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Forest Herding and Tree Foddering in Neolithic Europe: Comparing $\delta^{13}\text{C}$ Values in Caprine Enamel with Archaeobotanical Evidence at Lake Shore Settlements in Switzerland and the French Jura

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Abstract

Forest grazing and tree leaf foddering were once widespread in Europe. Stable carbon isotope analysis of faunal remains can help investigate the practice back to the Neolithic. The approach presupposes the empirical definition of a threshold $\delta^{13}\text{C}$ value beyond which a forest component in diet is arguable. This objective can be attained in contexts where animals feeding on forest trees were demonstrated independently. We analyzed caprine teeth from the sites of Arbon-Bleiche 3 (34th century BCE, Switzerland), where forest fodder was directly evidenced from macroremains in caprine faeces; and from Clairvaux (39th–37th c. BCE) and Chalain (32nd–30th c. BCE; French Jura) where it was suggested from thousands of branches accumulated in the occupation layers. Sequential isotope analysis in caprine tooth enamel revealed $\delta^{13}\text{C}$ values $\leq -14\text{‰}$ at Clairvaux and Chalain, and $\leq -15\text{‰}$ and down to -16.7‰ at Arbon during winter, the lowest recorded to date in Neolithic Europe. A more ^{13}C -depleted signal at Arbon, associated with significantly lower $\delta^{18}\text{O}$ values, may reflect the abrupt cooler and wetter climatic event recorded at this time in the Lake Constance sediments, causing harsher winters and the need for complementary feed in the form of tree leaves, as well as a potential tree-line decline leading to a greater proximity of the fir forest. Inter-individual variability reflects adaptability of extensive herding systems subjected to environmental uncertainties. These results confirm that in these chronocultural contexts, forests were fully integrated into husbandry systems, shaping practices and animal behaviors, and potentially contributing to the reshaping of the landscape.

Keywords Forest · Sheep · Sequential isotope analysis of enamel · Neolithic · Arbon-Bleiche 3 · Chalain · Clairvaux

Extended author information available on the last page of the article

Introduction

The diffusion and development of Neolithic agropastoral societies in Europe took place in predominantly forested landscapes, whose degree of openness varied regionally from dense canopies to mosaics of closed and more open areas (Githumbi *et al.*, 2022; Zanon *et al.*, 2018). These forests, exploited for firewood and construction timber, were also used for agropastoral activities, contributing early on to their opening and reshaping (Innes *et al.*, 2013; Rey *et al.*, 2025; Woodbridge *et al.*, 2018). If the modalities of cultivation on cleared woodland have been discussed (Bogaard, 2002; Pétrequin *et al.*, 2015; Saqalli *et al.*, 2014), how forested landscapes shaped Neolithic animal husbandry has been less explored. Today in Europe, the use of forests for pastoral purposes is mainly confined to traditional herding contexts and mountain areas. Yet, forest grazing and harvesting tree branches to feed cattle, sheep and goats were once very widespread all over Europe, as documented by ethnography and in recent history (Candel-Pérez *et al.*, 2022; Haas *et al.*, 1998; Halstead, 1998; Kotowski *et al.*, 2023; Petit & Watkins, 2003; Pétrequin *et al.*, 2015; Rasmussen, 1990; Varga *et al.*, 2020), long supporting the hypothesis of their existence in the Neolithic (Troels-Smith, 1960). Archaeology has provided indubitable evidence for it, in the form of remains of tree branches, twigs and leaves found in exceptionally well-preserved Neolithic stalling contexts, in dung layers and sometimes directly in animal faeces, attesting their use as litter and fodder (Rasmussen, 1989, 1990, 1993; Akeret & Jacomet, 1997, 1999; Delhon *et al.*, 2008; Kühn *et al.*, 2013; Jakobitsch *et al.*, 2023).

Forest grazing and gathering tree branches for fodder have been assessed in terms of their impact on forest cover (Hejzman *et al.*, 2014; Parker *et al.*, 2002; Rasmussen, 1989, 1990; Troels-Smith, 1960) and from the perspective of the method used to produce leafy fodder through tree taming (coppicing and pollarding; Candel-Pérez *et al.*, 2022; Dufraisse *et al.*, 2022; Rasmussen, 1989; Thiébault, 2006). At the other end of this technical system is the use of forest resources in husbandry to feed the flocks. The choice of tree species and the providing of fresh or dry leaves, in relation to their nutritional quality for different uses (to enhance milk yields in spring and summer, or as winter staple food), the quantity needed, the labor requirements for cutting, transportation and storing branches after drying, have been described by ethnoarchaeology, although in a limited number of socioeconomic and environmental contexts (Halstead, 1998; Hejzman *et al.*, 2014). Approaching the practice as part of the husbandry system in archaeological contexts necessitates determining what animals were given access to this resource and when in the year, in relation to the pastoral calendar. This aim can be achieved by turning to animal remains, including bones, teeth and faeces. The latter, when preserved, can provide direct proofs that tree leaves and twigs were consumed, while allowing direct association between the plant species and the animal who ate them (Rasmussen, 1993; Akeret & Jacomet, 1997, Akeret *et al.*, 1999; Kühn & Hadorn, 2004; Kühn *et al.*, 2013; Jakobitsch *et al.*, 2023), with the limitation that determining what animal produced the faeces can sometimes be challenging (Akeret *et al.*, 1999; Haas, 2004; Kühn & Hadorn, 2004).

Feeding on forest resources can also be detected from stable carbon isotope ratios ($\delta^{13}\text{C}$) in bones and teeth. The approach is not restricted to exceptionally well-preserved contexts and therefore allows investigations on a larger scale. Plants grown under dense forest canopy have lower $\delta^{13}\text{C}$ values compared to plants grown in open areas, a difference inherited in herbivores feeding on them (Bonafini *et al.*, 2013; Drucker *et al.*, 2008; van der Merwe & Medina, 1991). This principle has been used to assess consumption of forest resources by domestic livestock from $\delta^{13}\text{C}$ values measured in bone collagen (Bickle *et al.*, 2013; Fraser *et al.*, 2013; Gerling *et al.*, 2017; Gillis & Zanon, 2021) or tooth enamel (Balasse *et al.*, 2012; Berthon *et al.*, 2018; Blanz *et al.*, 2023; Fabre *et al.*, 2021, 2023; Gillis *et al.*, 2021, 2024; Tornero *et al.*, 2020). Grazing in wetlands, including riverbanks and freshwater marshes, has been proposed as an alternative explanation for lower $\delta^{13}\text{C}$ values in herbivores (Lynch *et al.*, 2008). However, field studies report diverging results on the effect of humid to waterlogged conditions on plant $\delta^{13}\text{C}$ values: foliar $\delta^{13}\text{C}$ values in willow are lower ($\sim 2\%$) in riverbanks compared to dry lands, but increase again in waterlogged conditions (in Northeastern Siberia; Fan *et al.*, 2018); at the level of plant communities, no difference was observed in $\delta^{13}\text{C}$ values between wetland and grassland vegetation in northern Greece (including grass, shrubs and trees; Vidas-Cardador *et al.*, 2025). Compound specific nitrogen isotope analysis of amino acids, which provides an alternative and complementary way of detecting consumption of woody material (versus herbaceous plants), independently of the canopy effect or hydrological conditions (Kendall *et al.*, 2019), could significantly contribute to the debate. For the moment this method has been applied much less frequently (Gillis *et al.*, 2024; Kendall *et al.*, 2020).

