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Neanderthal palaeoecology in the late Middle Palaeolithic of western Iberia: a stable isotope analysis of ungulate teeth from Lapa do Picareiro (Portugal)

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ABSTRACT: Adaptation to Late Pleistocene climate change is an oft-cited potential contributor to Neanderthal disappearance in Eurasia. Accordingly, research on Neanderthal behaviour – including subsistence strategies, mobility, lithic technology, raw material procurement and demography – often focuses on linking changes observable in the archaeological record to specific phases of climate and environmental change. However, these correspondences are often tenuous because palaeoclimatic and archaeological records are rarely available on the same scale. In Iberia, a critical location for understanding the demise of Neanderthals, some research indicates that Neanderthal populations were unable to recover from environmental degradations known as Heinrich Events, while other studies suggest that enclaves of Neanderthal populations survived for several millennia longer in refugial zones. Here, we present a palaeoenvironmental reconstruction study using analysis of $\delta^{13}C$ and $\delta^{18}O$ of herbivore tooth enamel recovered from two Mousterian deposits at Lapa do Picareiro, a site located in Portuguese Estremadura. We then use these data, combined with other site-based palaeoenvironmental indicators, to assess whether central Portugal acted as a refugium during periods of unfavourable climate, and to test whether Neanderthals in Portuguese Estremadura reorganised their mobility strategies after severe climate episodes. © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: herbivores; Middle Palaeolithic; Neanderthals; palaeoecology; stable isotope analysis

Introduction

About 40 000 years ago, Neanderthal populations disappeared as modern humans spread across Eurasia during the Middle to Upper Palaeolithic Transition (MUPT). Although a consensus may be emerging around demography as the main factor involved in the demise of Neanderthals, the underlying causes for demographic imbalances remain uncertain (Vaesen *et al.*, 2021). One major area of investigation focuses on responses to abrupt climatic and environmental deterioration (Finlayson and Carrión, 2007; Finlayson and Giles-Pacheco, 2000; Sepulchre *et al.*, 2007; Staubwasser *et al.*, 2018; Stewart, 2005, 2007; Vaesen *et al.*, 2021). This approach centres on the rapid and dramatic climatic oscillations of MIS 3, particularly the Greenland Stadials (cold) and Interstadials (warm) and the onset of Heinrich Events (e.g. Finlayson, 2004; Van Andel and Davies, 2003; Zilhão, 2006). A considerable amount of research suggests that Neanderthal populations were unable to adapt to or recover from the cold and dry conditions of these events (d'Errico and Sanchez-Goñi, 2003; Müller *et al.*, 2011; Van Meerbeeck *et al.*, 2009; Finlayson and Giles-Pacheco, 2000; Stewart, 2004a,b; Stewart *et al.*, 2003a). However, some studies suggest that late Neanderthal populations in southern Europe were shielded from adverse environmental conditions because they either remained in or contracted to refugial zones, or environments with more favourable conditions (see Jochim, 1987) during Heinrich Events (e.g. Sepulchre *et al.*, 2007).

The Iberian Peninsula holds important clues for understanding the dynamics that led to the demise of Neanderthals (e.g. Finlayson *et al.*, 2006; Zilhão *et al.*, 2017; Marín-Arroyo *et al.*, 2018; Haws *et al.*, 2020). The region was arguably the home of the last and potentially latest surviving Neanderthals (Finlayson *et al.*, 2006; Zilhão *et al.*, 2010); it is also a place where the MUPT is highly variable, with regions such as Vasco-Cantabria and Portuguese Estremadura containing their own distinct records (Straus, 2005, 2018; Zilhão, 2001; Bicho, 2004). Iberia has long been considered a refugium for both plant and animal communities during times of adverse climate conditions (Finlayson *et al.*, 2006) and a place where Neanderthal and modern human populations may have overlapped and even interacted (Marín-Arroyo, *et al.* 2018; Haws *et al.*, 2020).

However, linking observed changes in the archaeological record to specific climate phases is a difficult endeavour (see Discussion in Jimenez-Espejo *et al.*, 2007); the error ranges of radiometric dating techniques are usually too large to

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determine a precise climate phase, especially close to the limit of radiocarbon calibration curves, and palaeoclimatic reconstructions are limited, meaning we often need to rely on palaeoclimatic records obtained from sites that are hundreds of kilometres away. This, combined with the fact that Neanderthals adapted successfully to a variety of climates and environments over their preceding 300 000 years (e.g. Finlayson 2004), makes environmental arguments for their demise difficult to support. Nonetheless, Neanderthal behaviour appears to have been heavily influenced by the environment. Climatic and environmental factors did have a role in the distribution of Neanderthal sites, and often, major technological and behavioural reorganisations occurred after severe climate episodes (e.g. Pettitt, 2003; Banks *et al.*, 2021).

In this paper, we use $\delta^{13}C$ and $\delta^{18}O$ analysis of herbivore teeth from late Middle Palaeolithic deposits (51 800–42 420 cal a BP) at Lapa do Picareiro, a cave site in central Portugal, to explore the relationship between climate, environment and Neanderthal extinction in Portuguese Estremadura. We present $\delta^{13}C$ and $\delta^{18}O$ data from red deer (*Cervus elaphus*) and ibex (*Capra pyrenaica*) tooth enamel recovered from two Mousterian layers at Picareiro, Levels KK and JJ. We then compare these data with previously published regional and site-based geoarchaeological palaeoenvironmental records and to observed changes in occupation intensity and in raw material procurement to answer the following questions: (1) Do the $\delta^{13}C$ and $\delta^{18}O$ values of herbivore teeth at Picareiro provide local palaeoenvironmental information? (2) Is there evidence of a stable environment dominated by woodland forests and/or higher humidity levels during Neanderthal occupations that would indicate refugial conditions? (3) Was there a reorganisation in human behaviour and technology, observed through changes in occupation intensity and raw material procurement strategies, after episodes of severe climate change?

MIS 3, refugia, and ecological Neanderthal extinction

Environmental conditions during MIS 3 (~60–30k cal a BP) fluctuated dramatically and relatively quickly, with changes occurring over millennial and even centennial-scale cycles (Jouzel *et al.*, 1987; Voelker, 2002; Fletcher *et al.*, 2010). This period was marked by Greenland Interstadials, Stadials and Heinrich Events (when large quantities of icebergs floated into the North Atlantic Ocean as far south as 37°N, resulting in near-catastrophic disruption of the Atlantic Meridional Overturning Circulation; Grousset *et al.*, 2001; Rasmussen *et al.*, 2014). The latter caused considerable cooling of sea surface temperatures, which on land manifested as rapid onsets of extremely cold and dry conditions (Dansgaard *et al.*, 1993; Heinrich, 1988; Kissel, 2005; Rasmussen *et al.*, 2014).

In Iberia, these cycles resulted in the oscillation of the North Atlantic Polar Front between the northern strip of the Iberian Peninsula (Galicia to the Basque Country) and slightly south of central Iberia (~39°N) (Baas *et al.*, 1997; Hemming, 2004). The shifting polar front meant the boundary between the Eurosiberian and Mediterranean bioclimatic zones wavered. Greenland Interstadials and Stadials, and Heinrich Events continually modified the landscapes in which Neanderthals lived, with the cyclical deteriorations affecting human ecodynamics, technology and other aspects of culture (e.g. Melchionna *et al.*, 2018; Müller *et al.*, 2011; Obreht *et al.*, 2017; Staubwasser *et al.* 2018).

As might be expected given these conditions, relative stability in climate and environment seem have been crucial factors in the distribution of Neanderthals in Iberia (Finlayson and Giles-Pacheco, 2000; Stewart *et al.*, 2003a,b; Stewart, 2004a,b). A handful of contested dates suggest that Neanderthals survived until *c.* 37–35k cal a BP in its southern refugial extremes while modern humans persisted in the open steppe environments of the north (e.g. Straus *et al.*, 1993; Straus, 1996, 2018; Zilhão, 2000, 2006, 2009; Zilhão *et al.*, 2010, 2017). Other models posit that Neanderthals and modern humans had distinct ecological niches (d'Errico and Sanchez-Goñi, 2003; Sepulchre *et al.*, 2007; Finlayson, 2004; Finlayson and Giles-Pacheco, 2000; Finlayson and Carrión, 2007; Jimenez-Espejo *et al.*, 2007). It may be that particular niche parameters, or the specific biotic or abiotic variables that make up a niche, were more important drivers of Neanderthal distribution, and eventually disappearance, than others. Precipitation may have been a particularly important niche parameter: areas with higher levels of precipitation seem to have been home to more Neanderthal sites, suggesting that moisture, rather than temperature, was critical for Neanderthals (Jennings *et al.*, 2011).

However, the limited MUPT record in much of Iberia beyond the northern and eastern coastal regions, especially in Portugal, and often poor chronological control of transitional deposits mean that hypotheses and models are built upon relatively small sample sizes and contested radiocarbon dates. Late Neanderthal survival is increasingly questioned as re-evaluations of radiocarbon dates point to much older ages (e.g. Wood *et al.*, 2013; Higham *et al.*, 2014; Cunha *et al.*, 2019), and as discoveries of possible early Aurignacian sites may place modern humans in southern Iberia several millennia earlier than previously known (Haws *et al.*, 2020; Cortés-Sánchez *et al.*, 2019), if modern humans were its maker (see Straus, 2020). Furthermore, it is unlikely that the fate of Neanderthals was determined solely by climate, as Neanderthals lived through 300 000 years of successful adaptations to constantly changing environments (Finlayson 2004). Neanderthals had an extensive understanding of their surrounding landscape and the ecological communities within them, exploited multiple environments due to their seasonal mobility and varied subsistence strategies (e.g. Finlayson, 2004), made improvements in tool-making and raw material procurement (e.g. Baena *et al.* 2017) and often occupied diversity hotspots (e.g. Finlayson 2004). In other words, the observed plasticity in Neanderthal ecology leaves open the discussion on the significance of climate in the extinction of Neanderthals.

Perhaps most importantly, drawing direct links between the archaeological record and climatic events is nearly always challenging at best, due to differences in scale. For archaeologists working in Iberia, much of the palaeoenvironmental information available for the Late Pleistocene derives from pollen and deep-sea sediment cores, and to a lesser extent, ice cores. However, each palaeoclimatic proxy reflects information on a multitude of temporal and spatial scales. Reconstructions based on pollen records can reflect different catchment areas and therefore contain information pertinent to local, subregional, regional and continental scales. Pollen obtained from deep-sea marine sediments can reflect conditions that are basin-wide, resulting in records that are indicative of continental or regional conditions, while terrestrial pollen records are indicative of a more spatially limited area, reflecting regional, subregional and potentially local scales (see Jimenez-Espejo *et al.*, 2007 and Jones, 2016). In addition to pollen, deep-sea sediment cores contain foraminifera-based $\delta^{18}O$ records reflecting broad regional conditions (see Discussion in Jones, 2016). Ice cores produce oxygen isotope records on millennial and sometimes centennial scales, but these are based on the $\delta^{18}O$ composition of water in global-scale hydrological systems.

The archaeological record, too, is susceptible to issues of scale. At any given site, human occupation can be continuous (e.g. long term) or punctuated (i.e. short term), representative of a single event or, as is especially true of cave or rockshelter sites, a palimpsest of many events and constrained by large or small ranges of radiometric dates with differing error margins. Thus, linking archaeological evidence to specific climate phases is almost always an extremely conservative effort, where changes in human behaviour tend to be assigned to broad climate events such as Marine Isotope Stages. In reality, archaeological evidence of human activity could have formed on millennial or even centennial scales under environmental conditions that are essentially different from those used to broadly describe the assigned Marine Isotope Stage (see Discussion in Pederzani *et al.*, 2021). This makes it particularly difficult to assess whether reorganisations in technology and behaviour (*sensu* Pettitt, 2003; see Bradtmöller *et al.*, 2012 for the same concept applied to modern humans) occurred after severe climate events.

One way in which archaeologists have successfully secured a direct contextual connection between archaeological evidence and the climatic or environmental context of its deposition is through the creation of site-based faunal tooth enamel stable isotope records obtained from faunal assemblages that are either anthropogenic or in direct association with artefacts or other archaeological evidence of human activity (Pederzani *et al.*, 2021). By using local, site-based records in direct association with archaeological evidence, the issues of scale, though not completely resolved, are minimised.

