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Hanging around or moving on up? Multi-proxy perspectives on Bronze Age sheep/goats herding practices in the north-eastern Po Plain (northern Italy)

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ABSTRACT

During the Middle Bronze Age, farming settlements covered much of the Po Plain, but little is known about their herding strategies, e.g. in terms of mobility and foddering. According to faunal data and archaeological materials, herding practices focused on sheep husbandry for multiple products, including wool. Meanwhile, transhumance, involving the movement of flocks from the plain to the upland pastures, has been proposed to emerge during this period, but direct evidence for this practice is scant. To fill these gaps, we employed multiple isotope analyses of faunal remains embedded within palynological, archaeobotanical and micromorphological analyses to uncover sheep husbandry practices at two Middle Bronze Age sites (Oppeano 4D, La Muraiola di Povegliano Veronese) near Verona, northern Italy. These settlements have both stratigraphic evidence of animal penning investigated through high resolution multi-proxy geoarchaeological and archaeobotanical methods. Incremental carbon, oxygen and strontium analysis of sheep molars embedded within a bulk $\delta^{13}C/\delta^{15}N$ framework from domesticated and wild species indicates that transhumance was not practised at either site. Instead, we demonstrate the seasonal exploitation of local environments for pasturing animals with strong indications for the collection of plant resources for livestock (leafy-hay, grass hay) including the use of C_4 plants as cattle feed. This practice of fodder collection may have been an important step in the evolution of herding practices, as it allowed herds to remain within the local area and, at the same time, showing incipient pressure that might have led to the development of more mobile strategies.

1. Introduction

1.1. Research framework

Animal products form one of the cornerstones of human economies, directly connecting communities with their landscape (Kristiansen and Stig Sørensen, 2019; Sherratt, 1981). Livestock husbandry practices are moulded by human demographics, culture, and economic demand, while at the same time are heavily influenced by the local environmental context. Demographic pressure together with increasing social complexity have been seen as key aspects influencing subsistence strategies and the development of specialised economies across Europe (Carrer and Migliavacca, 2019; Kristiansen and Stig Sørensen, 2019). For example, demographic pressures drive an increase in food

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production, expanding cultivated land at the expense of pastures, as well as allowing the increase of specialised craftsmen and production of items, such as textiles, leading to not just changes in socio-economic dynamics but also in local ecosystems. Strongly associated with the European Bronze Age is the emergence of sheep with fine wool coats which transformed wool textile quality and thus becoming an important commodity to these communities (De Grossi Mazzorin, 2013; Sabatini et al., 2019, 2022). Maintaining large flocks within cultivated landscapes may have required herders to adopt novel strategies, such as transhumance, to prevent crop damage and conflict.

During the Middle Bronze Age (MBA; 1650–1350/1300 BCE, Cardarelli, 2010) in the Po Plain, northern Italy, population growth is evidenced by the formation of interconnected settlement systems (Cardarelli, 1997, 2010; Di Renzoni, 2006). These systems featured large ditched settlements called *Terramara* (Bernabò Brea et al., 1997; Cupitò and Leonardi, 2015) which showed uncommon complexity even within the frame of the European Bronze Age (Kristiansen and Stig Sørensen, 2019; Müller, 2015). Changes in land use (Debandi, 2021), crop diversification (Cremaschi et al., 2016; Mercuri et al., 2006a; Perego et al., 2022; Rottoli, 2024), specialised wool production (Sabatini et al., 2018) emerged at this time, while increased herd mobility has been suggested (Carrer and Migliavacca, 2019). The adoption of periodic seasonal movements of domestic herds between different and complementary grazing areas – from the alluvial plain to the mountains – has been proposed as a key component of Bronze Age communities in the Po Plain (Carrer and Migliavacca, 2019). Yet direct evidence of such practices remains scant. In the above-mentioned archaeological framework, multi-proxy bioarchaeological perspectives can strongly contribute to our understanding of the development and dynamics of northern Italian Bronze Age herding strategies.

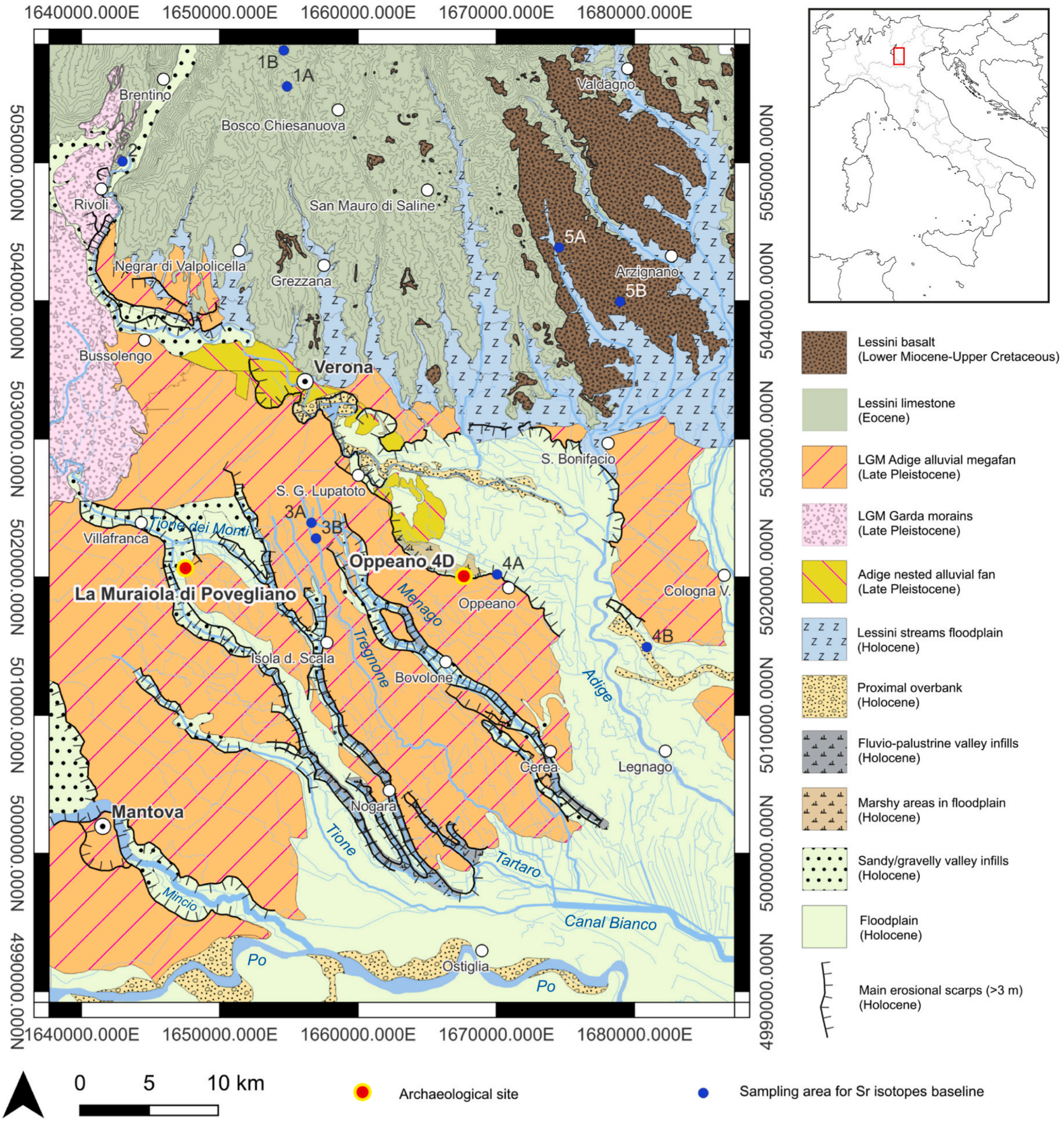


Fig. 1. Geomorphological map showing the floodplain between the Lessini Highlands and the present-day Po River. The map is based on Sorbini et al. (1984), Castiglioni (Castiglioni, 1997), and Carta Geologica d'Italia 1:100.000 sheets n° 48, 49, 62, 63 (modified from Polisca, 2025, Fig. 1). The archaeological sites of La Muraiola di Povegliano Veronese and Oppeano 4D are indicated, along with the sampling locations used to construct the local Sr isotope baseline (numbers and letters refer to the lithological units described in the text; see "Materials"). LGM: Late Glacial Maximum.

1.2. *Evolution of seasonal herding practice in bronze age northern Italy, a state of the art*

The abundance of sheep (*Ovis aries*) and goats (*Capra hircus*) within *Terramare* faunal assemblages highlights their importance compared to the other domestic animals (De Grossi Mazzorin, 2013; Debandi, 2021). Herding strategies, particularly fodder and pasture management, would have needed to be well-organised to balance with other land use demands, such as crop cultivation. Moreover, expansion of herd sizes in response to an increased demand for animal products, such as wool, would have driven herders to explore new territories and pasture areas. For example, during the Roman period, in the plain there were important centres for wool textile (i.e., Padova and Altino; Busana, 2024) and extensive agricultural production (Bonetto, 2024). The competition between agriculture and large herds for wool production has been proposed as a driver for the use of summer upland pastures. Considering the north-eastern Po Plain, the region of the present investigation, it has been proposed that its varied geomorphology (Fig. 1), i.e. floodplain, hills and mountains, across a relatively short distance encouraged the seasonal movement of herds (Bonetto, 2024; Migliavacca et al., 2015). Medieval written sources and those of later periods attest to the many agreements, as well as struggles, between mid-mountain communities – where herding was a primary economic activity – and landowners of the plain (e.g., Lessini Highlands in the Venetian Prealps; Sauro, 2018). Specialised shepherds were allowed to bring down large flocks from the mountains during winter, when the upland pastures used in summer were covered with snow (Bortoli, 2019; Chemin, 2019). More recently, herding strategies encompassed the large alluvial plain up to the lagoon, the fore alpine hills, and the highlands for pastures, until the 1970s when the opening up to other markets created a crisis in Italian wool production (Bortoli, 2019; Iannetti, 2021).

Focusing on the historical and ethnoarchaeological evidence, a palimpsest of archaeological evidence suggests the practice of transhumance since the late prehistoric period (De Guio, 2019). A survey of 600 pastoral structures – of uncertain chronology – identified in the Lessini Highlands highlighted the significance of seasonal transhumant practices in the region's recent past (Carrer and Migliavacca, 2019). The discovery of multipurpose tools, such as knives, daggers, and axe heads, dating to the MBA and Recent Bronze Age (RBA) along the main routes connecting the Lessini Highlands to the Adige Valley may support Bronze Age seasonal herd mobility (Migliavacca, 2014). Ethnoarchaeological studies indicate that such tools were often part of a shepherd's toolkit, used for defence and for clearing vegetation (Carrer and Migliavacca, 2019), although further evidence is needed to confirm this interpretation. Only for BA daggers recent organic residue analysis showed that they were mostly used for animal (wild game or domesticates) carcass butchering and carving (Caricola et al., 2022). Additionally, beginning in the MBA and into the RBA, the spread of archaeological sites, including ritual ones, e.g. sanctuaries (De Guio, 2019), into the hill and mountain ranges has been interpreted as possible establishment of way stations or control settlements along herding routes (Cupitò and Leonardi, 2015; Leonardi, 2006). Despite these elements, we lack an in-depth investigation of herd population dynamics, diet and mobility, which is crucial to understand herding strategies and this dynamic period and region.

1.3. *Review of terramare palaeo-environmental setting and subsistence practices*

The spread of the *Terramare* settlement systems during the MBA and RBA corresponds to a period of unprecedented human occupation of the Po Plain (Cardarelli, 2010; Cremaschi, 2009; Dalla Longa et al., 2019; Debandi, 2021). At an environmental level, in comparison to previous periods (Castelletti and Maspero, 1992; Rottoli, 1999; Rottoli and Castiglioni, 2009b; Wick, 1996; Zanon et al., 2018), differences can be found in woodland composition and density, and in the spread of synanthropic vegetation attesting the creation of new open habitats by the MBA-RBA farming communities (Mercuri and Sadori, 2012; Mercuri et al., 2013; Nisbet and Rottoli, 1997). This variety of natural and anthropogenic environments has been attested through several archaeobotanical records, but how extensive and subdivided within the landscape remains difficult to quantify. This is due to the fact that the floodplain, as such, was and remains a dynamic and patchy landscape. There is a scarcity of undisturbed and long sedimentary sequences encompassing the Bronze Age and previous/later phases (see “off-site” in Dal Corso et al., 2025; Ravazzi et al., 2022). Therefore, relying on standard methods alone, such as palynology, to reconstruct vegetation character and cover in the floodplain is challenging (e.g. Magri et al., 2015; Zanon et al., 2018). However, archaeobotanical records offer a high level of taxonomic detail to understand plant resources and to infer the environmental setting on and around *Terramara* sites.

Settlement structures (e.g. dwellings, fences, etc.) were built with wood, mostly from mixed deciduous woodlands (e.g. Cremaschi et al., 2021; D'Aquino et al., 2026;Rottoli and Castiglioni, 2009a), composed of deciduous oak species, ash, maple, lime, elm, hazelnut, and hornbeam (Accorsi et al., 1996; Magri et al., 2015). In particular, hornbeam became a fundamental element of the mesophile woods of the Po Plain beginning in the mid-4th millennium BCE (Magri et al., 2015; Ravazzi et al., 2013; Zanon et al., 2019), possibly due to changes in forest exploitation in relation to coppicing, the collection of leafy-hay, or browsing by livestock (Ravazzi and Pini, 2013). Arboreal resources used for fuel are evidenced by anthracological studies that reflect their local presence in the floodplain and neighbouring hills (Chiaffarelli et al., 2021; D'Aquino et al., 2026; Mercuri et al., 2015; Motella De Carlo, 1997; Nisbet and Rottoli, 1997; Rottoli and Motella De Carlo, 2004). Alder carr and other hygrophilous trees and shrubs from local riparian environments, typical of the riverine landscape, have been also attested (Dalla Longa et al., 2019; Florenzano et al., 2021). With species selected for specific purposes, such as alder for durable fence construction in water-saturated soil (D'Aquino et al., 2026), and deciduous oak for timber (Cremaschi et al., 2021; Nisbet and Rottoli, 1997). Episodes of deforestation for construction phases have been suggested at some sites (Chiaffarelli et al., 2021) as well as the periodic use of fire for land clearing (Mercuri et al., 2006a). Meanwhile, where pollen sequences are available, evidence of a wide spectrum of shrubs and light-demanding trees, that would have provided edible fruits, nuts, and berries, characterise the landscape during occupation phases (c.f. Dal Corso, 2018; Florenzano et al., 2021; Mercuri et al., 2006a, 2006b, 2015; Ravazzi et al., 2004). Archaeobotanical data demonstrates a clear interest in the consumption of fruits suggesting sophisticated management of these resources (Cremaschi et al., 2016), which were regularly harvested evidenced by stones/seeds that are found frequently in the carpological records (Chiaffarelli et al., 2021). The consumption of cornelian cherries was particularly relevant in this period, when concentrations of stones suggest processing/fermentation (Cremaschi et al., 2016; Nicosia et al., 2025; Rottoli and Castiglioni, 2009a).

Synanthropic vegetation from open habitats was also thriving in correspondence with the sites, where people and animals moved and lived, nutrients enriched the soil, and tree re-growth was prevented by fire, cutting, grazing, trampling, and buildings. This vegetation is particularly evident in the palynological records recovered from archaeological stratigraphy (Aceti et al., 2009; Dal Corso, 2018; Florenzano et al., 2021; Mercuri et al., 2006a, 2013, 2015; Nicosia et al., 2025; Ravazzi et al., 2004; Ravazzi and Valsecchi, 2001) through the so-called “anthropogenic pollen indicators” (Behre, 1981; Mercuri et al., 2013). Many of the synanthropic herbs attested at Bronze Age sites indicate wet pastures/meadows (e.g. plantain/*Plantago*, clovers/*Trifolium*, meadows buttercup/*Ranunculus acris*), dry pastures (e.g. white laceflower/*Orlaya grandiflora*), footpath and ruderal areas (e.g. nettle/*Urtica*, common sorrel/*Rumex acetosa*), weeds of arable fields with winter cereals (e.g. cornflower/*Centaurea*, bindweed/*Convolvolus,* poppy/*Papaver*), weeds of summer cereals or orchards (e.g.

goosefoot/*Chenopodium*), fallow land (e.g. common knotgrass/*Polygonum aviculare*), and some of them encompass more of the above mentioned categories (e.g. wild grasses/Poaceae, the dandelion and chicory tribe/Cichorieae tribe). Especially xerophytic vegetation of dry grasslands has been observed to emerge in the Bronze Age, likely associated with drained terrains used as rangelands (Nicosia et al., 2025; Perego et al., 2011; Pini et al., 2021). Synanthropic plant remains are also abundantly preserved in carpological assemblages from waterlogged settlements (Nicosia et al., 2025; Perego, 2017; Rottoli, 2001). In both carpological and palynological records, an additional pathway for plant remains to enter sites was through herbivore dung, besides inputs from human activities such as food preparation, constructions, basketry/fibres, medicine, and other uses (Nicosia et al., 2025; Perego, 2017; Polisca et al., 2025; Schepers and Van Haaster, 2015). Evidence for *Terramare* cereal consumption and processing has been attested by frequent carbonised caryopses and chaff found in the carpological records (Carra, 2009; Chiaffarelli et al., 2021; Mercuri et al., 2006b; Nicosia et al., 2025; Perego, 2017; Rottoli, 2001; Rottoli and Castiglioni, 2009a) and high values of related pollen (Mercuri et al., 2013; Nicosia et al., 2025). A diversified range of cereals characterises the period, with continuity from the Neolithic (barley, einkorn, emmer, free-threshing wheat, Timopheev's wheat, spelt) and novel introductions, i.e. millets. These small-grained panicoid cereals (broomcorn millet, foxtail millet, and barnyard grass) have a C_4 photosynthetic pathway and can be found since the MBA (Dal Corso et al., 2022; Debandi, 2021; Perego et al., 2022; Rottoli, 2024), some of which were directly radiocarbon dated (Filipović et al., 2020). Their relevance for people's diet is further confirmed by stable isotope analysis. Within the Veneto region, previous human palaeodietary reconstruction using carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from bone collagen included sampling of animal bones to produce a baseline (Tafuri et al., 2009, 2018; Varalli et al., 2016, 2022). Results showed that people in northeastern Italy started eating C_4 plants around the MBA (Tafuri et al., 2018), and by the RBA, these plants were consumed regularly.

Although pulses were already known in northern Italy (Breglia et al., 2025; Rottoli and Castiglioni, 2009b; Tecchiati et al., 2024), they are rarely found in *terramara* sites in the Po Plain (D'Aquino, 2025; Perego et al., 2022; Rottoli, 2024). Information about crop cultivation is scarce: a rotation system that integrates winter cereals, summer cereals, and fallow land has been proposed (Cremaschi et al., 2016). While alternation with pulses is not evident in the plain (Rottoli, 2024), soil nutrients could have been improved via animal manure either collected from stalls or by allowing animal grazing after harvest and/or in fallow lands, which would also have helped in that sense.

Zooarchaeological studies of faunal remains from *Terramare* culture sites have revealed in many cases a strong focus on sheep and goat husbandry (mostly sheep; Riedel and Tecchiati, 2003), with varying proportions of cattle (*Bos taurus*) and pigs (*Sus scrofa domesticus*) north and south of the Po River (De Grossi Mazzorin, 2013; Debandi, 2021). In sites south of the Po River, pigs usually constitute a significant part of the faunal assemblages (approximately 22–48%), whereas cattle are generally scarce, often below 20% (De Grossi Mazzorin, 2013; Maini et al., 2021). North of the Po River, the pattern is sometimes reversed: at the RBA site of Bovolone, for example, cattle are the most abundant domestic species, while pigs are less represented (Bertolini et al., 2015). In other northern sites, the proportions of cattle and pigs are more similar and, although not as numerous as caprines, remain an important component of the assemblage (around 20-30%) (Cupitò et al., 2024; De Grossi Mazzorin, 2013; De Grossi Mazzorin, 2015; Depellegrin and Tecchiati, 2016). Notable exceptions to these patterns are the MBA sites of Gaggio di Castelfranco Emilia and Baggiovara, both situated south of the Po River, where caprines are present in quantities respectively similar to and lower than those of pigs (De Grossi Mazzorin, 2013). Hunting generally played a marginal role at *Terramare* settlements (De Grossi Mazzorin, 2013). The most frequently hunted species were red deer (*Cervus elaphus*), whose antlers were exploited for the manufacture of objects and tools (Provenzano, 1997), followed by wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) (De Grossi Mazzorin, 2013).

