distant climate archives such as the NGRIP record.

isotope values - are more representative of hydroclimatic changes (e.g. Green et al., 2022) or changes in aridity in moisture-limited systems (e.g. Blumenthal et al., 2017; Reade et al., 2016). For each study using faunal oxygen isotopes as a palaeoclimatic indicator it is, furthermore, paramount to consider to which extent locally available drinking water sources are likely to be representative of isotopic effects in meteoric water. In this context it is particularly important to consider water transport by large rivers as well as time averaging or lags introduced by large water bodies or snowpacks and glaciers (Gat, 2010). The role of evaporation from rivers and lakes should be considered as well. Due to strong mixing effects, water bodies with long residence times (large rivers, large lakes, groundwater) exhibit little or no seasonal δ^{18}O variation (Gonfiantini, 1986; Halder et al., 2015; Kortelainen and Karhu, 2004). A pronounced seasonal signal in δ^{18}O data from sequentially sampled faunal enamel can therefore be used to indicate a negligible contribution of such water sources to animal drinking water throughout the year. However, a thorough discussion of such hydrological characteristics should be conducted on a case-by-case basis for each oxygen isotope palaeoclimate study. In addition to ensuring that surface waters predominantly represent isotopic changes in meteoric water, palaeoclimate studies using faunal δ^{18}O need to ensure that enamel δ^{18}O values closely represent those of liquid drinking water. This is normally achieved by choosing large-bodied mammals with high drinking requirements as study taxa. Due to these requirements and a preference for high-crowned teeth for sequential sampling, large herbivores are most commonly targeted with typical examples including large bovids, equids, suids, rhinoceros, and proboscideans (Pederzani and Britton, 2019; Reade et al., 2016; Sharma et al., 2004; Szabó et al., 2017; Uno et al., 2020; Zazzo et al., 2005). In cases where aridity is a climate variability of interest, combinations of obligate drinking and non-obligate drinking species can reveal changes in evaporation regimes while controlling for baseline hydroclimatic variability in $\delta^{18}O_{precip}$ (Levin et al., 2006). Underlying oxygen isotope differences between surface waters and plant waters also mean that comparing δ^{18}O values across different herbivore species may illuminate their feeding and drinking behaviour, and thus uncover ecological niches and relationships. Applications have particularly focused on differences between grazers and browsers (e.g. Asevedo et al., 2021; Sealy et al., 2020; Sponheimer and Lee-Thorp, 1999), and frugivory and feeding height in rainforest canopies (Carter and Bradbury, 2016; Fannin and McGraw, 2020). In cases where palaeotemperature is estimated it is critical to quantify and propagate errors when converting biomineral δ^{18}O to drinking water δ^{18}O and to temperatures (Pryor et al., 2014).

Oxygen stable isotope applications to this material often aim to take advantage of the incremental formation and lack of remodelling in tooth enamel to extract sub-annually resolved oxygen isotope time series through sequential sampling along the growth axis. Reconstructing summer and winter temperatures can be of particular interest, as both rainfall and temperature seasonality have strong impacts on vegetation and the seasonal availability of resources (Kwiecien et al., 2022). However, due to the complex and non-linear process of enamel formation and mineralisation described in earlier sections, the extraction of faithful seasonal environmental information from sequential $\delta^{18}O_{enamel}$ data presents a non-trivial challenge. Time averaging of the oxygen isotope signal from extended phases of mineralisation and from the sampling procedure introduces a damping of the seasonal amplitude in