We employ this approach using the red deer and ibex teeth from late Middle Palaeolithic deposits at Lapa do Picareiro, a cave site in central Portugal with occupations spanning the MUPT. We use this site-based palaeoenvironmental record to demonstrate the influence of climate and environment on Neanderthal populations in Portuguese Estremadura, a particularly understudied area in the study of Neanderthal extinction. Our goals for this study are threefold: (1) to assess whether the use of $\delta^{13}C$ and $\delta^{18}O$ analysis obtained from herbivore teeth can successfully reconstruct the local vegetation and moisture regimes in the area immediately surrounding Lapa do Picareiro during different late Neanderthal occupations and if these link to specific climate events; (2) to evaluate whether Portuguese Estremadura was a refugium for Neanderthals during periods of adverse climate conditions; and (3) to ascertain whether Neanderthals in the area reorganised their behaviour or technological systems after severe climate episodes through observations in raw material use in the different Neanderthal occupations at this site.

Isotopic relationships and environmental factors

The composition of $\delta^{13}C$ and $\delta^{18}O$ in animal teeth, particularly herbivore teeth, from archaeological remains is frequently used in assessments of the palaeodiets and palaeoenvironments of Neanderthals, modern humans and other hominins (e.g. Bocherens *et al.*, 1999, 2001; Jones *et al.*, 2019; Feranec *et al.*, 2010; Nelson and Rook, 2016; Faith, 2018). Here, we use this technique, applied to red deer and ibex tooth enamel, to assess whether the stable isotopic composition of herbivore tooth enamel can track environmental changes in moisture regimes and vegetation cover.

Environmental conditions, particularly the availability of water, are reflected in the $\delta^{13}C$ of plants and the tissues of the herbivores that eat them, in both modern and ancient contexts in western Europe (Drucker *et al.*, 2008). Thus, the $\delta^{13}C$ values obtained from herbivore tooth enamel mirror plant cover distributions, or the proportion of plants using C3 versus C4 photosynthetic pathways, of the territories in which an individual foraged during the period of tooth mineralisation (e.g. Fricke *et al.*, 1998; Nelson, 2005; Schoeninger, 1995). In a temperate environment such as Europe, where C3 plants dominate, the $\delta^{13}C$ values of C3 plants are typically driven by light and water stresses because C3 plants change respiration rates to cope with limited precipitation and large quantities of insolation (Ehleringer *et al.*, 1986). The $\delta^{13}C$ values of plants become enriched where evaporative stresses are high (forest upper canopies, open steppes and savannas) and depleted in environments where evaporative stresses are low, such as the vegetation available on forest floors (e.g. Vogel, 1980; Kohn, 2010; Cerling *et al.*, 1997). In temperate settings, the $\delta^{13}C$ composition of a plant located in open areas can be elevated by 2–5‰ in comparison with those encountered in closed forested environments, even for the same species of plants, confirming that the canopy effect operates in non-tropical environments as well (e.g. Drucker *et al.*, 2008). Thus, the $\delta^{13}C$ composition of tooth enamel from non-migratory herbivores can be a measure of how open (i.e. fewer trees due to drier conditions) or closed (i.e. more trees due to wetter conditions) (Drucker *et al.*, 2008) local vegetation systems were. However, interpreting this isotopic data requires an understanding of a herbivore's ecology.

Red deer is one such herbivore commonly used in this type of analysis because it is ubiquitous in archaeological assemblages, widely tolerant of different environments, and studies show that changes in local environmental conditions are reflected in the isotopic values of its tissues (Richards and Hedges, 2003; Drucker *et al.*, 2003, 2008, 2011; Stevens *et al.*, 2006, 2014). This ecologically plastic cervid can live in a variety of environments such as steppe, and boreal and closed temperate forests (Geist, 1998; Drucker *et al.*, 2008). Red deer are flexible in terms of diet, as they are considered an opportunistic mixed feeder (Straus, 1981; Hofman, 1989), foraging on forbs, foliage and other edible tree parts, grasses and sedges (Gębczyńska, 1980; Heptner *et al.*, 1989; Gebert and Verheyden-Tixier, 2001). These characteristics have been shown at various Palaeolithic sites, where the $\delta^{13}C$ composition of Late Pleistocene red deer bones (collagen) in western Europe displays a range of values ($\delta^{13}C_{diet} = c.\ -29$ to -24‰) that in context suggest that red deer occupied both open and closed habitats or foraged at a variety of elevations (Drucker *et al.*, 2008, 2011; Pilaar Birch *et al.*, 2016; Stevens *et al.*, 2014; Jones *et al.*, 2019, 2020; Feranec *et al.*, 2010). Modern red deer migration behaviour varies because many factors (e.g. food availability, climate, mate availability, wildlife management practices, anthropogenic disturbance) can affect their behaviour, with migrating distances ranging from 10 to 140 km, and migratory populations mostly located in the cold areas of North America (Boyce, 1991; Craighead *et al.*, 1972). In the Late Pleistocene the migrating behaviour is unclear, though some studies indicate that that observed for other ungulates such as reindeer during the Pleistocene has not been identified with Pleistocene red deer (Steele, 2002). The isotopic composition of the reconstructed diet of Palaeolithic red deer in northern Spain from La Riera (Asturias), Covalejos, El Castillo (Cantabria) and Valdegoba (Burgos) (roughly −26 to −24‰) suggests that red deer populations remained local (i.e. did not migrate), adapted to episodes of climate change, and foraged in relatively open temperate forest, mosaic-like environments ($\delta^{13}C_{\text{temperate forest}}$: −23‰ to −33‰, the latter value representing very closed-canopy forest; Kohn 2010; Hemming *et al.* 2005).

The remains of ibex, another common ungulate in Palaeolithic archaeofaunas in Iberia, can also be used in this type of stable isotope analysis. Ibex, though a resilient ungulate, has slightly less ecological plasticity than red deer. Ibex are typically considered high-altitude ungulates that prefer steep rocky areas in modern times, but archaeological data suggest they also occupied lower elevations during the Late Pleistocene (Freeman, 1973; Phoca-Cosmetatou, 2002). While they tend to graze more than red deer, ibex are flexible feeders, shifting altitudinally, searching for food, foraging at the wetter, higher altitudes during the dry summers, and at lower altitudes in the spring, when there is generally more precipitation at lower elevations (Parrini *et al.*, 2003). Other than the altitudinal movement, caprids like the ibex are assumed to have been non-migratory in the Late Pleistocene, moving to different areas in search of mates and adequate foliage (Ferrari *et al.*, 1988; Richard-Hansen and Campan, 1992). The $\delta^{13}C_{diet}$ data obtained from ibex tissues from the sites at Valdegoba and La Reira ranges from −26.4 to 21.9‰, which is slightly enriched for temperate forests, and slightly more elevated than red deer (e.g. Jones *et al.*, 2020; Feranec *et al.*, 2010). This indicates that Iberian ibex in the Late Pleistocene foraged in environments that were slightly more open or higher in altitude than red deer (Jones *et al.*, 2020; Feranec *et al.*, 2010).

As flexible feeders, the $\delta^{13}C$ values of red deer and ibex should reflect mostly herbaceous dicots and woody plants (depleted $\delta^{13}C$ values) during times of more closed-canopy, forested vegetation, and wetter climates like those of the interstadials. Enriched $\delta^{13}C$ values should reflect grasses or plants growing in open-canopy environments, such as the steppe that prevailed in southern Iberia during cold/arid stadial events and Heinrich Events. However, current evidence has shown that both red deer and ibex populations remained local during the Late Pleistocene in Europe, but this does not rule out the possibility that these ungulates had different mobility strategies at other times. It could be that variation in $\delta^{13}C$ of both taxa over time is the product of changes in mobility, either laterally or altitudinally, instead of being caused by climate change. One can approach this problem isotopically (Pilaar Birch *et al.*, 2016; Stevens *et al.*, 2011). For both red deer and caprids like ibex, large variations in the range of intratooth $\delta^{13}C$ (but more so for $\delta^{18}O$) observed in an individual can be a marker of limited lateral mobility wherein an individual faces seasonal climate changes in one location throughout the year which are then recorded in tooth enamel (Pilaar Birch *et al.*, 2016), whereas a smaller range in intratooth $\delta^{13}C$ values could be indicative of an animal moving laterally to different territories in search of foliage throughout the year, and this would dampen the isotopic signal of seasons in their teeth (see Pilaar Birch *et al.*, 2016). Assessing whether altitudinal movement is affecting the isotopic composition of animal tissues is possible because the $\delta^{13}C$ of plants increases by 0.7‰ with every 1000 m gain in altitude (Körner *et al.*, 1988).

While, in general, $\delta^{18}O$ of herbivore tooth enamel tracks the composition of the water consumed by any given animal (e.g. Quade *et al.*, 1992), $\delta^{18}O$ values can also be influenced by many variables, including the animal's physiology and habitat characteristics (e.g. elevation, distance to the coast, climate) (see Pederzani and Britton, 2019 and references therein). Like $\delta^{13}C$ values, $\delta^{18}O$ values of meteoric and leaf water are sensitive to light and water stresses and fractionate similarly to $\delta^{13}C$, where enriched values suggest more evaporative stress and lighter values suggest less evaporative stress (Quade *et al.* 1995). An important physiological property that guides the interpretation of $\delta^{18}O$ values is the way in which any given taxon consumes a majority of their water. Levin *et al.* (2006) have shown that evaporation-sensitive herbivores, those who take in a majority of their water through their food, will have $\delta^{18}O$ signals in their tissues that reflect the level of evaporation of leaf water. While ibex acquire most of their water from herbaceous dicots and to a lesser extent woody plants, red deer have more flexible drinking strategies, meaning they sometimes drink from bodies of water. Because the $\delta^{18}O$ composition of meteoric water reacts similarly to evaporative stresses, the $\delta^{18}O$ values of red deer will generally reflect the amount of evaporative stress in plants (e.g. herbaceous dicots, woody plants or grasses) and/or meteoric water with values decreasing during times of less evaporative stress (more precipitation or moisture) and increasing during periods of higher evaporative stress (less precipitation or moisture). However, the $\delta^{18}O$ values from ibex teeth should overwhelmingly reflect evaporative stress in the plants they consume. Variation in the $\delta^{18}O$ signature of ibex teeth can thus be explained by a change in foraging location (e.g. lateral or altitudinal) or environmental change. The $\delta^{13}C$ and $\delta^{18}O$ values observed in a herbivore's tooth enamel will either reflect where it feeds in the landscape or the environmental/climatic conditions that individual faced, or a mixture of both. Similar to $\delta^{13}C$, interpreting variations in $\delta^{18}O$ data is dependent on understanding the mobility strategies of the studied herbivore. Mobility of an individual can be assessed similarly as with $\delta^{13}C$, but a more robust measure uses $\delta^{18}O$: by evaluating the range size in $\delta^{18}O$ values (more variation = limited mobility, less variation = higher mobility) (Pilaar Birch *et al.*, 2016) and by comparisons with the rate at which the $\delta^{18}O$ composition of plants changes relative to altitude (Lachniet and Patterson, 2009; Andreu *et al.*, 2011; Hartman *et al.*, 2015). Studies of the former have shown that for non-migrating individuals, current data on modern populations suggest that red deer should display a range of 3–4‰ and ibex 2–4‰, while migrating populations of caribou (*Rangifer tarandus*) in North America showed approximately 1‰ in variation in $\delta^{18}O$ (Stevens *et al.*, 2011). In terms of elevation, while some studies suggest that there is a depletion of -1‰ in plant $\delta^{18}O$ values for every 250–280 m gained in elevation (e.g. Lachniet and Patterson, 2009; Andreu *et al.*, 2011; Hartman *et al.*, 2015), due to the numerous geographic characteristics that affect how $\delta^{18}O$ fractionate in a specific location (see Pederzani and Britton, 2019 and references therein), this calculation should be made in local systems or at the site-based level.

The fractionation patterns of $\delta^{13}C$ and $\delta^{18}O$ described above have been shown to be true regardless of feeding strategies in some cases (Drucker *et al.*, 2008; Bonafini *et al.*, 2013). However, changes in the isotopic composition of teeth from evaporative-sensitive taxa can also be linked to changes in palaeodiet that could be related to changes in food availability, other types of environmental change, or some other event that caused a shift in feeding behaviour (e.g. natural disasters). We side-step this issue by using more than one herbivore species to assess whether changes in $\delta^{13}C$ and $\delta^{18}O$ values reflect climate change and demonstrate the same trends over time.