The analysis of kill-off patterns of the main domestic species has revealed some variability in the management practices across the *Terramare* culture. With regard to sheep/goat husbandry, in some cases there is clear evidence of a strong focus on meat production, as indicated by the high proportion of animals slaughtered at a young and subadult age. Often, in these cases wool seems to be also exploited, as shown by the presence of mature adult individuals. Milk exploitation appears to have been of minor importance, given the scarcity of specimens culled before six months of age (Cupitò et al., 2024; De Grossi Mazzorin, 2013; De Grossi Mazzorin, 2015; Depellegrin and Tecchiati, 2016; Maini et al., 2021). In other cases, however, the data suggest a mixed economy aimed at both meat production and secondary products, including milk (Bertolini et al., 2015; De Grossi Mazzorin, 2013). Cattle tend to be kept as mature animals for traction and milk production (Bertolini et al., 2015; De Grossi Mazzorin, 2013; De Grossi Mazzorin, 2015; Depellegrin and Tecchiati, 2016; Maini et al., 2021). A post-lactation slaughter model for milk exploitation (Balasse and Tresset, 2002) seems most likely, given the lack of infant calves and the presence of young/subadult age groups, which also provide high-quality meat. As for pigs, kill-off patterns often show high percentages of individuals slaughtered before two years of age (Bertolini et al., 2015; Cupitò et al., 2024; De Grossi Mazzorin, 2015; Depellegrin and Tecchiati, 2016; Maini et al., 2021).

As illustrated above, age-at-death distributions are important for determining the animal production and husbandry strategies. Based on observations of modern Turkish herders, Payne (1973) proposed three models for sheep/goat based on survivorship curves: milk, meat, and wool. The age-at-death distribution for wool would include a large proportion of mature adults. However, in mixed model productions, young animals – particularly males – may have been slaughtered earlier for meat (Helmer et al., 2007). Recent analysis of sheep and goat teeth has been carried out at the Terramara of Montale (Emilia-Romagna, northern Italy, c. 1600/1550–1200/1150 BCE), where a large amount of sheep/goat remains together with numerous spindle whorls (>4500) have been recovered (Sabatini et al., 2018). Even though artefactual evidence highlights the importance of sheep wool processing, age-at-death analysis indicates a focus on meat production, with low frequency of mature adults (Sabatini et al., 2022), which does not support wool exploitation following the classic wool model (Payne, 1973). Previous zooarchaeological investigations into livestock seasonal movements have focused on presence and absence of specific age-at-death classes in complementary site types, i.e. upland sites are represented by a high percentage of neonatal remains, while lowland sites would have absence of younger age classes (SW France: Helmer and Vigne, 2004; Helmer et al., 2005; Bréhard et al., 2010; Balkans: Greenfield, 1999; SW Alps: Barker, 1999). A modern example of complementary site use is the Balkan Vlach herders (Ryder, 1994), where upland sites were used as birthing and milking stations during the spring, while the subadult animals and males remained at lowland settlements. At present, there has been no published comparison nor survey of sheep/goat mortality between upland/low land sites in northern Italy.

An understudied perspective of animal husbandry is direct analysis of micro- and macro-botanical remains from herbivore dung, coprolites, stabling layers, and further potential fodder sources recovered from well-preserved archaeological contexts. These datasets, especially single coprolites (Fuks and Dunseth, 2021), can provide important seasonal insights into fodder collections as well as animal movements. However, such fragile organic remains are rarely recovered under dry preservation conditions if mineralisation processes do not occur (Shillito et al., 2020). Waterlogged sites, mainly pile-dwellings from the surroundings of Lake Garda, provided paleo-environmental/dietary evidence from sheep/goat pellets indicating animals mainly grazing in open habitats, from cultivation areas to open dry/wet grasslands, pastures, and ruderal places around the settlements, with some evidence of woody plant consumption, e.g. at Lucone (Polpenazze del Garda, Brescia) and Lavagnone (Desenzano, Brescia). Here the botanical finds mostly indicate open habitats, from cultivation areas to open dry grasslands, pastures, and disturbed places around the settlements. Less frequent is the use of woodland areas for fodder and pasture, with species such as oak, hazel, blackberry and ivy (Perego, 2017; Perego et al., 2025). From dung studies in alpine pile-dwellings of the Bronze Age, mostly arboreal resources are observed, derived from the evergreen conifers, shrubs, and vines of the extended alpine woodlands, indicating winter foddering of livestock kept onsite in the cold season (Fiavè, Trento; Karg, 1998). Micromorphological studies of intra-site sediments from Italian Bronze Age sites have highlighted that livestock, particularly sheep/goat and bovids, were frequently penned within *Terramare* settlements, in both open and roofed structures (Cremaschi and Ottomano, 1996; Cremaschi et al., 2004; Nicosia et al., 2022, 2025; Polisca, 2025; Polisca et al., 2025). Data from the sites here investigated are provided in section 2.

This review highlights the need for detailed investigation of animal herding practices via an integrated, multidisciplinary approach to produce a nuanced understanding of Bronze Age societies and their herds in a very populated region for that time. Many questions remained unanswered, such as how did communities of the Po Plain manage the plant resources and environments for animal herds? Did they maintain year-round sedentary animal husbandry or were highland pastures used seasonally? Answering these questions will lead us to a deeper comprehension of Bronze Age socio-economic organisation and environmental impact, as well as the triggers for the development of transhumant practices.

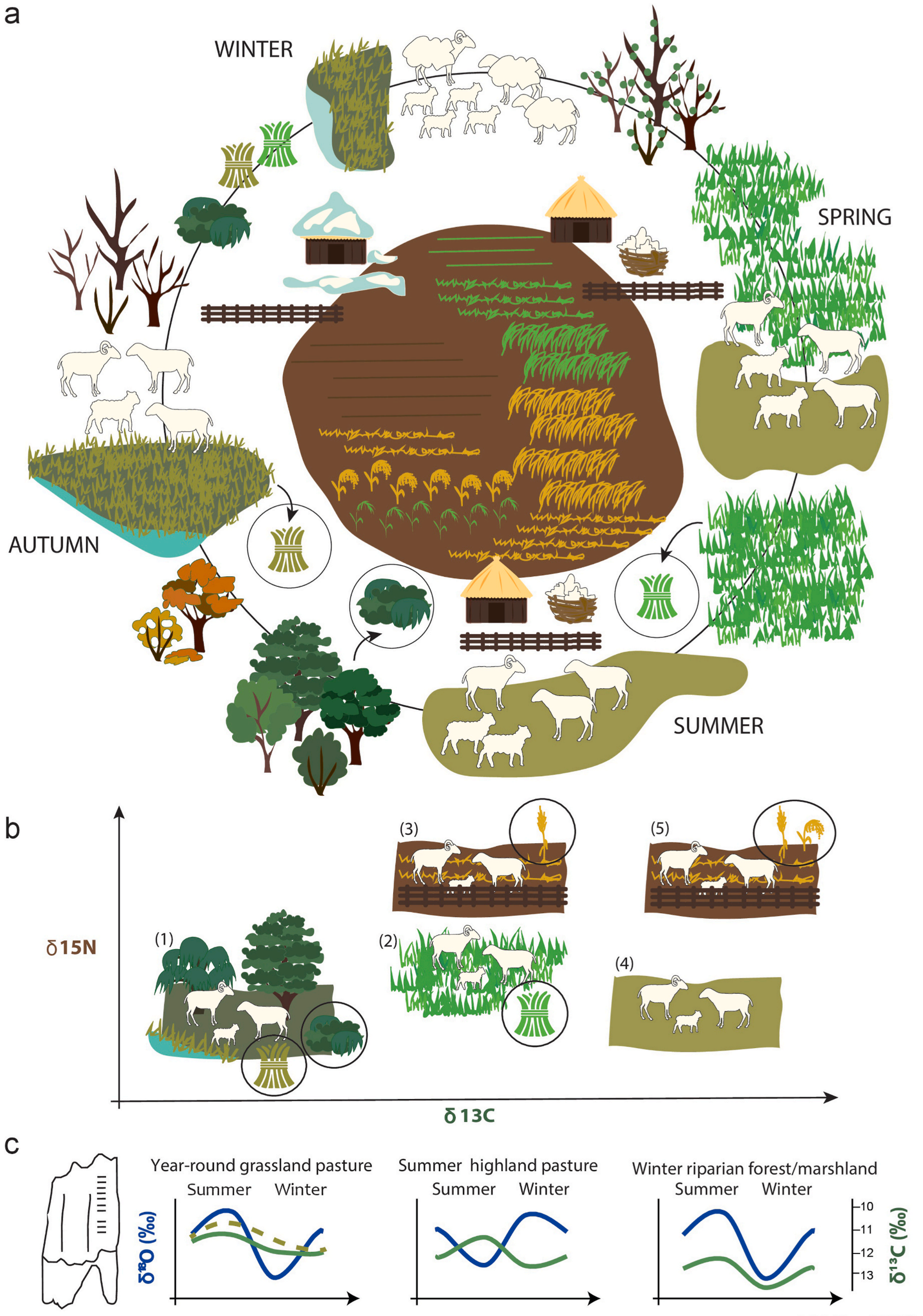
1.4. Model of sheep herding and its impact on isotope values

To ground our study in a theoretical isotope framework, Fig. 2a presents a model of sheep herding, against the seasonal dynamics of agricultural (internal circle) and natural landscape (external circle). The annual cycle of herding activities (Fig. 2a) begins each year with the birth of the new stock. Sheep are highly photosensitive and, as a result, have highly seasonal birthing periods (Balasse et al., 2017). Although modern sheep have undergone over ten thousand years of breeding by human populations (Jeanjean et al., 2025), the majority of herds have a breeding season from late summer to early winter with births occurring 5 months later (Balasse et al., 2017). This highly regimented system would have an impact on work organisation and seasonal availability of animal products. Oxygen isotopes can be used to predict birthing season, and based on previous analysis we assume that the birth season occurred late winter to early summer, similar to 5th-4th millennium BCE sheep from Romania (Balasse et al., 2017). The birth of animals may have taken place within the settlement, to prevent the loss of infants to exposure and predators. The mother's milk will sustain infants for the first two weeks, and then it will require additional sources of food (Tinley, 1949).

Domesticated species including sheep and goat have different dietary tolerances and physiologies. While goats, sheep, and cattle are ruminants and herbivores, they individually have preferences to specific types of plants with the former preferring browse while the latter two graze. This can influence herders in where they pasture their herds. Another factor is the size of a herd, where cattle herds may be small given their relative slow maturity in comparison to pigs and sheep/goat, who become sexually mature within their first year. To prevent overgrazing, animals may have been moved to pastures throughout the seasonal calendars. Within the context of the Po Plain, synanthropic, xerophytic and water rich environments offered herders a diverse range of pastures and sources of fodder (Fig. 2a: outer circle). Animals may have also had access to cultivated areas after the crop has been harvested (Fig. 2a: inner circle). Fodder may have been supplied when access to pasture is restricted by snow and floods, or during times when animals are penned for the collection of animal products, such as milk and wool, and/or to reduce overgrazing. Potential fodder collection from specific environments, such as grasslands and meadows for hay, marshlands for sedges (Sucholas et al., 2022) and woodlands for leafy-hay (Halstead et al., 1998) is indicated with an arrow directed circle, whereas their position in the outer circle highlights when these fodder stocks may have been fed to herds.

Stable isotope analysis of animal bone and teeth can be used to investigate husbandry practices, including forage and pasture management strategies (cf. Gillis et al., 2013; Knockaert et al., 2018; Madgwick et al., 2012; Varkuleviciute et al., 2021). The diet of the animal will be reflected in the isotope composition found in collagen (Fig. 2b) and bioapatite (Fig. 2c). A *caveat* to this is that bony tissue remodels over an animal's lifetime, with the rate varying according to both the type of bone and the age of the individual (Taguchi and Lopez, 2021). Growth rates plateau when an adult body mass is reached or due to growth stasis associated with weaning (McCracken et al., 1995). Consequently, we expect bone samples, depending on the age-at-death of the animal, to reflect the average diet over the animal's last 6-24 months (Webb et al., 2016). The δ^{13}C composition of animal tissues reflect the carbon component of protein and total diet in bone and enamel samples, respectively. For herbivores, δ^{13}C ratios directly indicate the source of animal feed, i.e. whether it comes from open pastures or from collected fodders because these ratios are influenced by the growing condition of a plant (Tieszen, 1991). The δ^{15}N ratios of bone can indicate the level of anthropogenic activity associated with a food source. For example, manured crop waste or plants growing within an area where animals are intensively penned will lead to plants exhibiting higher δ^{15}N values due to animal dung (Makarewicz, 2017a). Fig. 2b shows the hypothetical position for δ^{13}C and δ^{15}N of a sheep of a range of diets: forest pastures; open grasslands; cultivated crop wastes; collected fodders from forest/wetland environments, dry grasslands. As a place marker, in Central Europe, herbivores grazing on forest pastures have been found to have a range of δ^{13}C values from bone collagen samples between– 22.1‰ to– 27.6‰. This is based on bone collagen samples from red and roe deer and bison from the dense canopied deciduous Bialowieza forest (Poland), which exhibited an average value of– 25.3‰ (range:– 23.2‰ to– 27.1‰), while fallow and roe deer respectively had an average value of– 25.2‰ (Wytham Woods, UK:– 22.1‰ to– 26.1‰, Bonafini et al., 2013) and – 26.2‰ (Dourdan Forest, France: – 24.9‰ to – 27.6‰, Drucker et al., 2008). These values have been corrected by 1.5‰ for the Suess effect i.e. correction for the effect of fossil fuels (Friedli et al., 1986). With regard to δ^{15}N values, within plants they can provide an indication of soil conditions, such as humidity, as well as the levels of key nutrients, such as nitrates (Amundson et al., 2003; Fraser et al., 2011). The incorporation of manure into the soil can lead plant δ^{15}N values to increase by 4–9‰, where manure is enriched with ^{15}N due to the loss of ^{14}N by the animal during digestion and excretion (Robbins et al., 2005). Analysis of cereal grains from experimental farms has provided ranges of δ^{15}N values for different levels of manuring schemes: without manure (c. 2.5‰); with low quantities of manure (2.5–6‰); and with a long, moderate to intensive manuring regime (>6‰) (Fraser et al., 2011; Bogaard et al., 2013). One way of ensuring fields are manured is allowing animals to graze on fields after the harvest, which also provides animals with a fodder supply, thereby reducing overgrazing on surrounding natural pastures.

Seasonal mobility between different pastures can be explored via carbon (δ^{13}C), oxygen (δ^{18}O), and strontium (^{87}Sr/^{86}Sr) isotope ratios. These can help us to explore which pastures were used at different times of the year (Fig. 2c) by utilising the fact that isotope data reflect the local geology (^{87}Sr/^{86}Sr), environment and ecology (δ^{13}C, δ^{18}O). The δ^{13}C and δ^{18}O isotope values of sequential enamel samples from high-crowned ruminant molars are fixed during enamel mineralisation, and therefore provide a snapshot of an animal's diet within a specific period of its life. Seasonal changes in the diet reflected in δ^{13}C values can be tracked due to the temporal framework provided by those from δ^{18}O. This is due to ingested water being in almost equilibrium with local water source δ^{18}O values, which are in turn strongly correlated to mean annual



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(caption on next page)

Fig. 2. Models of sheep husbandry and its isotopic signature. a. Sheep herding annual cycle for a farming community in a temperate floodplain environment. Along the outer circle seasonal herd dynamics are represented within different landscapes (woodland, marshland, mesic grasslands, dry grassland) of which herders may choose to stock flocks. The potential collection of fodder from these environments as well as the timing of this collection is represented in the small circles. The inner pictograms on brown background represent the seasonal agricultural cycle of C_3 and C_4 cereals. The collection of fleece/wool and penning/stabling in the village are given between inner and outer circles; b. Hypothetical spacing of bone collagen values $\delta^{13}C/\delta^{15}N$ for sheep stocked within different environments (from left to right): (1) woodland/marshland (low $\delta^{13}C/\delta^{15}N$), (2) open pasture on mesic grassland, (3) penning on cultivated land or permanent pasture with diet of mainly C_3 plants (wild or cultivated) (high $\delta^{15}N$), (4) open pasture on dry grasslands(high $\delta^{13}C$), and (5) penning and feeding on a mixed diet of C_3/C_4 plants (cultivated)(high $\delta^{13}C/\delta^{15}N$); c. Incremented $\delta^{13}C$(green)/$\delta^{18}O$ (blue) for different seasonal herding strategies, from left to right: 1) Year-round grassland pasture, with summer grazing in dry grasslands highlighted (dotted line); 2) Summer highland pasture, where summer $\delta^{18}O$ values will be more similar to lowland winter values, dampening and potentially reversing the $\delta^{18}O$ values; 3) Winter forest/marshland grazing or leafy hay provision during winter. Graphic work MDC and REG using Adobe Illustrator.

ambient temperature. Therefore, low $\delta^{18}O$ corresponds to cold periods while high values during warm periods (Luz et al., 1984). Moreover, $\delta^{18}O$ values have been used to explore vertical seasonal movement of herds from the plains to higher areas during summer, based on the fact that $\delta^{18}O$ isotopes ratios at higher altitudes will be lower during the summer than those in the plain (Henton et al., 2010; Makarewicz, 2017b, Fig. 2c).

Strontium isotope ratios serve as a key proxy for investigating mobility patterns and the exchange/trade of animals, by identifying movement across different geological zones during an animal's lifetime. Animals incorporate bioavailable strontium from food and water into their bones and teeth. The $^{87}Sr/^{86}Sr$ ratios of the bioavailable strontium reflect the environments from which the food and water are sourced. These values are primarily determined by the age and composition of the underlying bedrocks, but can also be influenced by additional factors such as airborne dusts and sea sprays (Bataille et al., 2020; Holt et al., 2021). By comparing the $^{87}Sr/^{86}Sr$ ratios in animal tooth enamel with those of local plants, archaeologists can assess whether animals were raised locally. When these enamel ratios are evaluated against a well-validated $^{87}Sr/^{86}Sr$ isoscape, it becomes possible to identify potential nonlocal areas where the animals may have been raised (Holt et al., 2025; Lugli et al., 2022).

The $\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ ratios of sheep and goat teeth and bones have been used to study herd mobility in the NW Mediterranean (Knockaert et al., 2018; Sabatini et al., 2022; Tornero et al., 2018; Varkuleviciute et al., 2021). Recent studies conducted in different areas of the Pyrenees have focused on both modern animals and archaeological specimens. In particular, Tornero et al. (2018) carried out sequential analyses of $\delta^{13}C$ and $\delta^{18}O$ on tooth-enamel bioapatite from one of the last flocks still practising vertical mobility between the Ebro Valley and the central Pyrenees (Spain) to develop an interpretative model that can be applied to archaeological samples from the region. The analysed transhumant sheep show inverse covariance between $\delta^{13}C$ and $\delta^{18}O$. $\delta^{18}O$ values of meteoric water collected in both valley and mountain locations exhibit high values during summer and low values during winter, while $\delta^{13}C$ values decrease with altitude in the pastures along the altitudinal gradient. Knockaert et al. (2018) sampled caprines from a mountain site (Llo) and a coastal site (Portal-Viehl), dating respectively to the Middle and Late Bronze Age, in the eastern Pyrenees (France) and compared their values with those of modern sedentary and transhumant sheep. At Portal-Viehl there is no evidence of herd vertical mobility, while at Llo a full adaptation to a mountain environment is attested, but the question of vertical mobility remains unresolved. Moving to the Italian context, small-scale transhumance during the Neolithic (specifically during the Cardial phase, 5400-5300 BCE) has been identified for some sheep at Arene Candide (Liguria, northern Italy) through the analyses of sequential $\delta^{13}C$ and $\delta^{18}O$ bioapatite values (Varkuleviciute et al., 2021). Recent $^{87}Sr/^{86}Sr$ ratio analysis of sheep and goat teeth has been carried out at the aforementioned Terramara of Montale (Emilia-Romagna, northern Italy, c. 1600/1550–1200/1150 BCE), which has been interpreted as a key site for sheep herding and wool production (Sabatini et al., 2022). The $^{87}Sr/^{86}Sr$ analysis did not support herd movement over either short and long distances, further complicated by the investigated areas of the Apennines and the floodplain sharing very similar bioavailable $^{87}Sr/^{86}Sr$. As a result, whether Apennines were used as pasture remains unresolved (Sabatini et al., 2022).