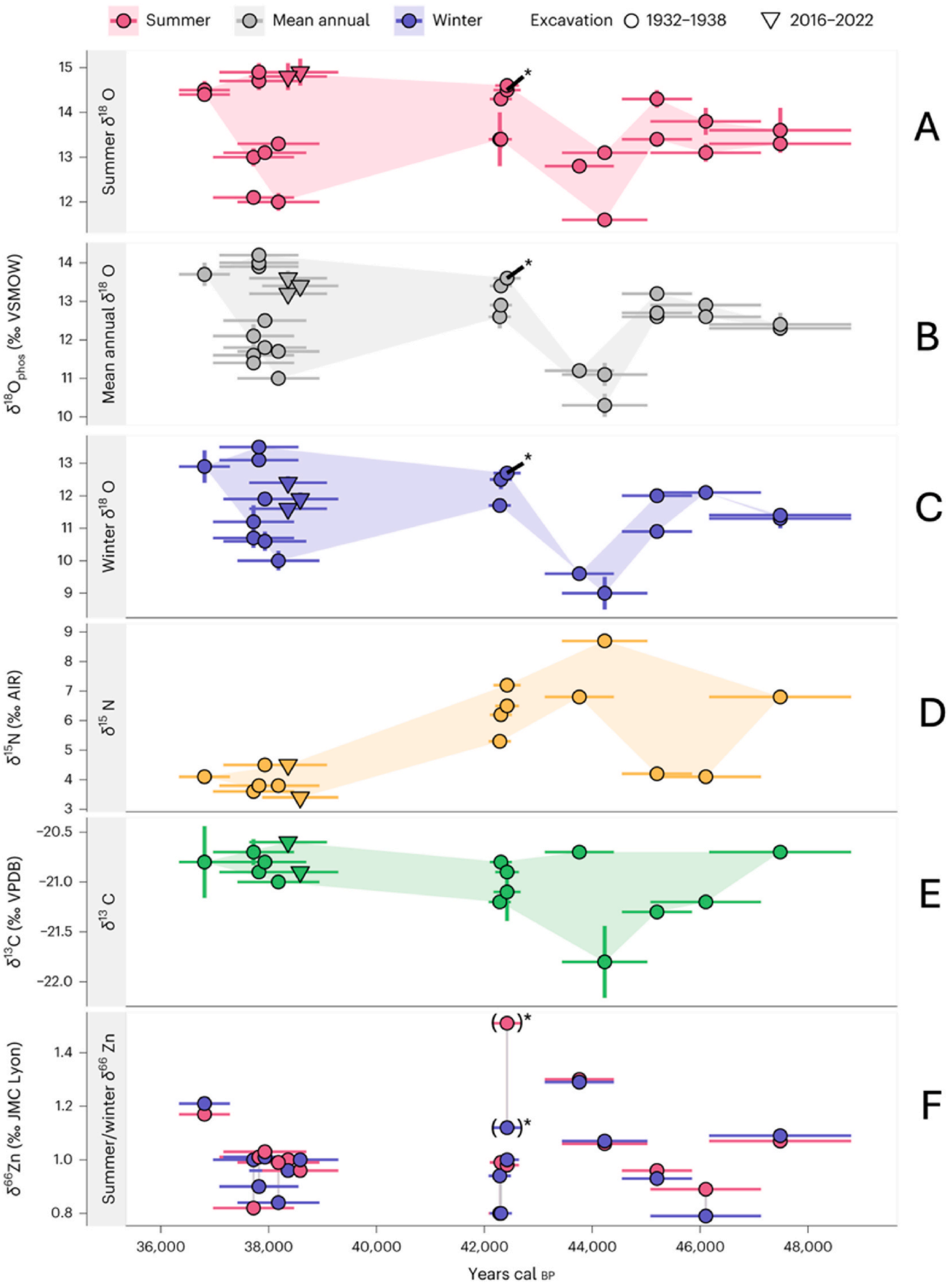

Fig. 7. (Adapted from Pederzani et al. 2024): Multi-isotope (oxygen, nitrogen, carbon and zinc) analyses of directly dated equid teeth show changes in climate and environment through the Upper Palaeolithic sequence of Ranis, Germany. Oxygen isotope data points represent $\delta^{18}O$ summer peak, winter trough and annual means of individual annual cycles represented in sinusoidal $\delta^{18}O$ time series obtained from sequentially sampled tooth enamel. Vertical error bars = measurement uncertainty, horizontal error bars indicate the 95 % calibrated age range of direct radiocarbon dates. One individual has been marked with an asterisk as it has been excluded from climatic interpretations because $^{87}Sr/^{86}Sr$ and $\delta^{66}Zn$ seasonal amplitudes are high enough that a seasonal movement cannot be completely excluded. Collagen analysed for $\delta^{13}C$ and $\delta^{15}N$ was obtained from tooth dentine for all 1932–1938 samples and from adhering mandible bone for the two 2016–2022 samples marked by triangle shapes. Oxygen isotope values are low values throughout the sequence and indicate a temperature decline from ~48 ka cal. BP to a temperature minimum at ~45–43 ka cal. BP. This minimum coincides with high $\delta^{15}N$ and $\delta^{66}Zn$ values, suggesting a hypergrazer niche of equids in open steppe environments or very dry soil conditions similarly indicative of an open environment. This is supported by high $\delta^{13}C$ values consistent with a steppe or tundra biome.

the measured $\delta^{18}O_{enamel}$ data compared to the original signal present in drinking water. A number of different sampling and modelling approaches have been developed to minimise this damping effect or estimate and computationally account for it (e.g. Blumenthal et al., 2019, 2014; Green et al., 2018; Passey et al., 2005a; Passey and Cerling, 2002). Some recent modelling approaches and high resolution analytical approaches have been shown to be very effective in recovering more faithful approximations of environmental oxygen isotope variation from enamel data (Green et al., 2018, 2022). However, the detailed enamel formation information for this work is not widely available for many species of interest and most seasonal oxygen isotope climate reconstructions remain less precise than mean annual inferences. It is important, however, that - due to differential dental wear, and thus enamel loss - the timing and periodicity of tooth formation is also considered in studies using 'bulk' samples of tooth enamel for the purposes of reconstructing mean annual temperatures (Britton et al., 2019).