Neanderthal reorganisation after severe climate

Neanderthal lifeways operated in a context of climate change, and at some sites there is evidence that deteriorations in climate are followed by changes in their technology, behaviour and networks (Pettitt, 2003). The Repeated Replacement Model expands on the idea of climate forcing cultural change in the context of modern human resilience (Bradtmöller *et al.*, 2012). This model, which borrows from socio-ecological adaptive models (Holling 2001; Walker *et al.*, 2006), places particular emphasis on Heinrich Events as 'release impacts' or external factors that 'lead to vital disturbances' in socio-ecological systems followed by various modes of reorganisation (p. 41, Bradtmöller *et al.*, 2012). One of the ways we identify a reorganisation in behaviour is by looking at site occupation intensity through lithic assemblage size and the presence or absence of archaeology. If the size (relative to the volume of sediment and other contextual properties) of a lithic assemblage shifts during or after severe climate episodes, it is possible that this is evidence of a shift in lifeways for Neanderthals. Another way reorganisations are visible in the archaeological record is through modification of lithic technology (changes in tool types, raw materials, retouch frequency, etc.) after climatic disturbances, and these modifications imply different organisational changes. Given that lithic assemblages are sometimes small in size and have few diagnostic pieces, reorganisations of lifeways can be difficult to observe. Emphasising raw material procurement strategies, however, overcomes this issue because changes in raw material types can be observed in assemblages with relatively small sample sizes. In addition, observed changes in the types and sources of raw materials can tell us about changes in mobility: if Neanderthals were procuring different raw materials after severe climate episodes, we can assume that they were changing their mobility strategies to procure the new ones.

Here, we evaluate behavioural change or reorganisation of lifeways at Lapa do Picareiro (central Portugal) by assessing whether occupation intensity (measured by lithic assemblage size) or raw material types changed after climatic disturbances observed in the palaeoenvironmental record generated in this study. If Neanderthal occupation intensity and procured raw materials changed after a Heinrich Event or stadial period identified in the stable isotope analysis, it is possible that this is evidence of a reorganisation in technology. However, if Neanderthals continue to use the same raw materials and site occupation remains the same regardless of climate change, could this mean refugial conditions did not force a reorganisation? It is important to note that we understand this is not a robust test of behavioural change or a reorganisation of lifeways, and we may not be able to fully answer this question. However, there is an advantage in making this type of observation: by analysing archaeological traces of human activity from the very deposits from which palaeoenvironmental conditions were isotopically reconstructed, we can generate a more secure connection between human activity and specific climate episodes.

Materials and methods

Study area and site

One potential Neanderthal refugium in Iberia is Portuguese Estremadura, an area considered a refugium during other periods of adverse conditions throughout the Pleistocene (Figueiral and Terral, 2002; Haws *et al.*, 2010). Estremadura is home to numerous well-known earlier Middle Palaeolithic sites including Gruta Nova da Columbeira, Gruta da Figueira Brava and Gruta da Oliveira, as well as the late Middle Palaeolithic site, Lapa do Picareiro. This limestone-rich region is a large-scale ecotone where marine ecosystems and terrestrial Mediterranean bioclimatic zones overlap (Haws *et al.*, 2010). The montane islands, plains and valleys of this area are home to Thermo- and Meso-Mediterranean communities of vegetation (Quézel, 1985). During the Late Pleistocene, Portuguese Estremadura was dominated by steppe-like environments and open mountain-type habitats with predominantly pine woodlands (González-Sampériz *et al.* 2010). Plant species distribution shifted slightly in elevation during periods of climate fluctuation; steppic herbs and shrubs generally dominate and tree occurrences are low during cold events (Sanchez-Goñi *et al.*, 2002). Warm events are characterised by peaks in Mediterranean forest cover (Haws *et al.*, 2010). However, western Iberian palaeoenvironmental reconstructions are based on an extremely limited number of correlations between marine and terrestrial records. Whereas MIS 3 was a period of relatively mild and stable environmental conditions even during Heinrich Events in some parts of southern Europe such as southern Italy (e.g. Columbu *et al.*, 2020), whether Portuguese Estremadura was a refugium during this time is still to be determined. Information about local environments in Iberia during MIS 3 is generally lacking, and the information available pertains to different proxies operating on different temporal and spatial scales (e.g. Denniston *et al.*, 2018).

Lapa do Picareiro is situated at 570 m above current sea level (a.c.s.l.), about 100 km northeast of Lisbon, on the west-facing slope of the Serra de Aire, a limestone massif north of the Tagus River Valley (Fig. 1) (Benedetti *et al.* 2019). Elevations within a 50 km radius of Picareiro range from roughly 200 to 660 m a.c.s.l. Excavations at Picareiro have yielded large amounts of animal bone, stone tool artefacts and charcoal from 40 strata, of which 36 are of Pleistocene age (E–NN). Deposits at Picareiro contain evidence of human occupation corresponding to the Middle Palaeolithic and the major Upper Palaeolithic phases, including the Aurignacian, Gravettian, Solutrean and Magdalenian (e.g. Benedetti *et al.* 2019; Bicho *et al.*, 2000, 2003, 2006, 2009; Bicho, 2004; Haws, 2006; Haws *et al.*, 2019, 2020, 2021). Picareiro is a unique site for Portugal with deposits spanning the MUPT; the latest Middle Palaeolithic occupation is dated to ~42k cal a BP and the earliest Upper Palaeolithic is dated to 41–38k cal a BP. The site has yielded one of the largest Palaeolithic archaeofaunal assemblages in Portugal, and preliminary taphonomic studies indicate that these animal remains were deposited by human activity as well as by carnivores and raptorial birds (e.g. Haws *et al.*, 2020).

These factors, combined with the presence of well-preserved ibex and red deer teeth encountered at varying depths of two late Middle Palaeolithic levels, Levels KK and JJ, make Picareiro an ideal location at which to explore the palaeoecology of the last Neanderthals in westernmost Iberia. For this paper, we analysed the $\delta^{13}C$ and $\delta^{18}O$ compositions of 22 red deer and ibex teeth from two late Mousterian occupations. The isotope samples are grouped into five units based on their provenience properties, as defined either as related to archaeology or by stratigraphic characteristics and position: KK, JJ-H1, JJ-dark lens, JJ-H2 and JJ-top (see Table 1, Fig. 2).

Level KK

Level KK (Fig. 3) is a ~10 cm thick Mousterian deposit, located roughly 8.35–8.64 m below datum (mbd). It is characterised by medium to large clasts with a yellowish red fine matrix that is slightly to moderately hard. This Mousterian level is tentatively radiocarbon-dated to 51.8–44.2k a cal BP, but this date is essentially the same as one from the overlying Level JJ Horizon. Alternatively, a composite deposition model based on the complete radiocarbon sequence dates suggests KK could date to ~55–57k cal a BP (Benedetti *et al.* 2019). Very few artefacts ($n = 3$) and few bones (faunal collections are still undergoing analysis and so final counts are not available) were encountered in this level; however, this may be due to the limited surface area that has been excavated to this level. One red deer lower second molar makes up this sample group.

Level JJ

The remaining four sample groups are located in Level JJ. Level JJ (Fig. 3) is a ~1 m thick deposit with archaeology representing

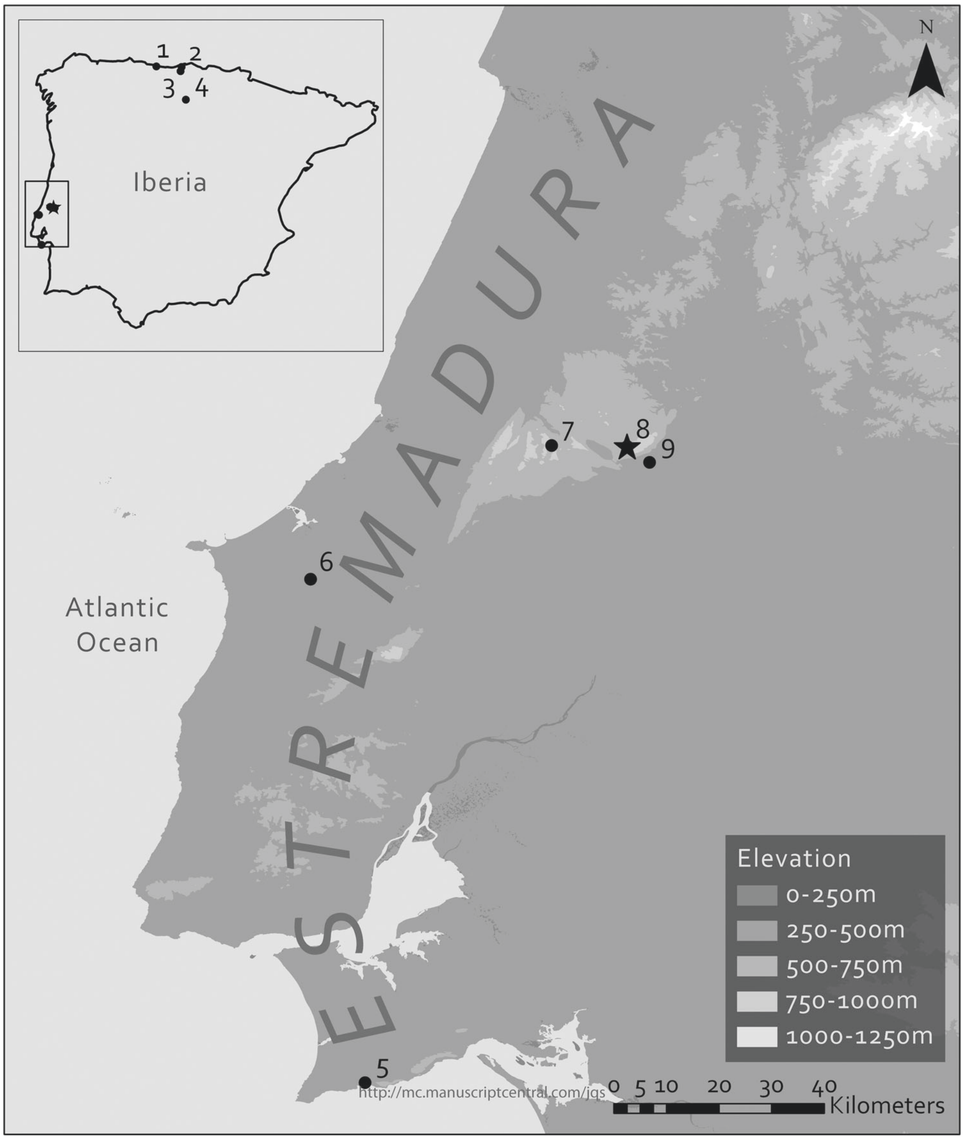

Figure 1. Map showing location of Picareiro and other sites mentioned in the text. 1: La Riera, 2: La Cueva de Covalejos, 3: El Castillo, 4: Valdegoba, 5: Figueira Brava, 6: Columbeira, 7: Buraca Gloriosa, 8: Lapa do Picareiro, 9: Oliveira.

the youngest definitively Middle Palaeolithic occupation at Picareiro (Benedetti *et al.* 2019). Stratigraphic integrity of these deposits is supported by the lack of significant inversions in radiocarbon dates, and minimal to no disturbances by burrowing animals (Benedetti *et al.*, 2019). Evidence of Middle Palaeolithic human occupation in Level JJ at Picareiro includes Mousterian lithic assemblages, tens of thousands of faunal remains (currently undergoing analysis) that show signs of butchery, and dispersed charcoal (see Figs. 2 and 4). The lithics are distributed in two horizons, Horizon 1 and Horizon 2, and are characterised by discoidal core/flake technology typical of the Mousterian (Figs. 2 and S1), and raw materials include chert, quartz and quartzite. The two artefact horizons are separated by a dark, organic-rich sediment lens (Fig. 3) that contains rare lithics and few bones. Based on preliminary analysis, human activities encountered in Level JJ include carcass butchering, processing and cooking, and ephemeral hearth activity. Level JJ has three phases of more intense human occupation associated with Horizon 1, Horizon 2 and the anthropic archaeofaunas in the top 20–30 cm of this layer, making it an ideal place to track changes in environment and Neanderthal behaviour over time.

Magnetic susceptibility data (Fig. 4, see also Fig. S2) show that the climate oscillated frequently during the deposition of JJ (see Benedetti *et al.*, 2019). Because of this, identifying the environmental context of Neanderthal occupation has been difficult. According to the magnetic susceptibility data, Heinrich Event 5 (peaked around 45k a cal BP) may have coincided with the deposition of the dark lens in between the lithic horizons (Fig. 4; Benedetti *et al.* 2019).

JJ-H1

JJ-H1 is found at roughly 8.35–7.73 mbd and contains lithic Horizon 1. It is characterised by medium clasts in a dark reddish brown, very muddy, matrix and radiocarbon dates targeting artefact Horizon 1 place it at *c.* 51.5–44.1k cal a BP. The magnetic susceptibility data suggest Level KK was deposited during Greenland Interstadial/Stadial 15 and Greenland Interstadial/Stadial 14. Seven red deer teeth and one ibex tooth form this group (see Table 1).

