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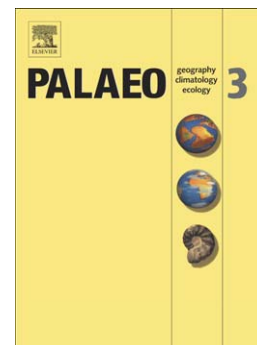
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Investigation of late Pleistocene and early Holocene palaeoenvironmental change at El Mirón cave (Cantabria, Spain): insights from carbon and nitrogen isotope analysis of red deer.

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Abstract:

El Mirón Cave was occupied by humans for over 40,000 years. Evidence of late Mousterian, Gravettian, Solutrean, Magdalenian, Azilian, Mesolithic, Neolithic, Chalcolithic, Bronze Age and Mediaeval occupations has been found in the cave. Understanding the local

environmental conditions during the occupations is crucial for gaining an insight into the lifeways of El Mirón's inhabitants as they relied on the surrounding region and its natural resources for their subsistence. 170 bones of hunted red deer recovered from the cave were sampled for carbon and nitrogen stable isotope analysis with the aim of reconstructing the palaeoenvironment and palaeoclimate during the human occupation. The results show the surrounding landscape underwent considerable environmental change during the late Pleistocene and early to mid Holocene. Shifts in $\delta^{13}\text{C}$ values between the Last Glacial Maximum, Heinrich stadial 1, Heinrich event 1, the Late-glacial interstadial and the onset of the Holocene reflect are likely to reflect changes in water availability and temperature. Deer $\delta^{15}\text{N}$ generally increased over time indicating the regeneration of soil biological activity and nitrogen cycling, which was temporarily halted during the Younger Dryas. Comparison of the El Mirón results with those of 300 deer from other regions of Europe show geographical variations in the timing and magnitude of the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This variation tracks local climate (temperature and water availability) and environmental (vegetation and forest development) changes.

Keywords: *Cervus elaphus*, Upper Palaeolithic, palaeoecology, palaeodiet, nitrogen cycle

Introduction:

El Mirón Cave is one of the longest and most complete cultural sequences in Europe investigated to date, with occupation spanning over 40,000 years through the last glacial and current interglacial periods. Evidence of late Mousterian, Gravettian, Solutrean, Magdalenian, Azilian, Mesolithic, Neolithic, Chalcolithic, Bronze Age and Mediaeval occupations has been found in the cave (Straus and González Morales, 2003, 2007a, 2010, 2012a,b). Understanding the local environmental conditions during the occupation of the cave is crucial for gaining an

insight into the lifeways of El Mirón's inhabitants as they relied on the surrounding region and its natural resources for their subsistence. Moreover local climate reconstructions will help further understanding of the role environmental change played in behavioural and cultural development within the Cantabrian region. A number of palaeoclimate and palaeoecological reconstructions have previously been undertaken at El Mirón and in Cantabria. They make use of climate proxies such as sediment microstratigraphy and micromorphology, pollen, charcoal, plant and faunal remains (e.g. Peñalba, 1994; Courty and Vallverdu, 2001; Ellwood et al. 2001; Peña-Chocarro et al. 2005a, 2005b; García Moreno, 2006; García Amorena et al. 2008; Cuenca-Bescós et al. 2009; Iriarte, 2009; Marín-Arroyo, 2010; González Sampériz et al. 2010; Farrand, 2012; Iriarte, 2012). Although valuable climatic information can be obtained via these techniques, they can be subject to taphonomic and diagenetic alteration. Thus the most powerful palaeoclimatic reconstructions are obtained using a multi-proxy approach. Stable isotope analysis of mammal bone collagen is a particularly valuable tool for palaeoclimatic reconstruction as the environmental information it provides complements that obtained via other proxies (Stevens and Hedges, 2004). Bone collagen isotope values reflect average conditions over the period of bone growth which is typically several years (Stenhouse and Baxter 1979; Hedges et al. 2007), thus isotopes indicate the typical ecological habitat in which animal lives. The palaeoenvironmental information obtained through isotope analysis of faunal remains can be directly linked to humans as the bones sampled are the remains of animals hunted by humans. Thus their isotope signatures reflect the local ecological niche in which the humans lived.

In this paper we aim to reconstruct the palaeoenvironmental conditions at El Mirón during the late Pleistocene and early to mid Holocene through isotope analysis of red deer, and to integrate the findings with those from other palaeoclimatic proxies at El Mirón and the wider

Cantabrian region. Red deer have been chosen as they are the most abundant large herbivore present throughout most of the sequence. Previous studies of red deer isotope signatures have shown that they are a good species for this type of analysis as they tolerate a wide variety of habitats, thus changes in their local environment are reflected in their isotope values (Richards and Hedges, 2003; Drucker et al. 2003a; Stevens, 2004; Stevens et al. 2006; Drucker et al. 2008, 2011a). In addition we compare the red deer isotope results from El Mirón to those at contemporary sites in other areas of Europe in order to consider how the environmental change seen at El Mirón across the Pleistocene-Holocene transition compares to that observed in other regions of Europe.

Carbon and nitrogen isotopes in bone collagen

Analysis of carbon and nitrogen isotope in bone collagen is widely applied with the aim of palaeodietary reconstruction (e.g. Bocherens et al. 1999; Richards and Hedges, 1999; Privat et al. 2002; Lightfoot et al. 2009; Craig et al. 2010; Hakenbeck et al. 2010; Stevens et al. 2010). More recently however it has been recognized that the technique can provide palaeoenvironmental information (e.g. Drucker et al. 2003a, 2003b; Richards and Hedges, 2003; Hedges et al. 2004; Stevens and Hedges, 2004; Bump et al. 2007; Drucker et al. 2008; Stevens et al. 2008; Drucker et al. 2009a; Szpak et al. 2010; Drucker et al. 2011a, 2011b, 2012). Underpinning this technique is the principle that the isotope signatures of different plants vary, are passed up the food chain to fauna (and then from fauna to fauna) and are recorded in the animal's body tissues such as bone collagen. Thus through isotope analysis of the bone collagen information about the diet of the animal can be obtained. Carbon and nitrogen isotopes in bone collagen reflect those of the dietary protein consumed over the last few years of the animals life as bones slowly remodel (Ambrose and Norr, 1993).

Environmental factors can influence animal isotope signatures in three ways. First, changing climatic or environmental conditions can result in an animal changing its dietary composition. This could be a change in the species of plants consumed or alternatively could be a change in the part of the plant consumed as plant roots, stems, seeds and leaves can have different isotope signatures due to plant physiology (Heaton, 1999).

Second, environmental factors can influence the isotopic signatures of soils and plants which are then passed up the food chain to animals. The primary control on plant $\delta^{13}\text{C}$ is photosynthetic pathway, but during the late Pleistocene / early Holocene European plants are thought to have almost exclusively used the C_3 photosynthetic pathway (Ehleringer et al 1997; Bocherens and Drucker 2013). Thus large-scale differences in $\delta^{13}\text{C}$ values such as those seen between C_3 and C_4 plants are not observed in fossil late Pleistocene plants or fauna from this region. Smaller scale variation in C_3 plant $\delta^{13}\text{C}$ values of the magnitude of a few ‰ are linked to environmental parameters. Light, water and nutrients availability, temperature, salinity, and atmospheric CO_2 $\delta^{13}\text{C}$ and partial pressure can cause a plant to increase its stomatal conductance and/or decrease its carboxylation rate, although water availability appears to be the most influential parameter (Heaton, 1999; Dawson et al. 2002). Thus the amount of isotopic fractionation during photosynthesis in each plant is dependent on the local environment. Correlations observed between plant $\delta^{13}\text{C}$ and light availability, nutrients availability, salinity and water use efficiency are typically positive whereas between plant $\delta^{13}\text{C}$ and water availability are generally negative (O'Leary, 1995; Yakir and Israeli, 1995; Hill et al. 1996; Sparks and Ehleringer, 1997; van Groenigen and van Kessel, 2002; Diefendorf et al. 2010; Kohn, 2010). Both positive and negative correlations have been observed between plant $\delta^{13}\text{C}$ and temperature (Heaton, 1999) However plant $\delta^{13}\text{C}$ had been shown to have a higher dependence on mean annual precipitation than mean annual

temperature (Kohn, 2010; Diefendorf et al. 2010). Changing CO₂ partial pressure and changing temperature collectively results in plant $\delta^{13}\text{C}$ being positively correlated with altitude (Körner et al. 1991). Under a forest canopy several of these parameters can synergistically result in particularly low $\delta^{13}\text{C}$ values in ground level plant relative to the same plant types in open environments (Vogel, 1978; Medina and Minchin, 1980; van der Merwe and Medina, 1989, 1991; Sonesson et al. 1992) and this phenomenon is known as the “Canopy effect”. Under a closed forest canopy, there is limited mixing between atmospheric and forest air CO₂. The isotopically light CO₂ released by rotting organic matter gets trapped under the canopy resulting in vertical stratification of the forest air $\delta^{13}\text{C}$ values. Limited light, nutrients, and water availability, along with intake of respired CO₂, exacerbate the depletion in ground level plant $\delta^{13}\text{C}$ values. Around 3‰ to 4‰ difference has been observed between leaf $\delta^{13}\text{C}$ of forest floor plants and from the top of the canopy (Schleser and Jayaskera, 1985; Broadmeadow et al. 1992; Brooks et al. 1997; Buchmann et al. 1997). The canopy effect is greatest in dense forest areas and more limited in open canopy woodland and at the edge of forests.

Temporal trends in animal bone collagen $\delta^{13}\text{C}$ values during the late Pleistocene and early Holocene have previously been observed in red deer, horse, reindeer and cattle across Northwest Europe (Drucker et al. 2003a; Richards and Hedges, 2003; Hedges et al. 2004; Stevens and Hedges 2004; Stevens, 2004; Hedges et al. 2005; Drucker et al. 2008, 2011a). As $\delta^{13}\text{C}$ temporal trends in initial data sets did not appear to differ between species or regions, most early investigations were in favour of a global driving factor, such as a change in atmospheric CO₂ partial pressure and $\delta^{13}\text{C}$ (Richards and Hedges, 2003; Stevens and Hedges, 2004; Stevens, 2004). However, the canopy effect, temperature and increased water availability were also considered possible driving parameters (Drucker et al. 2003a; Hedges

et al. 2005; Stevens et al. 2006). As data sets have expanded, it has become evident that temporal $\delta^{13}\text{C}$ trend may differ between species (Noe-Nygaard et al. 2005; Lynch et al. 2008) and within a species between regions (Drucker et al. 2008; 2011a). Thus local parameters such as the canopy effect and water availability are now more frequently cited as a major driving parameter. Where other proxy environmental data is available, one can more confidently determine whether temporal variations in faunal bone $\delta^{13}\text{C}$ values track vegetation changes, forest development or changes in water availability and so on. It is also possible that both global and local parameters may synergistically produce temporal changes in faunal $\delta^{13}\text{C}$.