Due to the spatial variation in $\delta^{18}O_{precip}$, palaeoclimatic reconstructions using mammalian skeletal remains need to ensure that sampled animals did not undergo long-distance migrations, as that would lead to a confounding of potentially opposing isotopic trends related to climate and geography. Independent evidence on spatial ecology from other isotope systems such as strontium (see section 6) is usually the best approach to confirm this. In this context it is particularly important to note that many mammal species have changed their migratory behaviour plastically throughout their evolutionary history (e.g. Bonhof and Pryor, 2022; Britton et al., 2011; O'Brien et al., 2024), making independent and contemporary evidence of spatial ecology a key to obtaining robust oxygen-isotope-based climatic reconstructions.

Precisely due to these geospatial effects in the oxygen isotope system, oxygen stable isotope analysis of mammalian skeletal remains is also an important tool for reconstructing animal movements and spatial ecology in their own right. Due to the relatively low geospatial rate-of-change of $\delta^{18}O$ in precipitation, studies of animal movement using $\delta^{18}O$ alone face challenges of low spatial resolution and equifinality with non-spatial $\delta^{18}O$ effects (Hodgkins et al., 2020). Oxygen-only studies of animal movement often focus on vertical movement, where larger isotopic gradients can be expected (Lazzerini et al., 2021). Therefore, $\delta^{18}O$ is most effectively paired with other geolocation proxies (such as sulfur, strontium or lead isotopes) to both identify migratory behaviour and to potentially identify likely areas that animals may have moved through, often on a seasonal basis. Oxygen isotope analysis may also be a useful means of seasonally anchoring these other isotopic proxies in intra-tooth studies of archaeo- or palaeo-faunal mobility (e.g. Barakat et al., 2023). Many of these studies of seasonal animal movement have made important contributions in highlighting the plasticity of mammal spatial ecology with implications for climate change adaptability and conservation of large herbivores.