JJ-dark lens and JJ-H2

The upper half of Level JJ contains both the JJ-H2 and JJ-dark lens groups. Upper JJ is characterised by medium to large clasts within a clay-rich matrix with a lens of dark reddish brown organic-rich fine sediment in the lower 20–25 cm of this unit.

Table 1. Information and summary statistics for all samples in this study. All of the δ^{13}C values in this table have been corrected to account for changes in atmospheric CO_2 in the past per Passey *et al.* (2009) and raw values can be found in Appendix B. δ^{13}Cdiet was calculated using the fractionation factor of -14‰ between enamel and diet according to Passey *et al.* (2005). L: lower (mandibular), U: upper (maxillary), M: molar, *n*: number of sequential samples per tooth, SD: standard deviation, CE: *C. elaphus*, CP: *C. Pyrenaica*, BD: below datum, ASL: above sea level.

Unit	Specimen ID	Tooth	*n*	δ^{13}C$_{MEAN}$	δ^{13}C$_{MIN}$	δ^{13}C$_{MAX}$	SD	δ^{13}C$_{diet\ MEAN}$	δ^{18}O$_{MEAN}$	δ^{18}O$_{MIN}$	δ^{18}O$_{MAX}$	SD	Taxon	DEPTH BD (m)	DEPTH ASL (m)
JJ-top	B9.1115	L, M1/M2	5	−14.2	−15.4	−13.4	0.75	−28.2	−1.2	−2.1	−0.5	0.65	CE	−7.027	564.456
	C10.428	L, P3	3	−11.2	−12.4	−10.1	1.14	−25.2	−3.8	−4.6	−2.9	0.85	CP	−7.040	564.443
JJ–H2	C9.1315	L, M1/M2	6	−12.7	−13.5	−11.3	0.87	−26.7	−3.5	−5	−1.7	1.27	CP	−7.310	564.173
	B10.418	L, M3	4	−11.7	−12.7	−10.4	1.08	−25.7	−3.2	−3.8	−2	0.84	CE	−7.369	564.114
JJ–dark lens	F7.Wall[†]	L, M2	7	−13.6	−13.9	−13.2	0.2	−27.56	−3.1	−4.43	−1.25	1.31	CE	−7.450	564.033
	A10.826	U, M3	5	−10.6	−12	−8.8	1.17	−24.6	−3.2	−3.7	−2.3	0.52	CE	−7.455	564.028
	A10.840	L, M1/M2	7	−11.8	−12.4	−11.2	0.45	−25.8	−3.2	−4.5	−2	1.08	CP	−7.481	564.002
	B10.426	U, M3	12	−10.8	−11.6	−9.5	0.54	−24.8	−1.6	−2.3	−0.5	0.6	CP	−7.525	563.958
	A10.873	U, M1/M2	5	−13.7	−14.9	−12.5	1.01	−27.7	−1.7	−3.4	−0.6	1.21	CE	−7.547	563.936
	ZZ11.1457[‡]	L, M2	2	−10.2	−12.1	−8.4	0.67	−24.2	−0.3	−0.8	0.3	0.18	CE	−7.590	563.893
	ZZ11.1457[‡]	L, M3	2	−13.8	−13.4	−14.3	2.63	−27.8	−1.7	−1.6	−1.8	0.76	CE	−7.590	563.893
	ZZ11.1497	U, M2	2	−13.3	−13.5	−13	0.36	−27.3	−0.2	−0.4	0.1	0.37	CE	−7.614	563.869
	A10.884	L, M2	5	−13	−14.4	−11.7	1.05	−27	−3.7	−4.5	−3.1	0.6	CE	−7.668	563.815
JJ–H1	A10.897	U, M3	5	−13.1	−13.6	−12.8	0.31	−27.1	−1.5	−3	−0.1	1.19	CE	−7.702	563.781
	A11.595	U, M1/M2	1	−14					−3.3				CE	−7.785	563.698
	ZZ11.1658	L, M2	5	−13.9	−14.7	−12.4	0.94	−27.9	−0.9	−1.6	−0.2	0.56	CE	−7.933	563.550
	A11.671	U, M3	3	−13.3	−13.7	−12.7	0.53	−27.3	−1.7	−3.5	−0.8	1.53	CE	−7.997	563.486
	ZZ11.1750	L, M3	7	−13.1	−14.1	−11.9	0.94	−27.1	−3	−4.2	−2.6	0.58	CE	−8.050	563.433
	ZZ11.1754[‡]	L, M1	4	−12.6	−15	−11.4	1.64	−26.6	−0.8	−1.9	−0.2	0.79	CE	−8.118	563.365
	ZZ11.1754[‡]	L, M2	3	−10.9	−12.2	−10.3	1.09	−24.9	−2.7	−3.7	−2.2	0.86	CE	−8.118	563.365
	A10.984	L, M1/M2	6	−12.2	−13.2	−10.9	0.78	−26.2	−1.1	−2.6	0.6	1.48	CP	−8.148	563.335
KK	A11.722	L, M2	4	−13.3	−14	−12.9	0.51	−27.3	−3	−3.7	−2.8	0.57	CE	−8.303	563.180

[†] This sample was obtained from a previous isotope study in which different pre-treatment protocols were used, which are listed in Appendix A.

[‡] Indicates teeth with corresponding specimen ID numbers that were sampled from the same mandible.

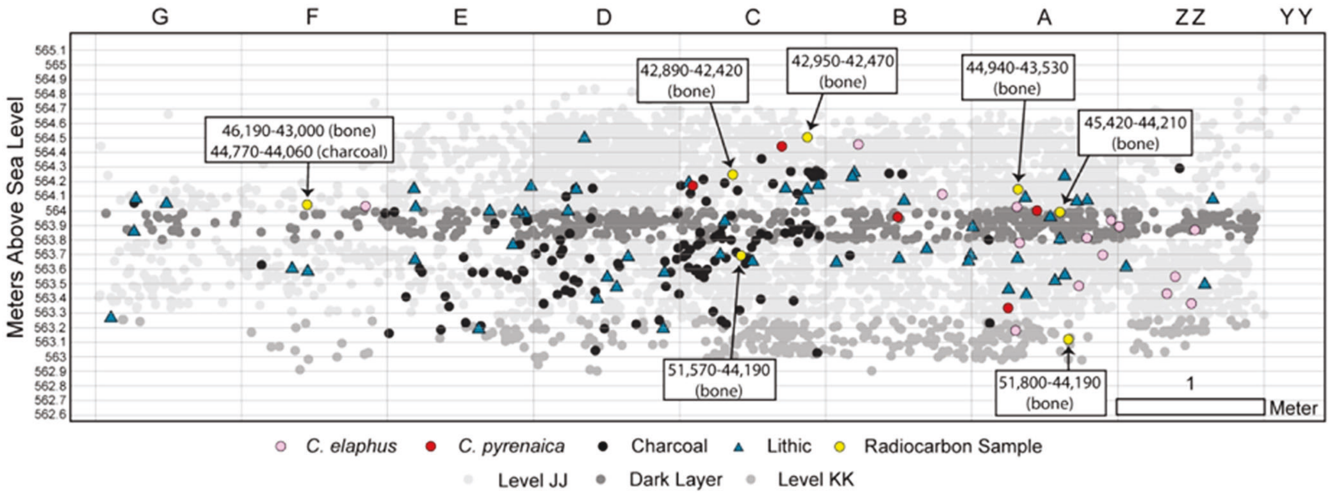

Figure 2. Spatial distribution of samples, lithics, faunal remains (grey circles) and calibrated radiocarbon dates (see Benedetti *et al.*, 2019 for more information). [Color figure can be viewed at wileyonlinelibrary.com].

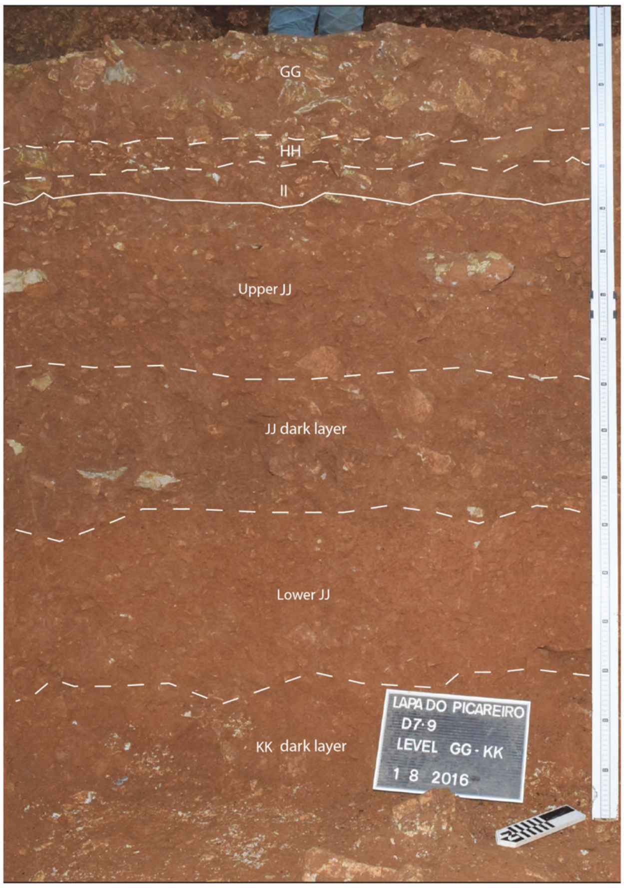

Figure 3. Stratigraphic profile showing Levels JJ and KK. Notice the dark band in the middle of Level JJ. [Color figure can be viewed at wileyonlinelibrary.com]

The lens of darker, organic-rich sediments wedged between the two lithic horizons at an approximate depth of 7.40–7.65 mbd (see Fig. 2) forms the JJ-dark lens group. Magnetic susceptibility data suggest this phase was deposited during Greenland Interstadial/Stadial 13 and Heinrich Event 5 (Fig. 4, Fig. S2). This layer contains few lithics ($n=7$) but several thousand bones. Seven red deer and two ibex teeth make up the JJ-dark lens group. JJ-H2 contains lithic Horizon 2. A radiocarbon dating assay targeting artefact Horizon 2 yielded a date of 44.9–42k cal a BP and corresponds to a depth of ~7.17–7.40 mbd. Magnetic susceptibility data suggest that JJ-H2 includes Greenland Interstadial/Stadial 12. For this group, one red deer tooth and one ibex tooth were selected.

JJ-top

The final sample group is JJ-top, and it comprises the top 20–30 cm of Upper JJ, located roughly at 6.87–7.17 mbd. One date places it at ~43–42.5k cal a BP. It displays the same stratigraphic properties as JJ-H2. This portion of Level JJ contained one lithic artefact, but preliminary results from ongoing analyses identified faunal remains with cut marks, percussion marks and breakage patterns consistent with butchering practices (Haws *et al.* 2020). One red deer tooth and one ibex tooth make up this group.

Stable isotope analysis

Information on the teeth sampled is available in Table 1. While ideally in this type of study, one would sample the same tooth (e.g. upper M3) across individuals in order to avoid using multiple teeth from the same individual that may have travelled vertically through sediments due to bioturbation, sample selection was driven by the limited availability of red deer and ibex teeth. Although the M3 is the most suitable for this analysis, we were forced to use whole teeth and tooth fragments from all molars and one premolar, including some instances where the identification of a tooth fragment could not go beyond M1/M2. Even though sampling is not ideal, we are confident that Lapa do Picareiro has minimal bioturbation and maintains stratigraphic integrity (see Discussion in Benedetti *et al.*, 2019). We sampled all but one tooth (ID = A11-595 in JJ-H1) sequentially to obtain ranges in variation of δ^{13}C and δ^{18}O values during enamel mineralisation as data obtained from bulk sampling dampens the signal of variation, (Reade *et al.*, 2015), though we do not assess seasonality in depth here. In two cases, we sampled two teeth from the same mandible (M1and M2 from ZZ11-1757 and M2 and M3 from ZZ11-1457) to assess the range of variation of a local individual red deer. In addition, the δ^{13}C and δ^{18}O values of one red deer sample (specimen ID = F7.Wall) was obtained from a previous analysis using a different pre-treatment protocol that produced virtually identical results as the protocol used on the remaining samples. Details of the two pre-treatment mass spectrometry protocols we used are available in Appendix A.