The primary control on plant $\delta^{15}\text{N}$ values is their ability to use nitrogen directly from the atmosphere. Leguminous plants live in symbiosis with bacteria attached to their roots which allow the plant to use nitrogen directly from the atmosphere. Thus their $\delta^{15}\text{N}$ is generally close to the atmospheric standard (AIR) $\delta^{15}\text{N}$ value of 0‰. By contrast non-leguminous plants cannot directly use atmospheric nitrogen (N_2) but instead depend upon soil inorganic nitrogen such as ammonium (NH_4^+) and nitrate (NO_3^-) which are created as part of the nitrogen cycle (Hoefs, 1997; Robinson, 2001). Globally, soil and plant $\delta^{15}\text{N}$ have been shown to decrease with decreasing mean annual temperature (and to a lesser extent with increasing mean annual precipitation) (Amundson et al. 2003). This is likely to be linked to the intensity of soil nitrogen cycling and the relative importance of within-ecosystem nitrogen cycling versus the relative importance of inputs and outputs (Austin and Vitousek, 1998; Hobbie et al. 1998; Handley et al. 1999; Brenner et al. 2001; Hobbie et al. 2005). In cold and/or wet ecosystems soil activity is reduced (especially in permafrost or glacial context) and little nitrogen is lost from the cycle, thus soil and plant $\delta^{15}\text{N}$ remain low (Handley et al. 1999). In hot and/or arid ecosystems a greater amount of nitrogen moves from the organic to the

mineral nitrogen pools, which are subject to preferential loss of ^{14}N through leaching, denitrification and ammonia volatilisation, resulting in higher soil and plant $\delta^{15}\text{N}$ (Austin and Vitousek, 1998; Handley et al. 1999). Due to changing temperatures and soil activity plant $\delta^{15}\text{N}$ is often positively correlated with altitude (Mariotti et al. 1980). As with carbon, variations observed in plant $\delta^{15}\text{N}$ are passed up the food chain and are recorded in animal bone collagen. Through isotope analysis of archaeological bones we can extract palaeoenvironmental information.

Third, isotopic signatures of animals could be influenced by physiological processes within the animal that are affected by environmental parameters. Elevated animal nitrogen isotope values in hot or arid contexts have often been attributed to physiological stress due to heat and lack of water (Heaton et al. 1986; Sealy et al. 1987; Cormie and Schwarcz, 1996; Gröcke et al. 1997). However, recent research has indicated that positive correlations between herbivore $\delta^{15}\text{N}$ and temperature / aridity are due to changes in diet $\delta^{15}\text{N}$ rather than physiological stress (Murphy and Bowman, 2006; Hartman, 2011)

Site location and characteristics

El Mirón is one of many large caves found in the highly karstified Lower Cretaceous (Aptian) limestone mountainous area of the Cantabrian *Cordillera* (Straus et al. 2001) (Figure 1). It is located at an altitude of 260 metres above sea level (m.a.s.l.) on the steep western face of the Monte Pando (43°14'48"N, 3°27'5"W) overlooking the Asón River Valley, (Straus and González-Morales, 2010, 2012a,b). El Mirón strategically dominates two major routes of communication. First, a north-south route between the northern Castilian plateau and the Cantabrian coast. The shore was *ca.* 27-25 km from the cave during the Pleniglacial and Tardiglacial. The low Tornos mountain pass (920 m.a.s.l.), only 13 km from El Mirón,

connects the coast with the *Meseta*. Second, the cave is near the easiest west-east route between Asturias/Cantabria, the Basque Country and south-western France, via the Carranza valley. The fluvial network surrounding the site also creates favourable conditions for habitation, with two rivers (the Calera and the Gándara), tributaries of the Asón, like the Carranza, converging near El Mirón (Figure 1c, Straus and González Morales, 2003, 2009a,b, 2010, 2012a,b).

Although discovered in 1903, archaeological excavations at El Mirón (led by Lawrence Guy Straus and Manuel González-Morales) only began in 1996 and are ongoing. The main foci of the excavations have been at the cave vestibule front (“Cabin”) and rear (“Corral”). These areas (respectively measuring 9-10 and 8-12 sq.m.) have been connected with a stratigraphic trench (“Trench”) 8 m long x 1 m wide (Straus and González-Morales, 2003; Marín-Arroyo, 2009a,b; Straus and González-Morales, 2010, 2012a,b). The stratigraphic sections for these three excavation areas and relationship between them are extensively detailed in Straus and González Morales (2012). The radiocarbon chronology for El Mirón and the different cultural attribution within the sequence are given in table 1.

Late Middle Palaeolithic (Mousterian) and Early Upper Palaeolithic (early Gravettian) cultural evidence at El Mirón is minimal (Straus and González-Morales, 2009b; González-Morales and Straus in press). These levels are characterised by a scarcity of artefacts and fauna and human occupation seems to have been ephemeral (Marín-Arroyo, 2009a, b). These levels were not the focus for isotopic analysis (with the exception of a single sample taken from an Early Upper Palaeolithic context: sample XLHB-170).

In the Solutrean period (contemporary with the Last Glacial Maximum) occupation was low-

intensity and discontinuous in nature. The high proportion of Solutrean points present in the relatively small lithic assemblage, together with the fact that many of them had been violently broken, has been interpreted as being indicative of seasonal hunting or fishing parties exploiting local resources, an interpretation which is confirmed by the faunal remains. The lithic assemblage contains many different forms, flint types and colours (e.g. microdébitage, bladelets, blades, plain flakes and cores), which might indicate contact and trade between the different areas of the Cantabrian region. Other artefacts include possible ornamental items, such as artificially or naturally perforated shells and red deer canines. The faunal remains are dominated by ibex (*Capra pyrenaica*) and red deer (*Cervus elaphus*). Their bones are highly fragmented, probably indicating intensive butchering, processing and probably marrow/brain extraction. Salmon and small fish are also present (Straus and González Morales, 2009b; Straus et al. 2011).

In the Magdalenian period the occupation of El Mirón was at its most intensive (Straus and González-Morales, 2005). The culturally richest layers belong to the Initial and Lower/Middle Magdalenian (i.e. pre-harpoon) period, when the population density was high, as can be seen in the abundance of contemporary sites in the region (e.g. Altamira, Castillo, Rascaño and Juyo in central Cantabria and other sites in Asturias, Gipuzkoa Vizcaya and Navarra). Artefacts include antler *sagaies*, bone needles and awls, perforated shells and teeth (notably red deer canines), abundant lithic *débitage*, small cores and retouched tools, engraved scapulae, a possible spearthrower and a decorated stone pendant (Straus and González-Morales, 2001; Straus and González-Morales, 2009a). The Upper Magdalenian is less rich in cultural materials, but includes a unilaterally barbed harpoon (Straus and González-Morales, 2003, 2010). The Azilian lithic assemblages are characterized by backed micropoints and thumbnail endscrapers, plus an ochre-stained pebble (Straus and González-

Morales, 2001; González-Morales and Straus, 2012a,b; Straus and González-Morales, 2012a).

The cave is thought to have functioned as a residential site during the Initial and Lower Magdalenian (Straus et al. 2001; Straus, 2005; Straus and González Morales, 2005; Risetto, 2005; González-Morales et al. 2007; Straus and González Morales, 2007a, 2007b; Marín-Arroyo, 2009b), with a human burial pertaining to the latter period (Straus et al. 2011). Again the faunal remains during this period are dominated by ibex and red deer, although other mammals such as equids (*Equus ferus*), roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*) and small carnivores are also present (Marín Arroyo, 2009b, 2010). The hunter-gatherer groups present in the area are thought to have followed the seasonal movements of their main prey, settling temporarily at strategic sites near the resources (Marín-Arroyo, 2010). The season of occupation during the Magdalenian and Azilian corresponds to late spring/early summer, except in the case of level 11, in which there is also limited evidence of occupation during the autumn (Marín-Arroyo, 2010). The scale of these seasonal movements (both for humans and the fauna), would not have been great, due to the high relief and shortness of most Cantabrian valleys (Straus, 1986, 1992; Straus et al. 2002; Marín-Arroyo, 2010).

With the start of the Holocene a diversification is seen in the faunal assemblages (Marín-Arroyo, 2010; Altuna and Mariezkurrena, 2012). Reindeer (never common in Cantabrian Spain and absent from El Mirón) disappeared, horse decreased and boar (*Sus scrofa*) and roe deer become more important, as a response to the expansion of forests. At the same time, a decrease in the size of red deer is observed (Altuna, 1995). This diversification of species in the assemblages is not necessarily due to natural diachronic changes in the abundance of

faunal resources but, rather, to increasing demographic pressure (Straus, 1997). This would have led human societies to optimise the resources in the surrounding areas and the adoption of more complex and specialised economic systems (Marín-Arroyo, 2010). The increase in population during the Azilian and Mesolithic would have favoured sedentism and the gradual abandonment of residential mobility (Marín-Arroyo, 2010). The Mesolithic is culturally barely attested at El Mirón, with scarce lithic artefacts and very few instances of boar, red deer and roe deer (Altuna et al. 2004; Altuna and Mariezkurrena, 2012).

The Neolithic, Chalcolithic and Bronze Age levels, have a greater number of lithics compared to the Mesolithic, and other artefacts such as decorated and undecorated ceramics, slag and a copper pin (Straus and González Morales, 2012a). Movement to sedentism culminated in the Neolithic, when the first evidence for agriculture (emmer wheat) and domesticated livestock (ovicaprines, cattle and pigs) is found at El Mirón (Peña-Chocarro et al. 2005a,b; Altuna and Mariezkurrena, 2012). In the early Neolithic, hunting continued to be a relatively important subsistence activity (red deer, ibex), in spite of the arrival of domesticates from the Near East. In the later Neolithic, however, hunting was notably reduced, with a decrease in boar and the complete disappearance of ibex and roe deer. In the Chalcolithic, hunting was an incidental subsistence activity which virtually disappeared in the Bronze Age (Altuna et al. 2004).