6. Hydrogen isotopes

Hydrogen has two naturally occurring stable isotopes, which, unlike isotopes of other elements, have their own names: protium (^{1}H) and deuterium (^{2}H, D). The ratio of ^{2}H to ^{1}H ($\delta^{2}H$) can be measured in the organic phase (bone or dentine 'collagen') and mineral phase (bone or enamel bioapatite) of mammal skeletal remains. Hydrogen exists in two forms in enamel bioapatite, with around 70 % as OH^{-} (c. 0.10 wt percent) and 30 % as HPO_4^{-} (c. 0.04 wt percent) (Drewicz et al., 2020; Driessens and Verbeeck, 1990). Studies analysing enamel bioapatite $\delta^{2}H$ are rare, in part due to the ease of measuring oxygen isotopes in bioapatite, which provide similar information. Further, the complexities of the analytical methods involved in dealing with biases introduced by labile water (both exchangeable structural hydrogen and adsorbed water) have limited research on enamel bioapatite $\delta^{2}H$ (Drewicz et al., 2020; Holobinko et al., 2011). Similar analytical difficulties impact organic tissue $\delta^{2}H$ analysis, but these have largely been overcome in recent years (Meier-Augenstein et al., 2013; Wassenaar et al., 2023). Around 77–81 % of hydrogen atoms in collagen are bound to carbon atoms and are non-exchangeable, whereas the other ~19–23 % are loosely bound in functional groups such as -OH, $-NH_2$, -SH or -COOH and are exchangeable with labile water (Clauzel et al., 2022; Cormie et al., 1994a; France et al., 2018; Meier-Augenstein et al., 2013; Sauer et al., 2009; Topalov et al., 2013). Measured $\delta^{2}H$ on the same sample of collagen will vary between different laboratories due to geographical and seasonal differences in the $\delta^{2}H$ of ambient water vapour which is absorbed by the sample and may impact collagen exchangeable $\delta^{2}H$ (Hobson, 2022; Meier-Augenstein et al., 2013). A range of approaches (e.g. comparative equilibrium) have been developed to account for adsorbed and exchangeable hydrogen, so that reported collagen $\delta^{2}H$ values are for non-exchangeable hydrogen only, and are comparable between laboratories (see (Hobson, 2022) for summary). The $\delta^{2}H$ of animal collagen reflects a combination of the $\delta^{2}H$ of drinking water and ingested food and body water, and therefore provides different information from $\delta^{18}O$ which also reflects oxygen taken in from air during metabolism (Hobson, 2022). The relative contribution of hydrogen from drinking water and ingested food is debated, but most studies suggest that the hydrogen in collagen is largely derived from diet rather than from water (Hobson et al., 1999; Topalov et al., 2019; Vander Zanden et al., 2016). In herbivores, there is a strong linear correlation between ingested water $\delta^{2}H$ and collagen non-exchangeable $\delta^{2}H$, and as leaf and stem $\delta^{2}H$ values reflect local precipitation $\delta^{2}H$ values, herbivore collagen non-exchangeable $\delta^{2}H$ can be used as a proxy for local precipitation $\delta^{2}H$ (Cormie et al., 1994a, 1994b; Reynard and Hedges, 2008). Some studies have shown that bone collagen $\delta^{2}H$ values reflect trophic levels, with $\delta^{2}H$ increasing in increments of 10 to 30 ‰ up the food chain (Birchall et al., 2005; Gröcke et al., 2017; Reynard et al., 2020; Reynard and Hedges, 2008; Topalov et al., 2013). However, there is some debate over whether this trophic enrichment results from the accumulation or exchange with ambient water at each trophic level, or from metabolic fractionation (Hobson, 2022).