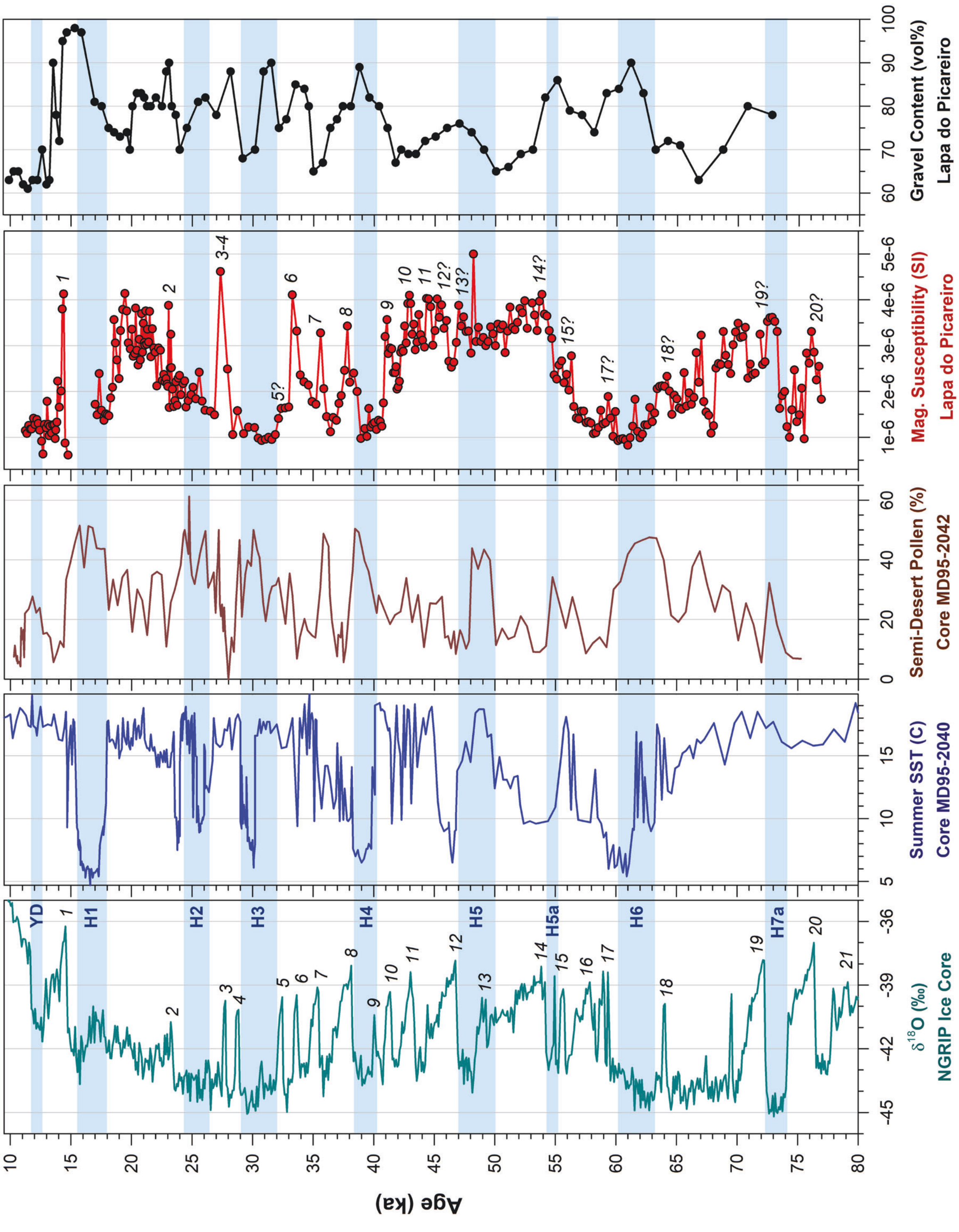

Figure 4. Magnetic susceptibility data obtained from Lapa do Picareiro (Benedetti *et al.*, 2019) and correlations with the δ^{18}O fluctuations in the NGRIP ice core record (Rasmussen *et al.*, 2014), the MD95-2040 deep-sea sediment record (Salguero *et al.*, 2010; Daniau *et al.*, 2007) and gravel content from Picareiro (Benedetti *et al.*, 2019). The Picareiro magnetic susceptibility data are plotted on the C^{14} age model presented in Benedetti *et al.* 2019, with some small adjustments for new radiocarbon dates presented in Haws *et al.* (2020). [Color figure can be viewed at wileyonlinelibrary.com].

Statistical analysis

Although parametric tests can be more robust, nonparametric tests are typically used for data that do not conform to any given distribution or data sets that fail to meet the assumptions of a parametric test (VanPool and Leonard, 2011), a situation common in isotopic analysis and which is indeed the case for our samples. To analyse variance between samples within a group and between groups, we use a Kruskal–Wallis test and a *post hoc* Mann–Whitney pairwise test with a Bonferroni correction. *P* values of <0.05 or less were considered statistically significant. All quantifications were completed using the PAST4 statistical package (Hammer *et al.* 2001).

We use Standard Ellipse Areas (SEAs) to analyse intergroup variance and to assess whether red deer and ibex were foraging in different environments. Although biplots have been a common way to present isotopic data and allow for visualisation of an animal's isotopic niche space, there are some issues with them (see Layman *et al.*, 2007). Biplots are susceptible to inaccuracies due to small sample sizes, which is usually the case with archaeological assemblages. The use of convex hull area has been used to describe the niche width of an organism (Quevedo *et al.*, 2009) or community (Layman *et al.* 2007). By incorporating Bayesian metrics into convex hull area calculations, Jackson *et al.* (2011) overcame this sampling issue with SEAs. Overlap in the isotopic niche space of two taxa would indicate that they occupy similar isotopic niches. Lack of overlap could be indicative of niche partitioning; a phenomenon where two competing taxa are driven to different patterns of resource use and/or niches by natural selection (Hector and Hooper, 2002; MacArthur, 1958). If the red deer and ibex δ^{13}C and δ^{18}O results reflect deteriorating environmental conditions during certain phases of occupation at Picareiro that would force these ungulates to partition their niches, we would expect to see considerable overlap in the isotopic niches of these two taxa, as has been observed in similar studies in Iberia (Jones *et al.*, 2018, 2019, 2020). The parameters used in the calculation of SEAs are available in Appendix C. All SEAs were completed using the statistical package SIBER in RStudio (Jackson *et al.* 2011; RStudio Team, 2020).

Results

δ^{13}C

The δ^{13}C values of both taxa range from −15.4 to -8.4‰ with the mean ratio of −12.6‰ for all samples. For all red deer teeth, δ^{13}C values range from −15.4 to −8.4‰ with a mean ratio of −12.9‰. Ibex δ^{13}C values had a smaller range, −13.5 to −9.5‰, with a mean ratio of −11.6‰, and the δ^{13}C values from ibex teeth are slightly more elevated than those of red deer. For red deer, δ^{13}C values seem to fluctuate increasingly through time as is visible in both the individual and aggregated δ^{13}C box plots while ibex samples show constant fluctuation of values (Figs. 5 and S4). The only statistically significant differences were observed in ibex samples. The variation of δ^{13}C values between groups was statistically significant ($H = 13.59$, $p = 0.003$), and this seems to be driven by the JJ-dark lens and JJ-H2 samples (see Table 2). The SEAs analysing variance between groups JJ-H1, JJ-dark lens and JJ-H2 groups also support this pattern (Fig. S3).

δ^{18}O

The δ^{18}O values of both taxa range from −5 to 0.6‰, with a mean value of −2.3‰ for all five groups. For red deer, δ^{18}O values range from −4.9 to 0.3‰ with a mean ratio of −2.3‰. The δ^{18}O composition of ibex teeth was very similar, with ranges from −5.0 to 0.6‰ and an identical mean ratio of −2.3‰. Boxplots of δ^{18}O ranges of individual red deer and ibex teeth can be found in Fig. 6. The δ^{18}O values obtained from red deer M1/M2 display a similar pattern to the δ^{13}C values, where there is an increase in fluctuation over time (Figs. 6 and S3). However, the M3 data do not show this pattern, potentially due to the smaller sample size. Meanwhile, ibex δ^{18}O values seem to decrease over time as is visible in

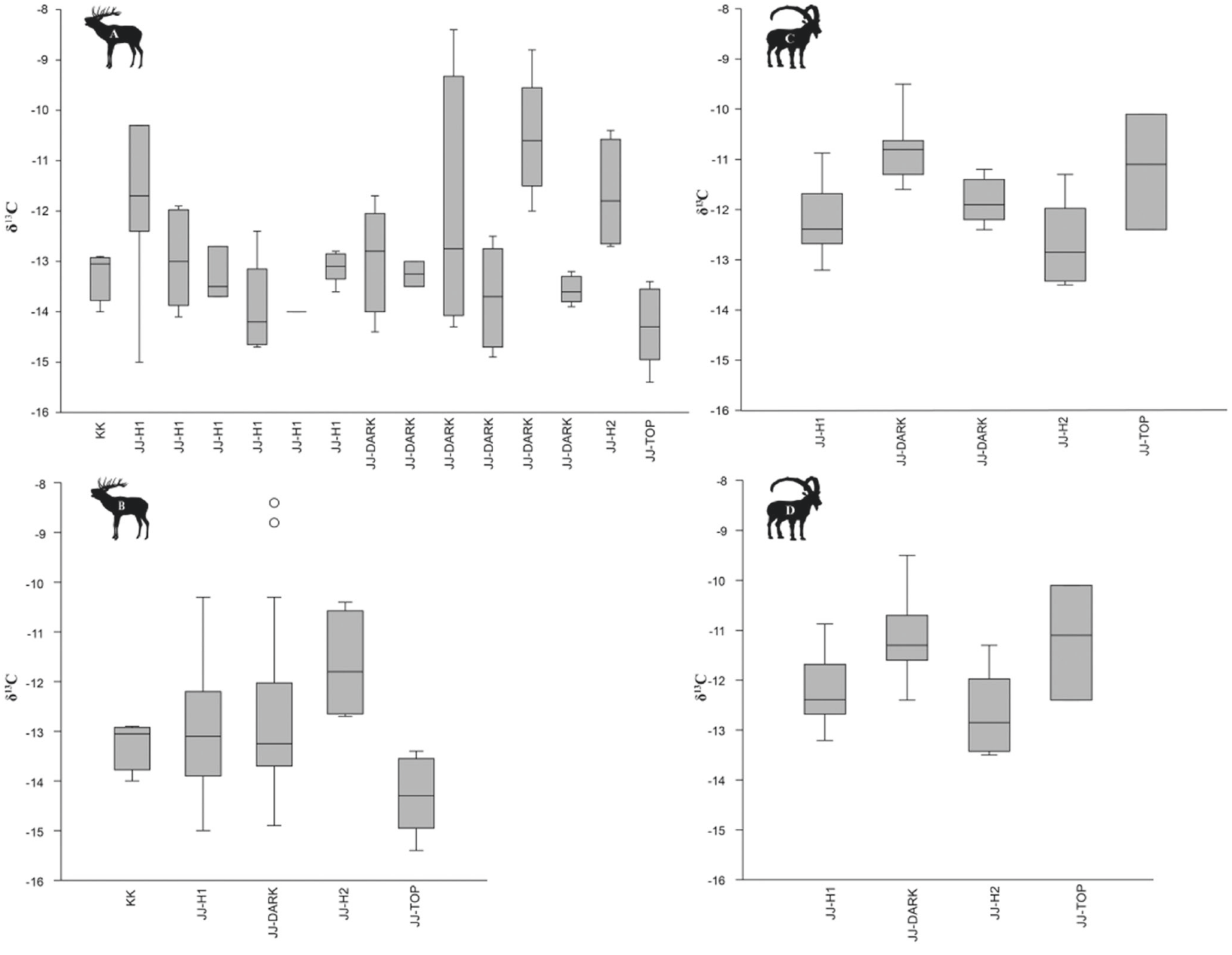

Figure 5. Boxplots showing ranges and standard deviations (whiskers) of δ^{13}C values obtained from (A) individual red deer samples, (B) red deer samples aggregated by group, (C) individual ibex samples, (D) ibex samples aggregated by group. Centre lines represent medians.

Table 2. Results of the *post hoc* Mann–Whitney test with a Bonferroni correction assessing intergroup variation in ibex samples. Significant values ($p \leq 0.05$) are in bold.

	JJ-H1	JJ-DARK	JJ-H2	JJ-TOP
JJ-H1		**0.04**	1	1
JJ-DARK	**0.04**		**0.02**	1
JJ-H2	1	**0.02**		0.5597
JJ-TOP	1	1	0.5597	

Figs. 6 and S4. No statistically significant differences were observed in δ^{18}O values for either red deer or ibex. All raw data are available in Appendix B.