Methodology

170 samples of red deer bone were selected for isotope analysis, 65 from the Cabin area, 15 from the mid-vestibule Trench and 90 from the Corral area. The archaeological periods represented were the Bronze Age (BA) (n=3), Chalcolithic (Chalc) (n=3), Neolithic (Neo) (n=10), Mesolithic (Meso) (n=4), Azilian (Az) (n=1), Final Magdalenian / Azilian (FM/AZ)

(n=17), Upper Magdalenian (UM) (n=15), Middle Magdalenian (MM) (n=15), Lower Magdalenian (LM) (n=38), Initial Magdalenian (IM) (n=8), Solutrean (Sol) (n=12) and Early Upper Palaeolithic (EUP) (n=1). A full list of sample provenance is given in online supplementary data file 1. The samples were prepared at the McDonald Institute for Archaeological Research using a modified Longin (1971) method. Approximately 500 mg bone pieces were cleaned by sandblasting and demineralised in 0.5M aq. hydrochloric acid at 4 °C until they had fully demineralised. Samples were rinsed in distilled water and gelatinised by heating in pH 3.0 aqueous solution at 75°C for 48 hours. The liquid fraction containing the dissolved collagen was filtered off, frozen overnight at -20°C, then stored at -80°C for 4 hours and finally lyophilised. The lyophilised collagen was weighed into tin capsules for isotope analysis. Isotope analysis was performed at the Godwin Laboratory, University of Cambridge, using a Costech automated elemental analyser coupled in continuous-flow mode to a Finnigan MAT253 mass spectrometer. Samples were analysed in triplicate (samples XLHB-1 to 36) and in duplicate (samples XLHB-37 to 170), where possible (full details in online supplementary data file 1). Carbon and nitrogen results are reported using the delta scale in units of 'per mil' (‰) relative to internationally accepted standards VPDB and AIR respectively (Hoefs, 1997). Based on replicate analyses of international (IAEA: caffeine and glutamic acid-USGS-40) and in-house laboratory standards (nylon, alanine and bovine liver standard) precision is better than $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Results

Collagen was successfully extracted from 142 of the 170 samples. Of the 28 samples that failed to produce sufficient collagen for analysis 26 came from the Corral excavation area, and 2 from the Cabin excavation area. Of the 148 samples from which collagen was successfully extracted, 127 had C/N atomic ratios between 2.9 and 3.6, which indicates good

collagen preservation (DeNiro, 1985). For the vast majority of these samples the %C values were greater than 35% and %N values were greater than 10%, suggesting the *in vivo* isotopic signature has not significantly altered. 15 samples had C/N atomic ratios above 3.6, indicative of poor preservation or contamination. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and C/N atomic ratios for all specimens are listed in online supplementary data file 1.

The deer $\delta^{13}\text{C}$ values range from -22.2‰ to -19.6‰ with a mean of -20.6‰ \pm 0.6 and the $\delta^{15}\text{N}$ values range from 0.6‰ to 4.5‰ with a mean of 2.9‰ \pm 0.6. In order to look for temporal variations in the deer isotope signature samples from the Cabin, Trench and Corral were collated and grouped by archaeological time period (See figure in online supplementary data file 2). As isotope results from the Magdalenian / Azilian layers were abundant, it was possible to subdivide the results on the chronological subdivisions given by Cuenca-Bescós et al. (2012) (See table 1 and online supplementary data files 1 and 2). The Early Upper Palaeolithic and the Azilian categories were not included in the statistical analysis of individual archaeological periods as only single data points were available from these two time periods. Summary statistics (no. of samples, mean, max, min, range, standard deviation) for each archaeological time period are given in table 2.

Considering the carbon first, a clear trend towards more negative $\delta^{13}\text{C}$ values can be seen over time (See figure in online supplementary data file 2). The mean $\delta^{13}\text{C}$ of deer from Holocene archaeological horizons (Meso, Neo, BA and Chalc) (-21.6‰ \pm 0.4, n=20) is significantly lower (Two-tailed student t-test, $p \leq 0.001$) by 0.8‰ relative to that of deer from late Pleistocene archaeological horizons (EUP, Sol, IM, LM, MM, UM, FM/Az, Az) (mean $\delta^{13}\text{C}$ = -20.4‰ \pm 0.3, n=107). Likewise, the mean values of each of the Holocene archaeological periods were statistically significantly different from the values of each of the

late Pleistocene periods (Tables 3 and 4). However, the differences between archaeological periods within either the late Pleistocene or the Holocene were not statistically significant (Table 4). The major shift in $\delta^{13}\text{C}$ of the magnitude of 1.1‰ occurs between the Final Magdalenien / Azilian mean $\delta^{13}\text{C}$ and the Mesolithic mean $\delta^{13}\text{C}$, although a change of 1.4‰ is observed between the Final Magdalenian / Azilian and Chalcolithic mean $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values for samples from the Cabin, Corral and Trench excavation areas are similar in the Upper Magdalenian, Final Magdalenian / Azilian, Mesolithic and Neolithic horizons. By contrast in the Lower Magdalenian and Middle Magdalenian the Corral deer mean $\delta^{13}\text{C}$ values (LM = $-20.5\text{‰} \pm 0.4$, $n=16$, MM = $-20.7\text{‰} \pm 0.3$, $n=7$) are significantly lower than those of the Cabin deer (LM = $-20.2\text{‰} \pm 0.2$, $n=22$, MM = $-20.3\text{‰} \pm 0.4$, $n=8$) (LM $p=0.001$, MM $p=0.043$).

Further examination of the stratigraphy and radiocarbon dates indicates that the differences observed between the Cabin and Corral deer $\delta^{13}\text{C}$ during the Lower and Middle Magdalenian are likely to be linked to chronology. Figure 2 shows the $\delta^{13}\text{C}$ data from the different layers in the three stratigraphic sections arranged in a single sequence as established by (Cuenca-Bescós et al. 2012) by means of radiocarbon dates as well as by partial physical correlation along the mid Vestibule Trench. Temporal variations can be seen within the single sequence. The sequence was divided into five $\delta^{13}\text{C}$ zones based on clear shifts in the $\delta^{13}\text{C}$ values (Figure 2). Of the four shifts in $\delta^{13}\text{C}$ observed between the zones, three do not occur at the boundaries between archaeological horizons. The first change in $\delta^{13}\text{C}$ occurs after layer 119 during the initial Magdalenian, with a shift of around 0.3‰ to more negative values. Although zones 1 and 2 appear to have distinctive $\delta^{13}\text{C}$ values (zone 1: $-20.3\text{‰} \pm 0.3$, $n=17$, zone 2: $-20.6\text{‰} \pm 0.3$, $n=19$), the difference between their mean $\delta^{13}\text{C}$ values is not statistically significant ($p=0.071$), even if the outlier in zone 2 (XLHB-135) is excluded. The small

magnitude of the change along with the amount of variation within the two zones may be responsible for the lack of statistical significance. The second change in $\delta^{13}\text{C}$ occurs after layer 110, with a shift of around 0.4‰ to more positive values. The mean $\delta^{13}\text{C}$ of zones 2 ($-20.6\text{‰} \pm 0.3$, $n=19$) and 3 ($-20.2\text{‰} \pm 0.3$, $n=28$) are significantly different ($p=0.002$). The third change in $\delta^{13}\text{C}$ occurs after layer 14 during the Upper Magdalenian, with a shift of around 0.3‰ to more negative values. The mean $\delta^{13}\text{C}$ of zones 3 ($-20.2\text{‰} \pm 0.3$, $n=28$) and 4 ($-20.5\text{‰} \pm 0.3$, $n=42$) are significantly different ($p=0.003$). The final change in $\delta^{13}\text{C}$ occurs after layer 305 at the end of the Azilian, with a shift of around 1.1‰ to more negative values. It should be noted however, that the single high $\delta^{13}\text{C}$ value during the Mesolithic layer 10.1 may indicate that the shift in $\delta^{13}\text{C}$ occurred during the Mesolithic period rather than at the end of Azilian (although this sample has not been directly dated). The mean $\delta^{13}\text{C}$ of zones 4 ($-20.5\text{‰} \pm 0.3$, $n=42$) and 5 ($-21.6\text{‰} \pm 0.4$, $n=20$) are significantly different ($p \leq 0.001$).

A broad temporal trend also exists in the nitrogen isotope over time when the samples are grouped by archaeological period (See figure in online supplementary data file 2). Unlike for carbon however, the $\delta^{15}\text{N}$ generally become more positive. The mean $\delta^{15}\text{N}$ of the Holocene deer ($3.7\text{‰} \pm 0.5$, $n=20$) is significantly higher by 1‰ relative to that of the late Pleistocene deer ($2.7\text{‰} \pm 0.5$, $n=107$) (Two-tailed student t-test, $p \leq 0.001$). However, the general trend to higher $\delta^{15}\text{N}$ values appears to be temporally reversed in the Final Magdalenian / Azilian period. Although the mean $\delta^{15}\text{N}$ of the late Pleistocene archaeological horizons (Sol, IM, LM, MM, UM, FM/Az) seem to differ, these differences are not large or statistically significant (Tables 3 and 4). The mean values of each of the Pleistocene archaeological periods are significantly different from the mean $\delta^{15}\text{N}$ values of the Mesolithic, Neolithic and Bronze Age (Tables 3 and 4) with the exception of the Middle Magdalenian and Final Magdalenian /

Azilian relative to the Neolithic. However, the mean $\delta^{15}\text{N}$ of all the Magdalenian samples (IM, LM MM, UM) ($2.8\text{‰} \pm 0.5$, $n=76$) is significantly different to that of the Neolithic period ($3.5\text{‰} \pm 0.5$, $n=10$) (Two-tailed student t-test, $p \leq 0.001$). By contrast, the mean $\delta^{15}\text{N}$ of the Chalcolithic deer is only significantly different to that of the Solutrean deer, however the Chalcolithic mean $\delta^{15}\text{N}$ is higher than that of each of the Pleistocene archaeological periods (Tables 3 and 4). The lack of statistical significance is likely to be related to the low number of Chalcolithic samples ($n=3$).