Investigating consumption of forest resources from bone and teeth $\delta^{13}\text{C}$ values presupposes to define a threshold beyond which a forest component in diet is arguable. In modern plants, $\delta^{13}\text{C}$ values $< -31.5\%$ refer to the understory of closed-canopy forests (Kohn, 2010). This value would translate to around -30% in pre-industrial times (when corrected for the fossil fuel effect; Freyer & Belacy, 1983), to -25% in bone collagen (applying a diet-collagen 5‰ spacing; Ambrose & Norr, 1993) and to -16.3% in enamel (applying a diet-enamel bioapatite 14.1‰ isotope enrichment in large herbivores; Cerling & Harris, 1999). These threshold values are conservative. For comparison, bone collagen $\delta^{13}\text{C}$ values measured in modern deer from dense deciduous Dourdan (France) and Białowieża (Poland) forests are on average -23.7% and rarely exceed -22.5% (corrected for the fossil fuel effect; Drucker *et al.*, 2008). Threshold $\delta^{13}\text{C}$ values varying between -23% and -22.7% in bone collagen or from -14.5% to -13.7% in enamel have also been used, with reference to large wild herbivores with a predominantly forest habitat; Mesolithic aurochs from Scandinavian forests (after Noe-Nygaard *et al.*, 2005), and aurochs and red deer from Neolithic contexts, presumed forest dwellers (Balasse *et al.*, 2012; Doppler *et al.*, 2017; Fraser *et al.*, 2013; Gerling *et al.*, 2017; Gillis & Zanon, 2021; Gillis *et al.*, 2024), respectively. Large herbivores (including bovids) dwelling in dense canopy evergreen forests in Eastern and Central Africa yielded enamel $\delta^{13}\text{C}$ values $\leq -14\%$ and mostly between -16% and -14% (Cerling *et al.*, 2015). However, the canopy effect on plant $\delta^{13}\text{C}$ values can differ according to the forest physiognomy—tree community and dominant species, height and degree

of opening—and its intensity at forest edges is also variable (Bonafini *et al.*, 2013; Crowley *et al.*, 2012; Kapos *et al.*, 1993).

In the present study, we contribute to defining the $\delta^{13}\text{C}$ values expected for animals feeding on forest tree leaves, by measuring them in the teeth of herbivores from archaeological contexts where tree leaf consumption was demonstrated from archaeobotanical evidence. The studied sites are Neolithic lake shore settlements in Switzerland and the French Jura, where exceptional preservation in waterlogged conditions has enabled very detailed reconstructions of the environmental setting through interdisciplinary studies. At Arbon-Bleiche 3 (Lake Constance, Switzerland, 4th millennium BCE), feeding on forest trees and shrubs was directly demonstrated from plant macroremains in caprine faeces (Akeret *et al.*, 1999; Kühn & Hadorn, 2004). At Clairvaux XIV and Chalain 19 (Jura lakes, France, 4th millennium BCE), it was strongly suggested from archaeobotanical findings consisting of thousands of twigs and small branches from tree species known for their possible use as fodder (Pétrequin & Pétrequin, 2015). Animal teeth offer the possibility to access the seasonal scale of woodland foddering through combined sequential analysis of carbon and oxygen isotope ratios. It allows to better characterize feeding on forest resources over the pastoral calendar and also increases chances to detect seasonal consumption, which could be less heavily printed in bone collagen where the dietary signal is averaged over multiple yearly cycles. Our objectives are to contribute to the definition of reference $\delta^{13}\text{C}$ values for enamel of domestic animals feeding on forest resources; to document the practice at the studied sites on a seasonal scale, and to test the hypothesis of different feeding behaviors between sheep and goats.

Studied Sites

Arbon-Bleiche 3

Arbon-Bleiche 3 is located on the shore of Lake Constance in northeastern Switzerland (Fig. 1) at an altitude of 397 m. Archaeological layers delivered a single phase of occupation dated to 3384–3370 BCE by dendrochronology, a period corresponding to the transition between the Pfyn and Horgen cultures (Leuzinger, 2000, 2012). The village was abandoned after being destroyed by fire, and soon after covered by a sudden rise in the lake level (Magny *et al.*, 2006), causing very good preservation of organic remains. The combined results of the palynological, carpological, and anthracological studies (Brombacher & Hadorn, 2004; Dufraisse & Leuzinger, 2009; Hosch & Jacomet, 2004) suggest that at the time when the village was occupied, the direct vicinity of the site was a mosaic of open cultivated fields, bushes and groves mixed with areas of light and denser forest. On the lake shores stretched a riparian forest with alder (*Alnus* sp.), willow (*Salix* sp.), and poplar (*Populus* sp.), a little further away developed a mixed ash forest (*Fraxinus excelsior*) and at a further distance a dense mixed oak forest, mixed with beech (*Fagus sylvatica*) and fir (*Abies alba*). These forests, largely exploited for edible plants, firewood and construction timber, were also frequented for hunting. Wild animals are well represented in the faunal assemblage (39% of determined remains), largely dominated by red deer

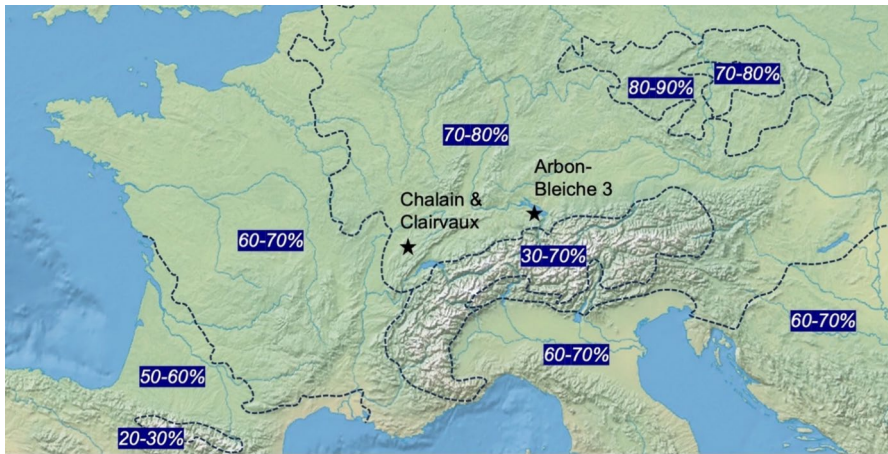


Fig. 1 Location of the sites, and forest cover at 3000 BCE (after Zanon *et al.*, 2018). Map by Flappiefh, CC BY-SA 4.0 <https://creativecommons.org/licenses/by-sa/4.0>, via Wikimedia Commons

(*Cervus elaphus*, 25%). Caprines, including sheep (*Ovis aries*) and goats (*Capra hircus*), came in the third position (8%) in the domestic stock, after pigs (*Sus domesticus*, 31%) and cattle (*Bos taurus*, 21%; Deschler-Erb & Marti-Grädel, 2004).