Underlying hydrogen isotopic patterns reflected in mammal collagen $\delta^{2}H$ are linked to the large-scale systematics of the hydro- and biospheres. Similar to oxygen isotopes, hydrogen isotopes in the hydrological cycle are influenced by geospatial and climatic factors, including latitude, altitude, distance from the coast, rainfall amount, temperature, aridity, and distance from the source, leading to spatial variation (Bowen and West, 2019). Globally, $\delta^{2}H$ and $\delta^{18}O$ in precipitation linearly co-vary, defining the Global Meteoric Water Line (GMWL) (Craig, 1961). The benefit of targeting mammal hydrogen isotopes over oxygen isotopes for palaeoenvironmental studies is the larger dynamic range of hydrogen in nature, and the fact that collagen $\delta^{2}H$ more closely tracks predicted amount-weighted mean precipitation $\delta^{2}H$ compare to $\delta^{18}O$ values (Hobson, 2022; Reynard et al., 2020; Wassenaar, 2019). However there are potential benefits to measuring $\delta^{2}H$ and $\delta^{18}O$ together. Deuterium excess (d), which records deviation from the GMWL (defined as $d = \delta^{2}H - 8\,\delta^{18}O$) varies worldwide and is affected by local aridity and the relative humidity of the originating air masses, and can therefore provide additional information beyond $\delta^{2}H$ or $\delta^{18}O$ alone (Pfahl and Sodemann, 2014). In recent years, the use of hydrogen isotopes in animal ecology has grown significantly, with data being used to track the movements and origins of migratory animals, diet and climate (Bowen et al., 2005; Dunn et al., 2023; Hobson and Kardynal, 2023; Hobson and Wassenaar, 1996; Holopainen et al., 2024; Rodríguez-Ochoa et al., 2024; Wassenaar and Hobson, 1998; Bearhop et al., 2003; Hobson et al., 2004; Hobson and Wassenaar, 1996, 1996; Sharp et al., 2003; Vander Zanden et al., 2016, 2018). By contrast there are fewer studies which have analysed $\delta^{2}H$ collagen from palaeo-contexts (Arnay-de-la-Rosa et al., 2010; Clauzel et al., 2022; Cormie et al., 1994b; France et al., 2018; Gröcke et al., 2017; Leyden et al., 2006; Reynard et al., 2020; Reynard and Hedges, 2008; Ryan et al., 2020; Sluis et al., 2019). Even fewer have focused on palaeoclimate reconstruction rather than diet or mobility. Most notably, Leyden et al. (2006) showed that $\delta^{2}H$ of North American Bison varied through the Holocene and tracked changes in moisture availability and temperature. Reynard et al. (2020) showed that spatial variations in precipitation δ^2H across the Mediterranean were preserved in herbivore bone collagen δ^2H values. In contrast, Gröcke et al. (2017) saw limited differences between three sites; one in Belgium dating to 40-27 kyrs BP, a second in Switzerland dating to 14–12 kyrs BP and another in France dating to 8 kyrs BP, and concluded that climate variability was not recorded in their mammal collagen δ^2H values. However, this study did not have many samples of each species, or a temporal sequence through time in a single location. Given that difficulties in dealing with δ^2H biases introduced by labile water have been largely overcome (Wassenaar et al., 2023) and that two collagen international standards have been recently developed (USGS88 and UGS89), it is likely hydrogen isotope studies of collagen from palaeo-contexts will increase exponentially over the next decade. The δ^2H of both bone and dentine collagen have significant potential as proxies for average and seasonal palaeoclimatic conditions, either paired with δ^{18}O or utilised in isolation. Intra-tooth dentine δ^2H may be used (like oxygen) for seasonally anchoring other isotopic proxies in archaeo- or palaeo-faunal mobility or palaeodietary studies and to advance understanding of the plasticity of mammal spatial or dietary ecology in relation to climate change.