Unlike in the carbon isotopes, the $\delta^{15}\text{N}$ values for the different excavation areas are similar in the Lower, Middle and Upper Magdalenian, Mesolithic and Neolithic periods. In the Final Magdalenian / Azilian however, the Trench deer mean $\delta^{15}\text{N}$ is significantly lower than that of the Corral deer (Mean $\delta^{15}\text{N}$ Trench = $2.1\text{‰} \pm 0.9$, $n=6$, Cabin = $3.1\text{‰} \pm 0.6$, $n=11$, Independent Student T-test $p=0.015$). Further examination of the stratigraphy and radiocarbon dates indicates that the difference observed between the Cabin and Trench deer $\delta^{13}\text{C}$ could also be linked to chronology. Figure 3 shows the $\delta^{15}\text{N}$ data from the different layers in the three stratigraphic sections arranged in a single sequence as established by (Cuenca-Bescós et al. 2012). There is a shift in the deer $\delta^{15}\text{N}$ values in the middle of the Final Magdalenian / Azilian. The Cabin deer $\delta^{15}\text{N}$ in the early part of the Final Magdalenian / Azilian range between 2.9‰ to 3.5‰ . By contrast the Cabin and Trench deer in the later part of the Final Magdalenian / Azilian are similar, ranging from 1.5‰ to 3.5‰ and 0.6‰ to 3.1‰ respectively, confirming that the differences between the different sequence appear to be linked to chronology. Temporal variations can be seen within the single sequence, with five distinct $\delta^{15}\text{N}$ zones visible (Figure 3). Unlike in the carbon, three of the four shifts in $\delta^{15}\text{N}$ observed between the zones occur at the boundaries between archaeological periods. The first change in $\delta^{15}\text{N}$ occurs after layer 118 (Corral) at the boundary between the Initial

Magdalenian and the Lower Magdalenian with a shift of around +0.4‰ to higher values. The mean $\delta^{15}\text{N}$ of zones 1 ($2.4\text{‰} \pm 0.4$, $n=21$) and 2 ($2.8\text{‰} \pm 0.4$, $n=68$) are significantly different ($p=0.016$). The second change in $\delta^{15}\text{N}$ occurs after layer 307 (Trench) at the boundary between the Upper Magdalenian and Final Magdalenian / Azilian boundary, with a shift of around +0.5‰ observed. Although $\delta^{15}\text{N}$ values above 2.9‰ are seen in both zones 2 and 3, no $\delta^{15}\text{N}$ value below 2.9‰ are observed in zone 3. The mean $\delta^{15}\text{N}$ of these two zones (zone 2: $2.8\text{‰} \pm 0.4$, $n=68$, zone 3: $3.3\text{‰} \pm 0.3$, $n=6$) are not however statistically significantly different. The third change in $\delta^{15}\text{N}$ occurs after layer 11.1 (Cabin) during the Final Magdalenian / Azilian, with a shift of around +0.8‰. Particularly low $\delta^{15}\text{N}$ values are seen in zone 4 in addition to values similar to those seen in zone 3. This zone has the largest spread of $\delta^{15}\text{N}$ values. The mean $\delta^{15}\text{N}$ of zones 3 (zone 3: $3.3\text{‰} \pm 0.3$, $n=6$) and 4 ($2.5\text{‰} \pm 0.9$, $n=12$) are significantly different ($p=0.090$). The final change in $\delta^{15}\text{N}$ occurs after layer 305 (Trench) at the end of the Azilian, with a shift of around 1.2‰ to higher values. The mean $\delta^{15}\text{N}$ of zones 4 ($2.5\text{‰} \pm 0.9$, $n=12$) and 5 ($3.7\text{‰} \pm 0.5$, $n=20$) are significantly different ($p \leq 0.001$).

Discussion

The temporal variations in the deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values seen through the El Mirón sequence provide an insight into the local environmental conditions in the area around the cave. Four major shifts are seen in both the carbon and nitrogen isotope signatures, enabling the isotope results to be grouped into five zones. Several of these shifts do not coincide with changes in archaeological technocomplex. Carbon zone 1 and nitrogen zone 1 are comparable in time. The same is true for carbon and nitrogen zones 5. Therefore carbon and nitrogen are discussed together for each of these two zones. Carbon zones 2 to 4 and nitrogen zones 2 to 4 differ in time scale, thus are discussed separately.

Carbon and nitrogen Zone 1: EUP, Sol and IM (c. 27 kyr cal BP to c. 20 kyr cal BP)

Limited information can be gleaned from the single specimen dating to the Early Upper Palaeolithic. However, this deer's $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are similar to those of the Solutrean deer. The Solutrean and Initial Magdalenian deer $\delta^{13}\text{C}$ values indicate these deer lived and consumed vegetation from an open cool environment. The Solutrean and Initial Magdalenian deer $\delta^{15}\text{N}$ values are relatively low, indicating low temperatures and limited biological activity and nitrogen cycling within the soil. This result is consistent with the evidence from the micromammals and pollen at El Mirón which suggest the Solutrean occupation occurred under the cool arid conditions of the Last Glacial Maximum (Straus and González Morales, 2009b; Straus et al. 2011). The micromammals recovered from the Solutrean levels are dominated by open grassland species, with species typical of barren rocky slopes also being abundant (Cuenca-Bescós et al. 2008, 2009; Straus and González Morales 2009b). Additionally the Solutrean levels show the lowest number of woodland species in the whole Mirón sequence and an abundance of a cold-climate indicator, *Microtus oeconomus* (Straus and González Morales, 2009b). Palynological results confirm an open landscape dominated by composites, grasses and heaths, although pine and birch trees were very occasionally present (Straus and González Morales, 2009b; Straus et al. 2011). Climate data from the wider region is also consistent with the interpretation of a cool open environment. Proxy data from marine cores around the Iberian Margins and from lake records on the Iberian Peninsula indicate that although temperatures were very cold, the LGM was not the coldest period during the Pleniglacial and may have been relatively humid (Moreno et al. 2012). Notably, the shift in $\delta^{13}\text{C}$ at the end of carbon zone 1 occurs one stratigraphic unit below the change in $\delta^{15}\text{N}$ at the end of nitrogen zone 1. It has previously been suggested that a delay can occur between a climate change and a detectable response in faunal $\delta^{15}\text{N}$ due to the complexity and nature of the soil-plant-animal nitrogen cycle (Stevens and Hedges, 2004; Stevens et al.

2008).

Carbon Zone 2: Late IM and early LM (c. 20 kyr cal BP to c.18.5 kyr cal BP)

The transition to slightly lower $\delta^{13}\text{C}$ values occurs during the Initial Magdalenian and coincides with the onset of the last deglaciation. The decrease in $\delta^{13}\text{C}$ values likely indicates a change in isotope composition and/or type of vegetation the deer consumed linked to increasing water availability as continental and marine climate data indicate this period was cold and humid (see Langlais, 2011 and reference therein). The decrease in deer $\delta^{13}\text{C}$ values cannot be due to the canopy effect because the micromammal assemblage at El Mirón indicate open environment (Cuenca-Bescós et al. 2009, 2012; Cuenca and Garcia, 2012), and deciduous trees and coniferous trees are thought to have had only a limited presence in the region at this time (McKeever, 1984; Uzquiano, 1992; Allen et al. 1996; Muñoz-Sobrino et al. 2004, 2007; González Samperiz et al. 2010).

Carbon Zone 3: Late LM and early MM (c. 18.5 kyr cal BP to c.16.3 kyr cal BP)

The transition to more positive deer $\delta^{13}\text{C}$ values at the start of zone 3 broadly coincides with the start of the Heinrich stadial 1* (HS1, onset c.18.0 - cal kyr BP, Elliot et al. 2002; Sánchez-Goñi and Harrison, 2010). The deer $\delta^{13}\text{C}$ values in this zone are similar to those in Zone 1 during the LGM, and indicate an open environment. The shift to slightly more positive deer $\delta^{13}\text{C}$ likely indicates decreasing water availability. This is consistent with evidence from marine and terrestrial records from the Iberian Peninsula and its margins, which shows a drop in sea surface temperatures and humidity (Grousset, 2001; Elliott et al. 2002, Rohling et al. 2003; Hemming, 2004; Naughton et al. 2009; Sánchez-Goñi and Harrison, 2010). It is likely that in the Iberian Peninsula this interval and not the global LGM was the coldest and most arid period (Moreno et al. 2012).

Zone 4: Late MM, UM, FM/Az, and Az (c.16.3 kyr cal BP to 11 kyr cal BP)

The transition to more negative deer $\delta^{13}\text{C}$ values at the start of zone 4 coincides with the onset of Heinrich event 1* (HE1 c.16.3 - 14.6 kyr cal BP, Naughton et al. 2009; Barker et al. 2009; Sánchez-Goñi and Harrison, 2010). The deer $\delta^{13}\text{C}$ values remain stable until the end of the Azilian suggesting consistent environmental conditions throughout this period. The shift to lower $\delta^{13}\text{C}$ values at this time could indicate increasing water availability. This is some time before the Late-glacial interstadial, when most palaeoclimate records show conditions began to ameliorate. An increase in woodland micromammal species at El Mirón during the Middle Magdalenian (start of Heinrich event 1) also suggests the start of forest expansion at this time. This forest expansion is unlikely to be driving the deer $\delta^{13}\text{C}$ values as the canopy effect acts as a threshold effect, meaning that a significant degree of forest closure is required to trigger visible depletion in the $\delta^{13}\text{C}$ values of understory plants. This degree of closure is very unlikely in the cold context of the Iberian Peninsula at this time. The results of

micromammal analysis from the Iberian Peninsula show the Heinrich event 1 marks an increase in the temperature of the coldest month, as well as an increase in the mean annual precipitation (López-García and Cuenca-Bescós, 2010; Cuenca- Bescós et al. 2012). Thus, collectively, the micromammals and stable isotope data suggest pre-Late-glacial increasing humidity in this region.

* Heinrich Stadial (HS) refers to the cold interval in a given region associated with an Heinrich Event (HE) (the interval of the formation of the ice raft detritus Heinrich layer). The duration of a HS may be longer than that of a HE (Sánchez-Goñi and Harrison, 2010). HS1 and HE1 occur during Greenland Interstadial 2-a (GS-2a).