The models presented here, along with the summary of isotope studies, provide a framework to explore Bronze Age herding dynamics and modalities embedded within the natural and anthropogenic landscapes. To do this a multi-isotope approach has been used, integrated with zooarchaeological, archaeobotanical, and palynological evidence from penning/stabling deposits to reconstruct a key point during the evolution of the agro-pastoral dynamics of the central-eastern Po Plain. The study focuses on the MBA sites of Oppeano “site number 4D” (hereafter, Oppeano 4D) and La Muraiola di Povegliano Veronese (hereafter “La Muraiola"), located in the middle of Verona plain (Fig. 1). The correlation of stable isotopic data from faunal material integrated with botanical records allows us to explore seasonal husbandry practices and to understand what local and non-local resources were available and used for rearing domestic herds, particularly sheep. Moreover, this will allow us to assess whether long-range herding practices evident in historical times originated during the MBA and to uncover the driving forces that led to their development.

2. Materials

2.1. Study sites of Oppeano 4D and La Muraiola

2.1.1. Oppeano 4D

The waterlogged site of Oppeano 4D is located within a depression on the Holocene floodplain of the Adige River. In 2014-2015, during a rescue excavation a multi-phase settlement was exposed with well-preserved domestic structures. Here we focus on the second settlement phase dating to the MBA 1-2, when eight contemporary wooden structures oriented north-south were built at the ground-level, with wooden walls, internal partitions and hearths (Fig. 3a) (Nicosia et al., 2022; Polisca, 2025).Soil micromorphology and faecal biomarker analysis indicated that the deposits inside the structures resulted from domestic and stabling activities (Nicosia et al., 2022, 2025). They consisted of finely laminated layers primarily composed of ash from the combustion of wood, cereal by-products, and food remains (i.e., burnt bones, shells), interspersed with *in situ* trampled herbivore dung, testified e.g. by faecal spherulites and biomarkers (Fig. 3b). These structures were interpreted as byre-houses, where people and livestock coexisted under the same roof. The abandonment of the site was likely driven by a rise in the groundwater table that triggered permanent waterlogged conditions until today.

The faunal remains from Oppeano 4D were mainly from domestic species (92.4%) with sheep and goats, many morphologically identified as sheep, constituting the dominant taxa, followed by cattle and pigs (Fig. 3c). The zooarchaeological data suggest agro-pastoral activities with sporadic hunting, likely aimed at preventing crop damage, so-called ‘garden hunting’ (Orton *pers. comm.*). Sheep/goat were initially slaughtered primarily at around 6 months old, while in the subsequent phase there was an increase in heavy lambs (6-12 months) as well as young adult individuals (2-4 years) (Supplementary Table S1). Referring to models proposed by Helmer et al. (2005), this may reflect mixed production of both meat and milk. Wool production has been classically identified as an increase of adults, which is not evident at this site from the dental remains.

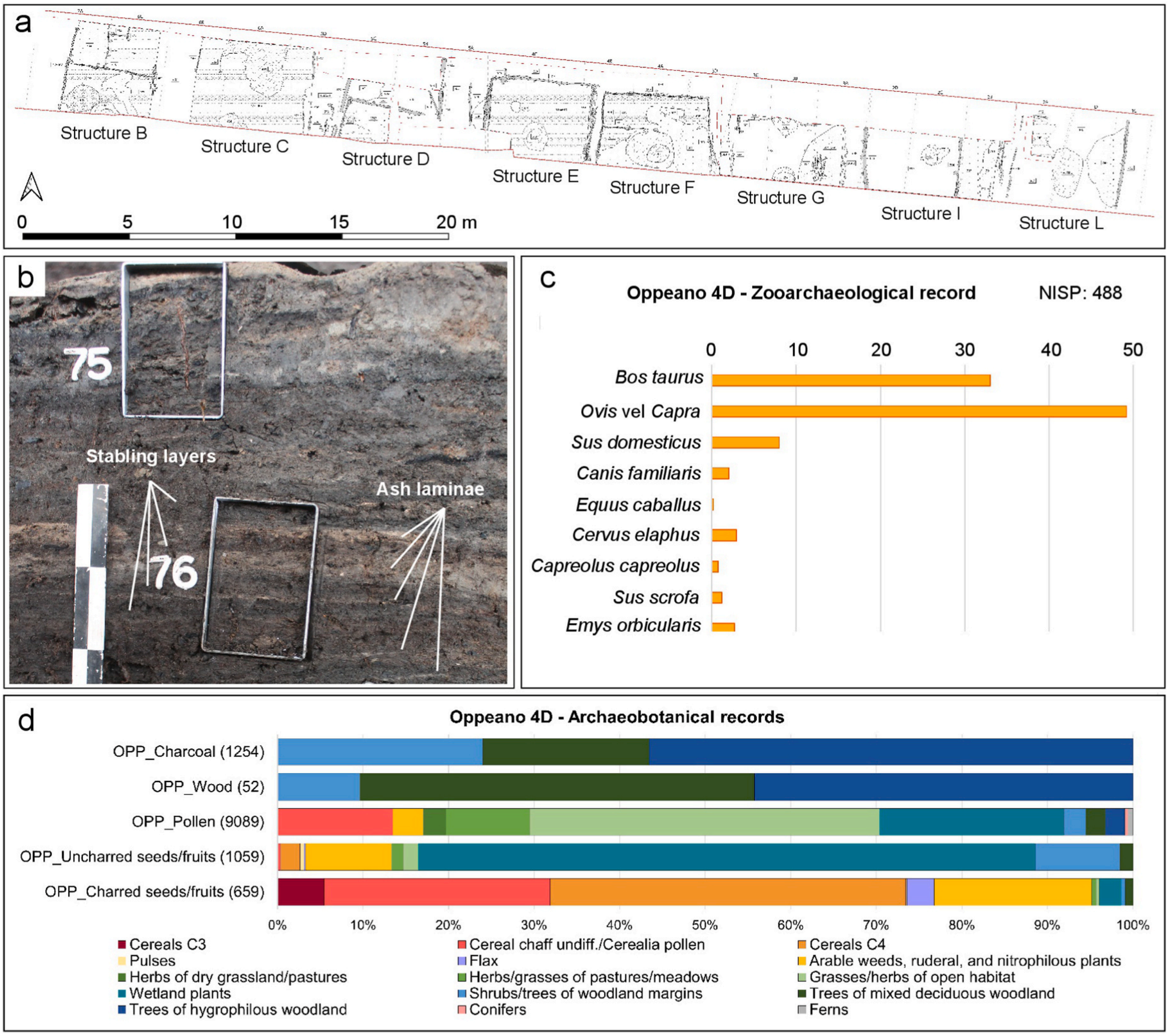

Fig. 3. a. Excavation plan of Oppeano 4D (modified from Nicosia et al., 2025, Fig. 2); b. Example of a finely laminated sequence of hearth rake-out and stabling layers from structure F at Oppeano 4D; c. Summary of faunal records from Oppeano 4D; d. Summary of archaeobotanical records from Oppeano 4D: percentage values are based on the total sum of finds specified into brackets (complete sample information on pollen and carpological datasets are available in Nicosia et al., 2025; for wood and charcoal, in D'Aquino et al., 2026), see Supplementary Table S2 for the plant *taxa* considered in each ecological plant group.

From the dung-rich deposits, the palynological and (uncharred) carpological records revealed a large variety of environments probably used as pastures and for fodder and bedding material (D'Aquino, 2025; Nicosia et al., 2025). Humid environments typical of the floodplain were evident from the abundance of sedges and alder (for wood use, see D'Aquino et al., 2026). Other open habitats, mostly anthropogenic, are represented by a large variety of grasses and forbs, such as xerophytes from dry grasslands, some typical pasture/meadows indicators, arable weeds, and nitrophilous/ruderal herbs from disturbed areas and fallow land. Abundant cereal chaff, some grains and rare pulses, and seeds of edible fruits are mainly carbonised and unrelated to the livestock. Charred seeds of barnyard grass, a wild and edible panicoid grass similar to millet, are particularly abundant. The most attested tree of the mesophilous woodland was deciduous oak, with little evidence of maple and elm (D'Aquino et al., 2026). An overview on the archaeobotanical records from Oppeano 4D is illustrated in Fig. 3d and complete taxa list per ecological plant group is provided in Supplementary Table S2.

2.1.2. *La Muraiola di Povegliano Veronese*

The Terramara site of La Muraiola di Povegliano Veronese is located in the spring belt, within an incision of the Late Pleistocene alluvial megafan of the Adige River (Castagnetti, 1977; Filippi, 1998; Zorzin, 1997). Excavations in the 1980s revealed a large moat-and-rampart system surrounding the settlement, along with domestic structures (Salzani, 1997). The site dates from MBA 1/2 to the RBA, although only limited evidence from RBA due to modern agricultural activities. New excavations, started in 2022 as part of the ERC-GEODAP project (Fig. 4a), revealed that the settlement contained both ground-level structures – such as external cooking plates, floors and livestock penning areas – and buildings on posts. Animal penning areas were clearly identified through the presence of phosphatic crusts (Fig. 4b), which formed through the cementation of herbivore dung in stocking areas due to peculiar diagenetic processes (see Polisca et al., 2025, where spherulites presence is also discussed). Livestock were a key in the formation of these deposits, with accumulations of trampled herbivore dung being observed both in external areas and within specific structures interpreted as barns (Polisca, 2025).

The zooarchaeological and archaeobotanical analyses are ongoing. However, the analysis colludes with previous fauna analyses from the 1980s excavations (Riedel, 1997), with a strong focus on sheep/goat herding (Fig. 4c). The preliminary age-at-death profiles of the La Muraiola sheep/goat assemblage indicate the presence of almost all age classes. A substantial proportion of individuals were culled by the age of 2 years (with many slaughtered between 6 and 12 months), whereas a

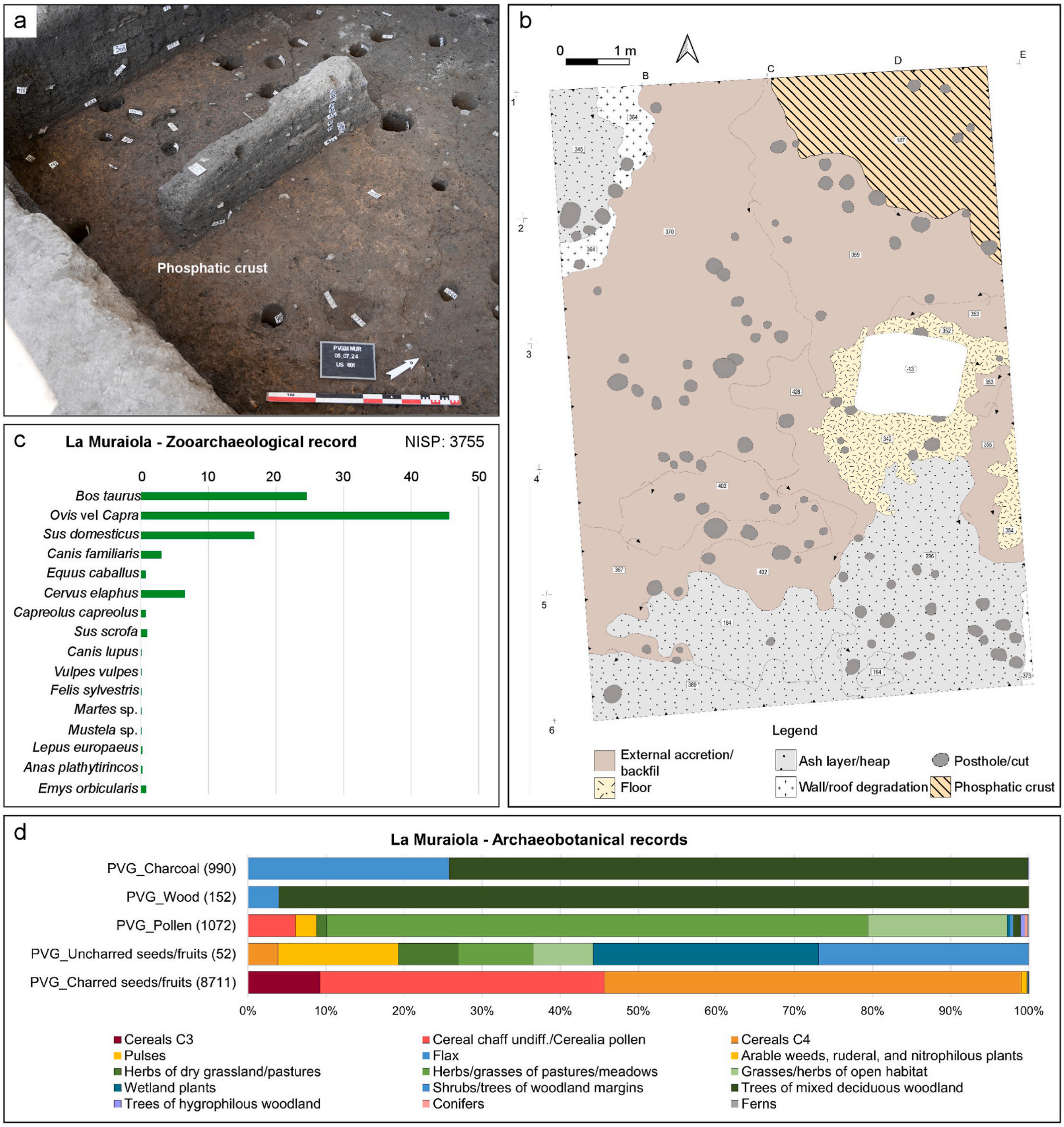

Fig. 4. a. Excavation plan of La Muraiola (2022–2025 excavations); b. Phosphatic crusts indicative of animal penning areas at La Muraiola (modified from Polisca, 2025, Fig. 5f); c. Summary of faunal records from La Muraiola; d. Summary of archaeobotanical records from La Muraiola: percentage values are based on the total sum of finds specified into brackets (complete sample information on pollen is available in Polisca et al., 2025; for carpological, wood, and charcoal datasets in D'Aquino, 2025), see Supplementary Table S2 for the plant *taxa* considered in each ecological plant group.

considerable number reached adulthood (3–4 years), with several specimens exceeding 4 years of age. Lambs culled between 2 and 6 months are also documented, although in smaller numbers (Supplementary Table S1). Neonates were attested – albeit in small quantities – from post-cranial elements.

The records of charcoal and mineralised wood fragments attest the use of mesophilous woodland with mixed oaks, hornbeam, elm, and of cornelian cherry from woodland margins, likely used for the collection of fruits and perhaps also for animal fodder/bedding (D'Aquino, 2025). Carbonised crop remains are abundant, i.e. rare pulses, abundant emmer and einkorn, and broomcorn millet (D'Aquino, 2025). A dense concentration of burnt broomcorn millet was found in a possible storage context close to an animal penning area (D'Aquino, 2025; Polisca et al., 2025). Panicoid phytoliths likely deriving from broomcorn millet have been found also in the phytolith record from the stabling crusts (Polisca et al., 2025; Supplementary Table S2). Seeds of wild plants from grasslands are rare, and are mainly from arable weed species of cultivated plots. However, the pollen record from phosphatic crusts (Polisca et al., 2025) presents herbs typical of pastures/meadows and of dry grasslands, in addition to being dominated by Cichorieae, observed to thrive in overgrazed pasturelands (Florenzano et al., 2015). Despite the site being close to springs, vegetation from humid habitats is almost absent in the archaeobotanical records: sedges occur only as rare mineralised seeds, likely preserved because of/in dung, and alder is absent also from the charcoal, mineralised wood, and pollen records. Dry preservation conditions can lead to a bias in the reconstruction of the natural vegetation in contrast to food plants, due to the under-representation of non-carbonised plant material associated with animal husbandry and to differential pollen preservation, with the resistant and highly recognizable pollen of Cichorieae being overrepresented. However, overall the archaeobotanical records associated with dung suggest a different foddering strategy than at Oppeano 4D, as evident from the overview on the archaeobotanical records from La Muraiola illustrated in Fig. 4d (complete taxa list per ecological plant group is provided in Supplementary Table S2).

2.2. *Faunal samples*

Ten sheep/goat mandibles from each site were selected (Table 1) for bulk bone collagen and incremental bioapatite sampling from the second (M2) and third molars (M3) for carbon and nitrogen, and for carbon, oxygen and strontium isotope analysis respectively. Sheep and goat are morphologically very similar; however, they can be distinguished based on morphological criteria (cf. Balasse and Ambrose, 2005; Boessneck et al., 1964; Gillis et al., 2011; Halstead et al., 2002; Zeder and Pilaar, 2010). Distinguishing between these two species is important as they have different physiology and feeding habits that may be reflected in the stable isotope results, as shown by Balasse and Ambrose (2005). Based on the morphological characteristics of mandibles and teeth (Gillis et al., 2011; Halstead et al., 2002), these mandibles were identified mainly as sheep, while sample OPP2 and possibly OPP3 may belong to goats. However, in the absence of confirmation from proteomics, all teeth will from now on be described as sheep/goat. We targeted the seasonal diet via incremental samples from M2 and M3, that represent approximately the first and second year of life. This is based on tooth formation in Soay sheep (Witzel et al., 2018), where the mineralisation of second molar crown completes between 9 and 11 months, while that of the third molars begin mineralisation at approximately 12 months and complete by 26 months.

In addition to molars, bone samples were taken for carbon and nitrogen isotope analysis. Mandible bone samples were taken from individual sampled previously for M2/M3 at both Oppeano 4D and La Muraiola. These samples from mandibles were taken in the area next to the M3/M2. Ten post-cranial bones samples were taken from other species from Oppeano 4D and 15 post-cranial bones were also sampled from La Muraiola site for carbon and nitrogen isotope analysis (Table 1).

2.3. *The ^{87}Sr/^{86}Sr baseline plant samples*

We targeted a 30 km radius around Oppeano focused on plants from

Table 1

List of samples selected for stable isotope analysis with: Sample Id; taxon; bone sampled; symmetry (L = left, R = right); tooth wear and fusion stage (Wear stages are based on Grant (1982); F = fused); age-at-death estimation (based on Payne (1973) and Barone (1995)) and the stable isotope analysed. Further archaeological information for each sample is found in Supplementary Table S6.

SAMPLE ID	Taxon	Bone sampled	Symmetry(L/R)	Tooth wear (Grant)/Fusion stage	Age (Payne/Barone)	SI
Oppeano 4D						
OPP_OC1	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	L	M$_2$: g M$_3$: g	2–4 years	O, C, N, Sr
OPP_OC2	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: g M$_3$: g	2–4 years	O, C, N, Sr
OPP_OC3	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: g M$_3$: g	4–6 years	O, C, N, Sr
OPP_OC4	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: g M$_3$: f	2–4 years	O, C, N, Sr
OPP_OC5	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: g M$_3$: g	2–4 years	O, C, N, Sr
OPP_BT1	*Bos taurus*	Astraglus	L	–	–	C, N
OPP_BT2	*Bos taurus*	Metatarsal - proximal	R	–	–	C, N
OPP_BT3	*Bos taurus*	Mandible	R			C, N
OPP_BT4	*Bos taurus*	Radius - proximal	R	F	>12/15 months	C, N
OPP_BT5	*Bos taurus*	Phalanx 1	–	F	>20/24 months	C, N
OPP_SD1	*Sus domesticus*	Tibia - distal	L	F	>24 months	C, N
OPP_SD2	*Sus domesticus*	Mandible	L	M$_3$: a	Subadult	C, N
OPP_SD3	*Sus domesticus*	Astragalus	L	–	–	C, N
OPP_SD4	*Sus domesticus*	Scapula	L	F	>12 months	C, N
OPP_CE	*Cervus elaphus*	Mandible	L	–	Adult	C, N
La Muraiola di Povegliano Veronese						
PVG_OC1	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: g M$_3$: g	4-6 years	O, C, N, Sr
PVG_OC2	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	L	M$_2$: g M$_3$: g	4-6 years	O, C, N, Sr
PVG_OC3	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: k M$_3$: g	>6 years	O, C, N, Sr
PVG_OC4	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	R	M$_2$: h M$_3$: g	>6 years	O, C, N, Sr
PVG_OC5	*Ovis aries/Capra hircus*	Mandible/M$_2$, M$_3$	L	M$_2$: g M$_3$: g	4-6 years	O, C, N, Sr
PVG_OC6	*Ovis aries*	Tibia - distal	R	F	>25-35 months	C, N
PVG_OC7	*Ovis aries/Capra hircus*	Radius - shaft	L	–	–	C, N
PVG_OC8	*Ovis aries*	Astragalus	R	–	–	C, N
PVG_OC9	*Ovis aries*	Metacarpal	R	F	>30-36 months	C, N
PVG_BT1	*Bos taurus*	Tibia - distal	L	F	>24-30 months	C, N
PVG_BT2	*Bos taurus*	Calcaneus	R	F	>36 months	C, N
PVG_BT3	*Bos taurus*	Metacarpal	R	–	–	C, N
PVG_BT4	*Bos taurus*	Astragalus	R	–	–	C, N
PVG_BT5	*Bos taurus*	Phalanx 1	–	F	>20-24 months	C, N
PVG_SD1	*Sus domesticus*	Radius - proximal	L	F	>12 months	C, N
PVG_SD2	*Sus domesticus*	Calcaneus	L	F	>24-30 months	C, N
PVG_SD3	*Sus domesticus*	Astragalus	R	–	–	C, N
PVG_SD4	*Sus domesticus*	Scapula	R	F	>12 months	C, N
PVG_CE1	*Cervus elaphus*	Astragalus	L	–	–	C, N
PVG_CE2	*Cervus elaphus*	Phalanx 1	–	F	–	C, N

the following lithological units (Supplementary Table S3): LU-1: Western portion of the Lessini Mts., calcareous bedrock, LU-2: Eastern portion of the morainic amphitheatre of the Garda Lake, calcareous bedrock, LU-3: Last Glacial Maximum megafan of the Adige River, LU-4: Holocene floodplain of the Adige River, and LU-5: Eastern portion of the Lessini Mountains, basaltic bedrock. The sampling was carried out on August 29th and September 1st 2022 by MDC and FP. In each lithological unit, we sampled 1 to 2 areas (A and B in Fig. 1) with arboreal vegetation that was at least 50 m from cultivated fields, modern rivers and channels, and major roadways. These precautions were to avoid contamination from fertilizers, pesticides, and water sources other than the local groundwater and soil.