Cattle and caprine faeces were recovered at Arbon-Bleiche 3. Their botanical contents, characterized by low frequency of seeds or fruits and low concentrations of pollen, refer to winter diet (late autumn to early spring; Akeret *et al.*, 1999; Haas, 2004; Kühn & Hadorn, 2004). High frequency and proportion of tree and shrubs macroremains in cattle dung attest to the importance of forest resources in their diet (*Abies alba*, *Viscum album*, *Hedera helix*, *Rosa/Rubus*, *Quercus*, and *Alnus* being the most frequently represented in this order; Kühn & Hadorn, 2004). Different patterns of mobility were described for cattle from strontium isotope analysis in teeth. Among those, cattle which had stayed in the vicinity of the site all year round delivered bone collagen $\delta^{13}\text{C}$ values averaging $-23.8 \pm 0.7\text{‰}$ (from -24.7‰ to -22.8‰ , $N=6$), compared to $-24.4 \pm 0.6\text{‰}$ in red deer ($N=6$; Gerling *et al.*, 2017), suggesting feeding in closed forests for the former as for the latter.

Several hundreds of sheep and goat faecal pellets recovered at the site were also analyzed for botanical contents (Akeret *et al.*, 1999; Haas, 2004; Kühn & Hadorn, 2004). Among the few plant macrofossils, the most frequent finds were prickles of Rosaceae (*Rosa* sp./*Rubus* sp.), *Abies alba* leaves, *Rubus* fruits (blackberries), and *Corylus avellana* anthers. Moreover, *Rubus* fruits and *Abies* leaves never occurred in the same pellets. *Rubus* fruits were grouped with Rosaceae prickles, while *Abies* leaves were grouped with *Corylus* anthers. The *Abies* leaves and *Corylus* anthers pellets also contained significant amounts of *Corylus* and *Alnus* pollen. From these findings the authors hypothesized that during winter, caprines pastured in the forests and forest edges where they could feed on blackberries, whose leaves remain green in the cold season and which could still bear dried-up fruits. They could have been additionally fed *Abies*, *Corylus*, and *Alnus* twigs when food was scarce, for instance on snowy days. It is not possible to distinguish sheep and goats' droppings

from their morphology (Akeret *et al.*, 1999; Jakobitsch *et al.*, 2023). However, given goats' taste for blackberries, whereas sheep would avoid the prickles; and given sheep's appetite for fir leaves, we hypothesize that the two faeces types could alternatively refer to sheep and goats with different food preferences, and that this could be reflected in different $\delta^{13}\text{C}$ values, with fir coming from the dense mixed oak forest having lower $\delta^{13}\text{C}$ values than blackberries which could be found in more open areas.

Clairvaux XIV and Chalain 19

The lakes of Clairvaux and Chalain are located in the Ain valley on the lowest plateau of the Jura mountains at an altitude of 500 m (Fig. 1). Neolithic groups from different chronocultural complexes settled successively on the lake sides from the beginning of the 4th millennium to around 2500 BC. Small villages were built in the wetlands. Houses intermittently occupied for short periods of time (a decade) were constructed on permanently submerged ground, in shallow water at low water level (Pétrequin & Pétrequin, 2021). The humid conditions have helped to preserve layers of organic remains in excellent condition. Communities from the so-called Burgundy Middle Neolithic (La Motte-aux-Magnins Group) occupied the shores of Lake Clairvaux from the 39th to the 37th c. BCE (Vielle & Pétrequin, 2015). The village of Clairvaux XIV belongs to this phase. It was occupied over six successive phases of 8–10 years (Pétrequin & Pétrequin, 2015). Chalain 19 was occupied in the Late Neolithic from the 32nd to the 30th c. BCE (Vielle, 2009) by communities from the Horgen culture and then the Early Clairvaux culture, deriving from the mixing of local populations with migrants from the Ferrières culture.

The Middle Neolithic communities settled in a predominantly oak forested environment, which had already been very locally reduced by previous farming activities on a very local scale. The transformation of the forest increased over the 4th millennium BCE with the development of forest-edge zones and intermediate types of vegetation (Dufraisse, 2005; Dufraisse *et al.*, 2015; Schaal & Pétrequin, 2015), possibly accentuated by itinerant agriculture requiring repeated forest clearance (Pétrequin, 2005; Pétrequin *et al.*, 2015). By the time of Clairvaux XIV, the vegetation had already undergone a degree of transformation comparable to that of the Lake Chalain basin in the 32nd c. BCE (Dufraisse *et al.*, 2015). The willow and poplar riparian woodland was not very developed. The lower Jura plateau was covered by a mixed ash forest with oak, maple (*Acer* sp.), Maloideae, and hazel; the upper plateau bore a mixed beech and oak forest with fir, elm (*Ulmus montana*), spruce (*Picea Abies*), and holly (*Ilex aquifolium*). At Chalain 19, the beech located on the first plateau was predominantly exploited before giving way to more heliophilous species (hazel, birch (*Betula* sp.), willow) and ash (Dufraisse, 2005).

Hunting played a key role at Clairvaux XIV and Chalain 19 (H–K layers). Large ungulates—mainly red deer, followed by roe deer and wild boar—are represented close to equilibrium with domestic animals at Clairvaux XIV, while they largely predominate at Chalain 19 (74% of determined remains), showing a lesser and more fluctuating importance of husbandry in the food economy at both sites. At Clairvaux

XIV, the domestic flocks were largely dominated by pigs, followed by caprines (2 to 17% of remains, mostly sheep) exploited for a mixed production of meat and milk, while cattle contributed only to a limited extent as a source of meat (Arbogast, 2015). At Chalain 19, pigs and bovines share the first place, while caprine husbandry (with sheep and goats equally represented) was more marginal (5% of remains) and oriented towards meat production (Arbogast, unpublished).

The thick preserved organic layers at Clairvaux XIV and Chalain 19 contained an important volume of twigs and small branches. Their botanical determination at Clairvaux XIV showed a selection of species edible by livestock. Leafy branches may have been collected and used as winter fodder. As no livestock pens or trampling marks, in permanently submerged soils with no mechanical resistance, were found during the excavations, the flock may have been provided fodder outside the village. As a secondary use, the remaining branches were brought to the village and strewn over the ground to cleanse and stabilize the soaked soil (Pétrequin & Pétrequin, 2015; Pétrequin *et al.*, 1998). Stable isotope analysis on bone collagen of wild and domestic ungulates at Chalain 3, Chalain 4 and Chalain 19 (31st c. BCE) showed $\delta^{13}\text{C}$ values averaging $-24.0 \pm 0.4\text{‰}$ for aurochs ($N=5$) and $-23.5 \pm 0.5\text{‰}$ for red deer ($N=14$; Drucker & Bocherens, 2009), attesting of a dense forest component in the landscape. Suids seem to have been mostly kept in open areas (Cucchi *et al.*, 2023), as well as cattle except for two of them with lower $\delta^{13}\text{C}$ values (-23.5‰ ; Drucker & Bocherens, 2009). Caprines were not included in these previous studies.

Material and Methods

The study material is composed of the lower second molars (M2) of 17 caprines from Arbon-Bleiche 3 (including 12 sheep and five goats), six sheep from Clairvaux XIV (from phases 3, 5 and 6) and five sheep from Chalain 19 (all from layer HK; Online resource 1). All teeth were extracted from dental rows, except for one isolated tooth (CLA Ovis3 M2). The sheep/goat distinction was made from tooth morphological criteria (Balasse & Ambrose, 2005; Gillis *et al.*, 2011; Halstead *et al.*, 2002; Helmer, 2000; Payne, 1985). In one instance it had to be confirmed by ZooMS (Online resource 2A).