Pollen and micromammal evidence from the Cantabrian region indicates that, with the warmer and more humid conditions of the Late-glacial interstadial, conifers expanded into higher altitudes, and deciduous trees, such as oak, hazel, alder, and birch, colonized the bottom of valleys replacing the steppe landscape (Leroi Gourhan, 1980; López García et al. 1996; Boyer-Klein, 1981; Dupré Ollivier, 1984; Peman, 1985; López García, 2000; Sánchez-Goñi and d'Errico, 2005; Cuenca-Bescós et al. 2012). This forest development does not, however, seem to have had a greater effect on the deer $\delta^{13}\text{C}$ values than the early forest expansion suggesting the forest was not particularly dense.

The deer $\delta^{13}\text{C}$ remain stable into the Final Magdalenian / Azilian period which coincides with the Younger Dryas event (Greenland Stadial 1, c. 12.9 cal kyr BP to 11.5 kyr cal BP). Micromammals from El Mirón suggest conditions were cold and dry, with a significant decrease in the amount of woodland. Pollen records from the Cantabrian region and the Iberian Peninsula show a sharp decline in the amount of tree pollen as the deciduous forests were broken up and temperate species existed in isolated areas within an open landscape. Temperatures dropped but humidity remained high within the region (Straus, 2011 and references therein; Uzquiano, 1998; Muñoz-Sobrino et al. 2007).

Thus, despite the varying temperatures and extent of woodland development through Heinrich event 1, the Late-glacial interstadial and the Younger Dryas, the deer $\delta^{13}\text{C}$ values remain constant. This lack of correlation demonstrates that water availability rather than temperature or forest development is the most convincing driving parameter of vegetation and deer $\delta^{13}\text{C}$ in this regions during the late Pleistocene period.

Nitrogen Zone 2: LM, MM and UM (c. 20 kyr cal BP to c.14.5 kyr cal BP)

The transition to slightly higher deer $\delta^{15}\text{N}$ values at the start of nitrogen zone 2 broadly coincides with the onset of the deglaciation after the LGM (Figure 3). The small rise in nitrogen isotope values indicates increased nutrient availability and soil biological activity due to increased temperatures. Soil development is likely to have been limited by loess accumulation. However, increased nutrient availability and soil biological activity would have enabled shrubs and trees to colonize previously inhospitable areas. The deer $\delta^{15}\text{N}$ remain relatively constant through to the end of the Upper Magdalenian, despite the regional evidence for changing climatic conditions through Heinrich stadial 1 and Heinrich event 1 and substantial climate amelioration in the early Late-glacial interstadial as discussed above. Thus, periods of low temperature during this interval do not seem to have had as great an effect on the nitrogen cycle as the conditions during in the LGM. This suggests that the nitrogen cycle is not quick to respond to changing climatic conditions.

Nitrogen Zone 3: Early FM/Az (c. 14.5 kyr cal BP to c.13.5 kyr cal BP)

The start of nitrogen zone 3 broadly occurs during the Late-glacial interstadial. The deer $\delta^{15}\text{N}$ at this time are similar to the higher $\delta^{15}\text{N}$ values seen in nitrogen zone 2 (Figure 3), however no low $\delta^{15}\text{N}$ are seen in this period. Thus, nitrogen zones 1 to 3 could potentially be viewed as a single zone in which deer $\delta^{15}\text{N}$ increase over time rather than three distinct zones. The $\delta^{15}\text{N}$ data from zone 3 indicates enhanced soil biological activity, greater nitrogen cycling, and increased nutrient availability at this time relative to preceeding periods due to increasing temperatures. Micromorphological and sedimentological analyses at El Mirón indicate soil regeneration and stability at this time (Courty and Vallverdu, 2001; Ellwood et al. 2001; Straus et al. 2001). The delay between the onset of the substantial climatic amelioration at the start of the Late-glacial interstadial and a detectable response in the deer $\delta^{15}\text{N}$ values again

indicates the slow response of the nitrogen cycle to climate change, probably due to the residence time of nitrogen in the soil-plant system and the rate of soil development.

Nitrogen Zone 4: Late FM/Az and Az (c. 13.5 kyr cal BP to c.11.5 kyr cal BP)

The onset of nitrogen zone 4 witnesses a shift to lower red deer $\delta^{15}\text{N}$ values, although some deer have $\delta^{15}\text{N}$ values similar to those in the preceding period (Figure 3). Notably, the lowest deer $\delta^{15}\text{N}$ value in the whole sequence is seen within this zone and several of the red deer $\delta^{15}\text{N}$ are comparable to those detected during the LGM. The transition to lower deer $\delta^{15}\text{N}$ occurs around 13.5 kyr cal BP, which broadly coincides with the onset of the Younger Dryas event (c. 12.9 kyr cal BP to 11.5 kyr cal BP). It is not possible to determine whether the inconsistency between the timing of the onset of the Younger Dryas and the shift in deer $\delta^{15}\text{N}$ values at El Mirón is real as the deer samples are not directly radiocarbon dated. The lower deer $\delta^{15}\text{N}$ values indicate substantially lower temperature during this period. Moreover, they suggest that despite its short duration, the Younger Dryas seems to have had a more major effect on the nitrogen cycle than the LGM. Micromorphological and sedimentological analyses at El Mirón suggest temperatures decreased threefold at this time and intense freezing of the soils occurred (Courty and Vallverdu, 2001; Ellwood et al. 2001; Straus et al. 2001). If taken at face value, the deer $\delta^{15}\text{N}$ values at El Mirón suggest conditions during the Younger Dryas were as severe as those during the LGM (and potentially more severe if only for a short period). This contradicts the general consensus that conditions in the Cantabrian region during the Younger Dryas were milder than during the LGM. Further research is required to determine whether this disparity truly indicates particularly harsh conditions at El Miron compared to the wider region or is due to our limited understanding of how climatic / environmental parameters include faunal $\delta^{15}\text{N}$ values.

Carbon and nitrogen zone 5: Meso, Neo, Chalc and BA (11 kyr cal BP to 4 kyr cal BP)

The transition to more negative deer $\delta^{13}\text{C}$ values and more positive $\delta^{15}\text{N}$ values at the start of zone 5 is the largest isotopic shift in the El Mirón sequence and coincides with the start of the Holocene. The $\delta^{13}\text{C}$ decrease likely indicates a change in isotope composition and/or type of vegetation the deer consumed linked to increasing water availability. It should however be noted that lower plant $\delta^{13}\text{C}$ values due to increased atmospheric CO_2 concentration could also be partly contributing to the observed change in deer $\delta^{13}\text{C}$. The $\delta^{15}\text{N}$ increase indicates increased temperatures, soil biological activity, nitrogen cycling and soil development. The isotope results are consistent with micromammal data, which suggest warm and humid conditions and rapid forest expansion at El Mirón (Cuenca-Bescós et al. 2008, 2009, 2012; Cuenca-Bescós and García Pimienta, 2012). Micromorphological and sedimentological data also point to soil development and stabilization due to increasing temperatures (Court and Vallverdu, 2001; Ellwood et al. 2001; Straus et al. 2001). Pollen and charcoal data from Cantabria and the Iberian Peninsula also indicate rapid expansion of forest after the Younger Dryas during the early Holocene (Carrión et al. 2010 and reference therein). Like in the Late-glacial interstadial, conifers expanded into higher altitudes, and deciduous trees colonized the bottom of valleys. As the deer isotope data is more limited from the Holocene, it is not possible to extensively examine whether the deforestation that occurred during the Mid Holocene (primarily due to clearance by humans) had a major impact on the deer $\delta^{13}\text{C}$ values. However, the deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ seem relatively unchanged through the Holocene.

Inter-regional comparison

The temporal variations seen in the red deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures at El Mirón can be compared to those seen in other areas of Europe. Comparative red deer carbon and nitrogen isotope data are available for 300 deer from the British Isles, Germany, Southwest France, the

French Jura, the Paris Basin, the Western Alps, Italy (Online supplementary data file 3). A small amount of data is also available from a few other sites in Spain (Online supplementary data file 3). Unfortunately data from other areas of Europe is not as abundant, evenly distributed through time or chronologically controlled as at El Mirón. Therefore, comparisons between regions must be made at a lower temporal resolution. Figures 4 and 5 show the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from other regions of Europe divided into time units that are contemporary with the cultural unit seen at El Mirón (regardless of the archaeological technologies present at these sites). This method of comparison allows geographical differences in temporal isotopic trends to be considered. These inter-regional faunal isotope comparisons builds on those previously published (Drucker et al. 2003a; Hedges et al. 2004; Stevens 2004; Stevens and Hedges, 2004; Drucker et al. 2008; Stevens et al. 2008; Drucker et al. 2010, 2012).

Considering the carbon first, during the late Pleistocene (Solutrean, Magdalenian and Azilian) limited variation in $\delta^{13}\text{C}$ is seen (at this resolution) (Figure 4). With the transition to the early Holocene (Mesolithic and Neolithic), a shift to more negative deer $\delta^{13}\text{C}$ values is seen in all geographical regions. However the magnitude of this shift differs between regions. The change in $\delta^{13}\text{C}$ values is most limited in the Western Alps and Italy, whereas in Spain (primarily data from El Mirón) and the UK the shift is slightly greater. A greater magnitude shift in deer $\delta^{13}\text{C}$ values is seen between the Azilian and Mesolithic in the Paris Basin and French Jura. The deer $\delta^{13}\text{C}$ values in the UK become more negative in the Neolithic and become similar to those in the Paris Basin, but by the Bronze Age they become more positive and similar to those seen in Spain. The relatively positive deer $\delta^{13}\text{C}$ values seen in all regions in the late Pleistocene indicate an open and relatively drier environment. With the onset of the Holocene the geographical disparity in the magnitude of the shift to more negative $\delta^{13}\text{C}$ values relates to local environmental conditions. The smaller magnitude $\delta^{13}\text{C}$ change seen in

more southerly regions (Italy and Spain) and higher altitude areas (Western Alps) is likely to reflect occupation of open habitats with vegetation $\delta^{13}\text{C}$ affected by changes in atmospheric CO_2 concentration and increasing water availability. However the limited $\delta^{13}\text{C}$ shift does not necessarily indicate total absence of dense forest as in the Western Alps the deer are thought to have occupied higher altitudes, avoiding valley bottoms where closed forests were present (Drucker et al. 2011a). The larger magnitude change in $\delta^{13}\text{C}$ seen in the Paris basin, French Jura and UK is likely to be due to the same factors but additionally to be a result of the more extensive development of dense forest canopies. The higher deer $\delta^{13}\text{C}$ values seen in the UK Bronze Age may reflect the fact that extensive forest clearance had occurred by this time.