We collected leafy material from trees and shrubs in managed and unmanaged woods, and from two historical gardens, as summarised in Supplementary Table S3. Both native and allochthonous plant species of the Po Plain and the pre-alpine Lessini Highlands were sampled (Supplementary Table S4). Native vegetation is based on the palynological studies of Holocene sequences in the region (Dal Corso, 2018). Leaves were hand-picked at different heights (between 50 and 300 cm from the soil) and at differing levels of exposure to sunlight. For consistency, the leaves were collected from a single plant per species (Supplementary Table S4). Within a plot, the plants were less than 50 m far away among each other. Healthy plants were selected, and leaves were left to air-dry indoors laying on a table, outside their bags, for two days and then stored in clean paper bags.

3. Methods

3.1. Preparation of isotope samples

Prior to sequential enamel sampling, the tooth surfaces were cleaned using an abrasive drill bit. A sequence of enamel samples were then drilled from enamel-root junction (ERJ) to the apex of the crown with a Komet drill bit (no. 835–104–010). For Oppeano 4D, the mean number of sequential samples taken was 10 for M2 and 14 for M3, while for La Muraiola, it was 8 and 9 samples respectively. The pre-treatment protocol was carried out for Oppeano 4D, which involved samples being soaked in 0.1M Acetic Acid per mg for 5 h, rinsed in distilled water 5 times and then dried in a freeze dryer (Tornero et al., 2013), while powders from La Muraiola were not. All samples were analysed for δ^{18}O and δ^{13}C isotopes. Furthermore, 2 samples per tooth from Oppeano 4D and one sample per tooth from La Muraiola have been taken and analysed for ^{87}Sr/^{86}Sr. Different protocols should not have affected the interpretation of results since we are principally concerned with relative, rather than absolute, values and consequently the differing pre-treatment protocol should not impact on the shape of curves.

In preparation for sampling for strontium isotope analysis, tooth surfaces were also cleaned using an abrasive drill bit. A single sample was then taken for each tooth from near the occlusal surface. Samples were further cleaned in an ultrasonic bath, rinsed, and dried. The clean enamel samples, weighing 20-40 mg, were stored in clean microcentrifuge tubes and transferred to a clean working area (class 100, laminar flow) at Cardiff Earth Laboratory for Trace Element and Isotope Chemistry (CELTIC) for further sample preparation and ^{87}Sr/^{86}Sr isotope analysis. To prepare plants for strontium chemistry, the plants were first freeze dried. Then an approximately 0.2-0.3 g sample of each plant was crushed and combined with samples of plants from the same sampling plot, resulting in a mixed sample of approximately 1.0-1.5 g. These samples were stored in clean microcentrifuge tubes and transferred to CELTIC.

For δ^{13}C and δ^{15}N isotope analysis, collagen was extracted using a modified Longin (1971) method (Brown et al., 1988). Mass spectrometry was performed using a Flash 1112 series elemental analyser coupled with a Finnigan DELTA V Advantage (Thermo Fisher Scientific) using established protocols (Scorrer et al., 2021). Analytical precision (1σ) of the in-house calibrated standards (Scorrer et al., 2021) were 0.08 and 0.07 for δ^{13}C and δ^{15}N, respectively.

3.2. Isotope analysis

The isotope composition of the structural carbonate within the sequential enamel samples was analysed for δ^{18}O and δ^{13}C at the Cardiff University Stable Isotope Facility. Samples were acidified for 5 min with >100% ortho-phosphoric acid at 70 °C and analysed using a Thermo MAT253 dual inlet mass spectrometer coupled to a Kiel IV carbonate preparation device using protocols described in Scorrer et al. (2021). The resultant isotope values are reported as per mil (^{18}O/^{16}O) normalised to the VPDB scale using an in-house carbonate reference material (BCT63) calibrated against NBS19 certified reference material. The long-term reproducibility for δ^{18}O BCT63 is ± 0.04 per mil and ±0.03 for δ^{13}C (1σ). Oxygen carbonate values ($\delta^{18}O_{C\ VPDB}$) were converted to phosphate ($\delta^{18}O_{P\ VSMOW}$) using the formula from Chenery et al. (2012).

In the CELTIC laboratories, mixed plant samples for strontium isotope analysis were transferred to clean beakers, 2 mL of concentrated HNO_3 was added, and the samples were left to digest under a fume hood for at least a week. Next, 2 mL of 30-32% H_2O_2 was added to each sample and the samples were left to digest under a fume hood for at least 2-3 days. The lids were then removed, and the samples were placed on a hot plate to dry down for 24 h. After the samples were dried, 1 mL of 8 M HNO_3 was added to each sample, and they were allowed to flux on a hot plate at 120 °C for at least 24 h until fully dissolved. The redissolved digested samples were transferred to clean microcentrifuge tubes using unique clean pipette tips and centrifuged for 2-3 min. Only the liquid portion of each sample was loaded into columns for strontium extraction. Bulk enamel samples for strontium isotope analysis were digested in 8M HNO_3 and heated overnight at 120 °C. The dissolved samples were then loaded into columns for strontium extraction.

Strontium extraction used Sr Spec™ resin following a revised version of the protocol of Font et al. (2007). The samples were loaded into resin columns in 1 ml 8M HNO_3. Matrix elements (including calcium and traces of rubidium) were then eluted in several washes of 8M HNO_3 and the samples placed on a hotplate (120 °C) overnight. This process was then repeated for a second pass to remove all remaining calcium. Once the purified samples were dry, the samples were re-dissolved in 2% HNO_3. The strontium isotope ratios were measured using a Thermo Fisher Scientific Neoma MC-ICP-MS/MS installed May 2024 at Cardiff University. Instrumental mass bias was corrected for using the exponential law and a normalization ratio of 8.375209 for ^{88}Sr/^{86}Sr (Nier, 1938). Residual krypton (Kr) and rubidium (^{87}Rb) interferences were monitored and corrected for using ^{84}Kr and ^{86}Kr (^{83}Kr/^{84}Kr = 0.20175 and ^{83}Kr/^{86}Kr = 0.66474; without normalization) and ^{85}Rb (^{85}Rb/^{87}Rb = 2.5926), respectively. Accuracy of the method is assessed by measurement of the in-house EC-5 coral standard during all analytical sessions, which gives an ^{87}Sr/^{86}Sr value of 0.709162 ± 0.000020 (2σ, n = 217), consistent with the expected value of approximately sea water (0.709180). Data is also corrected against a NIST SRM 987 value of 0.710248 (Avanzinelli et al., 2015). The values are reported to 5 decimal places.

The δ^{13}C and δ^{15}N isotope analysis of collagen samples was carried out at the National Environmental Isotope Facility at the British Geological Survey (UK) using an Elementar vario ISOTOPE cube elemental analyser (EA) coupled to an isoprime precisION isotope ratio mass spectrometer (IRMS) with an onboard centrION continuous flow interface system. The EA inlet converts organic materials in solid sample matrices into pure gases via high-temperature combustion. The post-combustion gas mixture is then separated and focused into individual molecular species for quantitative analysis of nitrogen and carbon content and are then passed online to the IRMS for the determination of their stable isotope composition. Carbon and nitrogen isotope data are reported in delta (δ) notation in per mille (‰) relative to the international reference scales VPDB and AIR, respectively. Sample δ^{13}C and δ^{15}N were normalised to VPDB and AIR, respectively, using a multipoint calibration including B2215 (δ^{13}C −22.92‰, δ^{15}N +4.26‰), USGS88 (δ^{13}C −16.06‰, δ^{15}N +14.96‰), USGS40 (δ^{13}C −26.39‰, δ^{15}N −4.52‰), USGS61 (δ^{13}C −35.05‰, δ^{15}N −2.87‰), and USGS63 (δ^{13}C −1.17‰, δ^{15}N +37.83‰). An internal laboratory collagen standard, SADCOW (δ^{13}C −22.6‰, δ^{15}N +4.4‰), was used as a secondary reference material to check the calibration. External precision (1σ) for the within-run standards was <0.1‰ for δ^{13}C and δ^{15}N. Acetanilide (71.09 %C and 10.36 %N) was used to calculate the carbon and nitrogen elemental content of samples, and C/N is reported as the atomic ratio.

3.3. *Dietary value inference*

The enrichment of ^{13}C values between diet and bioapatite has been shown to vary between species depending on dietary composition, physiology, and body size (Cerling and Harris, 1999; Passey et al., 2005; Zazzo et al., 2010). For diet-bioapatite spacing, we used the 14.5‰ based on ruminants (Cerling et al., 2021). For collagen, we applied a 5.1‰ - enrichment between diet and collagen (Ambrose and Norr, 1993).

3.4. *Statistical analysis*

Isotope results were statically tested using PAST (Hammer), the significance level was set to <0.05. As all sample groups consisted of fewer than 30 individuals, only non-parametric tests were employed (Kruskal-Wallis/Mann-Whitney), given the limited reliability of normality tests for small datasets. No statistical tests were performed when there were fewer than 10 samples. When pairwise Mann–Whitney tests were conducted following the Kruskal–Wallis test, Bonferroni correction was applied to adjust the resulting *p*-values. All standard deviation is given to 1σ.

4. Results

4.1. *Sequential enamel carbon and oxygen isotopes for sheep/goat individuals*

The δ^{13}C values of the Oppeano 4D M2s ranged from −12.7 to −5.1‰ with an average amplitude of 4.4‰ (range: 2 to 6.5‰), while the M3 values fall between −13.6 and −4.6‰, with an average amplitude of 5.1‰ (range: 3.9 to 6.7‰, Table 2; Fig. 5a–j). Where repeated samples were taken, a typical standard error between samples was 0.05‰. Overall, the range in values suggests that animals were consuming plants with a large variation in δ^{13}C. The paired molars for each individual showed good correspondence between teeth, suggesting no significant missing records. On average, OPP3 had the lowest amplitude observed in M2 of 2‰, and in M3, the lowest δ^{13}C (−13.7‰) values observed at Oppeano 4D (Fig. 5e/f), while OPP5 had the highest δ^{13}C values (−5.1, −4.6‰) and largest amplitude (6.5, 6.7; Fig. 5h/j). The Kruskal-Wallis test showed that there was a significant difference between sample medians ($Hc = 25.6$, $p < 0.05$); specifically, after the *p* value correction, the Mann-Whitney pairwise test exhibited significant differences between individual OPP_OC5 and individuals OPP_OC1 and OPP_OC3 (respectively $p = 0.0008$ and $p = 0.001$). At La Muraiola (Fig. 5k–t), both M2 and M3 have similar δ^{13}C value ranges (M2: −12.3 to −9.8‰; M3: −13.2 to −9‰). Moreover, the values from M2 and M3 exhibit low amplitude between the highest and the lowest values (an average of 1.5 and 1.9‰ respectively). At La Muraiola, a significant difference between sample medians is attested as well ($Hc = 51.5$, $p < 0.05$) and the Mann-Whitney pairwise test (after *p* values correction) showed that PVG_OC1 and PVG_OC3 were not significantly different from one another, but they both differed significantly from all other individuals. This is because both PVG_OC1 and OC3 present the lowest amplitude for M2 (0.7 and 0.6‰ respectively) and for M3 (1.2 and 1.7‰ respectively). On the other hand, the other specimens (PVG_OC2, PVG_OC4, and PVG_OC5) did not show significant differences among themselves. The distribution of the δ^{13}C values was significantly different between sites, with La Muraiola exhibiting a smaller range overall (Mann-Whitney for δ^{13}C, $U = 4116$, $p=0.03$).

The δ^{18}O values, observed in all sheep/goat teeth from Oppeano 4D, present a sinusoidal curve (Fig. 5). The M2 values range from −7.7 to −0.8‰ and exhibit large variation in amplitude between values (1.8 to 5.1‰). OPP_OC3_M2 had the lowest amplitude (1.8‰), considerably lower than that observed in its respective M3 (4.1‰) and in other individuals. The M3s overall exhibited a larger range of values (−8.4 to −0.1‰) than M2s, with an average amplitude of 5.5‰. The δ^{18}O values from La Muraiola generally present a different picture than that observed at Oppeano 4D. For the M2s, the δ^{18}O values vary between −6.2 and −3.7‰ with a lower amplitude than exhibited in Oppeano 4D teeth (1.2 to 2.1‰). Sheep are non-obligate drinkers and can receive most of their daily water intake from leaf-water. The δ^{18}O composition of leaf-water is strongly influenced by seasonal changes in temperature, and results in a large amplitude between the highest and the lowest values (Levin et al., 2006). A low δ^{18}O variation could be an indication

Table 2

Summary of the δ^{18}O and δ^{13}C results from incremental samples of sheep/goat molars. The mid-point is calculated Max + Min/2, while the amplitude is Max-Min. N represents the number of incremental samples taken for each tooth. The complete list of values can be found in Supplementary Table S5.

		δ^{18}O				δ^{13}C			
SAMPLE ID	N	Max	Min	Mid-point	Amplitude	Max	Min	Mid-point	Amplitude
OPP_OC1_M2	13	−2.8	−7.7	−5.3	4.9	−9.1	−12.5	−10.8	3.4
OPP_OC1_M3	16	−0.8	−6.7	−3.8	5.9	−8.3	−12.9	−10.6	4.6
OPP_OC2_M2	9	−1.6	−4.4	−3	2.8	−6.2	−11.3	−8.8	5.0
OPP_OC2_M3	16	−2.5	−8.5	−5.5	6.0	−6.8	−12.3	−9.6	5.4
OPP_OC3_M2	7	−3.3	−5.1	−4.2	1.8	−10.1	−12.1	−11.1	2.0
OPP_OC3_M3	12	−1.8	−5.9	−3.9	4.1	−9.6	−13.6	−11.6	3.9
OPP_OC4_M2	12	−0.8	−5.9	−3.4	5.1	−7.5	−12.7	−10.1	5.2
OPP_OC4_M3	15	−1.9	−6.8	−4.4	4.9	−6.8	−11.8	−9.3	4.9
OPP_OC5_M2	10	−1.3	−4.8	−3.1	3.5	−5.1	−11.5	−8.3	6.5
OPP_OC5_M3	12	−0.1	−7.0	−3.6	6.9	−4.6	−11.3	−8.0	6.7
PVG_OC1_M2	8	−4.1	−5.2	−4.7	1.2	−9.9	−10.5	−10.2	0.6
PVG_OC1_M3	9	−3.9	−5.5	−4.7	1.6	−9.8	−10.9	−10.4	1.2
PVG_OC2_M2	9	−4.1	−6.2	−5.2	2.1	−10.2	−12.5	−11.4	2.3
PVG_OC2_M3	9	−4.5	−7.8	−6.2	3.3	−10.3	−12.5	−11.4	2.3
PVG_OC3_M2	6	−3.8	−5.9	−4.9	2.1	−9.8	−10.4	−10.1	0.6
PVG_OC3_M3	8	−3.4	−6.0	−4.7	2.6	−9.0	−10.7	−9.9	1.7
PVG_OC4_M2	6	−3.7	−4.9	−4.3	1.2	−10.6	−11.7	−11.2	1.1
PVG_OC4_M3	9	−4.4	−9.3	−6.9	4.9	−10.6	−13.2	−11.9	2.6
PVG_OC5_M2	9	−3.7	−5.5	−4.6	1.7	−10.9	−12.3	−11.6	1.4
PVG_OC5_M3	9	−4.9	−7.9	−6.4	2.9	−10.8	−12.6	−11.7	1.9

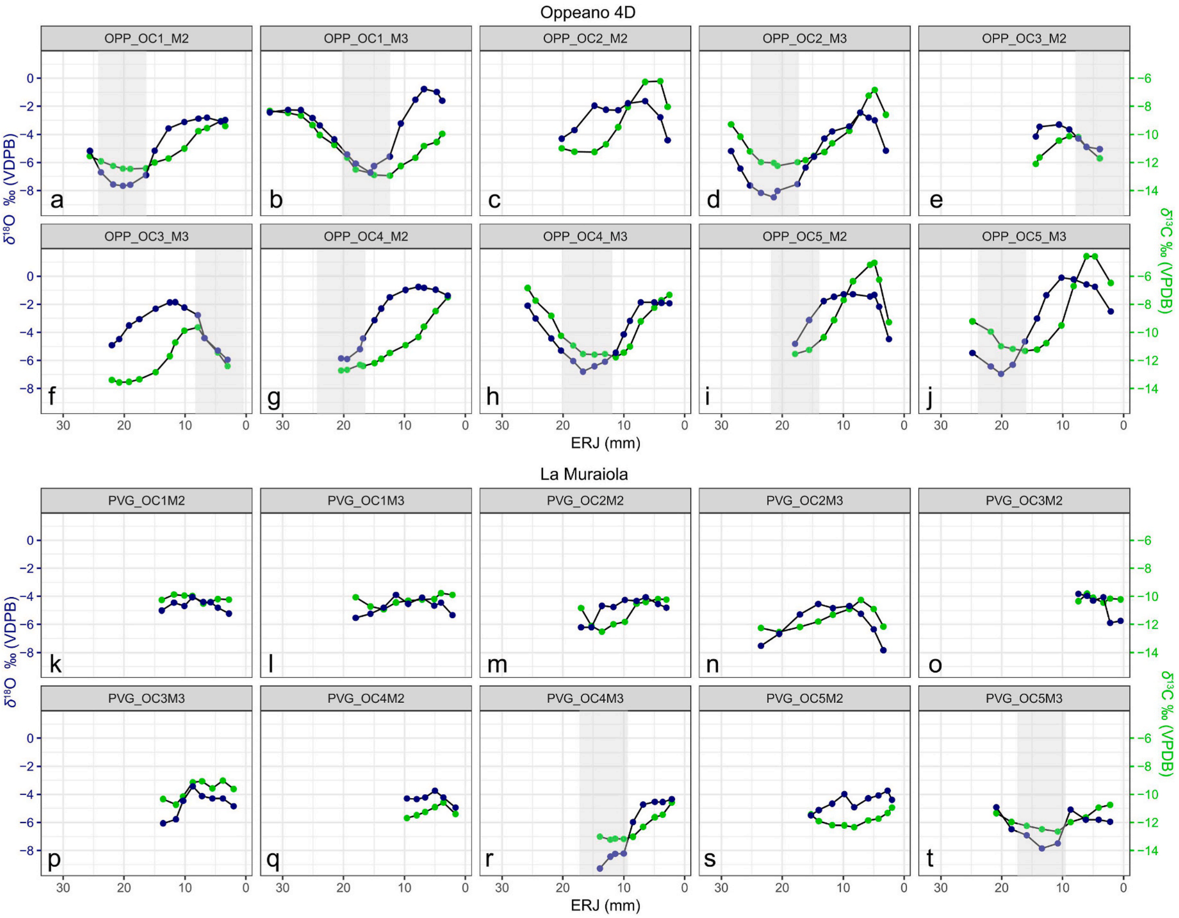

Fig. 5. δ^{18}O (blue) and δ^{13}C (green) results on Oppeano 4D (OPP) and La Muraiola (PVG). ERJ: The distance from the enamel root junction.

of water imbibed from water sources with low δ^{18}O, such as springs (Makarewicz and Pederzani, 2017). At La Muraiola, a similar larger amplitude was observed in M3s, however the average of 3.3‰ was lower than those observed in Oppeano teeth (range: −9.3 to −3.4‰; amplitude: 1.7 to 4.9 ‰). Individual PVG_OC4 showed the highest amplitude, 4.9‰, and its values, as well as those from PVG_OC2 and PVG_OC5, are the most similar to individuals from Oppeano 4D, while PVG_OC1 and PVG_OC3 showed the lowest variation (Fig. 6).