Discussion

Because the mineralisation of different teeth happens at different times in the first few years of an individual's life, the time period recorded in each tooth (P vs M1 vs M2 vs M3) varies, and this has implications for the interpretation of isotopic data because different portions of different seasons may be recorded in a tooth. This is evident, for example, in the combined relatively large δ^{13}C and δ^{18}O ranges of the M1 and M2 of sample ZZ11-1754 and M2 and M3 of ZZ11-14, demonstrating that one tooth may not show the full extent of the isotopic composition of their diet. In addition, in δ^{18}O, nursing has an enrichment effect (Roberts *et al.*, 1998), meaning that nursing signals (elevated δ^{18}O values) are observed most strongly in the M1, and to a lesser extent in the M2 (Stevens *et al.*, 2011). This is evident when comparing the two teeth from ZZ11-1754, where δ^{18}O values are enriched in the M1 compared with the M2. That being said, Figs. 7A and 7B are a scatterplot of ranges of δ^{18}O and δ^{13}C by tooth type and a biplot of δ^{18}O and δ^{13}C by tooth type. In both of these plots, there seems to be no relationship between tooth type and the range of variation or δ^{18}O and δ^{13}C values. Still, we interpret δ^{18}O data obtained from an M1 or M1/M2 with caution.

Do the δ^{13}C and δ^{18}O values of herbivore teeth from Picareiro provide local palaeoenvironmental information?

The Picareiro δ^{13}C results trend similarly to various cold and warm periods identified at the same depths in the magnetic susceptibility record of the site (Fig. 8). Generally, depletions observed in the isotopic record (indicating an increase in forested canopies) are paralleled by increases in SI units in the magnetic susceptibility data (increase in precipitation) (Balsam *et al.*, 2011) and the opposite is also true. In depths corresponding to Greenland Stadial and Interstadial events 14 and 13 and Heinrich Event 5, the δ^{13}C data fluctuate accordingly, with more enriched values during periods associated with drier, more open-canopy environments and less forest cover and more depleted values during periods of more humid, more closed-canopy or forested environments (Fig. 8). However, similar trends in the magnetic susceptibility and isotope data were not observed in all instances (Greenland Stadial and Interstadial 12). It is possible that the tooth from the depths corresponding to Greenland Stadial 12 belongs to an individual that was alive during a pulse of slightly more forested conditions that does not temporally correspond with the magnetic susceptibility data. While we are operating at the site-based scale in our efforts to link human activity to climate phases, these proxy records may not operate at the same scale throughout the entire sequence. Regardless, it is clear that the mean δ^{13}C$_{diet}$ values of individual red deer and ibex from varying depths of the Picareiro sequence fall within the isotopic range for temperate forests. The most enriched values (~24‰) are consistent with reconstructed δ^{13}C$_{diet}$ values obtained from herbivores living in an open-canopy environment while the most depleted signal (~−28‰) suggests that the canopy of local forests were not completely closed (Drucker *et al.*, 2008). Variation in the isotopic data could be reflecting changes in vegetation over time and not just variation due to mobility. While δ^{13}C values do not always indicate evidence of environmental change and can instead reflect differences in feeding behaviour, a shift in foraging areas, or a mixture of both (Faith 2018), in this instance we argue that the changes observed in δ^{13}C values over time at Picareiro are influenced more heavily by environmental change than diet or altitudinal mobility. In some instances, the environmentally driven fluctuations in δ^{13}C data are further supported by offshore pollen data showing forest expansion during vegetation records of Greenland Interstadial 14, a trend that matches the depleted δ^{13}C values for group JJ-H1 (Fletcher *et al.* 2010; Roucoux *et al.*, 2015).

The range of δ^{18}O intratooth data for most red deer and all ibex individuals suggests that they belong to local populations, because the ranges exceed 1‰, which is the observed range in modern migrating caribou populations in North America (Stevens *et al.*, 2011). The exceptions are the ranges of four red deer individuals in two sampling groups KK ($n = 1$) and JJ-dark lens ($n = 3$) which had ranges close to or less than 1‰. It could be that these four red deer individuals travelled to different areas and were more mobile, or that incremental sampling did not pick up on the full range of variation within a tooth. Thus, it seems that a majority of the individuals sampled here belonged to non-migratory populations, meaning that this type of analysis functions at an appropriate scale for securely linking climate change and human behaviour.

Without local baseline information and, in the case of herbivores in particular, without information on the sources of δ^{18}O, it is difficult to understand exactly how δ^{18}O fractionates in an ecosystem (Hamilton *et al.*, 2018). For alpine species such as ibex, differentiating climate and environmental influences from dietary influences on δ^{18}O is particularly difficult. However, some observations can be made. The altitude at which an individual is foraging greatly influences the values of δ^{18}O recorded in their tissues (e.g. Hartman *et al.* 2015). Studies evaluating how the δ^{18}O composition of water changes with altitude across Portugal suggests that for every 100 m gained in elevation, a depletion of ~0.24‰ occurs (Thatcher *et al.*, 2020), which is less than values observed elsewhere (~−1‰ for every 250–280 m or ~0.35–0.4‰ for every 100 m) (e.g. Lachniet and Patterson, 2009; Andreu *et al.*, 2011; Hartman *et al.*, 2015). The elevation gradient for the area immediately surrounding Picareiro is ~200–660 m, and if the ibex from Picareiro were foraging in the immediate vicinity of the cave and altitude was the main driver of the fluctuation in their δ^{18}O values, we would expect to see a range of ~0.6‰, which is consistent with the differences in the interindividual mean ibex δ^{18}O values, but not consistent with the range of all ibex δ^{18}O values for all groups (~5.6‰). For the group that contained more than one ibex sample, JJ-dark lens, the range of δ^{18}O values was 4‰, meaning that environmental fluctuation did have some influence on these values, suggesting that the ibex δ^{18}O values could be slightly more indicative of environmental and/or climate change and less so for foraging location, at least for the JJ-dark lens phase of occupation. The δ^{18}O data for both taxa become enriched during drier phases and depleted in wetter phases, oscillating for the most part

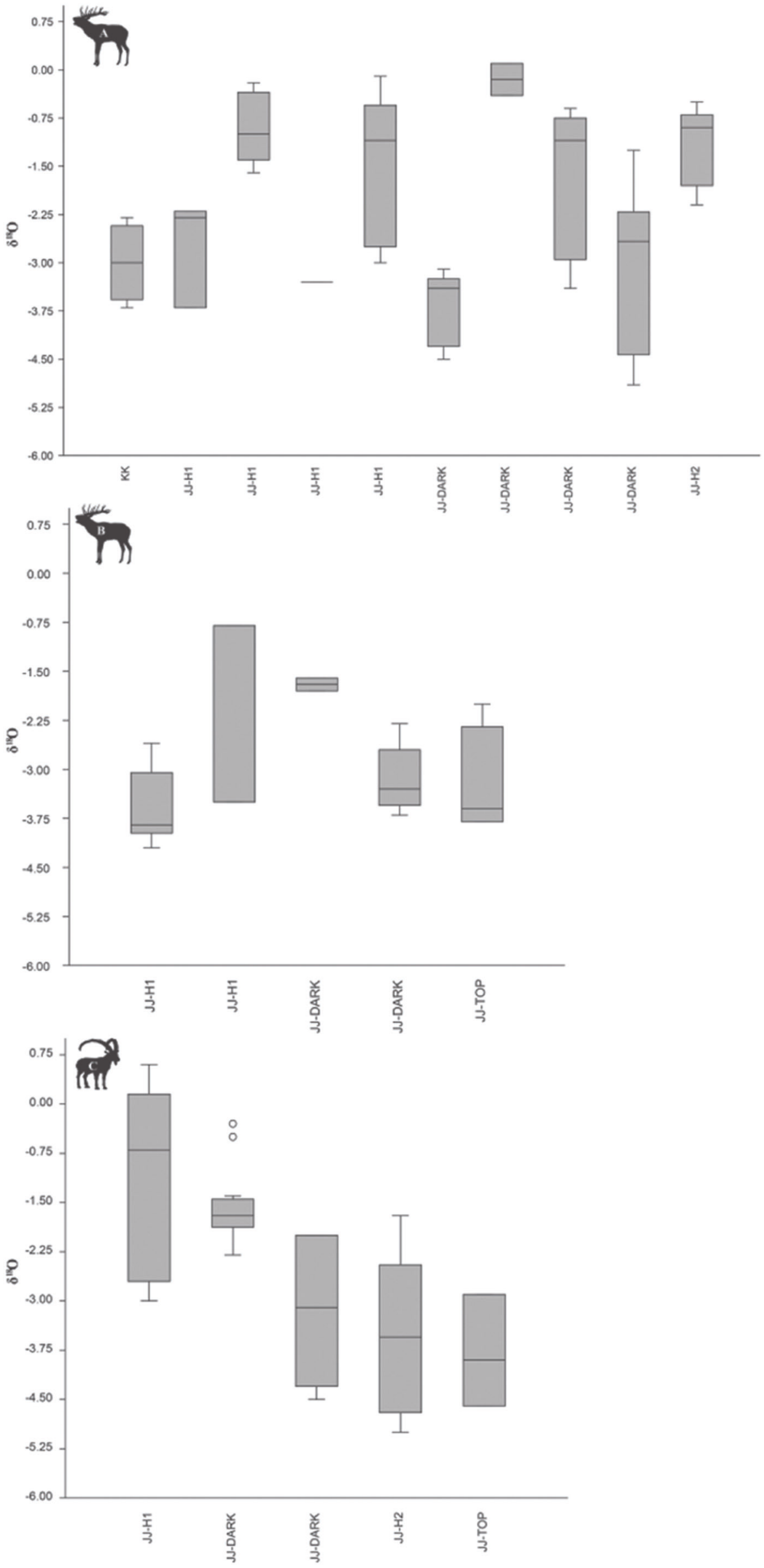

Figure 6. Boxplots showing ranges and standard deviations (whiskers) of $\delta^{18}O$ values obtained from (A) individual red deer samples, (B) red deer samples aggregated by group, (C) individual ibex samples. Centre lines represent medians.

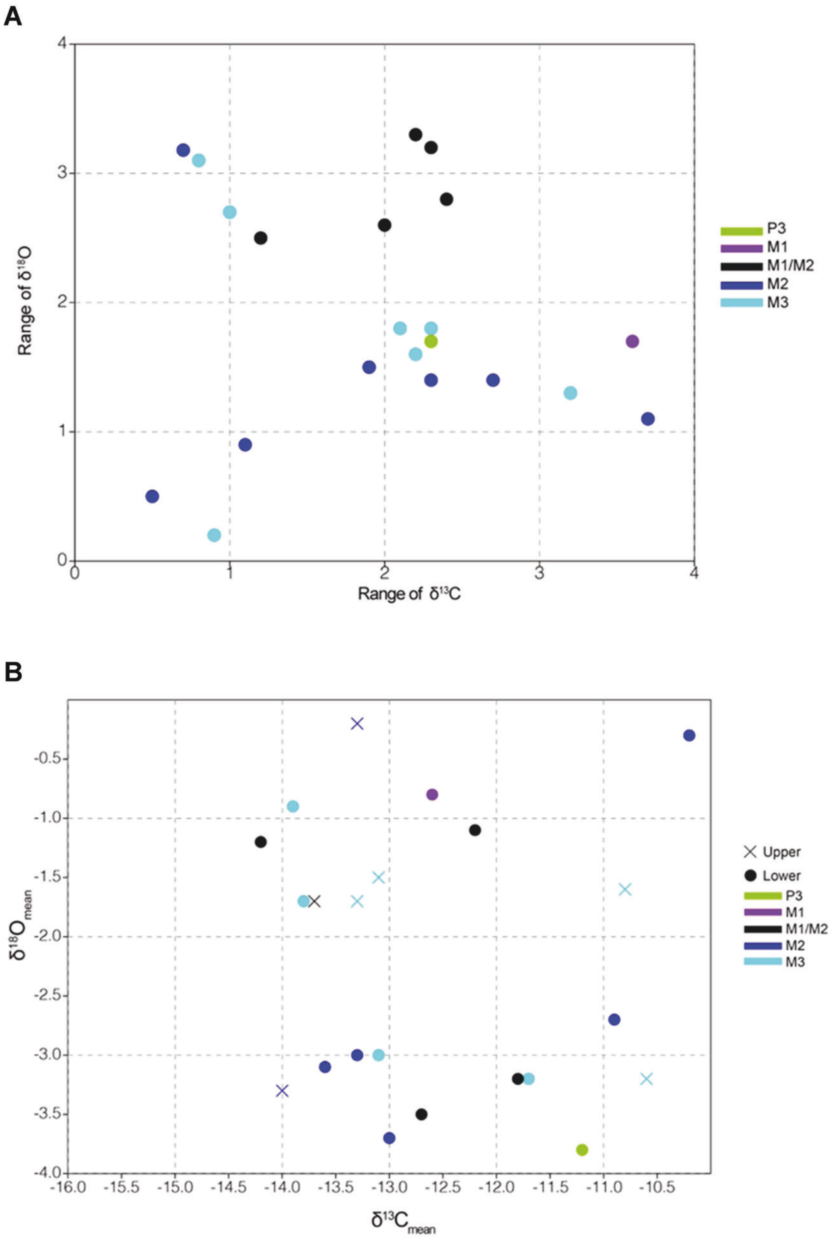

Figure 7. (A) Scatterplot showing the variation in intratooth range of individuals by the tooth sampled. (B) Biplot showing mean carbon and oxygen isotope values by tooth. [Color figure can be viewed at wileyonlinelibrary.com].

congruently with δ^{13}C values (although with some exceptions) suggesting that the δ^{18}O results overall are tracking fluctuations in environment and potentially climate (Fig. 8). However, without an understanding of how δ^{18}O fractionates in Portuguese Estremadura, a record of precipitation and temperature for the time period assessed that would help specify the effect of altitude on δ^{18}O in the region, and the limited number of ibex samples in this study ($n = 5$) mean that we use caution in the interpretation of ibex δ^{18}O until we have more specific palaeoenvironmental and modern baseline data.