The seasonal cycle is traced from the stable oxygen isotope ratios ($\delta^{18}\text{O}$) in the carbonates of enamel mineral fraction (bioapatite). Oxygen in bioapatite derives from body water, whose $\delta^{18}\text{O}$ value, determined by oxygen input (mainly drinking and plant water) and output fluxes, results from a combination of environmental factors, animal behavior and physiology (Chen *et al.*, 2017; Longinelli, 1984). A linear correlation was found between $\delta^{18}\text{O}$ values in animal skeleton and $\delta^{18}\text{O}$ values in local annual precipitation (Land *et al.*, 1980; D'Angela & Longinelli, 1990). The latter vary seasonally, mostly with air temperature in continental Europe, leading to higher $\delta^{18}\text{O}$ values during summer and lower during winter (Rozanski *et al.*, 1993). Data from the Global Network of Isotopes in Precipitations confirm this scheme at Thonon-les-Bains (the closest station to Clairvaux and Chalain with precipitation $\delta^{18}\text{O}$ record, located 60 km further east on the meridional shore of Lake Lemman, altitude 385 m) and at Constance on the southwestern shore of Lake Constance

(IAEA/WMO, 2025). The resulting cyclical variations are recorded in enamel oxygen isotope ratios during mineralization and can be reconstructed using sequential sampling in enamel (Bryant *et al.*, 1996; Fricke & O'Neil, 1996). The $\delta^{13}\text{C}$ values in bioapatite are linked to that of the plants eaten (Krueger & Sullivan, 1984). The combined measurement of stable carbon and oxygen isotope ratios in enamel carbonates therefore allows to investigate diet on a seasonal scale (Balasse *et al.*, 2002).

Enamel was sampled on the vestibular side of the posterior lobe after removal of the cementum layer and cleaning of the enamel outer surface by gentle drilling. Enamel was sampled as a series of bands perpendicular to the tooth growth axis (Fig. 2). Each sample is located in the tooth crown using its distance from the enamel-root junction (erj). Enamel powders were pre-treated to eliminate diagenetic

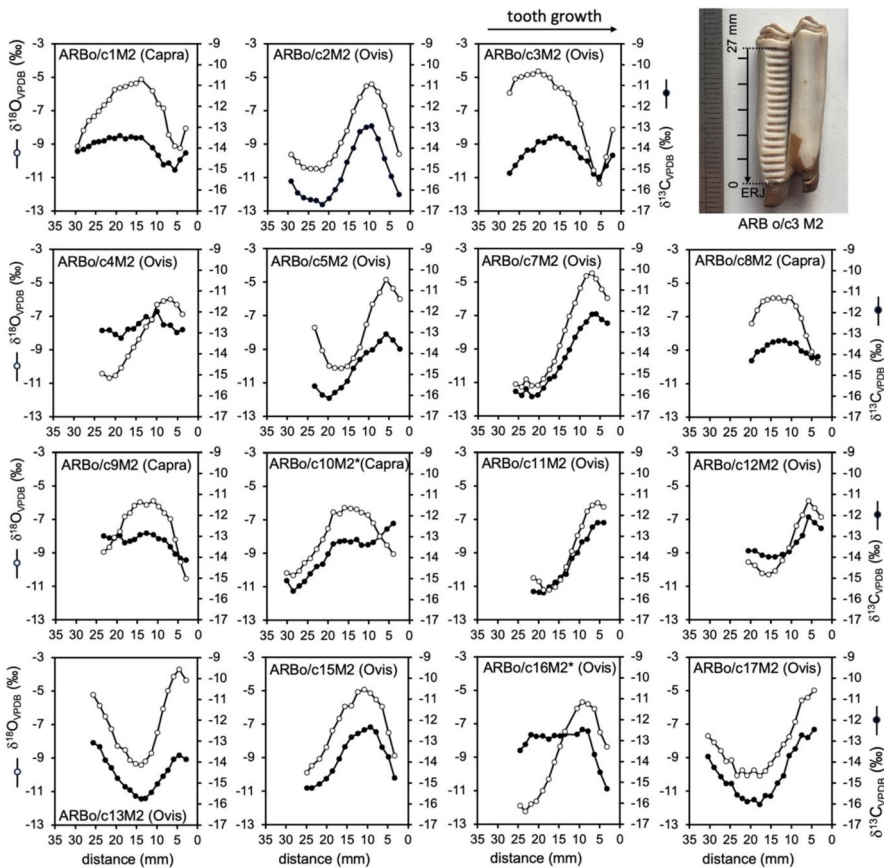


Fig. 2 Results from the sequential analysis of the stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope ratios in sheep (*Ovis*) and goat (*Capra*) lower second molars (M2) from Arbon-Bleiche 3 (ARB); picture of a tooth showing sequential sampling of enamel (scale in mm). The arrow shows the direction of tooth growth. Teeth marked with (*) show a rupture in the co-variation of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences. The results from ARB o/c6 and ARB o/c14, paired with ARB o/c2 and ARB o/c8 respectively, are shown in Online resource 4B

carbonates (0.1 M acetic acid for 4 h at room temperature, 0.1 ml/mg), rinsed using distilled water and freeze-dried. Pre-treated enamel samples weighing ~600 µg were reacted with 100% phosphoric acid at 70 °C in individual vessels in an automated cryogenic distillation system (Kiel IV device), interfaced with a Delta V-Advantage isotope ratio mass spectrometer at the SSMIM IRMS service (MNHN, Paris), except for six teeth from Arbon-Bleiche 3 (ARB o/c5, o/c9, o/c11, o/c15, o/c16 and o/c17) which were analyzed on the same analytical equipment at the ISTEP IRMS service (Sorbonne Université, Paris). The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (V-PDB scale) were normalized to the international IAEA NBS-18 ($\delta^{18}\text{O} = -23.01\text{‰}$; $\delta^{13}\text{C} = -5.01\text{‰}$) and NBS-19 ($\delta^{18}\text{O} = -2.20\text{‰}$; $\delta^{13}\text{C} = 1.95\text{‰}$) standards. The analytical precision, estimated from the analysis of 4 to 8 Marbre LM (our in-house standard) in each analytical session, was always $\leq 0.12\text{‰}$ for $\delta^{13}\text{C}$ values and $\leq 0.11\text{‰}$ for $\delta^{18}\text{O}$ values. In order to check the repeatability of the measurements between the two laboratories, 15 enamel powders from ARB o/c2 M2 were divided in two subsamples and analyzed in each laboratory.

Results

The results are shown extensively in Online resource 3A and in Figs. 2 and 3 and summarized in Table 1 and in Online resource 3B. Results from the test of repeatability between the two laboratories are shown in Online resources 4A&B. The mean difference (ISTEP-SSMIM) between measurements over a sequence of 15 samples is $0.08 \pm 0.17\text{‰}$ for $\delta^{13}\text{C}$ values and $-0.08 \pm 0.09\text{‰}$ for $\delta^{18}\text{O}$ values, and the trends of intra-tooth variation are almost identical. From tooth morphology and from the stable isotope sequences, six teeth could be paired (ARB o/c2 and ARB o/c6; ARB o/c8 and ARB o/c14; CLA Ovis1 and CLA Ovis2). To avoid redundancy, the results from the analysis of ARB o/c6, ARB o/c14 and CLA Ovis2 are not shown in the figures of the main text and were not included in inter-individual and inter-sites comparisons. However, they are given in Online resource 3A. A comparison of the results obtained in paired left and right molars shows identical $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ intra-tooth sequences (Online resource 5).