Significant differences were also found between individuals (Fig. 6) at Oppeano 4D but not at La Muraiola (Oppeano Kruskal-Wallis: *Hc* = 9.976, *p* = 0.04; La Muraiola: Kruskal-Wallis, *Hc* = 6.67, *p* = 0.1). The Mann-Whitney pairwise test shows a significant difference between individual OPP_OC5 and OPP_OC1, OPP_OC2, OPP_OC3, but after the correction of the *p* values no statistical difference remains

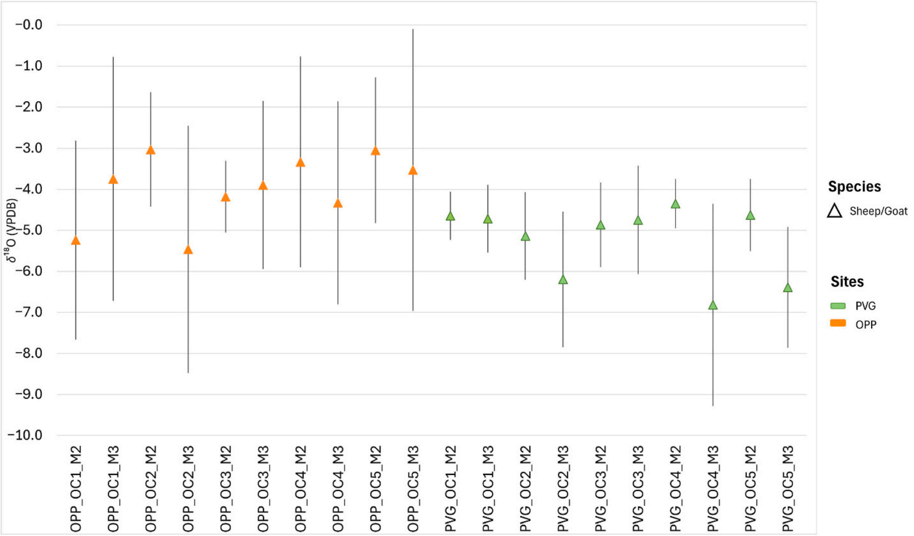

Fig. 6. Comparison of δ^{18}O values in sheep/goat from Oppeano 4D (OPP) and La Muraiola (PVG).

significant. However, if we look at the oxygen values it is evident how individual OPP_OC5 presents the highest value, attested in the M3 (−0.1‰). Overall, there is a significant difference between values and the variance observed at the two sites (Mann-Whitney: U = 2985.5, $p < 0.001$).

There is a strong correspondence between carbon and oxygen isotope curves at both sites, i.e. the δ^{13}C values are low when the δ^{18}O is low i.e. cold periods, and *vice versa*. At Oppeano 4D, δ^{13}C values show c. 4 to 5‰ difference between summer and winter, with values reaching a maximum −4-6‰ in warm periods (OPP_OC5_M3) and values less than −11‰ were observed coinciding with low δ^{18}O (Fig. 6). While at La Muraiola, instead, we observe a low amplitude of c. 1 to 2 ‰ throughout the year with individual PVG4_M3 exhibiting the lowest δ^{13}C value of −13.2‰ that occurs with low δ^{18}O values i.e cold period. Applying the fractionation adjustment of 14.5‰, the average δ^{13}C diet-inferred values range for La Muraiola is between −26.5 and −24.6‰, falling within the expected range for an environment composed of C_3 plants. The values from Oppeano 4D are similar (−26.4 to −22.7‰) albeit more enriched in ^{13}C, which may reflect a wider grazing catchment that were not exploited by or available to La Muraiola herds.

4.2. Strontium isotope results from sheep/goat samples

The results of the baseline plants suggest a fairly small range of ^{87}Sr/^{86}Sr ratios in the areas around Oppeano 4D and La Muraiola (Table 3). Samples LU-1 and LU-2 were taken on top of Eocene limestone substrates and gave ratios of 0.708338 and 0.708085. LU-3 was taken on top of the Late Pleistocene alluvial megafan and gave a ratio of 0.709148. LU-4 was taken on top of a Holocene overbank and gave the highest ratio of the sampled plants at 0.710581. LU-5 was taken on top of a Lower Miocene-Upper Cretaceous basalt and gave a very low ratio of 0.705475, reflecting the unradiogenic composition of basalts.

The ^{87}Sr/^{86}Sr ratios in enamel samples from Oppeano 4D individuals showed little variation (mean: 0.7107 ± 0.00005, Fig. 7). There was no significant difference observed between samples of M2s and M3s (Mann-Whitney: U = 44, $p = 0.7$). The results do not provide evidence of animals grazing on the higher ground to the north of the site (i.e., pre-Alps). This area is characterised by lower ratios (<0.709) than are observed in the Oppeano 4D dataset. OPP3 had a ratio of 0.7119 at the crown apex in M2, >0.001 greater than the mean of other individuals. The closest known comparable ^{87}Sr/^{86}Sr ratios are found approximately 80 km to the north, in the area of the Alps around modern Trento and Bolzano. Measured ^{87}Sr/^{86}Sr ratios in this area are varied, however. Some plants, soil leachates, and mineral waters gave ^{87}Sr/^{86}Sr ratios similar to or more strongly radiogenic than Opp3M2.1, while some fauna, plants, and soil leachates gave much less radiogenic ratios more closely reflecting the underlying limestone and dolomite bedrocks (Lugli et al. 2022). The amplitude of δ^{18}O values from Opp3M2 was the lowest within the dataset, and may suggest that this animal was raised in a different herd, in another area and subject to a different management regime. OPP4 was also an outlier, with an average ^{87}Sr/^{86}Sr ratio of 0.7098, similar to the plant baseline value given by LU-3. The comparison of the ^{87}Sr/^{86}Sr data with δ^{18}O values, revealed an interesting pattern observed in all teeth except OPP3_M2 where the ^{87}Sr/^{86}Sr ratios shifted very slightly down (c. 0.00005) from ‘winter’ to ‘summer’ (based on δ^{18}O values). This suggests that there is a relatively consistent pastoral management system, where animals moved between different summer and winter pastures.

The La Muraiola samples (N = 10) had a mean ^{87}Sr/^{86}Sr ratio of 0.7089 ± 0.0002. They were significantly different from those observed at Oppeano 4D (Mann-Whitney: U = 0, $p < 0.0001$). There were no marked differences between teeth of the same individuals, providing no evidence for longer term movement during early life. Moreover, the low amplitude in δ^{18}O values, suggests that possibly animals imbibed water from a source with a low seasonal amplitude in values with limited input

Table 3
Results of strontium analysis of baseline plant samples and sheep/goat specimens from Oppeano 4D and La Muraiola.

Site	Sample	^{87}Sr/^{86}Sr ratio	2SE	Material
Plant baseline	LU-1	0.708338	9.28E-06	*Acer campestre, Cornus mas, Corylus avellana, Fraxinus ornus, Fagus sylvatica*
Plant baseline	LU-2	0.708085	7.76E-06	*Fraxinus ornus, Ostrya carpinifolia, Prunus mahaleb,* deciduous *Quercus (pubescens?)*
Plant baseline	LU-3	0.709148	6.94E-06	*Acer campestre, Cornus mas, Fraxinus excelsior, Prunus mahaleb*
Plant baseline	LU-4	0.710581	6.68E-06	*Carpinus betulus, Fraxinus excelsior, Ulmus*
Plant baseline	LU-5	0.705475	7.52E-06	*Acer campestre, Castanea sativa, Corylus avellana, Ulmus galbra/minor?*
La Muraiola	PVG_OC1_M2	0.709088	9.64E-06	M_2
La Muraiola	PVG_OC1_M3	0.708781	8.98E-06	M_3
La Muraiola	PVG_OC2_M2	0.709125	8.72E-06	M_2
La Muraiola	PVG_OC2_M3	0.709245	9.24E-06	M_3
La Muraiola	PVG_OC3_M2	0.708725	1.10E-05	M_2
La Muraiola	PVG_OC3_M3	0.708721	8.90E-06	M_3
La Muraiola	PVG_OC4_M2	0.709072	9.72E-06	M_2
La Muraiola	PVG_OC4_M3	0.709031	1.05E-05	M_3
La Muraiola	PVG_OC5_M2	0.708671	8.22E-06	M_2
La Muraiola	PVG_OC5_M3	0.708672	1.19E-05	M_3
Oppeano 4D	Opp1M2.1	0.710491	1.03E-05	M_2
Oppeano 4D	Opp1M2.2	0.710743	7.50E-06	M_2
Oppeano 4D	Opp1M3.1	0.710756	9.94E-06	M_3
Oppeano 4D	Opp1M3.2	0.710459	9.34E-06	M_3
Oppeano 4D	Opp2M2.1	0.710909	1.24E-05	M_2
Oppeano 4D	Opp2M2.2	0.711021	1.02E-05	M_2
Oppeano 4D	Opp2M3.1	0.710804	1.10E-05	M_3
Oppeano 4D	Opp2M3.2	0.710931	5.52E-06	M_3
Oppeano 4D	Opp3M2.1	0.711958	6.12E-06	M_2
Oppeano 4D	Opp3M2.2	0.711083	6.34E-06	M_2
Oppeano 4D	Opp3M3.1	0.711163	6.76E-06	M_3
Oppeano 4D	Opp3M3.2	0.710912	9.42E-06	M_3
Oppeano 4D	Opp4M2.1	0.709824	8.54E-06	M_2
Oppeano 4D	Opp4M2.2	0.710088	8.04E-06	M_2
Oppeano 4D	Opp4M3.1	0.709836	8.12E-06	M_3
Oppeano 4D	Opp4M3.2	0.709775	7.18E-06	M_3
Oppeano 4D	Opp5M2.1	0.710769	8.90E-06	M_2
Oppeano 4D	Opp5M2.2	0.710914	7.58E-06	M_2
Oppeano 4D	Opp5M3.1	0.710559	9.16E-06	M_3
Oppeano 4D	Opp5M3.2	0.711010	8.70E-06	M_3

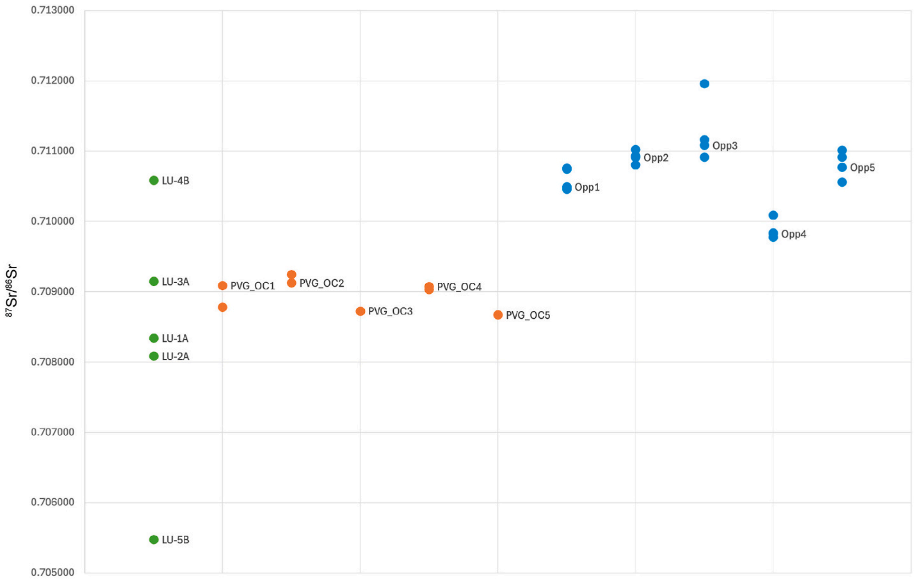

Fig. 7. Results of $^{87}Sr/^{86}Sr$ from baseline plants and faunal (sheep/goat) material from Oppeano 4D and La Muraiola.

from leaf-water.

4.3. Bone collagen carbon and nitrogen isotopes

The concentrations of carbon and nitrogen and the atomic ratios of the analysed samples fall within ranges proposed by van Klinken (1999) indicating that the collagen was of a good quality. In detail, at Oppeano 4D the C:N ratio ranges between 2.7 and 3.3, with %C values ranging from 36.7 to 44.1% and %N values from 12.9 to 18%; at La Muraiola, the C:N ratio varies between 3.2 and 3.3, with %C between 36.8 and 45% and %N ranging from 13.2 to 16.2%.

The δ^{13}C values from La Muraiola faunal samples range from −21.1 to −15.1‰ (N = 20, Table 4, Supplementary Fig. S1). The sheep/goat samples' δ^{13}C values range from −20.9‰ to −17.3‰ (N = 9). Turning to cattle, δ^{13}C values were enriched by c. 2‰ than those observed in sheep/goat (−18.4 to −15.9‰, N = 5). This suggests that sheep/goat and cattle may have not shared the same pastures, with the diet of the latter potentially containing some C_4 plants (Depaermentier et al., 2025). The pig samples range from −19.6 to −15.1‰ (N = 4), with two individuals (PVG_SD2 and PVG_SD3) that have similar values to that of the deer samples (average: −20.8‰), while one animal (PVG_SD1: −15.1‰), as in the case of cattle, exhibits values of a diet composed partially of C_4 plants (Depaermentier et al., 2025). This would fit within the wider context of the arrival of millet and its cultivation (Tafuri et al., 2018). At Oppeano 4D (N = 15), the range of carbon isotope values was greater than La Muraiola (−21.6 to −13.3‰). Sheep/goat individuals ranged from −19.8 to −17.5‰. This low variation in sheep/goat values found in Oppeano 4D may reflect the fact that all samples came from mandibles, while samples from La Muraiola came from different skeletal elements. Cattle at Oppeano 4D show a wide range of carbon isotope values, between −19.1 and −13.3‰ (N = 5), with one individual (OPP_BT3) clearly indicating the consumption of C_4 plants. As for the pigs from Oppeano 4D (N = 4), they exhibit little variability in comparison to those from La Muraiola, with values ranging from −21.1 to −20.1‰ and being close to those of the single red deer examined for the site. Two samples of red deer from La Muraiola and the single sample from Oppeano 4D, provided a δ^{13}C wild herbivore δ^{13}C 'baseline' of between −21.6 to −20.5‰, albeit based on a small sample (N = 3).

The overall average δ^{15}N value for Oppeano 4D individuals was 5.0 ± 0.7‰ (from 3.8 to 6.1‰), slightly lower than at La Muraiola (5.3 ± 1.2‰; from 3.1 to 7.4‰), with a cattle sample (PVG_BT3) exhibiting the lowest value of 3.1‰, while the highest value was observed in a sheep/goat sample (PVG_OC8: 7.4‰). Breaking it down by species, we observed that sheep/goat from La Muraiola had values between 4.4 and 7.4‰, which was on average lower than pig samples, which exhibited a higher average 6.5 ± 1.1‰ (range: 4.9 to 7.2‰). The δ^{15}N for sheep/goat and pig values from Oppeano 4D, have a lower average than observed in La Muraiola (Table 4). While cattle samples from La Muraiola were lower than those from Oppeano 4D (La Muraiola: from 3.1 to 5.2‰; Oppeano 4D: from 3.8 to 5.7‰). Interestingly, a single red deer sample from La Muraiola (PVG_CE1) exhibited a similar value to that observed in domesticates (5.5‰), perhaps reflecting that plants growing in the region were enriched in ^{15}N naturally due to local soil conditions (c.f. Schlütz et al., 2023).

Table 4
Summary of the δ^{13}C and δ^{15}N results (maximum, minimum and average) from Oppeano 4D (OPP) and La Muraiola (PVG). The complete list of values can be found in Supplementary Table S6.

SITE	SPECIES	N	δ^{13}C (‰ VPDB)			δ^{15}N (‰ Air)		
			Max	Min	Average	Max	Min	Average
OPP	Sheep/goat	5	−17.5	−19.8	−18.5	5.6	4.9	5.2
OPP	Cattle	5	−13.3	−19.1	−17.1	5.7	3.8	4.6
OPP	Pig	4	−20.1	−21.1	−20.6	6.2	4.6	5.4
OPP	Red deer	1	−21.6	−21.6	−21.6	4.2	4.2	4.2
PVG	Sheep/goat	9	−17.3	−20.9	−19.5	7.4	4.4	5.4
PVG	Cattle	5	−15.9	−18.4	−17.0	5.2	3.1	4.6
PVG	Pig	4	−15.1	−19.6	−17.9	7.2	4.9	6.5
PVG	Red deer	2	−20.5	−21.1	−20.8	5.5	3.6	4.5

4.4. Comparison of carbon and nitrogen isotope results from veneto region (Italy)

In Fig. 8, the bulk collagen stable isotope data presented here were compared with those published from other Bronze Age sites located in the province of Verona (Tafuri et al., 2009, 2018; Varalli et al., 2016, 2022). We only included species data from each site where two or more samples were available. Therefore, we excluded the values from sheep/goat, pigs, and deer bones from Olmo di Nogara. First, we consider the red deer values, whose collagen δ^{13}C values range from −21.6 to −17.4‰ ($N = 5$). These values fall within the range from other stable isotopic studies from sites from central and southern regions, −22.4 to −18.0‰ ($N = 14$, N of sites $= 7$; Davitashvili, 2024).

Returning to the domesticated animals, if collagen results are only considered, the overall range of δ^{13}C values from sheep/goats was between −20.9 to −17.3‰ with the lowest values observed in La Muraiola. However, when we consider the bioapatite values, then Oppeano 4D has the widest range in values (Diet inferred: −27.4 to −19.1‰; Fig. 9). The remarkable difference of c. 2‰ between δ^{13}C values from cattle and sheep/goats at La Muraiola, was not evident at other sites, where δ the range of δ^{13}C values for sheep/goats and cattle tend to be more similar. It is worth noting that only at La Muraiola and Oppeano 4D there was a suggestion of C_4 plant consumption in at least two cattle individuals (PVG_BT3 and OPP_BT3).

Turning to pigs, among the sites examined in this study, the specimens from Fondo Paviani stand out for their wide range of δ^{13}C values, including markedly higher than other sites, an indication of a diet with a C_4 plant component. A single individual from La Muraiola exhibits δ^{13}C values consistent with the consumption of C_4 plants (PVG_SD1). The samples from Fondo Paviani date to the RBA, a period during which millet became more common in northern Italy (Cavazzuti et al., 2019). There is also the question of identification of domesticated pigs, which is hampered by similar shape and size between the domestic and wild individuals. At La Muraiola, the δ^{13}C values may help us distinguish between species, where two individuals (PVG_SD2 and PVG_SD3) exhibit values that overlap with that of the red deer, while another (PVG_SD1) may have a diet with some contribution from C_4 plants, suggesting an animal eating a diet composed of waste from human food sources. The first two are metrically similar to domesticated pigs. Overall, this demonstrates that domesticated pigs have a wide dietary niche, which is evident from the wide variation observed in our comparative cohort. The variation is greatest at La Muraiola and Fondo Paviani in comparison to Arano di Cellore and Oppeano 4D.

For δ^{15}N values, there are a number of similarities and differences between sites for all species. Focusing on red deer, the red deer samples from all sites were all below 5.5‰, with the highest value observed in La Muraiola. It should be noted that a sample from red deer at Olmo di Nogara had a value of 6.3‰ (Tafuri et al., 2018). This falls within the broad range exhibited in other Bronze Age red deer samples from central and southern Italy (central: 4.2 to 5.3‰; southern: 3 to 8.5‰, Davitashvili, 2024). With respect to domesticated animals, all species from Oppeano 4D and Arano di Cellore exhibit values below 6‰, although ruminants from the latter site exhibit c.3 ‰ variation (Varalli et al., 2016). This may be a reflection of young animals within the sample. Sheep/goat at La Muraiola overlap with these sites, although they exhibit a larger range, with values reaching a maximum of 7.4‰. Cattle in general have values below 6‰, except at Fondo Paviani (7.2‰) (Tafuri et al., 2018) and Olmo di Nogara (7.3‰) (Tafuri et al., 2018); also at the latter site, sheep/goat exhibited high values (7.2‰) (Tafuri et al., 2018). Pigs overall are variable with samples from some sites exhibiting values as high as 9.7‰ (Fondo Paviani: Tafuri et al., 2018) while at Arano di Cellore as low as 3.6‰ (Varalli et al., 2016). The high values would be consistent with the omnivore nature of pigs and the consumption of protein-rich food waste or manured crop waste. Indeed, there appears a trend towards ^{15}N enrichment observed in other species from sites dating to the later phases of the Bronze Age (Olmo di Nogara, Fondo Paviani). Those samples identified as domesticated pigs with low values such as at Arano di Cellore, may be wild animals.