The deer nitrogen isotope values vary both geographically and temporally (Figure 5). Similar variations in $\delta^{15}\text{N}$ values have been seen in other herbivores including reindeer, horse and bovids (e.g. Drucker et al 2003; Stevens, 2004; Stevens and Hedges 2004; Stevens et al 2008; Drucker et al 2012). During the late Pleistocene the deer $\delta^{15}\text{N}$ are generally low, with broadly similar values in seen in the Jura, Western Alps, the UK and Spain, and slightly higher values in Southern France and the Paris Basin. Italy however is the exception as higher values are seen in this region. Over time the deer $\delta^{15}\text{N}$ values increase in all regions (for which data are available), however this change is more gradual and of a more limited magnitude in some regions (e.g. Spain and the Western Alps) than in other regions (Paris Basin, French Jura) and is particularly large in the UK. The pace of change in $\delta^{15}\text{N}$ values seen in the graph is, however, probably not a true reflection of speed of $\delta^{15}\text{N}$ increase due to the limited sample size from some regions and the temporal grouping of data. The isotope results suggest that the nitrogen cycle in southern Italy was not greatly affected by the climate conditions during the late Pleistocene, which is consistent with the general consensus that conditions in the Mediterranean remained relatively mild at this time. The small rise in $\delta^{15}\text{N}$ in Spain (primarily

El Mirón) and Western Alps suggests an increase in nitrogen cycling and soil development due to increasing temperatures. The larger increase in $\delta^{15}\text{N}$ seen in the UK, Paris Basin and French Jura indicates a substantial increase in nitrogen cycling and extensive soil regeneration and development due to increasing temperatures. This larger increase in $\delta^{15}\text{N}$ is witnessed in regions where the deer $\delta^{13}\text{C}$ data indicates dense canopy forest became established.

Conclusion

The carbon and nitrogen isotope analyses of red deer from the well dated archaeological sequence at El Mirón have shown that the habitat occupied by the deer underwent considerable environmental change between the end of the Pleistocene and the Holocene. In the rest of the sequence changes in the red deer isotope signatures were much more attenuated, and some times only slightly larger than measurement error. Variations in the carbon isotopes show that the LGM, Heinrich stadial 1, Heinrich event 1, the Late-glacial interstadial (GI-1) and the onset of the Holocene all had an impact on the ecosystem occupied by the red deer. However, subtle changes in the local environmental conditions within the Late-glacial interstadial (GI-1) were not detected in the carbon isotopes. Comparison of the red deer carbon isotopes with those from other regions of Europe show that although the vegetation changed within the habitat they occupied, the forest was never as dense enough to result in a canopy effect as seen in more northern regions. Further isotopic analysis of more forest dwelling species such as roe deer would help determine whether a dense forest canopy was also absent from the wider landscape surrounding El Mirón. The deer nitrogen isotopes at El Mirón generally increased over time indicating the regeneration of soil biological activity and nitrogen cycling, which was temporarily interrupted during the Younger Dryas. Although the deer $\delta^{15}\text{N}$ at El Mirón have varied overtime, the magnitude of variation is not as

great as that observed in other regions of Europe. This is in line with the well-known habitat and dietary flexibility of *Cervus elaphus* (Straus, 1981 with references therein).

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Figure 1: Location of El Mirón Cave in the Iberian Peninsula (A), the Asón River Valley (B) and Monte Pando (C) (Modification of map drawn by L.G. Straus, R. Stauber and M. González Morales).

Online supplementary data set 2: El Mirón red deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the Cabin (black circles), Trench (red triangles) and Corral (blue crosses) grouped by archaeological time period.

Figure 2: El Mirón red deer $\delta^{13}\text{C}$ from the different layers in the Cabin (black circles), Trench (red triangles) and Corral (blue crosses) stratigraphic sections arranged in a single sequence as established by (Cuenca- Bescós et al. 2012).

Figure 3: El Mirón red deer $\delta^{15}\text{N}$ from the different layers in the Cabin (black circles), Trench (red triangles) and Corral (blue crosses) stratigraphic sections arranged in a single sequence as established by (Cuenca- Bescós et al. 2012).

Figure 4: Box plots of red deer $\delta^{13}\text{C}$ data from Europe divided into time units that are contemporary with the cultural units seen at El Mirón (regardless of the archaeological technologies present at the different sites). (Solutrean 20-17ka ^{14}C BP, Magdalenian 17-12ka ^{14}C BP, Azilian 12-10ka ^{14}C BP, Mesolithic 10-6ka ^{14}C BP, Neolithic 6-4.5ka ^{14}C BP, Chalcolithic 4.5-3.5ka ^{14}C BP, Bronze Age 3.5-2.5ka ^{14}C BP).

Figure 5: Box plots of red deer $\delta^{15}\text{N}$ data from Europe divided into time units that are contemporary with the archaeological units seen at El Mirón (see Figure 4 caption).

Table 1: Radiocarbon chronology at El Mirón for archaeological horizons sampled for this study. Full information on material dated and radiocarbon technique used is given in Straus and González-Morales 2012a,b.

Table 2: Summary statistics by archaeological time period .

Table 3: Cabin excavation: One-way Anova with Post Hoc Bonferroni Correction: for carbon isotopes (white section of table) and nitrogen (grey section of table).

Table 4: Collated sequence (Cabin, Corral and Trench). One-way Anova with Post Hoc Bonferroni Correction: for carbon isotopes (white section of table) and nitrogen (grey section of table).

Online supplementary data file 1: Sample provenance and isotope results.

Online supplementary data file 2: El Mirón red deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the Cabin (black circles), Trench (red triangles) and Corral (blue crosses) grouped by archaeological time period.

Online supplementary data file 3: Published red deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the British Isles, Germany, Southwest France, the French Jura, the Paris Basin, the Western Alps, Italy and Spain.