In all teeth, the variation of $\delta^{18}\text{O}$ values follows a sinusoidal pattern, reflecting the seasonal cycle (Figs. 2 and 3). Both winter (lowest) and summer (highest) $\delta^{18}\text{O}$ values are lower at Arbon compared to Clairvaux and Chalain, resulting in lower annual values at Arbon: the middle values of the intra-tooth sequences ($[\text{min} + \text{max}]/2$) averages $-7.9 \pm 0.6\text{‰}$ at Arbon, compared to $-6.2 \pm 0.4\text{‰}$ at Clairvaux and $-5.7 \pm 0.4\text{‰}$ at Chalain (Online resource 3B and Fig. 4). In most teeth, the $\delta^{13}\text{C}$ values covary in phase with the $\delta^{18}\text{O}$ values: the lowest $\delta^{13}\text{C}$ values were recorded during winter, and the highest during summer (Figs. 2 and 3). Intra-tooth variation in $\delta^{13}\text{C}$ values diverges from this general pattern in four instances, for part of the year (in ARB o/c10 and ARB o/c16) or the entire year (in CLA Ovis7 and CHA Ovis5). The lowest/winter $\delta^{13}\text{C}$ values reach -16.7‰ to -13.3‰ at Arbon, -14.6‰ to -13.4‰ at Clairvaux, and -15‰ to -12.7‰ at Chalain, while the highest/summer $\delta^{13}\text{C}$ values vary from -13.4‰ to -12‰ at Arbon and -13.2‰ to -11.7‰ at Clairvaux and Chalain (Online resource 3B and Fig. 4).

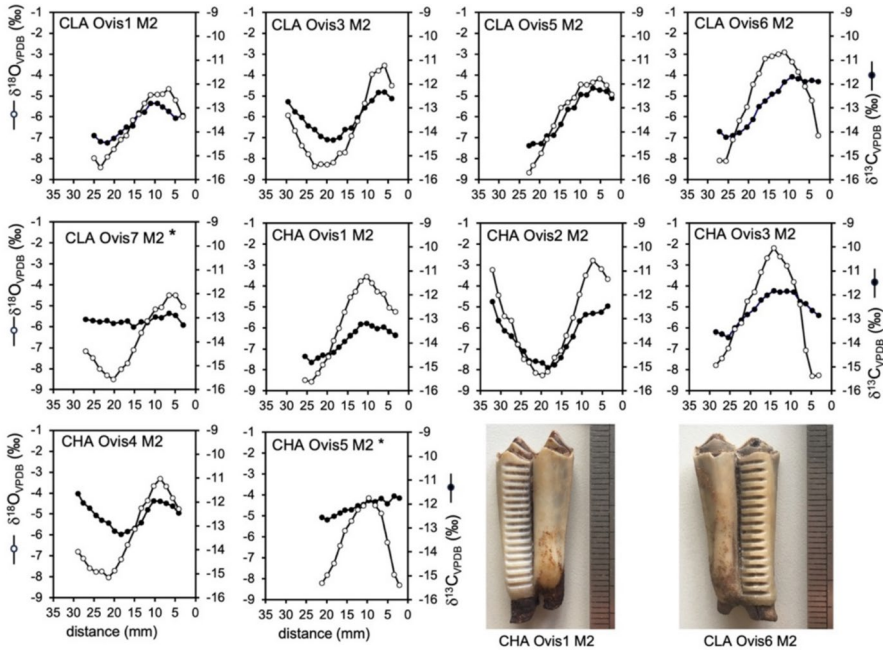


Fig. 3 Results from the sequential analysis of the stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope ratios in sheep lower second molars (M2) from Clairvaux XIV (CLA) and Chalais 19 (CHA); pictures of a tooth from each site showing sequential sampling of enamel (scale in mm). Teeth marked by (*) do not show a co-variation of the $\delta^{18}\text{O}$ and ($\delta^{13}\text{C}$) sequences. The results from CLA Ovis2, paired with CLA Ovis1, are shown in Online resource 4B

Discussion

Repeatability of the Analytical Protocol

Investigating the repeatability of results between paired left and right molars allows to assess the preservation of the isotopic signal as well as the repeatability of the analytical protocol. The very good matching between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences measured in paired teeth demonstrate the good preservation of the original signal in all tested teeth, and shows that the successive steps of the analytical protocol—enamel sampling; measurement of the distances to locate samples in tooth crown; IRMS analysis—did not induce significant biases; and that the effect of the pretreatment on the integrity of bioapatite $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values, demonstrated elsewhere (Koch *et al.*, 1997; Balasse *et al.*, 2012; Pellegrini & Snoeck, 2016; Varkulevičiūtė *et al.*, 2025) was, in this case, systematic. Finally, the excellent repeatability between the two laboratories allows us to merge both datasets.

Table 1 Results from the sequential analysis of the stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope ratios in the caprine teeth from Arbon Bleiche-3 (ARB), Clairvaux XIV (CLA), and Chalain 19 (CHA)

Tooth	Species	$\delta^{18}\text{O}$ (‰)		$\delta^{13}\text{C}$ (‰)		Estimated Collagen $\delta^{13}\text{C}$ (‰)
		Min	Max	Min	Max	
ARB o/c1 M2	Goat	-9.2	-5.1	-15.0	-13.4	-22.8
ARB o/c2 M2*	Sheep	-10.5	-5.4	-16.7	-12.9	-23.4
ARB o/c3 M2	Sheep	-11.4	-4.7	-15.4	-13.4	-23.0
ARB o/c4 M2	Sheep	-10.7	-6.0	-13.3	-12.0	-21.2
ARB o/c5 M2	Sheep	-10.1	-4.9	-16.1	-13.1	-23.2
ARB o/c6 M2*	Sheep	-10.6	-5.3	-16.7	-13.1	-23.5
ARB o/c7 M2	Sheep	-11.3	-4.5	-16.1	-12.1	-22.7
ARB o/c8 M2**	Goat	-9.8	-5.9	-14.3	-13.3	-22.4
ARB o/c9 M2	Goat	-10.5	-5.9	-14.1	-12.9	-22.1
ARB o/c10 M2	Goat	-10.3	-6.3	-15.6	-12.4	-22.6
ARB o/c11 M2	Sheep	-11.2	-6.0	-15.7	-12.3	-22.6
ARB o/c12 M2	Sheep	-10.3	-5.9	-14.0	-12.1	-21.6
ARB o/c13 M2	Sheep	-9.4	-3.7	-15.8	-13.1	-23.0
ARB o/c14 M2**	Goat	-10.1	-5.8	-14.4	-13.3	-22.5
ARB o/c15 M2	Sheep	-9.9	-4.9	-15.2	-12.3	-22.4
ARB o/c16 M2	Sheep	-12.2	-5.7	-15.3	-12.5	-22.5
ARB o/c17 M2	Sheep	-10.1	-5.0	-16.0	-12.5	-22.8
CLA Ovis1 M2***	Sheep	-8.4	-4.7	-14.5	-12.8	-22.2
CLA Ovis2 M2***	Sheep	-8.6	-4.7	-14.7	-12.9	-22.4
CLA Ovis3 M2	Sheep	-8.4	-3.5	-14.3	-12.3	-21.9
CLA Ovis5 M2	Sheep	-8.7	-4.2	-14.6	-12.2	-22.0
CLA Ovis6 M2	Sheep	-8.1	-2.9	-14.2	-11.7	-21.6
CLA Ovis7 M2	Sheep	-8.5	-4.5	-13.4	-12.8	-21.7
CHA Ovis1 M2	Sheep	-8.6	-3.6	-14.8	-13.2	-22.6
CHA Ovis2 M2	Sheep	-8.3	-2.8	-15.0	-12.3	-22.3
CHA Ovis3 M2	Sheep	-8.3	-2.2	-13.8	-11.8	-21.4
CHA Ovis4 M2	Sheep	-8.0	-3.3	-13.3	-11.7	-21.1
CHA Ovis5 M2	Sheep	-8.3	-4.1	-12.7	-11.7	-20.8