5. Discussion

5.1. Sheep/goat husbandry at Oppeano 4D and La Muraiola: variations in animal diets and local husbandry strategies

Sheep husbandry is central to understanding the Italian Bronze Age economy, because of its implications concerning wool production within the framework of the evolution of social complexity and specialised craft production characteristic of the period. Furthermore, uncovering past

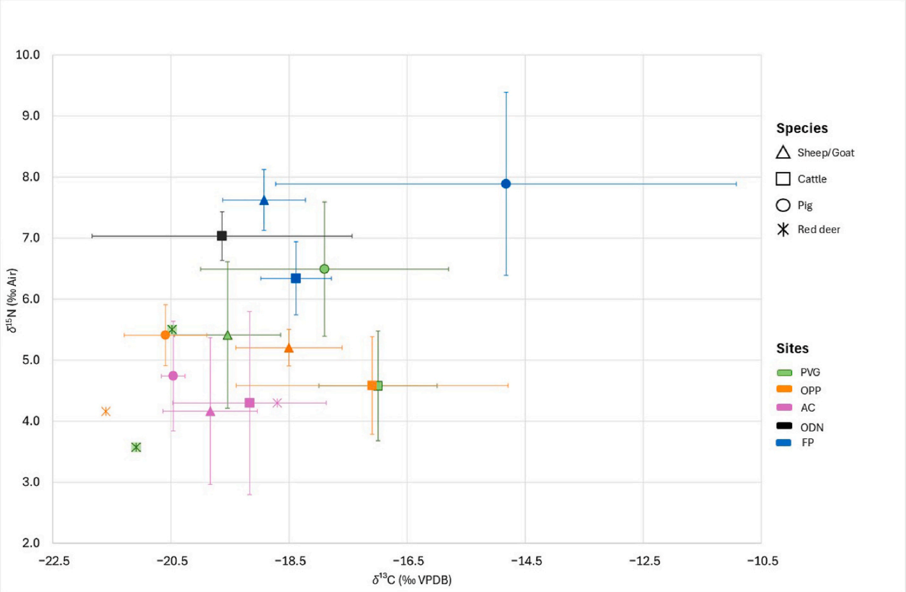

Fig. 8. Bulk collagen δ^{13}C and δ^{15}N results from La Muraiola (PVG) and Oppeano 4D (OPP) (this study), together with published results from the Early Bronze Age (EBA) site of Arano di Cellore (AC), the MBA-RBA site of Olmo di Nogara (ODN) and the RBA-Final Bronze Age (FBA) site of Fondo Paviani (FP) (Tafuri et al., 2009, 2018; Varalli et al., 2016, 2022).

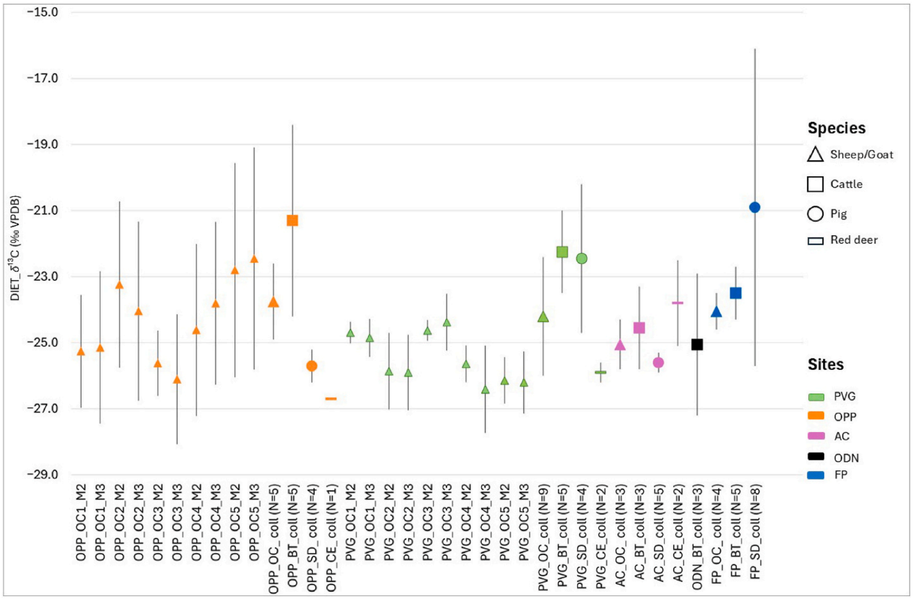

Fig. 9. Comparison between the maximum, minimum and mean inferred diet δ^{13}C values from enamel and collagen samples. The enamel carbon isotope are from the M2 and M3 samples from sheep/goat individuals from La Muraiola (PVG) and Oppeano 4D (OPP), while the collagen carbon isotope results are based on multiple individuals from sheep/goat, cattle, pig and red deer (the number in brackets is the sample size) from OPP, PVG (this study), the EBA site of Arano di Cellore (AC), the MBA-RBA site of Olmo di Nogara (ODN) and the RBA-FBA site of Fondo Paviani (FP) (Tafuri et al., 2009;Tafuri et al., 2018; Varalli et al., 2016;Varalli et al., 2022). The fractionation adjustment for diet follows 14.5‰ (Cerling et al., 2021) for bioapatite and 5.1‰ (Ambrose and Norr, 1993) for collagen.

pasture and fodder management strategies can help us uncover Bronze Age land use dynamics. Our case study of two MBA sites demonstrates that, while belonging to the same archaeological culture, the isotope data indicate different pastoral strategies that appear both tied to local resource availability and environments.

At Oppeano 4D, seasonal variation in the diet of sheep/goat was detected. The ^{13}C-enriched $\delta^{13}C_{bioap}$ values (M2 and M3: −5.1 and −4.6‰ respectively) may indicate these herds had access to open grassland pasture during summer. Moreover, these high values indicate sheep grazed in a relatively arid environment during summer. There is a strong signal of pollen from dry secondary grasslands found at the site. Secondary grasslands are enhanced by farming and grazing flocks in drained calcareous substrates (Perego et al., 2011, 2025; Rösch, 2018), similar to substrate on the ancient Adige megafan close to the site (Sorbini et al., 1984), or on smaller alluvial ridges (Marcolin and Zanetti, 2012), and dunes with coarse sediment within the floodplain (Tosco, 1958) (Fig. 1). The δ^{18}O signal from individual teeth at this site exhibit a large amplitude, which suggests a strong leaf-water effect. This is commonly observed in non-obligate ruminants, such as sheep and goats, in arid environments (Levin et al., 2006). The collagen values also suggest pasturing on open environments, supported by the relatively low δ^{15}N values (average: 5.2‰) that are indicative of herds grazing in areas with evidence of limited or low-level manuring (Fraser et al., 2011). Moreover, these δ^{15}N values suggest a low stocking rate, and/or no restricted movement within the pasture, such as corralling, indicating that the animals grazed for at least part of the year possibly under an extensive grazing strategy in open habitats and not in corrals/cultivated plots (Fig. 2b). Overall, from the perspective of the stable isotope analysis, there is strong indication that sheep were managed under a non-intensive system with access to open dry grasslands pastures during summer.

The evidence from the stabling layers at Oppeano 4D, brings further nuances to sheep herding practices. Faecal biomarkers have been attributed mainly to ruminants, which indicates that animals were housed on the site (Nicosia et al., 2025). This may have occurred at specific times of the year, for example for lambing and subsequent milking of females, and fleece collection from the flock as a whole. The latter activity was supported by the presence of puparia of sheep tick (*Meolophagus ovinus* L.) found within carpological remains (Nicosia et al., 2025). This species is usually associated with sheep shearing and wool processing (Buckland and Perry, 1989; Kenward, 2009). Integrating the scenarios proposed from the stable isotopic and archaeobotanical analyses, we propose that the pollen from the dry grasslands may have entered the structures via animal fleeces, via sediment attached to animal hooves, and in dung, when fleeces were collected in the summer (cf. Tinley, 1949).

In contrast to the summer, in winter the diet of Oppeano 4D sheep was depleted in ^{13}C ($\delta^{13}C_{bioap}$ minimum values for M2 and M3: −12.7 and −13.6‰) associated with low δ^{18}O values. Adjusting these values for fractionation would give inferred-dietary values of −27.2 and −28.1‰, which would suggest a diet composed of plants coming from either wetlands, dense forest pasture, or leafy-hay (Fig. 2b). There were water-rich environments with woodland carrs and marshland sedges in the palaeovalley where the site is located, which have been conspicuously attested by the botanical records (D'Aquino et al., 2026; Nicosia et al., 2025). The twigs and buds of deciduous oak and maple have also been found, which may derive from sparse stands of mesophilous woodland and, with regard to oak, possibly woodworking leftovers (D'Aquino et al., 2026). These twigs and wood splits may have been used as bedding/litter during winter or when animals were in the byre-houses. It is unlikely that sheep were pastured on marshland in winter, due to flooding and foot rot (Shahack-Gross, 2017: 267). Therefore, we propose that animal diets during winter were supplemented by either leafy-hay or collected sedges.

In comparison, for most sheep/goats of La Muraiola, incremental δ^{13}C sampling of molars indicates a lack of seasonal variation in their diet consistent with year-round grazing in open vegetation (Fig. 2b). Nitrogen isotopes provide us a potential insight into stocking densities and penning intensity. It is interesting to note that some of the collagen samples from sheep/goat individuals at La Muraiola exhibited δ^{15}N values higher than those from pigs. There is clear archaeological evidence of penning on site in the form of phosphatic crusts (Polisca et al., 2025), composed of sheep/goat dung pellets. The palynological record of the phosphatic crusts is mainly composed by non-arboreal pollen that indicate the site was situated within an open anthropogenic landscape, characterised by arable fields, with areas of disturbed ground, grasslands, open woodlands, and shrubs (D'Aquino, 2025; Polisca et al., 2025). Mineralised wood fragments from twigs and small branches testify to the exploitation of woodland resources for leafy-hay or bedding material for sheep/goat herds procured from mixed deciduous woodlands with hornbeam, deciduous oak and light-demanding shrubs from woodland margins, such as cornelian cherry (D'Aquino, 2025). The use of winter leafy-hay is supported by low δ^{13}C values occurring with low δ^{18}O (lowest values for M2 and M3: −12.5 and −13.2‰) observed in some sheep/goat individuals. Overall, there is a suggestion that at La Muraiola herds were pastured in open areas close to the sites and supplemented with collected fodders from both grasslands and woodlands.

5.2. Testing mobility of Middle Bronze Age sheep/goat husbandry at Oppeano 4D and La Muraiola

The ^{87}Sr/^{86}Sr results from sheep/goat teeth, when compared to baseline samples, provide no evidence of long-distance seasonal mobility and support local rearing of the flocks by the MBA communities of Oppeano 4D and La Muraiola (Fig. 7). Plants were analysed for ^{87}Sr/^{86}Sr, from five lithological units within a relatively short distance (ca. 30 km) from the sites. The variation in ^{87}Sr/^{86}Sr ratios between units is relatively small, particularly between the calcareous bedrock (LU-1: Western portion of the Lessini Mts., LU-2: Eastern portion of the morainic amphitheatre of the Garda Lake). These two units represent the closest upland pastures to the study sites in the floodplain and, if summer seasonal mobility took place, we assume that it would be in these regions. However, none of the teeth exhibited ratios consistent with these units. Moreover, despite being very close (ca. 28 km), herds from Oppeano 4D and La Muraiola were not raised in the same lithological unit. Respectively, the individuals from Oppeano 4D mainly cluster with the signal of the Holocene floodplain of the Adige River (LU-4) where the site is located. Although there are differences of up to 0.0014 between the ^{87}Sr/^{86}Sr ratios of the individuals from Oppeano 4D and the ^{87}Sr/^{86}Sr ratio of LU-4, this is consistent with the variability of measured ^{87}Sr/^{86}Sr ratios of similar archives from the same locations, noted particularly on some Holocene sediments (Holt et al. 2025). Only one individual (OPP_OC3) exhibits ratios of its first year potentially indicating it was born outside the Holocene floodplain, possibly in a part of the Alps around modern Trento and Bolzano (Lugli et al. 2022). Another individual (OPP_OC4) tends towards the nearby Late Pleistocene Adige megafan (LU-3). In comparison, sheep from La Muraiola grazed mainly on the Late Pleistocene Adige megafan where the site is located. Although the vast majority of animals are consistent with being raised in the vicinity of the sites, equifinality is invariably a problem for confident assignment of origins and these ratios are also consistent with origins in central Emilia Romagna, Liguria and Lazio (Lugli et al. 2022). These are less likely areas of origin, but cannot be entirely excluded.

Concerning mobility, the comparison of seasonal δ^{18}O values has in the past been used for identifying seasonal movements to upland pastures (Messana et al., 2023), resulting in a dampening of the sinusoidal δ^{18}O signal. This is assumed to be the result of animals consuming snow-melt fed streams with low δ^{18}O values in the highlands in summer, and returning to the plains in the winter, where they consume water with similar or lower δ^{18}O values. Sheep from La Muraiola exhibited a low amplitude in δ^{18}O values compared to those from Oppeano 4D. As discussed, the high variation observed at Oppeano 4D is likely the result of a strong leaf-water effect associated with pasturing on dry grassland vegetation. In contrast, the La Muraiola animals appear to have grazed not on dry grasslands but in the vicinity of a spring-fed stream. While mountain rivers often exhibit greater seasonal variability in their δ^{18}O signal due to snowmelt and rainfall (Brighenti et al., 2023), spring-fed rivers maintain a more consistent signal, as groundwater undergoes fewer rapid changes (Pederzani and Britton, 2019; Regione Emilia-Romagna, 2016:76). The exploitation of spring-fed rivers at La Muraiola likely accounts for relatively low variability in δ^{18}O values. However, the tendency towards less radiogenic ratios at La Muraiola (closer to LU1) raises the possibility that transhumance could be taking place, but the δ^{18}O isotope data suggests that this is unlikely.

From the stable isotope and archaeobotanical datasets, we propose that plant resources as both pasture and fodder from multiple local environments in the plain were sufficient to allow the livestock to remain within the vicinity of the respective sites year-round. The ^{87}Sr/^{86}Sr results indicate little evidence for mobility both local and long distance: flocks were likely grazing on grasslands in the plain, with the possibility of some additional fodders collected from woodlands and marshland potentially to prevent overgrazing and protect cultivation areas from grazing. Finally, at both settlements there is the geoarchaeological attestation of stabling deposits and penning areas formed by regularly repeated deposition of dung and litter during times when the livestock were kept on-site. This also supports small-scale village-based husbandry strategies for local consumption of animal product (milk, meat and wool), alongside other regular agricultural routines and production. Meanwhile, the presence of livestock in the vicinity of (or within) domestic structures also underlines the crucial importance of these animals and their products for these MBA communities (cf. Fokkens, 1999; Olausson, 1999; Zimmerman, 1999).

5.3. Use of collected wild and cultivated plant resources as animal feed

Our analysis demonstrates that plant resources from a variety of local environments were exploited for husbandry. In terms of pasturelands, repeated grazing on the same pastures might have favoured the development of resistant synanthropic herbs, expanded open habitats, and prevented wood regeneration. At La Muraiola, the large abundance of pollen of Cichorieae, a tribe of the Asteraceae family including perennial herbs such as dandelion and chicory, could suggest overgrazing or intensive grazing in penned locations (Florenzano et al., 2015; Mercuri et al., 2013). However, it must be noted that this family may be overrepresented due to its preservation. Both sites, and other records in the northern Po Plain, attest secondary grasslands that developed in newly open areas on drained locations (Dal Corso, 2018; Nicosia et al., 2025; Perego et al., 2011, 2025; Pini et al., 2021; Polisca et al., 2025; Zanon et al., 2018).

Meanwhile, there is strong archaeobotanical, micromorphological and isotope evidence for collected plant resources for fodder. Collected fodder allowed communities to feed their animals when access to pastures was restricted, as well as preventing pasture exhaustion. Given the strong geoarchaeological evidence for onsite penning within structures, the collection and probable storage of additional fodder supplies and plant bedding materials were necessary. At both sites, the botanical records from dung-rich penning areas contain an abundance of wild herbs and grasses likely derived from different sources besides digested vegetal matter itself, i.e. fodder, litter, and seeds or pollen inadvertently carried via wool or on the hoof (Nicosia et al., 2025; Polisca et al., 2025). The palynological data from stabling layers at Oppeano 4D, especially evidenced different kinds of open habitats close to the settlement. These include passageways and uncultivated areas potentially used for pastures/meadows, alongside other habitats spanning from wetlands with sedges in the valley to areas with dry substrate and xerophytic vegetation on fluvial terraces. When considering plant physiology, some vegetation would respond and serve differently than others for hay collection. For example, we suggest that hay from inside the structures at Oppeano 4D was collected from disturbed/anthropogenic open environments (e.g., meadows/pasture, verges) and not dry grassland vegetation due to the latter containing short and shrubby plants (e.g., sunrose), which makes poor quality hay (Ziliotto et al., 2004). Herbs from other open habitats nearby the site generally grow taller, thus being easier and more convenient to harvest/mow (see for comparison Lodwick, 2017; Reed, 2024). This hay may have been provisioned to animals during the birthing/milking or shearing season.

Leafy-hay from deciduous and hygrophilous woodlands is usually connected to winter fodder (e.g., Jakobitsch et al., 2023; Karg, 1998). The stable isotope results of Oppeano 4D sheep/goats indicate the inclusion of wetland plants or forest resources. This matches botanical evidence of fragments of tree twigs and bark from woodland carrs alongside sedges that favour wetlands. While marshland would not be suitable pasture during winter due to flooding, sedges from these environments would provide a plentiful source of fodder as known in recent traditional husbandry strategies (Sucholas et al., 2022). Also at La Muraiola, the mineralised wood fragments from twigs and small branches testify the exploitation of forest resources for leafy-hay and/or bedding material from mixed deciduous open woodlands, including cornelian cherry. While consumption of resources from open woodlands is problematic to identify in the isotope record, collaboration between archaeobotanical and stable isotope evidence points to the use of leafy-hay during winter.

Finally, crop cultivation was largely attested in the archaeobotanical records at both sites, with little cereal remains in the stabling/penning layers suggesting that cereals were mainly consumed by humans. Stable nitrogen isotope values from sheep/goat and cattle from La Muraiola suggest that sheep on average had access to plant stuff that were more enriched with ^{15}N. The values suggest plants that were receiving low to moderate levels of manure according to Bogaard et al. (2013). This could suggest that animals had access to manured cereals processing waste, such as crop stubble. The isotope analysis helped to disentangle further the use of crops for fodder, especially for C_4 plants. At both sites, there is clear indication of faunal species-specific feeding practices. According to Bender (1971), δ^{13}C values of C_3 plants normally range between −22 and −33‰, whereas C_4 plants have a range of −10 to −20‰ (Bender, 1971; O'Leary, 1988). This has been further developed recently in Depaermentier et al. (2025), who have examined region specific variation in stable isotopic values of C_4 and C_3 plants, and demonstrated that local growing conditions influence plant isotopic values. For Northern Italy, they propose that c.−17 ± 0.7‰ for C_4 plants consumers, while the value for a mixed C_3/C_4 diet will be closer to that of C_3 plants. At Oppeano 4D, there are some cattle individuals exhibiting high diet inferred δ^{13}C values, for example, OPP_BT3 exhibits a diet inferred value of −18.4‰, suggesting C_4 component. The frequently attested wild edible millet, barnyard grass (*Echinochloa crus-galli*) at Oppeano 4D, may have been a source of fodder for cattle, a practice known at present (Quattrocchi, 2006). Interestingly, the barnyard grass grains are mostly charred (D'Aquino, 2025; Nicosia et al., 2025), similarly to the other cereals, suggesting they were also consumed by humans. Another source of C_4 plants is broomcorn millet, of which only a few charred grains were attested. In contrast, at La Muraiola, a rich deposit of burnt broomcorn millet was uncovered within a barn where animals were penned. At this site, a single sample from cattle (PVG_BT3) and pig (PVG_SD1) exhibit diet inferred δ^{13}C values of −21.0‰ and −20.2‰ that may also indicate a C_4 plant component to these species diet. This may have been provisioned seasonally; further incremental analysis of cattle teeth is needed to test this hypothesis.