Our δ^{13}C results are similar to the isotopic information obtained from herbivore teeth in other archaeological MIS 3 contexts from El Castillo Cave Level 20E (undated) and Valdegoba Cave Levels 5 and 6 (undated), although with a larger range in isotope values (Fig. 9) (Jones *et al.*, 2019; Feranec *et al.*, 2010). This is likely due to the larger sample size in this study in comparison to those obtained at the other two sites. Regardless, it seems like the Neanderthals occupying the three sites inhabited generally stable habitats with similar proportions of open and closed vegetation cover, indicative of mosaic environments. However, it is notable that the δ^{18}O results generated in this study are more enriched than those of both El Castillo and Valdegoba. The depleted Valdegoba δ^{18}O values are likely a product of its altitude (930 m a.c.s.l. on the *meseta* of Old Castile), while the El Castillo (190 m a.c.s.l., 17 km from the present Cantabrian shore) values plot in between Picareiro and Valdegoba (Fig. 9). But again, due to limited sample sizes, the limited number of stable isotope studies of herbivore teeth for MIS 3 in Iberia, and the lack of absolute dates for El Castillo Level 20 E and Valdegoba Level 5/6, this pattern may or may not hold with new data.

While we are confident that some of our red deer δ^{13}C and δ^{18}O and ibex δ^{13}C data reflect some climatic oscillations and associated environmental changes of MIS 3, it is difficult to tease out to what degree altitude, diet and climate influence the ibex δ^{18}O values. In addition, the changes observed produced no statistically significant results with the exception of the ibex δ^{13}C composition. However, the use of the Bonferroni correction means that our quantifications increase the probability of making a Type II error, and the lack of significant variations in red deer isotope values and ibex δ^{18}O values could be an artefact of sample sizes or the statistical tests used. More herbivore and environmental isotopic data are needed from both ancient and modern contexts to resolve this issue.

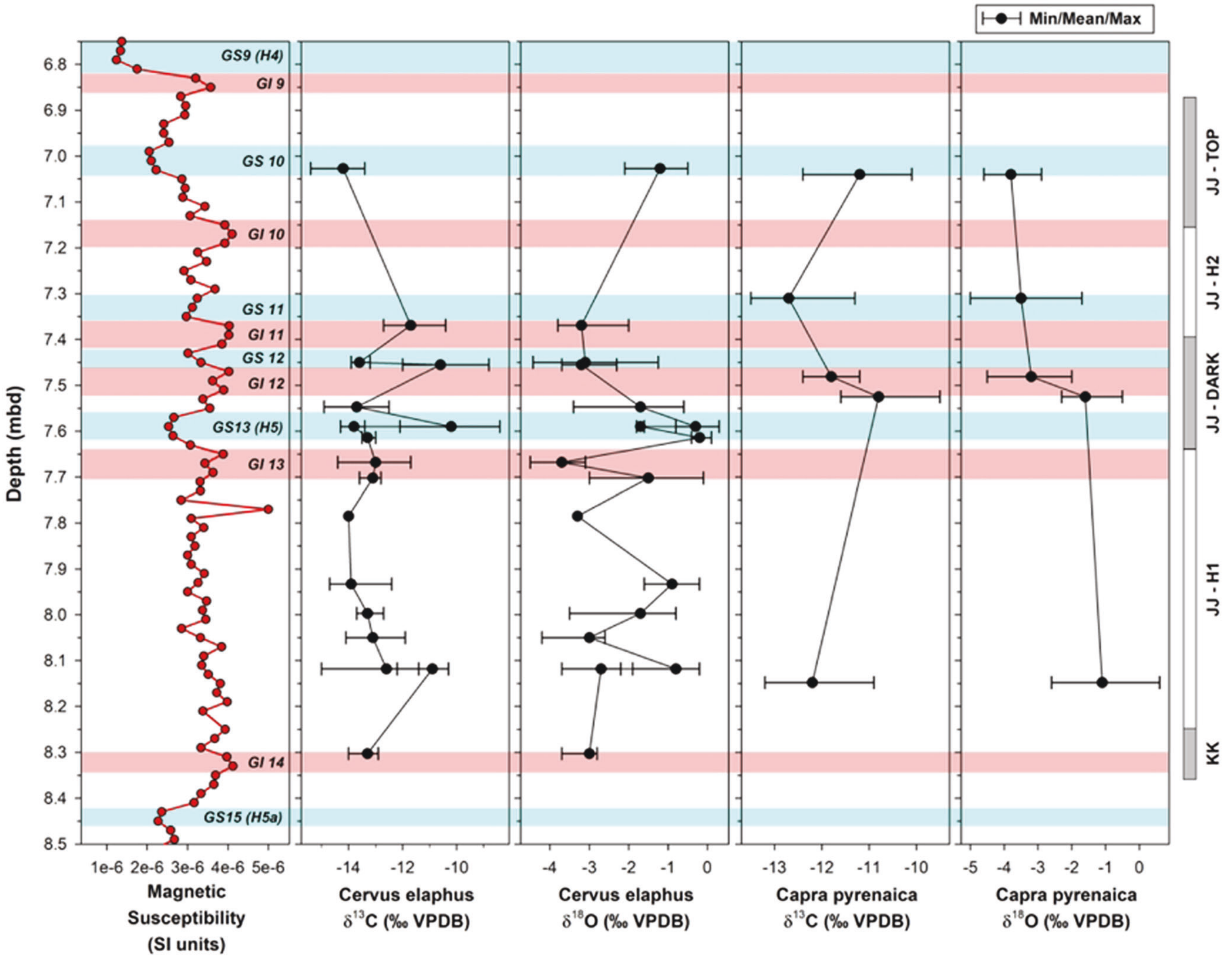

Figure 8. Comparison of δ^{13}C and δ^{18}O data to magnetic susceptibility data. Blue shading indicates potential cold phases. Red shading indicates potential warm phases. [Color figure can be viewed at wileyonlinelibrary.com].

Do we see evidence of a stable environment dominated by woodland forests and/or higher humidity levels during Neanderthal occupations that would indicate refugial conditions? Was there a reorganisation in human behaviour and technology, observed through changes in occupation intensity and raw material procurement strategies, after episodes of severe climate change?

Using the fractionation factor between $\delta^{13}C_{diet}$ and $\delta^{13}C_{enamel}$ of −14‰ for medium-sized herbivorous ungulates (Cerling and Harris, 1999; Passey *et al*., 2005; see Table 1 for mean $\delta^{13}C_{diet}$ values), our results suggest that the δ^{13}C composition of the plant diet of red deer and ibex ranges from −29.4‰ to 22.4‰, averaging −26.5‰. These averaged results suggest environmental conditions biased towards drier communities and are congruent with δ^{13}C values typical of European temperate forests ($\delta^{13}C_{temperate\ forest}$: −23‰ to −33‰; Kohn 2010; Hemming *et al*. 2005) as well as the modern *Quercus ilex* and *Q. suber*-dominated temperate forests in Évora ($\delta^{13}C_{avg.\ temp.\ forest}$: −27.7‰) (Hemming *et al*., 2005), and the vegetation above Buraca Gloriosa in Portugal ($\delta^{13}C_{avg\ veg\ BG}$: −27‰) (Thatcher *et al*., 2020). Given that the range in δ^{13}C values of plants in closed versus open environments is relatively small (2–5‰), our results indicate that environmental conditions likely changed during the deposition of Levels KK and JJ. In some cases, our data reflect enriched dietary δ^{13}C values similar to those obtained in extremely dry environments such as the Atacama desert or *Pinus* forests in dry settings (>−23‰) and in others, our data reflect δ^{13}C values that plot closer to closed-canopy rainforest environments (<-31‰; Kohn, 2010). Below, we describe the environmental setting for each phase of occupation assessed in this study.

Level KK

The red deer molar from Level KK had a mean $\delta^{13}C_{diet}$ value of −27.3‰, meaning that the red deer were foraging in mosaic environments that were predominantly dry but somewhat forested. The mean δ^{18}O values of this tooth (−1.2‰) are more enriched than modern $\delta^{18}O_{precipitation}$ values modelled for Portuguese Estremadura, which range between −5‰ and −3‰, indicating that conditions may have been drier than they are currently (Hatvani *et al*. 2020). Due to the limited sample of teeth and lithics in this section, more data are required to make further assumptions about the environmental conditions of the Neanderthal occupation in Level KK.

JJ-H1

In group JJ-H1, the mean δ^{13}Cdiet values are slightly enriched (−27‰), suggesting a minor shift towards a drier and more open landscape relative to the one sample from Level KK. Within this group, there is a range of mean δ^{13}C values of −24.9‰ to −27.9‰. Changes in the composition of vegetation where red deer were foraging were gradually oscillating from