Max maximum value in the intra-tooth sequence, *min* minimum value in the intra-tooth sequence. The collagen $\delta^{13}\text{C}$ value was estimated from the middle value in the tooth sequence (see Methods). (*), (**), and (***) are respectively paired teeth

How Is Forest Feeding Reflected in Enamel $\delta^{13}\text{C}$ Values?

The $\delta^{13}\text{C}$ values measured at Arbon, Clairvaux and Chalain are compared to those previously published for caprines (mostly sheep) in Neolithic continental Europe (Online resource 6). Figure 5 shows the annual minimum/winter values retrieved from intra-tooth sequences. Arbon delivered the lowest values of the dataset, with four caprines yielding $\delta^{13}\text{C}$ enamel values $\leq -16\text{‰}$ previously unreached in Europe, and 11 caprines with $\delta^{13}\text{C}$ values $\leq -15\text{‰}$ previously reached only

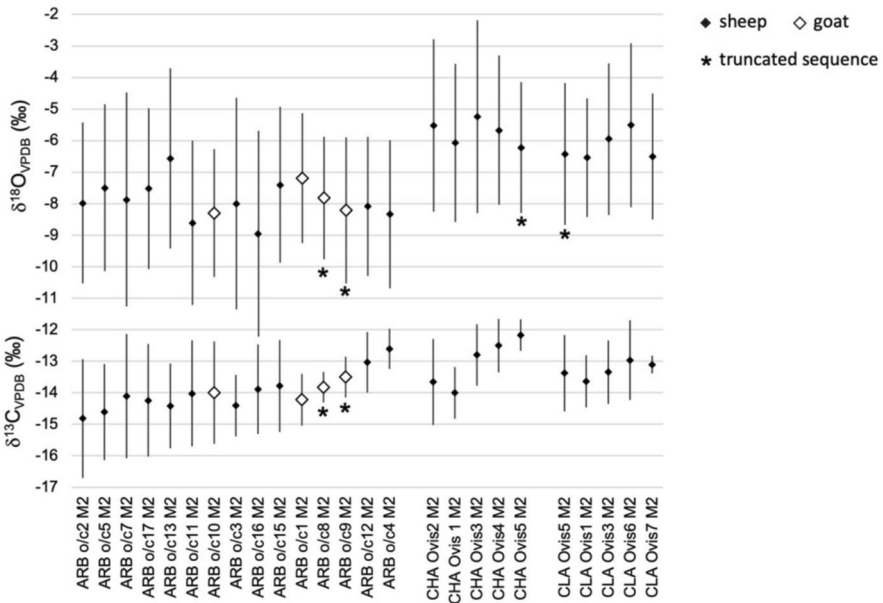


Fig. 4 Range of intra-tooth variation of the stable carbon and oxygen isotope ratios in the caprine teeth from Arbon-Bleiche-3 (ARB), Clairvaux (CLA), and Chalain (CHA). Within each site, the teeth are ordered according to the lowest $\delta^{13}\text{C}$ value of the intra-tooth sequence

in one sheep at Bercy (Paris basin, early 4th millennium BCE; Balasse *et al.*, 2012). This -15‰ threshold is also attained in one instance at Chalain (CHA Ovis2 M2), while most annual minimum $\delta^{13}\text{C}$ values at Clairvaux are $\leq -14\text{‰}$ also within the lowest values of the distribution. At the three sites, the annual maximum/summer values are also among the lowest measured in Europe (Online resource 6). It should be noted that the preexisting corpus is biased in favor of data from the Mediterranean and Dinaro-Carpathian regions (Zanon *et al.*, 2018), where the forest cover would have been less dense than in our study area in the western part of the Central Europe biogeographic region (Zanon *et al.*, 2018); future studies may shift the mode of the distribution towards lower $\delta^{13}\text{C}$ values.

In Fig. 6, the minimum/winter $\delta^{13}\text{C}$ values measured in each intra-tooth sequence are compared to values previously measured in red deer bone collagen at the respective sites. To allow this comparison, the caprine enamel $\delta^{13}\text{C}$ values were corrected by -8.6‰ (bioapatite-collagen spacing for sheep in Clementz *et al.*, 2009; corrected values in Online resource 3B). We are aware that plant diet with different protein content and digestibility (namely browse versus graze) can lead to different spacing in ruminants (Codron *et al.*, 2018) and consider the resulting corrected values indicative. At Arbon, most caprine teeth delivered $\delta^{13}\text{C}$ values falling seasonally within one standard deviation around the mean of those measured in red deer. At Clairvaux and Chalain also, a majority of sheep yielded winter $\delta^{13}\text{C}$ values in the range of those measured in the red deer hunted at Chalain (Fig. 6).

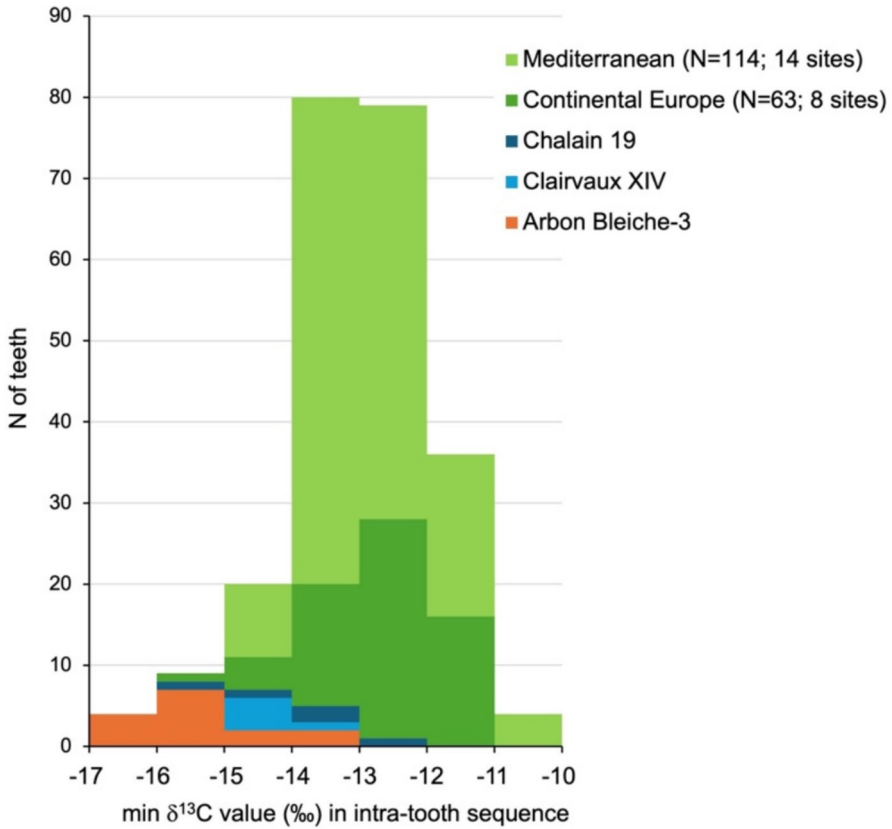


Fig. 5 Minimum/winter $\delta^{13}\text{C}$ values from sequential sampling in enamel, in Neolithic caprines from continental Europe (total number of teeth $N=232$, data and references in Online resource 6)