5.4. Choice and sustainability of plant resources and environments for animal husbandry

Cross-correlating our datasets provides us with a rich picture of MBA herders, who exploited a local catchment within the floodplain, with potential seasonal alternation of marshlands, fluvial banks, and alluvial terraces. These landscapes hosted different kinds of vegetation as well as a richness of plant resources that allowed local year-round management of the herds. Indeed, it appears that cattle, sheep/goats, and pigs were kept in areas surrounding the settlements, and for at least for part of the year, both settlements show frequent evidence of sharing living space among people and their animals. The byres and fenced pens served as protected locations to keep livestock safe from predators at night and to ensure accessibility for the seasonal collection of seasonal products such as wool and milk.

The integration of collected fodders into the diet of all species suggests that herders were aware of the fodder potential of local environments. Plants from synanthropic environments dominate the archaeobotanical records of the dung-rich deposits. These include many open habitats where grasses and forbs were used for pasture and as hay fodder, besides cultivated fields for human consumption. At both sites, we can observe the use of plants from humid and woodland environments during periods in the seasonal calendar when sheep herds returned to the fold. The impact of husbandry led to the creation and maintenance of open environments (see for comparison in the Alps, e.g. Garcés-Pastor et al., 2025, and in other areas of Europe e.g. Dal Corso et al., 2025). While difficult to quantify, in combination with agriculture and woodland exploitation, confirms the picture of considerable landscape opening during the MBA in the Po Plain.

Among the four animal species investigated here, there is little evidence of grazing consistently on plants growing on nitrogen-rich or manured land. Overall, it suggests extensive herding strategies, supplemented with collected fodders with restricted use of manured cereal stubble or by-products as fodder. Ongoing isotope analyses on cereals from these sites in the future will elucidate cultivation practices. Archaeobotanical evidence indicates millets, barnyard grass, and broomcorn millet were provided or accessible to livestock. Millets were probably available for human consumption and employed as fodder to feed cattle when penned for milking or other purposes. The question is what is the carrying capacity of the landscape under the presented model (Fig. 10). The integration of fodder into the husbandry strategy of sheep and other domesticates may have been a response to the reduction of land to pasture animals due to an increase in cultivation areas to feed expanding populations. The next step in this model may be the stocking of animals on cultivated areas after harvest, to increase agricultural production. Finally, once more land is turned over to cultivation, herders may then be pushed to explore alternative pastures at a greater distance from the site.

6. Conclusions and future perspectives

This investigation, integrating geoarchaeological, archaeobotanical, zooarchaeological, and isotope evidence, elucidates MBA sheep herding dynamics in the Po Plain, opening a window on past lives and economies (Fig. 10). The integration of botanical and isotope archives allowed a more precise reconstruction of animal diet. For example, the consumption of leafy-hay can result in consumer values being depleted in ^{13}C, while there is always a problem with equifinality, here we could directly point to leafy-hay coming from open woodland. In contrast to the initial expectation, the study indicated that sheep herds were reared within the vicinity of the study sites, challenging the preconception that during the MBA herders were driven to expanding herding ranges to distant regions at different altitudes. However, the study does indicate that communities linked by material culture maximised and tuned their herding strategies in response to local environments available to them for both grazing and fodder collection. The movement of animals between grazing areas has been mainly suggested as a strategy to reduce the risk of overgrazing, increase access to rich pastures enhancing production, and avoid cultivation areas. An interesting open question remains concerning the difference of livestock treatment between the two sites, that further research on those and other sites will help to delineate.

Competition with cultivated land and absence of feed for winter seemed not to be a problem at these case study sites, which saw the collection of supplementary fodders from a range of environments leafy-hay, and possibly of grass hay too, as useful strategies to maintain herds. This apparent resource sustainability within the floodplain may have come under pressure after centuries of similar land-use by expanding village communities and their herds; at La Muraiola, indeed, a significant zooarchaeological record has been recovered (around 10,000 bones from an excavated area of 70 m^2). Focusing on hay making, this activity

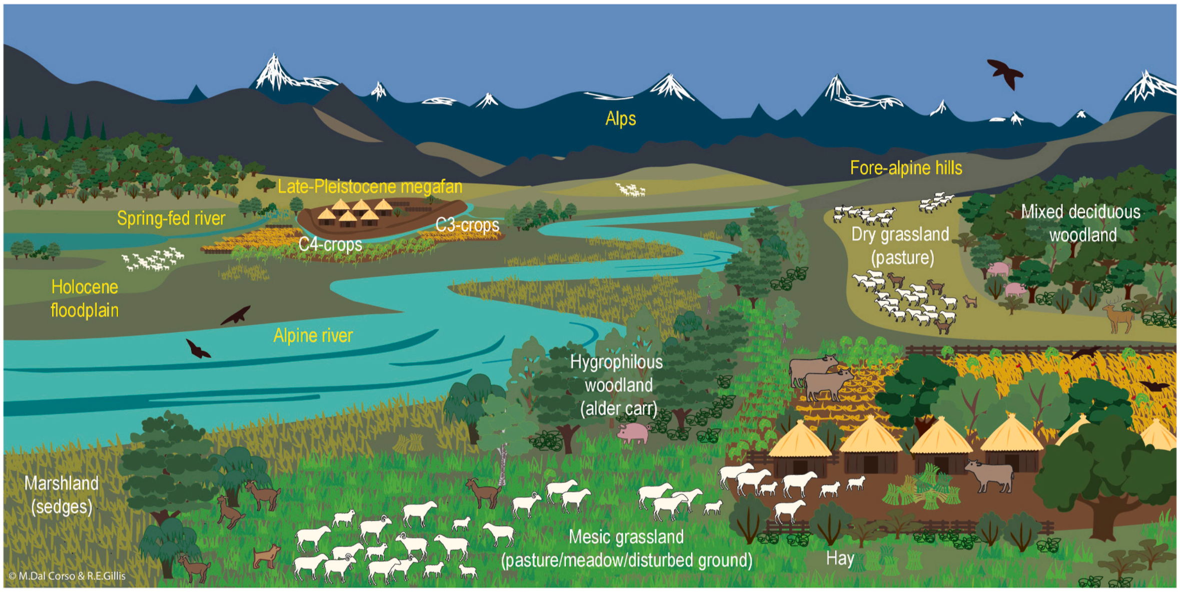

Fig. 10. A reconstruction of the MBA landscape at the sites of Oppeano 4D (in the palaeovalley, on the right) and of La Muraiola (in the upper plain, on the left). Vegetation and possible scenarios of land use partitions for animal husbandry and agriculture are illustrated. Graphic work MDC and REG using Adobe Illustrator.

has traditionally been considered an Iron Age prerogative (Eriksson, 2020), mainly due to the presence of iron tools. Hay making is associated with many social aspects, ethnographic evidence emphases the use of collective labour in traditional agro-pastoral systems (Iannetti, 2021; Smerdel, 2014), as well as technological and environmental aspects, worthy of further investigations. The botanical and isotopic data presented here suggests that wild forbs/grasses harvest was already established in the MBA, possibly derived from mesic grasslands and open habitats on disturbed ground nearby the sites. From medieval to modern times, we know that pastoral mobility and strategies have also been shaped by political aspects, land ownership, social order, and market requirements, but whenever it has been possible to consider ethnographic and traditional comparisons of husbandry for farmers' subsistence (see for instance "morra" in the Appennines, Sonsini and Angelucci, 2012), a rather small mobility was compensated by diversity of fodder resources.

The comparison between the data from this study and those published for the region highlighted the limited corpus of isotope data from faunal records available for the northern Italian Bronze Age. Further analysis with higher numbers of samples would be also beneficial to more accurately detect signs of intensive or extensive grazing, as demonstrated by e.g. Schlütz et al. (2023), Vaiglova et al. (2018). Moreover, increased sampling of wild species will help us develop isoscapes that can be fine-tuned with botanical evidence. Further incremental tooth analyses are needed to clarify the seasonality of herd management and the emergence of transhumance, providing insight into how animals were managed both temporally and spatially. In this regard, while within pre- and protohistoric mobility the directional pattern is often supposed to be lowland to highland, in contrast to historical times, it would be particularly valuable to also investigate faunal assemblages from mountain sites through combined zooarchaeological and isotopic approaches. This will allow a better nuanced understanding of what, when, and why transhumance strategies emerged and to develop an articulated model for its evolution.

Authors contributions

REG, RM and MDC designed the study; MSM, REG, KSE, EH, MDC and FP sampled and processed material for stable isotopic analysis; AN, M-AM and AL carried out the stable isotopic analysis; MSM and REG carried out statistical analysis; MSM, REG and MDC wrote the paper and produced figures with contributions from other authors; CN provided research funds from GEODAP project; CN and SDA provided funds from SIS-BRO project. GP, FP, and FB collected samples in the fields and improved the final version of the manuscript.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2026.109961.

Data availability

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

References

Accorsi, C.A., Bandini Mazzanti, M., Mercuri, A.M., Rivalenti, C., Trevisan Grandi, G., 1996. Holocene forest pollen vegetation of the Po plain - northern Italy (Emilia Romagna Data). Allionia 34, 233–275.

Aceti, A., Ravazzi, C., Vescovi, E., 2009. Analisi pollinica della successione laminata nella vasca di Noceto. In: Bernabò Brea, M., Cremaschi, M. (Eds.), Acqua E Civiltà Nelle Terramare: La Vasca Votiva Di Noceto. Skira, pp. 121–131.

Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1–37. https://doi.org/10.1007/978-3-662-02894-0_1.

Amundson, R., Austin, A.T., Schuur, E.A.G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., Baisden, W.T., 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Glob. Biogeochem. Cycles 17. https://doi.org/10.1029/2002GB001903, 2002GB001903.

Avanzinelli, R., Conticelli, S., Francalanci, L., 2015. High precision Sr, Nd, and pb isotopic analyses using the new generation thermal ionisation mass spectrometer ThermoFinnigan Triton-Ti®. Period. Mineral. 74, 147–166.

Balasse, M., Tresset, A., Bălăşescu, A., Blaise, E., Tornero, C., Gandois, H., Fiorillo, D., Nyerges, É.Á., Frémondeau, D., Banffy, E., Ivanova, M., 2017. Animal board invited review: sheep birth distribution in past herds: a review for prehistoric Europe (6th to 3rd millennia BC). Animal 11, 2229–2236. https://doi.org/10.1017/S1751731117001045.

Balasse, M., Ambrose, S.H., 2005. Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C4 grassland environments. J. Archaeol. Sci. 32, 691–702. https://doi.org/10.1016/j.jas.2004.11.013.

Balasse, M., Tresset, A., 2002. Early weaning of Neolithic domestic cattle (Bercy, France) revealed by intra-tooth variation in nitrogen isotope ratios. J. Archaeol. Sci. 29, 853–859. https://doi.org/10.1006/jasc.2001.0725.

Barker, G., 1999. Hunting and farming in prehistoric Italy: changing perspectives on landscape and society. Pap. Br. Sch. Rome 67, 1–36. https://doi.org/10.1017/S0068246200004517.

Barone, R., 1995. Anatomia Comparata Dei Mammiferi Domestici, I. Edagricole - Edizioni Agricole della Calderini, Bologna. Osteologia, 1995th.

Bataille, C.P., Crowley, B.E., Wooller, M.J., Bowen, G.J., 2020. Advances in global bioavailable strontium isoscapes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 555, 109849. https://doi.org/10.1016/j.palaeo.2020.109849.

Behre, K.E., 1981. The interpretation of anthropogenic indicators in pollen diagrams. Pollen Spores 23, 225–245.

Bender, M.M., 1971. Variations in the 13C/12C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. Phytochemistry 10, 1239–1244. https://doi.org/10.1016/S0031-9422(00)84324-1.

Bernabò Brea, M., Cardarelli, A., Cremaschi, M. (Eds.), 1997. Le Terramare. La Più Antica Civiltà Padana. Electa, Milano.

Bertolini, M., Zanini, S., Thun Hohenstein, U., 2015. Nuovi dati sullo sfruttamento e gestione delle risorse animali tra il Bronzo antico ed il Bronzo recente nei territori del medio-basso Veronese e il basso Polesine. In: Leonardi, G., Tiné, V. (Eds.), Preistoria E Protostoria Del Veneto. STUDI DI PREISTORIA E PROTOSTORIA-2, Firenze, pp. 321–326.

Boessneck, J., Müller, H.-H., Teichert, M., 1964. Osteologische Unterscheidungsmerkmale zwischen Schaf (Ovis aries Linné) und Ziege (Capra hircus Linné). In: Kühn-Archiv. Akad.-Verlag, pp. 1–129.

Bogaard, A., Fraser, R., Heaton, T.H.E., Wallace, M., Vaiglova, P., Charles, M., Jones, G., Evershed, R.P., Styring, A.K., Andersen, N.H., Arbogast, R.-M., Bartosiewicz, L., Gardeisen, A., Kanstrup, M., Maier, U., Marinova, E., Ninov, L., Schäfer, M., Stephan, E., 2013. Crop manuring and intensive land management by Europe's first farmers. Proc. Natl. Acad. Sci. USA 110, 12589–12594. https://doi.org/10.1073/pnas.1305918110.

Bonafini, M., Pellegrini, M., Ditchfield, P., Pollard, A.M., 2013. Investigation of the 'canopy effect' in the isotope ecology of temperate woodlands. J. Archaeol. Sci. 40 (11), 3926–3935. https://doi.org/10.1016/j.jas.2013.03.028.

Bonetto, J., 2024. Tra pianura e Prealpi: pecore, agricoltori e transumanze. In: Busana, M.S., Rodeghiero, M.M. (Eds.), Lanam Fecit: L'Economia Della Lana Sul Filo Della Storia. Ronzani Editore, pp. 27–38.

Bortoli, G., 2019. La pastorizia nella storia dei Sette Comuni. In: Lana Pecore Pastori Tra Il Monte E Il Piano. Attilio Fraccaro Editore, Bassano, pp. 44–57.

Breglia, F., Prillo, V.G., Dal Corso, M., Manfrin, M.S., D'Aquino, S., Polisca, F., Germinario, L., Piazzalunga, G., Salzani, P., Nicosia, C., 2025. Reassessing neolithic subsistence in Northern Italy through a critical review and new evidence from Molino Casarotto. Sci. Rep. 15, 44494. https://doi.org/10.1038/s41598-025-28005-6.

Bréhard, S., Beeching, A., Vigne, J.-D., 2010. Shepherds, cowherds and site function on middle Neolithic sites of the Rhône valley: an archaeozoological approach to the organization of territories and societies. J. Anthropol. Archaeol. 29, 179–188. https://doi.org/10.1016/j.jaa.2010.02.001.

Brighenti, S., Engel, M., Dinale, R., Tirler, W., Voto, G., Comiti, F., 2023. Isotopic and chemical signatures of high Mountain Rivers in catchments with contrasting glacier and rock glacier cover. J. Hydrol. 623, 129779. https://doi.org/10.1016/j.jhydrol.2023.129779.

Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified longin method. Radiocarbon 30, 171–177. https://doi.org/10.1017/S0033822200044118.

Buckland, P., Perry, D., 1989. Ectoparasites of sheep from Stóraborg, Iceland and their palaeoecological significance (Piss, parasites and people: a palaeoecological perspective). Hikuin 15, 37–46.

Busana, M.S., 2024. La produzione tessile nel Veneto romano. In: Busana, M.S., Rodeghiero, M.M. (Eds.), Lanam Fecit: L'Economia Della Lana Sul Filo Della Storia. Ronzani Editore, Dueville, pp. 97–108.

Cardarelli, A., 1997. Terramare: l'organizzazione sociale e politica delle comunità. In: Le Terramare: La Più Antica Civiltà Padana. Electa, Milano, pp. 436–442.

Cardarelli, A., 2010. The collapse of the Terramare Culture and growth of new economic and social systems during the late Bronze Age in Italy. Scienze dell'Antichità 15, 449–520.

Caricola, I., Charles, A., Tirillò, J., Charlton, F., Barton, H., Breglia, F., Rossi, A., Deflorian, M.C., De Marinis, A.M., Harris, S., Pellegrini, A., Scacchetti, F., Boccuccia, P., Miari, M., Dolfini, A., 2022. Organic residue analysis reveals the function of bronze age metal daggers. Sci. Rep. 12, 6101. https://doi.org/10.1038/s41598-022-09983-3.

Carra, M., 2009. Alimentazione, ambiente ed economia di sussistenza su base vegetale. Studio archeobotanico preliminare dei macroresti provenienti dal sito di Solarolo. IpoTesi Preistoria 2 (1), 281–291.

Carrer, F., Migliavacca, M., 2019. Prehistoric transhumance in the Northern Mediterranean. In: Sabatini, S., Bergerbrant, S. (Eds.), The Textile Revolution in Bronze Age Europe. Cambridge University Press, pp. 217–238. https://doi.org/10.1017/9781108656405.009.

Castagnetti, A., 1977. La pianura veronese nel Medioevo. In: Borelli, G. (Ed.), Una Città E Il Suo Fiume. Banca Popolare Di Verona, Verona, pp. 33–138.

Castelletti, L., Maspero, A., 1992. Analisi di resti vegetali di Camo Ceresole del Vhò di Piadena e di altri siti neolitici padani. Nat. Brescia. 27, 289–305.

Castiglioni, G.B., 1997. Geomorphological map of Po Plain.

Cavazzuti, C., Skeates, R., Millard, A.R., Nowell, G., Peterkin, J., Bernabò Brea, M., Cardarelli, A., Salzani, L., 2019. Flows of people in villages and large centres in Bronze Age Italy through strontium and oxygen isotopes. PLoS One 14, e0209693. https://doi.org/10.1371/journal.pone.0209693.

Cerling, T.E., Bernasconi, S.M., Hofstetter, L.S., Jaggi, M., Wyss, F., Rudolf Von Rohr, C., Clauss, M., 2021. CH4/CO2 ratios and carbon isotope enrichment between diet and breath in herbivorous mammals. Front. Ecol. Evol. 9, 638568. https://doi.org/10.3389/fevo.2021.638568.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363. https://doi.org/10.1007/s004420050868.

Chemin, A., 2019. Le vie di transumanza tra pianura e montagna. Una rilettura storica dei territori e dei segni delle vie della lana. In: Lana Pecore Pastori Tra Il Monte E Il Piano. Attilio Fraccaro Editore, Bassano, pp. 34–43.

Chenery, C.A., Pashley, V., Lamb, A.L., Sloane, H.J., Evans, J.A., 2012. The oxygen isotope relationship between the phosphate and structural carbonate fractions of human bioapatite. Rapid Comm Mass Spectrometry 26, 309–319. https://doi.org/10.1002/rcm.5331.

Chiaffarelli, G., Indipolage Kariyawasam, T., Proserpio, B., Rottoli, M., 2021. I macroresti vegetali nelle strutture al margine del Villaggio Grande della Terramara Santa Rosa di Poviglio. In: Cremaschi, M., Pizzi, C. (Eds.), Terramara Santa Rosa Di Poviglio: Le Strutture Idrauliche Al Margine Del Villaggio Grande (Scavi 1998–2011), Origines 35. Istituto Italiano di Preistoria e Protostoria, Firenze, pp. 389–401.

Cremaschi, M., 2009. Foreste, terre coltivate ed acque, l'originalità del progetto terramaricolo. In: Bernabò Brea, M., Cremaschi, M. (Eds.), Acqua E Civiltà Nelle Terramare: La Vasca Votiva Di Noceto. Skira, Milano, pp. 34–45.

Cremaschi, M., Griggs, C., Kocik, C., Mutti, A., Zerboni, A., Manning, S.W., 2021. Dating the Noceto vasca Votiva, a unique wooden structure of the 15th century BCE, and the timing of a major societal change in the Bronze Age of northern Italy. PLoS One 16, e0251341. https://doi.org/10.1371/journal.pone.0251341.

Cremaschi, M., Mercuri, A.M., Torri, P., Florenzano, A., Pizzi, C., Marchesini, M., Zerboni, A., 2016. Climate change versus land management in the Po Plain (Northern Italy) during the Bronze Age: new insights from the VP/VG sequence of the Terramara Santa Rosa di Poviglio. Quat. Sci. Rev. 136, 153–172. https://doi.org/10.1016/j.quascirev.2015.08.011.