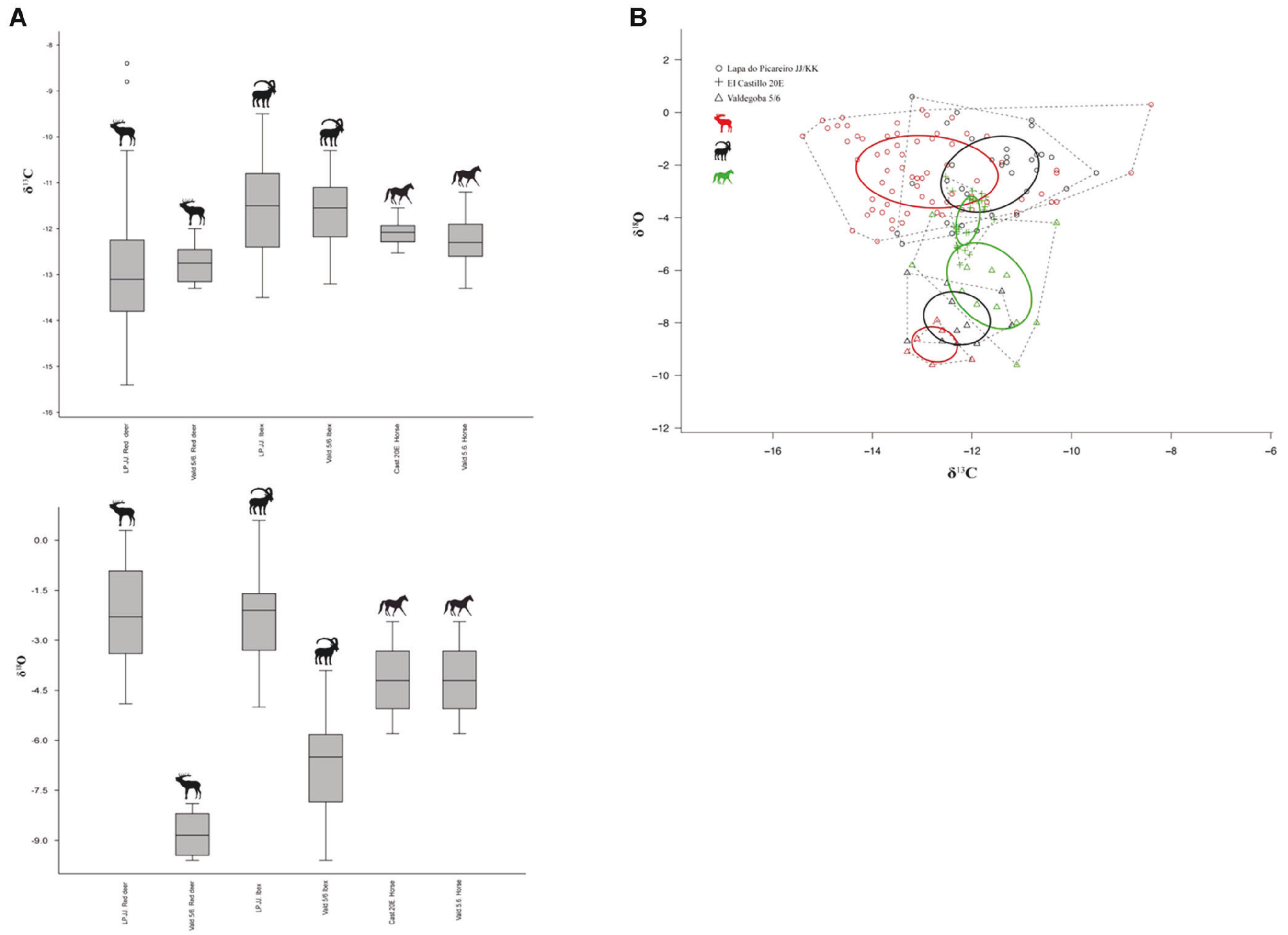

Figure 9. (A) Top. Boxplots of red deer, ibex and horse δ^{13}C data from Levels KK and JJ of Lapa do Picareiro, Level 5/6 of Valdegoba Cave and Level 20E of El Castillo Cave. Bottom. Boxplots of red deer, ibex and horse δ^{18}O data from Levels KK and JJ of Lapa do Picareiro, Level 5/6 of Valdegoba Cave and Level 20E of El Castillo Cave. (B) Standard ellipse areas showing the isotopic niche space occupied by herbivores from Levels JJ and KK of Lapa do Picareiro, Level 5/6 of Valdegoba Cave and Level 20E of El Castillo Cave. [Color figure can be viewed at wileyonlinelibrary.com].

temperate forest conditions during warmer periods such as Greenland Interstadial 14, to drier periods with similar δ^{13}C values of plants typically encountered in dry *Pinus*-dominated communities (Fig. 8) (Kohn, 2010). The ibex δ^{13}C values for this group are too limited in number to observe changes through time. In this section, the δ^{18}O values of red deer reach the range of the modern $\delta^{18}O_{precipitation}$ values for this area, while the ibex δ^{18}O values in this group are more enriched (Figs. 8 and S5). The red deer δ^{18}O data from teeth located in a 20 cm interval of −8 to −7.8 mbd do not fluctuate in tandem with the δ^{13}C data, and this discrepancy can be explained by the flexible drinking strategies of red deer, thus reflecting meteoric water values rather than the evaporative stress of leaf water. The δ^{13}C values indicate a shift towards wetter, more forested environments and it could be that there was enough precipitation during this time and, therefore, more pooled water from which red deer could drink. Since the δ^{18}O composition of meteoric water subjected to any level of evaporative stress becomes more enriched (lighter O^{16} evaporates more readily than the heavier O^{18}; Quade *et al.*, 1992), the elevated δ^{18}O values of red deer in this 20 cm interval could be reflecting a shift in water acquisition strategies. This could explain the broader niche space occupied by red deer in comparison to ibex (Fig. 9A), but this could also be due to red deer's more flexible feeding strategy. More local palaeoenvironmental records to corroborate this are needed. Increasing sample sizes, the number of taxa sampled, and obtaining information regarding the fractionation of δ^{18}O in the local ecosystem are necessary to test this hypothesis.

JJ-dark lens

In the JJ-dark lens group, the mean δ^{13}Cdiet values range from −24.8‰ to −27.8‰, with a mean of −26.3‰, reflecting another shift towards drier, more open-cambd do not fluctuate in tandemnopy environments in which red deer and ibex foraged. The δ^{18}O values in JJ-dark lens samples generally display similar oscillations to the δ^{13}C data; however, as observed in Fig. 10, the oscillations in environmental conditions are more drastic in this group, or occur more frequently in a smaller timespan, in comparison to JJ-H1, particularly for Heinrich Event 5 and potentially Greenland Interstadial 13 and Greenland Stadial 12. In the red deer δ^{13}C and δ^{18}O data, an enrichment of ~2–3‰ is observed in the samples located at the depths corresponding to Heinrich Event 5 (−7.56 to −7.65 mbd), which is congruent with the characteristics of this Heinrich Event. In the depths that correspond to H5, only two lithics were encountered, suggesting that Neanderthal occupations at Picareiro Cave during this period were extremely sparse. The δ^{13}C and δ^{18}O data obtained from both taxa indicate a shift towards wetter conditions during Greenland Interstadial 12, while the drier stadial conditions of Greenland Stadial 12 are only visible in the red deer δ^{13}C.

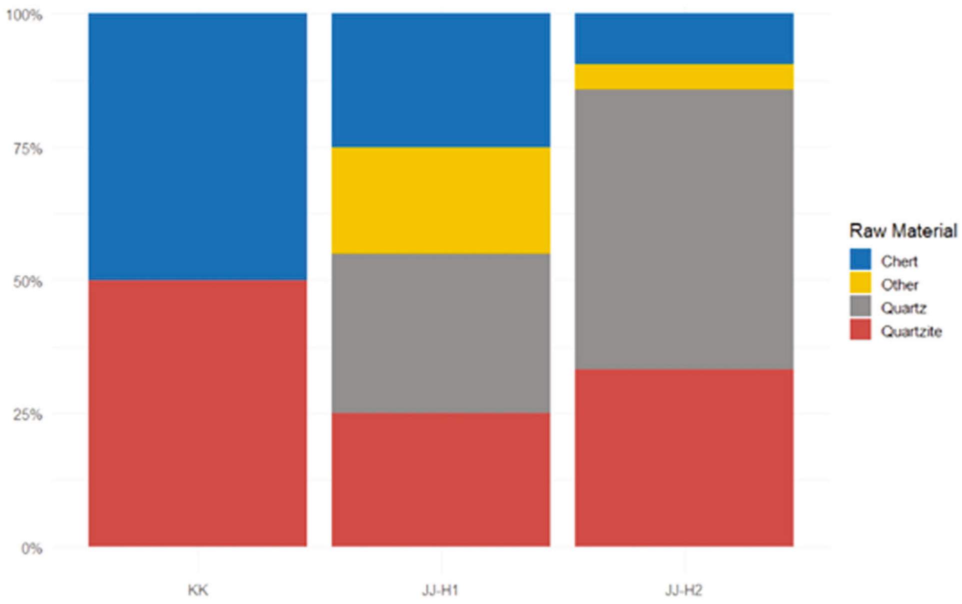

Figure 10. Proportion of raw material types encountered in Level KK, Horizon 1 (JJ-H1) and Horizon 2 (JJ-H2). [Color figure can be viewed at wileyonlinelibrary.com].

It is worth noting that the climatic changes observed in isotopic data for Heinrich Event 5 do not skew more heavily towards drier and more open conditions compared with fluctuations shown in other groups in the entire sequence, but instead suggest a period of climatic instability. This instability could be a driver of the more notable niche partitioning (i.e. less overlap in SEAs) between red deer and ibex (Fig. S5B). Overall, during this period of more dramatic environmental and climatic deterioration, occupation of the cave by Neanderthals seems to have decreased, with a majority of the lithics encountered in this deposit coinciding with the depth of Greenland Interstadial 12. The similar isotopic data ranges for Heinrich Event 5 and other cold periods in the sequence could be attributed to the fact that on the Atlantic margin of the Iberian Peninsula, the deposition of lower quantities of ice-rafted debris may mean that Heinrich Event 5 was a shorter event in this area than in other parts of Europe (de Abreu *et al.*, 2003). In other words, conditions during Heinrich Event 5 were not any colder or any drier than stadials in Portuguese Estremadura, but considerably more unstable than stadials.

JJ-H2

The samples from JJ-H2 immediately above the JJ-dark lens group suggest a return to slightly wetter conditions and more closed vegetation cover and could be representative of Greenland Interstadial 12, as evident in the depletion of red deer and ibex δ^{13}C and δ^{18}O values, potentially followed by another oscillation towards drier, more open-canopy vegetation cover revealed by the enrichment in red deer δ^{13}C values. The red deer and ibex isotopic niches in this sample group overlap, and we hypothesise that food resources might have been abundant enough during this time period that no competition, and therefore no niche partitioning, occurred (Fig. S5). Lithic Horizon 2 suggests a more intense Neanderthal occupation during this time; however, the interpretations we can make regarding the occupation's environmental context are limited since only two teeth make up this group.

Nonetheless, an interesting change in Neanderthal behaviour occurs between lithic Horizons 1 and 2. The raw material procurement strategies shift from a more diversified use of raw materials in Horizon 1 (in JJ-H1) to an assemblage dominated by quartz and quartzite in Horizon 2 (in JJ-H2) (Fig. 10), suggesting that a reorganisation in lifeways, as dictated by the Repeated Replacement Model (e.g. Bradtmöller *et al.*, 2012) and observed at some Neanderthal sites (Pettitt, 2003), may have occurred after the onset of Heinrich Event 5. The instability of Heinrich Event 5 likely forced a reorganisation in Neanderthal raw material procurement and therefore mobility strategies and could be indicative of the fragmentation and isolation of Neanderthal habitats.

JJ-Top

Interpretation of the isotopic composition of the samples in this group is limited due to its small sample size. The two samples from JJ-top provide contradictory information. While the red deer δ^{13}C mean ratio is the lightest of the entire sequence, suggesting a shift to slightly more closed vegetation cover in comparison to JJ-HE 2 samples, the δ^{13}C mean ratio from the ibex sample in this group becomes enriched. Meanwhile, the δ^{18}O mean ratio of the red deer sample becomes enriched in this section, whereas the ibex δ^{18}O mean ratio becomes depleted. This could be indicative of different foraging environments, wherein red deer sought food in areas of more closed vegetation cover and drank from enriched pools of water while ibex foraged in more open areas under limited evaporative stress.

Conclusion

The data presented here provide local-scale environmental information on vegetation cover and moisture levels during MIS 3 that have direct connections to archaeological activity. Even though limited sample sizes and missing information on local δ^{18}O fractionation systems made it difficult to make assertions during certain phases of Neanderthal occupation at Lapa do Picareiro, the δ^{13}C and δ^{18}O values of red deer and ibex tracked local environmental changes associated with climate events such as Greenland Stadial/Interstadial 14, Greenland Interstadial 13 and Heinrich Event 5. The patterns observed here are corroborated by other palaeoenvironmental proxies from Picareiro and supported by regional palaeoclimate records.

Based on these data, we can tentatively conclude that the environment in which the individuals sampled lived fluctuated between mosaic (and relatively humid) environments with patches of forest and open vegetation on the one hand and much drier open steppe on the other. While Neanderthal occupation intensity does seem to decrease during climatic downturns (like that of Heinrich Event 5) at Lapa do Picareiro, neither humidity levels nor vegetation cover seem to be driving factors of Neanderthal behaviour. While a reorganisation in mobility strategies seems to have occurred after Heinrich 5, at Picareiro, Neanderthal occupation of the site was not driven by the presence of favourable environmental conditions (i.e. warm and wet), but by the stability of environmental conditions, as evidenced by the sparse occupation during the particularly unstable Heinrich Event 5 and relatively stable conditions when the JJ-H1 artefact horizon was deposited. Whether this region acted as a refugium for Neanderthal populations might be more related to climatic stability than niche parameters like vegetation cover or moisture regimes. In this case, searching for the environmental processes occurring in a habitat proves to be more valuable than identifying refugia.

Supporting information

Additional supporting information can be found in the online version of this article.

Figure S1. (A) Bone with anthropic impact mark from JJ-dark lens. (B) Bone with anthropic impact mark from JJ-H1. (C) Bone with anthropic impact mark and cut marks from JJ-H1. (D) Middle Palaeolithic core. (E) Middle Palaeolithic sidescraper.

Figure S2. Figure adapted from Benedetti *et al.* (2019) showing the magnetic susceptibility record and corresponding stratigraphic units from Lapa do Picareiro.

Figure S3. Standard ellipse areas showing the isotopic niche represented in red deer individuals in JJ-H1 (top) and JJ-dark lens (bottom).

Figure S4. Standard ellipse areas showing the isotopic niche of ibex individuals in JJ-H1 (black), JJ-dark lens (red) and JJ-H2 (green).

Figure S5. Standard ellipse areas of all ibex and red deer samples from (A) JJ-H1, (B) JJ-dark lens and (C) JJ-H2.

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Conflict of interest statement—The authors declare that they have no conflicts of interest.

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