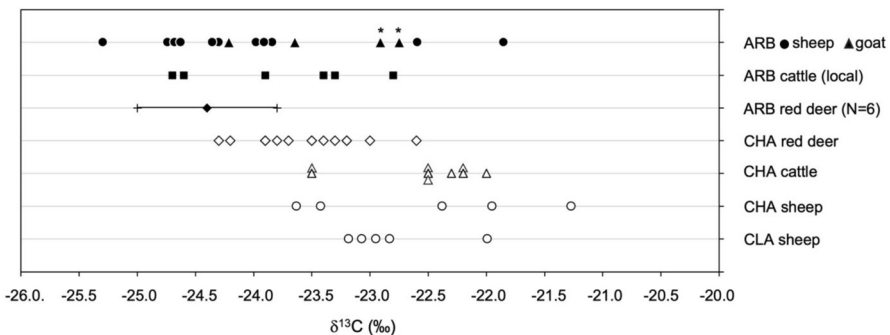


Fig. 6 Comparison of the minimum/winter $\delta^{13}\text{C}$ values in intra-tooth sequences (converted to collagen value using a—8.6‰ bioapatite-collagen spacing for sheep; Clementz *et al.*, 2009) with those measured in bone collagen in red deer and cattle at Arbon-Bleiche 3 (Gerling *et al.*, 2017) and Chalain (Chalain 3, 4, and 19; Drucker & Bocherens, 2009); * truncated intra-tooth sequences (=the true minimum value could be lower)

A More Pronounced Contribution of Forest Resources in Winter, Reflecting Forest Pasturing or Fodder Provisioning

At the three sites, the intra-tooth variation in $\delta^{13}\text{C}$ values shows that the contribution of forest resources in the diet of caprines is more pronounced in winter (Figs. 2 and 3), which could reflect the need to compensate for the scarcity of grass pastures, possibly accentuated by snowy winters. At Arbon, the macrobotanical remains in the caprine faeces were mostly composed of evergreen species (*Abies alba*, *Rubus*, *Viscum album*) or plant parts that would have been available in late autumn/winter (*Rubus* fruits) or late winter/early spring (*Corylus* catkins). These plants could have been browsed on the stump during winter by sheep and goats on their own. As for *Abies alba*, the most frequently used for the construction of piles and boards at Arbon (Dufraisse & Leuzinger, 2009; Leuzinger, 2000), they were taken to the site as whole trees, and their branches could have been collected and provided as fodder or directly eaten by caprines from the tree at the site (Akeret *et al.*, 1999).

At Clairvaux and Chalain, a more pronounced contribution of forest resources in winter raises the question of the availability of tree leaves at this time of the year, as the surrounding landscape would have comprised deciduous forests and the important volume of twigs and sticks found at the site was mostly composed of deciduous trees/bushes (dominated by beech, hazel, Maloideae, dogwood, poplar, lime) additionally to some evergreen plants (ivy). Following the hypothesis that the twigs and small branches recovered at the site had indeed been used as fodder, twigs may contribute marginally to sheep diet, but the latter prefer leaves to branches, and it is more likely that these branches were bearing leaves when provided to them. This would then suggest that leafy branches were collected before leaf fall, probably in the end of summer or early autumn, for a deferred use in winter. The storage of dried leafy branches for use as fodder throughout the year or during the bad season is documented in middle mountain contexts in North-western Greece, Northern India, and Nepal (Halstead, 1998; Pétrequin *et al.*, 2015).

The Reasons for Lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ Values at Arbon-Bleiche 3 Compared to Clairvaux XIV and Chalain 19

Arbon caprines have delivered significantly lower winter $\delta^{13}\text{C}$ values than the sheep from Clairvaux and Chalain taken together (Wilcoxon rank test, $W=25.55$, $p=0.007$) while the values measured in sheep from the two sites in the French Jura were not significantly different ($W=11$, $p=0.84$). Lower winter $\delta^{13}\text{C}$ values at Arbon could either mean a greater contribution of forest resources to caprine diet, or differences in the forest physiognomy leading to a more ^{13}C -depleted forest signal at Arbon. Both hypotheses are not mutually exclusive. Lower $\delta^{13}\text{C}$ values in red deer bone collagen at Arbon ($-24.4 \pm 0.6\text{‰}$; Gerling *et al.*, 2017) compared to Chalain ($-23.5 \pm 0.5\text{‰}$; Drucker & Bocherens, 2009 and Fig. 5) and lower summer $\delta^{13}\text{C}$ values in caprine enamel at Arbon compared to Chalain and Clairvaux (a significant difference: $W=39$, $p=0.05$) could suggest a denser forest cover at Arbon, especially in the southern, hilly zones of the territory (Leuzinger, 2000). Specifically,

the good representation of fir leaves in caprine faeces at Arbon may explain particularly low $\delta^{13}\text{C}$ values as fir forests are very dark. Last, Arbon-Bleiche 3 being one of the few sites occupied during the 34th c. BCE to have been recovered in the area, it is expected that the impact of human activities on the forest cover would have been more limited compared to the Clairvaux and Chalain contexts where several villages were occupied contemporaneously. Indeed, the palynological record in lowland lakes from the Swiss plateau highlights that the beech forests in southwestern Central Europe have experienced episodic deforestation during the 39th–37th and during the 32nd–30th c. BCE at the periods of occupation of Clairvaux XIV and Chalain 19 respectively, whereas the 34th c. BCE was a phase of reforestation (Rey *et al.*, 2025).

It is interesting to note that Arbon also stands out with markedly lower $\delta^{18}\text{O}$ values in the time series recorded in caprine teeth (Online resource 3B and Fig. 4): in comparison to the data measured at Clairvaux and Chalain, Arbon shows significantly lower maximum $\delta^{18}\text{O}$ values (by 1.6‰ on average; Wilcoxon rank test, $W=6$, $p=0.0001$) and considerably lower minimum $\delta^{18}\text{O}$ values (by -2.1 ‰ on average; no overlap between both datasets), suggesting cooler summers and colder winters at Arbon. Low $\delta^{18}\text{O}$ values in caprine tooth enamel at Arbon may be linked to the tripartite climate event documented in the paleoenvironmental record of Lake Constance between 3600 and 3350 BCE (5550–5300 cal BP) by three episodes of successively higher lake level, the last one occurring during the latter period of the village occupation and in the decade following its abandonment (Magny & Haas, 2004; Magny *et al.*, 2006). Cooler and wetter conditions on the local scale find an echo in higher lake levels on a regional scale and also coincide with glacier advance and a tree-limit decline in the Alps (Magny & Haas, 2004). Lower ambient temperatures at Arbon with harsher winters could have accentuated the need to rely on complementary feed such as tree leaves, while a lowering of the tree-limit would also mean a greater proximity of the forest.