7. Strontium isotopes

Strontium has four naturally occurring isotopes, three of which are stable (^{84}Sr, ^{86}Sr, ^{88}Sr). The fourth isotope, ^{87}Sr, is radiogenic and is formed over time through the β-decay of ^{87}Rb. Despite its radiogenic nature, archaeologists and mammalian palaeontologists generally treat ^{87}Sr as stable. This is because the half-life of ^{87}Rb is 48.8 billion years but mammals only appeared around 250 million years ago, and hominins have only evolved over the past few million years. Strontium isotopes are typically measured in the mineral phase (bone or enamel bioapatite) of mammal skeletal remains as strontium substitutes for calcium in the bioapatite. Whilst strontium isotopes in enamel are generally resistant to diagenesis, it is widely accepted that the strontium isotopes in bone and dentine are often altered by diagenesis (Budd et al., 2000; Hoppe et al., 2003; Nelson et al., 1986; Trickett et al., 2003), although the exception is calcined (burnt) bone which preserves the ^{87}Sr/^{86}Sr of bone in the years prior to death (Snoeck et al., 2015, 2018). While there have been a growing number of studies using the stable isotopes of strontium (δ^{88}/^{86}Sr) of bones and teeth as a trophic level indicator (Guiserix et al., 2022; Knudson et al., 2010; Lewis et al., 2017), the vast majority of studies have focused on using the ^{87}Sr/^{86}Sr ratios of mammal remains to explore past mobility and migratory behaviour (see reviews: Bentley, 2006; Bataille et al., 2020; Holt et al., 2021; Montgomery, 2010; Richards and Britton, 2020). The ratio of ^{87}Sr/^{86}Sr in mammal bones and teeth is directly influenced by the ratio of ^{87}Sr/^{86}Sr in the plants they consume. This ratio, in turn, is determined by the soils and water that the plants rely on and is ultimately connected to the underlying lithologies and atmospheric deposition. The relative amount of ^{87}Sr to ^{86}Sr is dependent on factors such as the age of the rock, its mineral composition, and its original chemical content (Bentley, 2006; Capo et al., 1998). The spatial palaeoecology and migratory behaviour of mammals (including humans) have been explored through bulk and sequential sampling of teeth (e.g., Barakat et al., 2023; Britton et al., 2023a, 2011; Hoppe et al., 1999; Lugli et al., 2019; Price et al., 2017; Wooller et al., 2021). Over the past 15 years there has been increasing recognition that the bioavailable ^{87}Sr/^{86}Sr can deviate from those of the underlying geology due to environmental processes. With researchers primarily interested in mobility and migration, there has been a drive to map and create isoscapes of bioavailable strontium in order to facilitate provenancing (Barberena et al., 2021; Bataille et al., 2018, 2020; Britton et al., 2020; Evans et al., 2009, 2010; Holt et al., 2021; Kootker et al., 2016; Lugli et al., 2022; Tang and Wang, 2023; Wang and Tang, 2020; Wong et al., 2021). However, there is an underexploited opportunity to use ^{87}Sr/^{86}Sr of non-migratory mammals with small home ranges to explore changes in specific climatic/environmental conditions that could influence 'baseline' ^{87}Sr/^{86}Sr at a specific location. For example, coastal regions receive a significant atmospheric deposition of marine derived strontium in the form of heavy rainfall and sea-spray. This results in coastal regions being saturated with a marine ^{87}Sr/^{86}Sr value (~0.7092) instead of reflecting the underlying geology. As with sulfur, past changes in sea level have impacted terrestrial bioavailable ^{87}Sr/^{86}Sr as regions became less or more coastal, changing the geography of the coastal ^{87}Sr/^{86}Sr signal (Evans et al., 2009; Johnson et al., 2022; Montgomery, 2010; Montgomery et al., 2004). The deposition of wind-blown sediments can result in exotic ^{87}Sr/^{86}Sr being introduced to a region. In arid environments, the contribution of wind-blown sediments can fluctuate with climate and changing weather patterns (Capo et al., 1998; Chadwick et al., 1999; Ganor and Foner, 2001; Johnson et al., 2022; Yaalon, 1997). Glacial and fluvial erosion, which are influenced by climatic conditions, can also bring non-local ^{87}Sr/^{86}Sr into an area, altering the relationship between the underlying bedrock and surficial deposits (Bataille et al., 2018, 2020; Holt et al., 2021). Long term forestation impacts the ^{87}Sr/^{86}Sr isotope signature of the biosphere as leaf litter accumulation in the forest over time leads to soil acidity, which in turn leaches out the carbonate component of the soil, removing it as a contribution to the bioavailable ^{87}Sr/^{86}Sr signature (Johnson et al., 2022). With carefully selected tooth samples it would be possible to use ^{87}Sr/^{86}Sr isotopes of specific mammal species to study all of these environmental changes. However, perhaps due to the complexities in disentangling these influences and the circularity of needing to demonstrate a lack of movement in order to achieve these goals (perhaps using ^{87}Sr/^{86}Sr), current studies on past faunal ^{87}Sr/^{86}Sr signatures have primarily focused on understanding how mammal spatial ecology and migratory behaviour have responded to climate and environmental change, rather than directly investigating the climate and environmental change itself. Compared to other isotopes (such as carbon and nitrogen), there is also currently a lack of understanding as to how dietary variation can impact the ^{87}Sr/^{86}Sr of different organisms living at the same location. The extent of carnivory (particularly of potentially migratory animals), the intensity of consumption of marine foods, and even the parts (and root depth) of plants consumed, may influence the ^{87}Sr/^{86}Sr of dietary inputs of animals living on the same lithology (Blum et al., 2000). Ideally, prior to the more expansive application of ^{87}Sr/^{86}Sr within archaeology and/or palaeoecology, these potential influences would be better characterised, for example, through experimental controlled feeding or observational field studies.