Figure 1

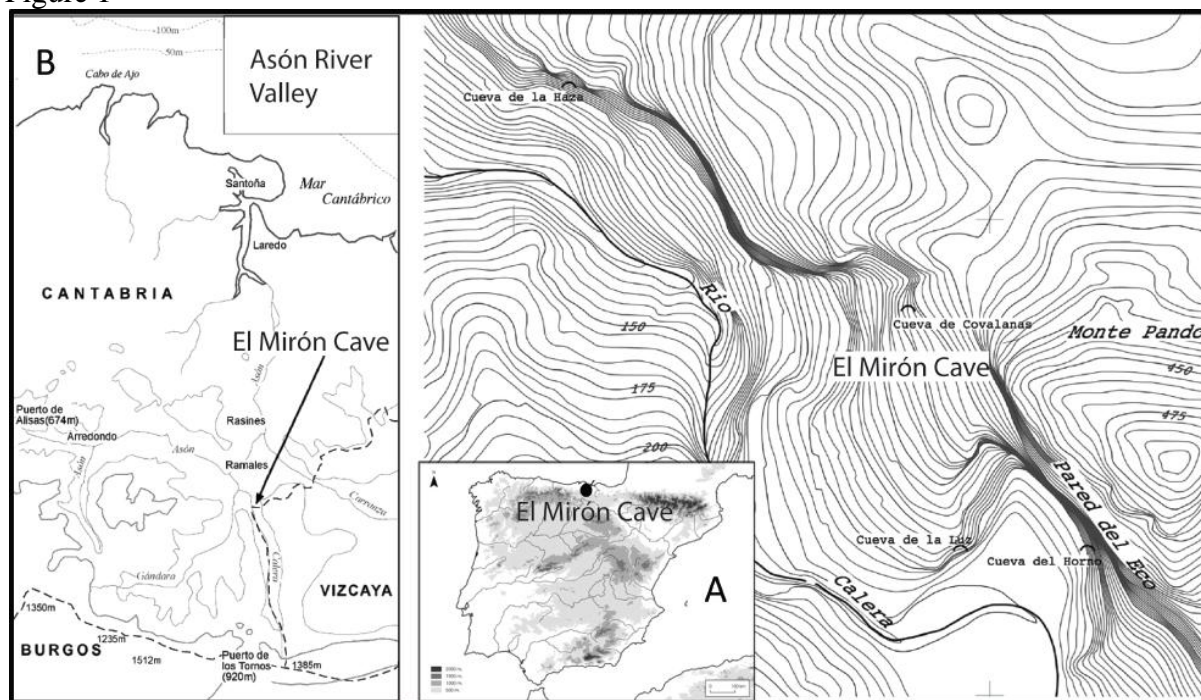


Figure 2

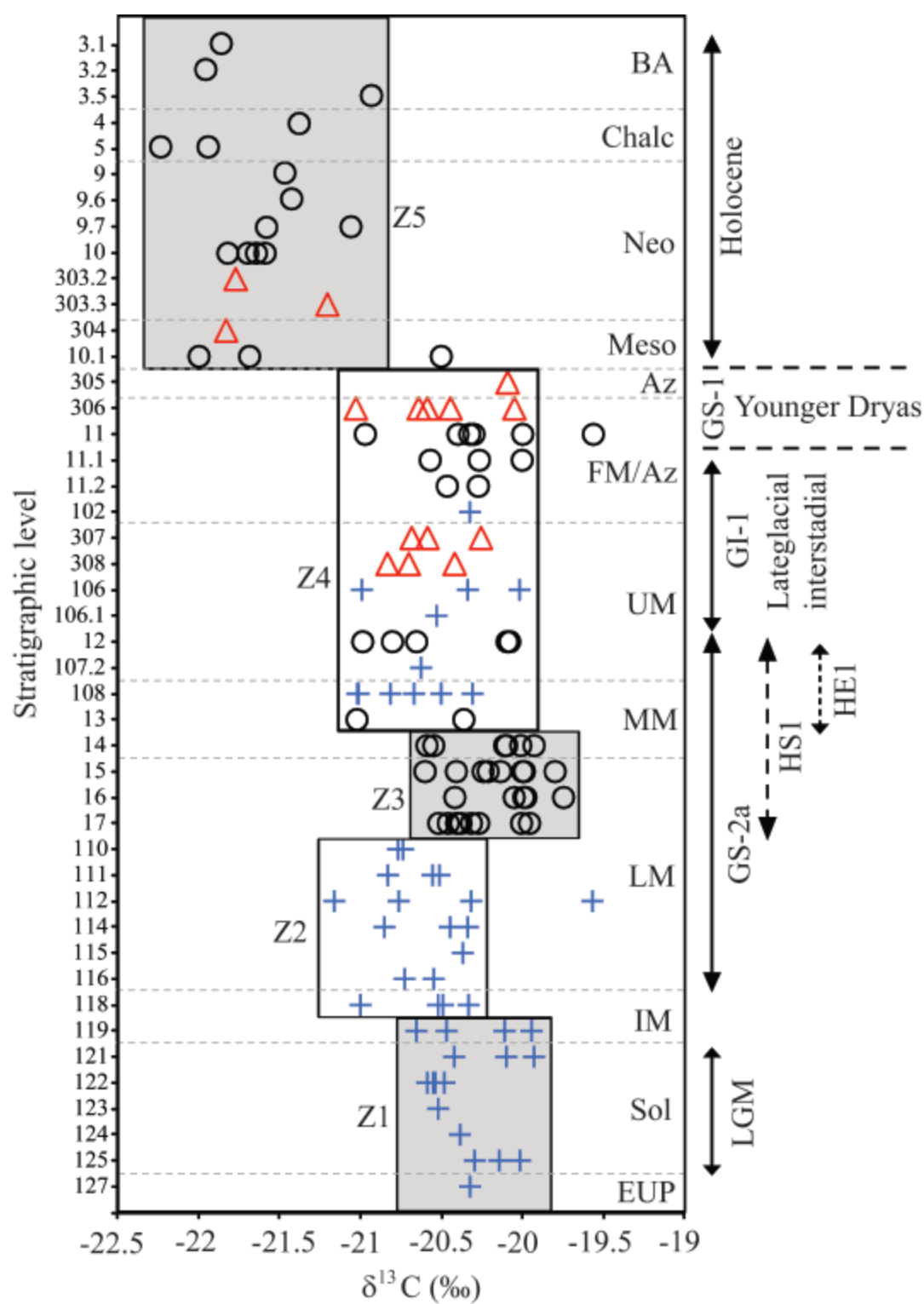


Figure 3

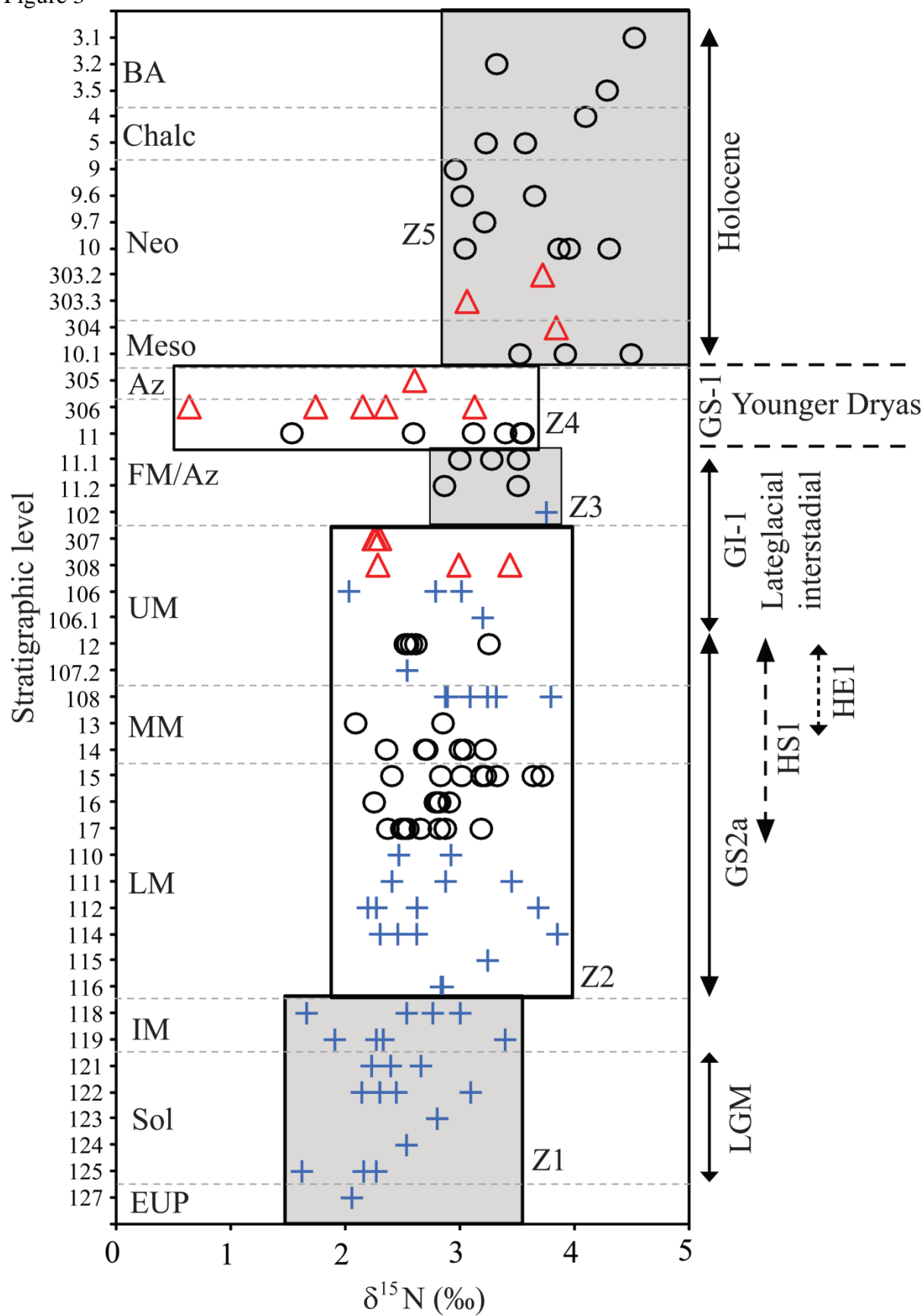


Figure 4

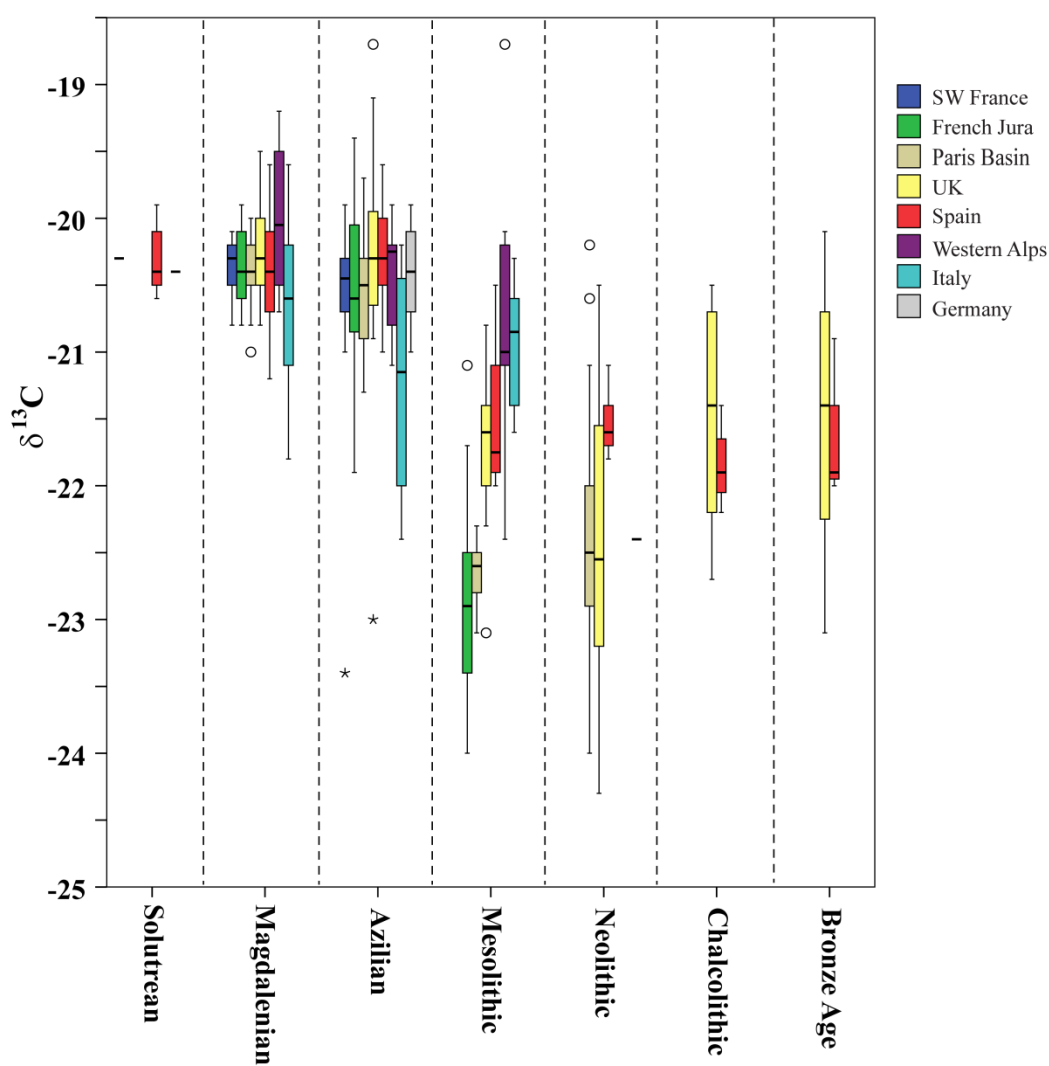


Figure 5

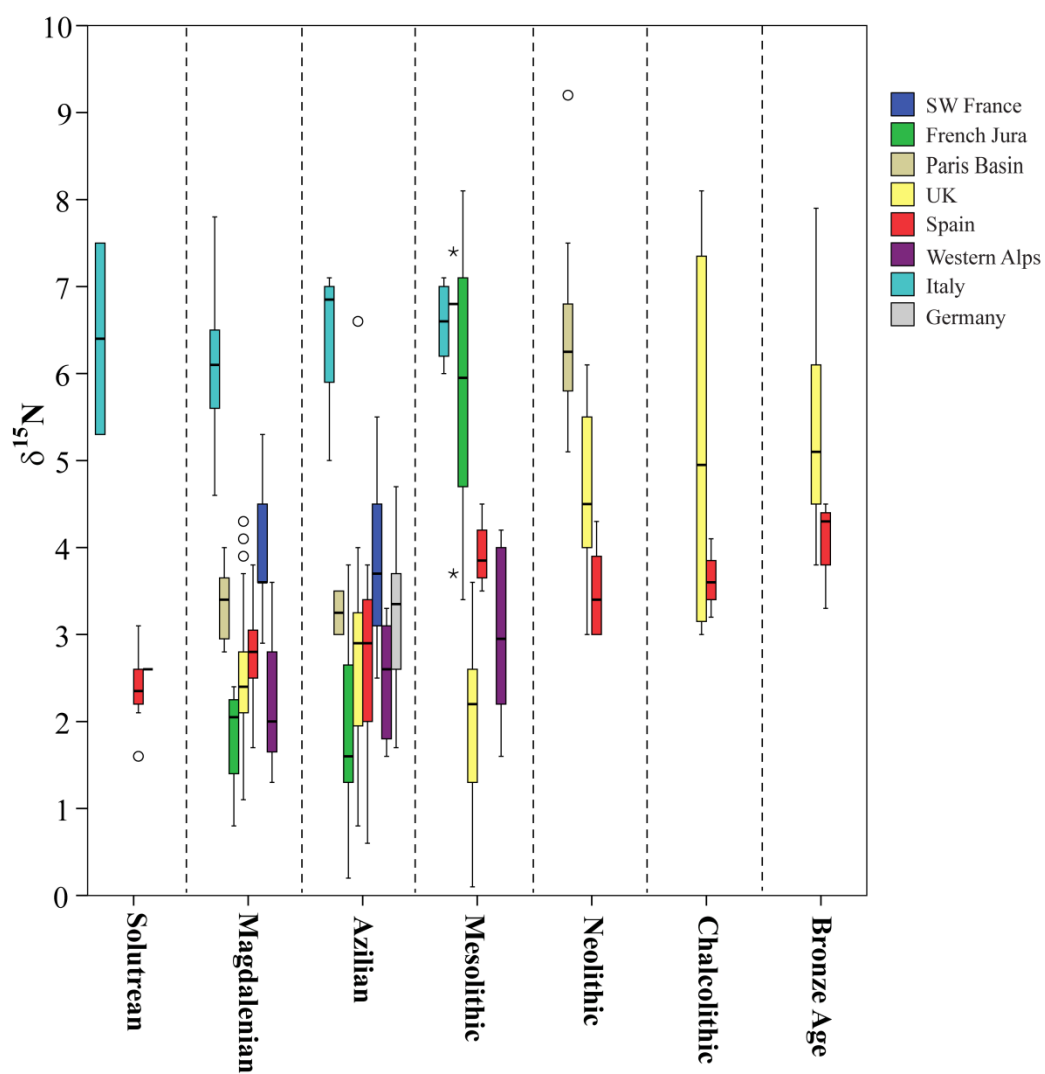


Table 1:

Archaeological period	Cabin	¹⁴ C dates	Trench	¹⁴ C dates	Corral	¹⁴ C dates
Bronze Age	3.1	3700± 40 BP (GX-25851)				
Chalcolithic	5	3820±240 (GX-22127)				
	5.1	4120±50 (GX-22130)				
	7	3740±120 (GX-22460)				
Neolithic	8.1	4680±60 (GX-22131)	302	4910±80 (GX-28211)		
	9	5170±170 (GX-22128)	303	5500±90 (GX-25854)		
		5280±40 (GX-24461)	303.1	5520±70 (GX-25855)		
	9.6	5250±150 (GX-24462)	303.3	5550±40 (GX-30910) 5790±90 (GX-25856)		
	10	5570±50 (GX-23414) 5690±50 (GX-23413)				
Mesolithic	10.1	8380±175 (GX-24463) 8700±40 (GX-25852) 9550±50 (GX-24464)				
Azilian			305	10270±50 (GX-24467)		
Final Magdalenian / Azilian	11	11785±55 (OxA-22087)				
	11.1	11205±55 (OxA-22088) 11720±140 (GX-23391)	306	11650±50 (GX-24468)	102.1	11950±70 (GX-23417)
Upper Magdalenian	12	12970±70 (GX-22132)	308	12350±180 (GX-28210)	105	13490±40 (UG-9286)
Middle Magdalenian	13	14930±70 (OxA-22089)			106	12460±180 GX-32382)
	14	14600±190 (GX-32383)			108	13660±70 (GX-22703) 13710±70 (GX-32381) 14710±160 (GX-23397) 14850±60 (GX-27114)
Lower Magdalenian	15	15010±260 (GX-23392) 15220±300 (GX-23393)	312	15850±170 (GX-31932)	110	14760±70 (OxA-22091) 14795±75 (OxA-22092) 16130±250 (GX-23396)
	16	15180±100 (GX-23415)			111	16370±190 (GX-23395) 15530±230 (GX-24469)
	17	15470±240 (GX-24466)			112	15430±75 (OxA-22090)
		15450±160 (GX-27115)			114	16460±50 (GX-28209)
		15700±190 (GX-25858)			115	13800 ±840 (GX-23394)
		15610±90 (OxA-22093)			116	15220±100 (GX-23416) 17400± 80 (GX-29439)
		15370±80 (GX-32654)				
Initial Magdalenian	18	16080±40 (UGAMS-3366r)	313	17400±270 (GX-31194)	117	17050±60 (GX-25857)
	19	16600±40(UGAMS-3365r)			118	15460±190 (GX-31933)
	21	16050±40(UGAMS-3364r)			119	16960±80 (GX-25857)
Solutrean					119.2	16320±160 (GX-32656)
					121	18390±300 (GX-32655)
					125	18980±360 (GX-24470)
					126	18950±350 (GX-24471)
Early Upper Palaeolithic					127	19230±50 (UG-7216)
					128	27580±210 (GX-27113)

Table 2: Summary statistics by archaeological time period

Archaeological period	n=	Mean d13C	St Dev d13C	Min d13C	Max d13C	Range d13C	Mean d15N	St Dev d15N	Min d15N	Max d15N	Range d15N
Early Upper Palaeolithic	1	-20.3	-	-	-	-	2.1	-	-	-	-
Solutrean	12	-20.3	0.2	-20.6	-19.9	0.7	2.4	0.4	1.6	3.1	1.5
Initial Magdalenian	8	-20.4	0.3	-21.0	-19.9	1.1	2.5	0.6	1.7	3.4	1.7
Lower Magdalenian	38	-20.4	0.3	-21.2	-19.6	1.6	2.8	0.4	2.2	3.8	1.6
Middle Magdalenian	15	-20.5	0.4	-21.0	-19.9	1.1	2.9	0.4	2.1	3.8	1.7
Upper Magdalenian	15	-20.5	0.3	-21.0	-21	0	2.7	0.4	2.0	3.4	1.4
Final Magdalenian / Azilian	17	-20.4	0.4	-21.0	-19.6	1.4	2.8	0.9	0.6	3.8	3.2