Inter- and Intra-species Variability

Two types of faecal pellets were observed at Arbon, some containing *Rubus* fruits and Rosaceae prickles, and others containing *Abies* leaves associated with *Corylus* anthers. This dichotomy is not observed in caprine teeth $\delta^{13}\text{C}$ values (Figs. 4 and 6). If the lowest winter $\delta^{13}\text{C}$ values are measured in sheep, the two highest are also measured in sheep (ARB o/c12 and ARB o/c4—the sheep identity of the latter being confirmed by ZooMS and tooth morphology; Online resource 2A&B) while one goat (ARB o/c10) also delivered low $\delta^{13}\text{C}$ values in winter. Sheep and goat did not yield significantly different $\delta^{13}\text{C}$ values, either in winter (Wilcoxon-Mann Whitney rank T -test, $W=33$, $p=0.17$) nor on an annual basis ($W=28.5$, $p=0.43$). Although a larger goat sample would be needed to confirm, in the light of available results it would be hazardous to conclude that the two types of faecal pellets correspond to the two caprine species. The former hypothesis of different faecal contents reflecting different feeding behavior/practices on a daily basis still stands (Akeret *et al.*, 1999; Kühn & Hadorn, 2004).

At each site, a few animals diverge from the most commonly observed pattern of covariation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ intra-tooth sequences reflecting two main dietary poles (warm season/cold season): at Arbon, the pattern of seasonal variation in $\delta^{13}\text{C}$ values in ARB o/c10 and ARB o/c16 suggests some deviations from this pattern, with a contribution of a third dietary source with a higher $\delta^{13}\text{C}$ value in the latest autumn/winter in the former and a dietary regime with stable $\delta^{13}\text{C}$ value from late winter to early summer in the latter (Figs. 2); at Clairvaux and Chalain, CLA Ovis7 and CHA Ovis5 show little variation in $\delta^{13}\text{C}$ values suggesting stable diet throughout the year (Fig. 3). Such divergences from the expected scheme of seasonal covariation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values have been interpreted in other contexts as potentially reflecting foddering with hay (Balasse *et al.*, 2013; Blanz *et al.*, 2023). Beyond this hypothesis, it is difficult to determine more precisely the type of fodder. The most interesting is that such inter-individual variability among small assemblages accumulated over very short periods of time (at Arbon and Clairvaux) suggests opportunistic feeding by caprines, and more generally reflects adaptability of animal behavior and husbandry practices, as expected in any extensive herding system to face climatic or other environmental hazards.

Lastly, differences in feeding strategies between caprines and cattle could also be investigated. The available $\delta^{13}\text{C}$ values for cattle at these sites were measured in bone collagen, reflecting average diet on a (pluri)annual basis, but not allowing for an estimation of the importance of the contribution of forest resources to cattle diet on a seasonal basis. Inversely, the middle value (Min + Max/2) of the intra-tooth sequence in caprine enamel may be used to approach the $\delta^{13}\text{C}$ value on an annual basis. The middle $\delta^{13}\text{C}$ values in caprine intra-tooth sequence average $-22.6 \pm 0.6\text{‰}$ at Arbon (vs $-23.8 \pm 0.8\text{‰}$ in cattle; Gerling *et al.*, 2017), $-21.9 \pm 0.3\text{‰}$ at Clairvaux, and $-21.6 \pm 0.8\text{‰}$ at Chalain (vs $-22.6 \pm 0.5\text{‰}$ in cattle; Drucker & Bocherens, 2009), reflecting an overall higher contribution of forest resources to cattle diet compared to caprines, as highlighted previously on a larger dataset from central and northern Europe by Gillis and Zanon (2021), although the inverse pattern (lower $\delta^{13}\text{C}$ values in sheep teeth compared to cattle) was also observed (Fabre *et al.*, 2021).

Conclusion

At Arbon-Bleiche 3, caprines consuming forest tree leaves had enamel $\delta^{13}\text{C}$ values that seasonally fell below -15‰ and as were low as -16.7‰ , previously unreached in Neolithic Europe. These results significantly broaden the range of possible values expected for animal husbandry in Neolithic Europe. At Clairvaux XIV and Chalain 19, where tree branch fodder had been strongly suggested from abundant macrobotanical remains, the $\delta^{13}\text{C}$ values measured in caprine teeth reached occasionally $< -15\text{‰}$, and more regularly $< -14\text{‰}$. It should be emphasized that these new reference values should only be applied outside this chronological and geographical area with caution. Plant $\delta^{13}\text{C}$ values vary with physical, environmental and climatic parameters, leading to spatial variability in the $\delta^{13}\text{C}$ values of global vegetation, detectable on the European scale: higher $\delta^{13}\text{C}$

values are expected on the Mediterranean margins of Europe (Wang *et al.*, 2024). The Arbon reference probably stands for Neolithic Central Europe and its western margins, where forest cover still largely predominated until Late Neolithic.

The exceptionally low $\delta^{13}\text{C}$ values measured in caprine teeth at Arbon, associated with low $\delta^{18}\text{O}$ values, suggest a dense forest cover and lower ambient temperatures, potentially related to the following: (1) cooler and wetter conditions during the latter period of the village occupation, recorded in the paleoenvironmental record of Lake Constance in the form of an abrupt lake level rise (Magny *et al.*, 2006); (2) harsher winters accentuating the need for complementary feed in the form of tree leaves; (3) a potentially concomitant tree-line decline causing a greater proximity of the fir forest; and (4) a lesser impact of human activities on forests during the 34th c. BCE in the area.

If the contribution of forest plants to caprines' diet was already directly evidenced from archaeobotanical contents in faeces at Arbon, we were able to demonstrate it at Clairvaux and Chalain. Sequential sampling in enamel additionally allowed to determine that this consumption was more important in winter at all sites. It appears that in these environmental contexts, forest plants could massively contribute to caprine diet to compensate for the scarcity of pastures in open areas during winter, but also contribute to some extent for the rest of the year as attested by rather low maxima in the $\delta^{13}\text{C}$ values during summer. Besides, $\delta^{13}\text{C}$ values measured previously in cattle bone collagen at the study sites suggest that the latter could deliver even lower seasonal values in their tooth enamel than caprines. All this indicates that, in these chronocultural contexts, forest areas were fully integrated into husbandry systems, shaping the pastoral calendar and practices as well as animal behaviors, and potentially also contributing to the reshaping of the landscape.

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Author Contribution Marie Balasse conceptualized the study. Material preparation, data acquisition and analysis were performed by Marie Balasse, Laurent Emmanuel and Denis Fiorillo. The first draft of the manuscript was written by Marie Balasse. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability Data generated in this study are included in this article and its supplementary information files available at: <https://doi.org/10.48579/PRO/NDWAUM>.

Declarations

Competing interests The authors declare no competing interests.

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