8. Zinc isotopes

Analysis of zinc isotopes in fossil skeletal remains is a relatively new field of research (Jaouen and Pons, 2017). Zinc (Zn) is found in nature with five stable isotopes (^{64}Zn, ^{66}Zn, ^{67}Zn, ^{68}Zn, and ^{70}Zn). Various ratios of these isotopes have been measured, with δ^{66}Zn (derived from ^{66}Zn/^{64}Zn) being the most frequently applied. Studies have primarily focused on measuring zinc in the mineral portion of bones and enamel (Bourgon et al., 2020, 2021; Jaouen et al., 2016). Research has shown that tooth enamel and enameloid bioapatite can preserve biogenic δ^{66}Zn values for long periods, even in tropical conditions (Bourgon et al., 2020; Jaouen et al., 2022; McCormack et al., 2021, 2022). This preservation has been observed for tens of millions of years, dating back to the Miocene era (Bourgon et al., 2020; McCormack et al., 2022). However, the extent to which biogenic δ^{66}Zn values are preserved in bone is not well understood and dentine δ^{66}Zn has been shown to be prone to diagenetic alteration (Weber et al., 2021), thus it is important to exercise caution when interpreting fossil bone δ^{66}Zn values. A comparison of the Zn concentration and δ^{66}Zn isotopic data has been suggested as way of checking biogenic preservation and the extent of diagenetic alteration, as zinc leaching or uptake from the burial environments may be expressed as a mixing line (Bourgon et al., 2020). Further research is needed to determine the conditions under which bone biogenic δ^{66}Zn values are preserved/altered.

Zinc isotopes in mammal bones and teeth are derived from their diet, as zinc is an essential trace element that serves important biological functions. Zinc isotopes undergo mass-dependent fractionation within an organism, resulting in different δ^{66}Zn values among various body tissues (Balter et al., 2010; Moynier et al., 2013). Soft tissues, such as muscle and kidney, exhibit lower δ^{66}Zn values than hard tissues, such as bone (Balter et al., 2010; Jaouen et al., 2013). When comparing palaeo-skeletal remains, it is necessary to consider the offset in δ^{66}Zn values between different bioapatite tissues of the same individual, as bone and tooth dentine typically exhibit values that are, on average, 0.2 ‰ higher than those of tooth enamel. As carnivores and omnivores consume animal soft tissues, a trophic level effect is observed in mammal zinc isotopes, with δ^{66}Zn values decreasing by approximately 0.4 ‰ with trophic level (Jaouen et al., 2016). However, exact trophic level fractionation factors have not been experimentally determined. It should be noted that carnivores that consume both bone and soft tissues exhibit higher δ^{66}Zn values than those that consume only soft tissues (Balter et al., 2010; Bourgon et al., 2020; Jaouen et al., 2016).