Azilian	1	-20.1	-	-	-	-	2.6	-	-	-	-
Mesolithic	4	-21.5	0.7	-22.0	-20.5	1.5	3.9	0.4	3.5	4.5	1
Neolithic	10	-21.5	0.2	-21.8	-21.1	0.7	3.5	0.5	3.0	4.3	1.3
Chalcolithic	3	-21.8	0.4	-22.2	-21.4	0.8	3.6	0.5	3.2	4.1	0.9
Bronze Age	3	-21.6	0.6	-22	-20.9	1.1	4	0.6	3.3	4.5	1.2

Table 3: Cabin excavation: One-way Anova with Post Hoc Bonferroni Correction: for carbon isotopes (white section of table) and nitrogen (grey section of table).

Archaeological Period	N=	Lower Magdalenian	Middle Magdalenian	Upper Magdalenian	Final Magdalenian /Azilian	Mesolithic	Neolithic	Chalcolithic	Bronze Age
Lower Magdalenian	22					$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$
Middle Magdalenian	8					$p = 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$
Upper Magdalenian	5					$p = 0.001$	$p \leq 0.001$	$p = 0.001$	$p = 0.004$
Final Magdalenian /Azilian	11					$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$
Mesolithic	3	$p = 0.008$	$p = 0.006$	$p = 0.011$					
Neolithic	8	$p = 0.053$	$p = 0.053$						
Chalcolithic	3								
Bronze Age	3	$p = 0.004$	$p = 0.003$	$p = 0.006$	$p = 0.062$				

Table 4: Collated sequence (Cabin, Corral and Trench). One-way Anova with Post Hoc Bonferroni Correction: for carbon isotopes (white section of table) and nitrogen (grey section of table). x = excluded due to insufficient samples.

Archaeological Period	N=	Early Upper Palaeolithic	Solutrean	Initial Magdalenian	Lower Magdalenian	Middle Magdalenian	Upper Magdalenian	Final Magdalenian /Azilian	Azilian	Mesolithic	Neolithic	Chalcolithic	Bronze Age
Early Upper Palaeolithic	1		x	x	x	x	x	x	x	x	x	x	X
Solutrean	12	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Initial Magdalenian	8	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Lower Magdalenian	38	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Middle Magdalenian	15	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Upper Magdalenian	15	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Final Magdalenian /Azilian	17	x							x	p≤0.001	p≤0.001	p≤0.001	p≤0.001
Azilian	1	x	x	x	x	x	x	x		x	x	x	x
Mesolithic	4	x	p≤0.001	p≤0.001	p=0.006	p=0.034	p=0.002	p=0.008	x				
Neolithic	10	x	p≤0.001	p=0.006	p=0.044		p=0.012		x				
Chalcolithic	3	x	p=0.015						x				
Bronze Age	3	x	p≤0.001	p=0.001	p=0.010	p=0.040	p=0.003	p=0.012	x				

Highlights

- We measured the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bone collagen of red deer from El Mirón Cave
- Results show changes in local environment during the late Pleistocene and Holocene
- Shifts in deer $\delta^{13}\text{C}$ reflect changes in water availability
- Shifts in deer $\delta^{15}\text{N}$ track regeneration of soil biological activity
- Comparison with European data shows $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ changes differ between regions