Mammal zinc isotopes have the potential to provide information on palaeoenvironmental conditions because they are ultimately derived from soils and plants, thus not only reflect the bioavailable δ^{66}Zn baselines but also the processes which alter them. In soils, δ^{66}Zn variability is primarily driven by the lithology of the underlying bedrock. However, as with other isotopes, bioavailable δ^{66}Zn values are also affected by physical, chemical, and biological processes. Bioavailable δ^{66}Zn is influenced by a wide range of factors, such as hydrology, weathering, soil mineralogy, microbial activity, soil pH, organic matter, and biological activity (see Junqueira Tassiane et al., 2024 for review). Plant δ^{66}Zn values differ from bioavailable δ^{66}Zn values due to fractionation during uptake and transport. Heavier zinc isotopes accumulate in roots, giving them higher δ^{66}Zn values, while lighter isotopes are transported to peripheral parts like leaves, which show lower values. Taller plants, such as trees and shrubs, generally exhibit low δ^{66}Zn values, while shorter plants, like grasses and herbs, tend to have higher values. This can result in differential δ^{66}Zn values between grazers and browsers, which has been observed in some ecosystems, but not all (Bourgon et al., 2020; Jaouen et al., 2016, 2022; Pederzani et al., 2024) (Fig. 7 F).

Spatial difference in herbivore bone and enamel δ^{66}Zn have been reported, with tropical herbivore δ^{66}Zn being lower than those from other regions (Bourgon et al., 2020, 2021; Jaouen et al., 2016, 2022), although the cause of this difference has yet to be explored. Temporal trends in faunal baseline δ^{66}Zn have yet to be reported, however, due to the infancy of the application of zinc isotopes in fossil bones and teeth. However, δ^{66}Zn of mix feeder herbivores could potentially be used to determine whether they were grazing or browsing and thus track changes in vegetation distribution over time (Pederzani et al., 2024). In theory, herbivore δ^{66}Zn values could be used to track the climate/environmental processes that impact bioavailable δ^{66}Zn baselines. However, much work is required to understand the relationship between these processes and mammal δ^{66}Zn values in modern ecosystems before we can reliably use them as palaeo-proxies.

9. Conclusion

Multi-isotope analysis of bones and teeth is a powerful tool for reconstructing past climatic and environmental changes, and also the ecological behaviours of different species, offering advantages over single-isotope approaches. When combined, (see Pederzani et al. 2021, 2024a for examples of multi-isotope studies (Fig. 7A–F), these analyses provide substantial insights into changes in climate and environmental conditions as well as how animals responded, revealing shifts in niche partitioning (e.g. Reiss et al., 2023; Britton et al., 2023b), trophic dynamics (e.g. Yeakel et al., 2013), and spatial ecology (e.g. Heddell-Stevens et al., 2024) that inform our understanding of broader ecosystem changes. While we are aware of many environmental controls on the isotopic composition of bones and teeth, our understanding is more complete for carbon, nitrogen, oxygen, and strontium than for hydrogen, sulfur, and zinc. Analytical advances in the last decade mean that these latter isotopes are likely to become a focus for research in the coming decades. Further ground-truthing studies exploring the relationships between stable isotopes in bone and tooth samples and environmental parameters are necessary for the continued development of fossil faunal stable isotopes as palaeo-proxies. Furthermore, these should be coupled with studies that focus on how a taxon's physiology, or individual's dietary or spatial habits can influence resulting tissue isotopic values, and thus how 'baseline' changes can be disentangled from behavioural plasticity, which themselves may be caused by changes in broader environmental, climatic or ecological parameters. Ultimately, however, stable isotopes from bones and teeth are much more than just palaeo-proxies for past environments or behaviours. The isotopic archive offered in faunal remains provide a record natural and also anthropogenic change within ecosystems, and even the ecological responses to those changes. In this sense, these data can provide valuable baseline data for modern ecology, revealing the plasticity of animal behaviours and the interactions between those behaviour and climatic change. The use of the data thus goes beyond archaeological, palaeoecological or palaeontological study, but is relevant to animal conservation efforts in the present day and also to contemporary ecosystem restoration and rewilding policies and practices (e.g. Bocherens et al., 2015; Shaikh et al., 2025).

CRediT authorship contribution statement

Rhiannon E. Stevens: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Sarah Pederzani:** Writing – original draft, Writing – review & editing. **Kate Britton:** Writing – original draft, Writing – review & editing. **Sarah K. Wexler:** Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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Data availability

All data and/or code is contained within the submission.

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