Cremaschi, M., Ottomano, C., Trombino, L., 2004. Aspetti micromorfologici e pedologici nei processi di formazione della stratigrafia archeologica. In: Bernabò Brea, M.A., Cremaschi, M. (Eds.), Il Villaggio Piccolo Della Terramara Di Santa Rosa Di Poviglio, pp. 117–150. Scavi 1987–1992.

Cremaschi, M., Ottomano, C., 1996. Il testimone stratigrafico di Monte Castellaccio - aspetti micromorfologici per lo studio dei processi di formazione del sito. In: Pacciarelli, M. (Ed.), Musei Civici Di Imola. La Collezione Scarabelli. 2. Preistoria. Grafis, Bologna, pp. 148–157.

Cupitò, M., Ambrosioni, C., Dal Corso, M., Manfrin, M.S., Mileto, S., Pecci, A., Rottoli, M., Tecchiati, U., 2024. Agricoltura, allevamento e alimentazione nella tarda età del Bronzo della pianura veronese : il caso studio del sito di Fondo Paviani. In: Migliavacca, M., Martinelli, N., Salzani, P., Saracino, M. (Eds.), Food and Wine in Ancient Verona = Cibo E Vino Nella Verona Antica. 2: Mangiare E Bere Nella Preistoria E Protostoria. Edizioni Quasar, pp. 79–94.

Cupitò, M., Leonardi, G., 2015. Il Veneto tra Bronzo antico e Bronzo recente. In: Leonardi, G., Tiné, V. (Eds.), Preistoria E Protostoria Del Veneto. STUDI DI PREISTORIA E PROTOSTORIA-2, Firenze, pp. 201–239.

D'Aquino, S., 2025. La vita quotidiana dell'Età del Bronzo attraverso lo studio dei reperti di origine vegetale: due siti del Bronzo Medio del Veneto a confronto. Università degli Studi di Padova (PhD Dissertation).

D'Aquino, S., Stefani, I., Polisca, F., Bernabei, M., Nicosia, C., Dal Corso, M., 2026. The lost woodlands of the Po plain: wooden resources from the middle Bronze Age site of

Oppeano 4D (Verona, northern Italy). Veg. Hist. Archaeobotany. https://doi.org/10.1007/s00334-026-01089-4.

Dal Corso, M., 2018. Environmental History and Development of the Human Landscape in a Northeastern Italian Lowland During the Bronze Age: a Multidisciplinary case-study. Habelt, Kiel.

Dal Corso, M., Salavert, A., Marinova, E., Gillis, R.E., 2025. Exploring the role of plant–animal interactions in the long-term development of heritage landscapes in Europe. Philos. Trans. R. Soc. B 380, 20240204. https://doi.org/10.1098/rstb.2024.0204.

Dal Corso, M., Zanon, M., Heron, C., Rottoli, M., Cupitò, M., Dalla Longa, E., 2022. Tracing millet through biomarker analysis in archaeological sites in alluvial plains: The first miliacin data from the northern Italian Bronze Age. In: Kirleis, W., Dal Corso, M., Filipović, D., et al. (Eds.). Leiden: Sidestone Press, Leiden, pp. 231–252.

Dalla Longa, Elisa, Dal Corso, M., Vicenzutto, D., Nicosia, C., Cupitò, M., 2019. The Bronze Age settlement of Fondo Paviani (Italy) in its territory. Hydrography, settlement distribution, environment and in-site analysis. J. Archaeol. Sci.: Reports 28, 102018. https://doi.org/10.1016/j.jasrep.2019.102018. https://linkinghub.elsevier.com/retrieve/pii/S2352409X19303967.

Davitashvili, A., 2024. Creating stable isotopic database of faunal remains – Bronze Age Italy. Folia Praehistorica Posnaniensia 29, 37–55. https://doi.org/10.14746/fpp.2024.29.03.

De Grossi Mazzorin, J., 2013. Considerazioni sullo sfruttamento animale in ambito terramaricolo. In: De Grossi Mazzoroin, J., Curci, A., Giacobini, G. (Eds.), Economia E Ambiente Nell'Italia Padana Dell'Età Del Bronzo. Le Indagini Bioarcheologiche. Edipuglia, Bari, pp. 257–263.

De Grossi Mazzorin, J., 2015. Fondo Paviani e Frattesina: economia animale di due central places della tarda età del Bronzo veneta. In: Leonardi, G., Tiné, V. (Eds.), Preistoria E Protostoria Del Veneto. STUDI DI PREISTORIA E PROTOSTORIA-2, Firenze, pp. 389–400.

De Guio, A., 2019. Storie e scorie, di formaggio e di rame. In: Rodeghiero, G.F. (Ed.), Lana Pecore Pastori Tra Il Monte E Il Piano. Attilio Fraccaro Editore, Bassano, pp. 11–24.

Debandi, F.I., 2021. Sistemi Di Gestione Economica E Alimentazione Nelle Comunità Dell'Età Del Bronzo Con Particolare Riferimento All'Italia Settentrionale. Bononia University Press. https://doi.org/10.30682/disciarche27.

Depaermentier, M.L.C., Kempf, M., Motuzaitė Matuzevičiūtė, G., 2025. Environmentally adjusted δ13C thresholds for accurate detection of C4 plant consumption in Europe. Commun. Earth Environ. 6, 1021. https://doi.org/10.1038/s43247-025-03031-4.

Depellegrin, V., Tecchiati, U., 2016. I resti faunistici dell'abitato protostorico di Terranegra (Legnago, Verona). Sezione di Museologia Scientifica e Naturalistica 12, 103–110. https://doi.org/10.15160/1824-2707/1303. Paginazione.

Di Renzoni, A., 2006. L'evoluzione del sistema insediativo delle terramare: alcuni casi studio. In: Studi in Onore Di Renato Peroni. Borgo San Lorenzo, pp. 471–484.

Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E., Bocherens, H., 2008. Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. Palaeogeogr. Palaeoclimatol. Palaeoecol. 266, 69–82. https://doi.org/10.1016/j.palaeo.2008.03.020.

Eriksson, O., 2020. Origin and development of managed meadows in Sweden: a review. Rural Landscapes: Society, Environment, History 7, 2. https://doi.org/10.16993/rl.51.

Filipović, D., Meadows, J., Corso, M.D., Kirleis, W., Alsleben, A., Akeret, Ö., Bittmann, F., Bosi, G., Ciută, B., Dreslerová, D., Effenberger, H., Gyulai, F., Heiss, A.G., Hellmund, M., Jahns, S., Jakobitsch, T., Kapcia, M., Klooß, S., Kohler-Schneider, M., Kroll, H., Makarowicz, P., Marinova, E., Märkle, T., Medović, A., Mercuri, A.M., Mueller-Bieniek, A., Nisbet, R., Pashkevich, G., Perego, R., Pokorný, P., Pospieszny, Ł., Przybyła, M., Reed, K., Rennwanz, J., Stika, H.-P., Stobbe, A., Tolar, T., Wasylikowa, K., Wiethold, J., Zerl, T., 2020. New AMS 14C dates track the arrival and spread of broomcorn millet cultivation and agricultural change in prehistoric Europe. Sci. Rep. 10, 13698. https://doi.org/10.1038/s41598-020-70495-z.

Filippi, E., 1998. Qualche nota sul fiume Tartaro. In: Il Tartaro Tra Passato E Presente: Le Acque, La Pesca, La Fauna Ittica. Consorzio Di Bonifica Agro Veronese. Isola della Scala, pp. 5–16.

Florenzano, A., Clò, E., Zappa, J., Furia, E., Torri, P., Mercuri, A.M., 2021. Paesaggio vegetale sulla base delle analisi del riempimento dei pozzi al margine del Villaggio Grande della Terramara Santa Rosa di Poviglio. In: Cremaschi, M., Pizzi, C. (Eds.), Terramara Santa Rosa Di Poviglio: Le Strutture Idrauliche Al Margine Del Villaggio Grande (Scavi 1998–2011), Origines 35. Istituto Italiano di Preistoria e Protostoria, Firenze, pp. 373–387.

Florenzano, A., Marignani, M., Rosati, L., Fascetti, S., Mercuri, A.M., 2015. Are Cichorieae an indicator of open habitats and pastoralism in current and past vegetation studies? Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 149, 154–165. https://doi.org/10.1080/11263504.2014.998311.

Fokkens, H., 1999. Cattle and martiality. Changing relations between man and landscape in the Late Neolithic and the Bronze Age. In: Fabech, C., Ringtved, J. (Eds.), Settlement and Landscape. Proceedings of a Conference in Aarhus, Denmark, May 4-7 1998, Jutland Archaeological Society Publications. Jutland Archaeological Society, Højbjerg, pp. 35–43.

Font, L., Nowell, G.M., Graham Pearson, D., Ottley, C.J., Willis, S.G., 2007. Sr isotope analysis of bird feathers by TIMS: a tool to trace bird migration paths and breeding sites. J. Anal. At. 22, 513. https://doi.org/10.1039/b616328a.

Fraser, R.A., Bogaard, A., Heaton, T., Charles, M., Jones, G., Christensen, B.T., Halstead, P., Merbach, I., Poulton, P.R., Sparkes, D., Styring, A.K., 2011. Manuring and stable nitrogen isotope ratios in cereals and pulses: towards a new archaeobotanical approach to the inference of land use and dietary practices. J. Archaeol. Sci. 38, 2790–2804. https://doi.org/10.1016/j.jas.2011.06.024.

Friedli, H., Lötscher, H., Oeschger, H., Siegenthaler, U., Stauffer, B., 1986. Ice-core record of the ^{13}C/^{12}C ratio of atmospheric CO_2 in the past two centuries. Nature 324, 237–238. https://doi.org/10.1038/324237a0.

Fuks, D., Dunseth, Z.C., 2021. Dung in the dumps: what we can learn from multi-proxy studies of archaeological dung pellets. Veg. Hist. Archaeobotany 30, 137–153. https://doi.org/10.1007/s00334-020-00806-x.

Garcés-Pastor, S., Heintzman, P.D., Zetter, S., Lammers, Y., Yoccoz, N.G., Theurillat, J.-P., Schwörer, C., Tribsch, A., Walsh, K., Vannière, B., Wangensteen, O.S., Heiri, O., Coissac, E., Lavergne, S., Van Vugt, L., Rey, F., Giguet-Covex, C., Ficetola, G.F., Karger, D.N., Pellissier, L., Schabetsberger, R., Haas, J.N., Strasser, M., Koinig, K.A., Goslar, T., Szidat, S., PhyloAlps, Consortium, Brown, A.G., Tinner, W., Alsos, I.G., 2025. Wild and domesticated animal abundance is associated with greater late-holocene alpine plant diversity. Nat. Commun. 16, 3924. https://doi.org/10.1038/s41467-025-59028-2.

Gillis, R., Bréhard, S., Bălăşescu, A., Ughetto-Monfrin, J., Popovici, D., Vigne, J.-D., Balasse, M., 2013. Sophisticated cattle dairy husbandry at Borduşani-Popină (Romania, fifth millennium BC): the evidence from complementary analysis of mortality profiles and stable isotopes. World Archaeol. 45, 447–472. https://doi.org/10.1080/00438243.2013.820652.

Gillis, R., Chaix, L., Vigne, J.-D., 2011. An assessment of morphological criteria for discriminating sheep and goat mandibles on a large prehistoric archaeological assemblage (kerma, Sudan). J. Archaeol. Sci. 38, 2324–2339. https://doi.org/10.1016/j.jas.2011.04.012.

Grant, A., 1982. The use of tooth wear as a guide to the age of domestic ungulates. In: Wilson, B., Grigson, C., Payne, S. (Eds.), Ageing and Sexing Animal Bones from Archaeological Sites, BAR British Series. BAR - British Archaeological Reports, Oxford, pp. 91–108.

Greenfield, H.J., 1999. The advent of transhumant pastoralism in the temperate Southeast Europe: a zooarchaeological perspective from the central balkans. In: TRANSHUMANT PASTORALISM IN SOUTHERN EUROPE. Recent Perspectives from Archaeology, History and Ethnology, pp. 15–36.

Halstead, P., Collins, P., Isaakidou, V., 2002. Sorting the sheep from the goats: morphological distinctions between the mandibles and mandibular teeth of AdultOvis and capra. J. Archaeol. Sci. 29, 545–553. https://doi.org/10.1006/jasc.2001.0777.

Halstead, P., Tierney, J., Butler, S., Mulder, Y., 1998. Leafy hay: an ethnoarchaeological study in NW Greece. Environ. Archaeol. 1, 71–80. https://doi.org/10.1179/env.1996.1.1.71.

Helmer, D., Gourichon, L., Sidi Maamar, H., Vigne, J.-D., 2005. L'élevage des caprinés néolithiquesdans le sud-est de la France: saisonnalitédes abattages, relations entre grottes-bergerieset sites de plein air. Anthropozoologica 40 (1).

Helmer, D., Gourichon, L., Vila, E., 2007. The development of the exploitation of products from Capra and Ovis (meat, milk and fleece) from the PPNB to the Early Bronze in the northern near East (8700 to 2000 BC cal.). Anthropozoologica 41 (2), 41–69.

Helmer, D., Vigne, J.-D., 2004. La gestion des cheptels de caprinés au Néolithique dans le Midi de la France. In: Approches Fonctionnelles En Préhistoire, Actes Du Xxve Congrès Préhistorique De France Nanterre 2000, pp. 397–407.

Henton, E., Meier-Augenstein, W., Kemp, H.F., 2010. The use of oxygen isotopes in sheep molars to investigate past herding practices at the Neolithic settlement of ÇatalhÖyÜk, central Anatolia. Archaeometry 52, 429–449. https://doi.org/10.1111/j.1475-4754.2009.00492.x.

Holt, E., Evans, J.A., Madgwick, R., 2021. Strontium (87Sr/86Sr) mapping: a critical review of methods and approaches. Earth Sci. Rev. 216, 103593. https://doi.org/10.1016/j.earscirev.2021.103593.

Holt, E., Lugli, F., Schirru, D., Gigante, M., Faillace, K., Millet, M.-A., Andersen, M., Madgwick, R., 2025. Comparing machine learning isoscapes of 87Sr/86Sr ratios of plants on the island of Sardinia: implications for the use of isoscapes for assessing the provenance of biological specimens. Sci. Total Environ. 989, 179880. https://doi.org/10.1016/j.scitotenv.2025.179880.

Iannetti, M., 2021. Bellina che sei Nata alla montagna. Donne, agro-pastoralismo E Migrazioni a Pietracamela. Bambun.

Jakobitsch, T., Dworsky, C., Heiss, A.G., Kühn, M., Rosner, S., Leskovar, J., 2023. How animal dung can help to reconstruct past forest use: a late Neolithic case study from the Mooswinkel pile dwelling (Austria). Archaeol. Anthropol. Sci. 15, 20. https://doi.org/10.1007/s12520-023-01724-5.

Jeanjean, M., Mureau, C., Valenzuela-Lamas, S., Nieto Espinet, A., Jiménez Manchón, S., Colominas, L., Gardeisen, A., Renaud, A., Saña Segui, M., Gourichon, L., Bonhomme, V., Ros, J., Bouby, L., Evin, A., 2025. 8000 years of morphometric evolution of sheep, goat and pig in the northwestern Mediterranean basin. Holocene 35, 491–506. https://doi.org/10.1177/09596836251313633.

Karg, S., 1998. Winter- and spring-foddering of sheep/goat in the Bronze Age site of Fiavè-Carera, Northern Italy. Environ. Archaeol. 1, 87–94. https://doi.org/10.1179/env.1996.1.1.87.

Kenward, H.K., 2009. Invertebrates in archaeology in the North of England. Research Department Reports. English Heritage.

Knockaert, J., Balasse, M., Rendu, C., Burens, A., Campmajo, P., Carozza, L., Bousquet, D., Fiorillo, D., Vigne, J.-D., 2018. Mountain adaptation of caprine herding in the eastern Pyrenees during the Bronze Age: a stable oxygen and carbon isotope analysis of teeth. Quat. Int. 484, 60–74. https://doi.org/10.1016/j.quaint.2017.05.029.

Kristiansen, K., Stig Sørensen, M.L.S., 2019. Wool in the Bronze Age: concluding reflections. In: Sabatini, S., Bergerbrant, S. (Eds.), The Textile Revolution in Bronze

Age Europe. Cambridge University Press, pp. 317–332. https://doi.org/10.1017/9781108656405.014.

Leonardi, G., 2006. L'insediamento nell'ambito collinare e montano veneto nell'età del bronzo: il territorio veronese e vicentino. In: Studi in Onore Di Renato Peroni, pp. 435–444.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proc. Natl. Acad. Sci. USA 103, 11201–11205. https://doi.org/10.1073/pnas.0604719103.

Lodwick, L.A., 2017. Agricultural innovations at a late Iron Age oppidum: archaeobotanical evidence for flax, food and fodder from Calleva Atrebatum, UK. Quat. Int. 460, 198–219. https://doi.org/10.1016/j.quaint.2016.02.058.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. Nature 230, 241–242. https://doi.org/10.1038/230241a0.

Lugli, F., Cipriani, A., Bruno, L., Ronchetti, F., Cavazzuti, C., Benazzi, S., 2022. A strontium isoscape of Italy for provenance studies. Chem. Geol. 587, 120624. https://doi.org/10.1016/j.chemgeo.2021.120624.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochem. Cosmochim. Acta 48, 1689–1693. https://doi.org/10.1016/0016-7037(84)90338-7.

Madgwick, R., Mulville, J., Stevens, R.E., 2012. Diversity in foddering strategy and herd management in late Bronze Age Britain: an isotopic investigation of pigs and other fauna from two midden sites. Environ. Archaeol. 17, 126–140. https://doi.org/10.1179/1461410312Z.00000000011.

Magri, D., Agrillo, E., Di Rita, F., Furlanetto, G., Pini, R., Ravazzi, C., Spada, F., 2015. Holocene dynamics of tree taxa populations in Italy. Rev. Palaeobot. Palynol. 218, 267–284. https://doi.org/10.1016/j.revpalbo.2014.08.012.

Maini, E., Lattao, V., Corazza, S., Gorello, L.E., Thun Hohenstein, U., 2021. La fauna della Terramara di Pilastri di Bondeno: analisi archeozoologica e tafonomica dei resti raccolti nelle campagne 2016-2018. In: Vidale, M., Bergamini, S., Osti, G., Prillo, V. G., Reggio, C., Trevisan, F. (Eds.), I "Pilastri" Della Terramara. Alle Radici Dell'Economia Del Territorio Di Bondeno (Ferrara). Edizioni Antilia, Treviso, pp. 295–342.

Makarewicz, C.A., 2017a. Winter is coming: seasonality of ancient pastoral nomadic practices revealed in the carbon (δ13C) and nitrogen (δ15N) isotopic record of Xiongnu caprines. Archaeol. Anthropol. Sci. 9, 405–418. https://doi.org/10.1007/s12520-015-0289-5.

Makarewicz, C.A., Pederzani, S., 2017. Oxygen (δ18O) and carbon (δ13C) isotopic distinction in sequentially sampled tooth enamel of co-localized wild and domesticated caprines: complications to establishing seasonality and mobility in herbivores. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 1–15. https://doi.org/10.1016/j.palaeo.2017.01.010.

Makarewicz, C.A., 2017b. Sequential δ13C and δ18O analyses of early Holocene bovid tooth enamel: resolving vertical transhumance in Neolithic domesticated sheep and goats. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 16–29. https://doi.org/10.1016/j.palaeo.2017.01.028.

Marcolin, C., Zanetti, M., 2012. Prati di pianura. Aspetti Paesaggistici, Naturalistici Ed Ecologici. Nuovadimensione, Portogruaro (VE).

McCracken, B.A., Gaskins, H.R., Ruwe-Kaiser, P.J., Klasing, K.C., Jewell, D.E., 1995. Diet-dependent and diet-independent metabolic responses underlie growth stasis of pigs at weaning. J. Nutr. 125, 2838–2845. https://doi.org/10.1093/jn/125.11.2838.

Mercuri, A.M., Accorsi, C.A., Bandini Mazzanti, M., Bosi, G., Trevisan Grandi, G., Cardarelli, A., Labate, D., Olmi, L., Torri, P., 2006b. Cereal Fields from the Middle-Recent Bronze Age as found in the terramara di Montale, in the Po plain (Emilia Romagna, Northern Italy), based on pollen, seeds/fruits and microcharcoals. In: Morel, J.P., Tresserras, J., Matamala, J.C. (Eds.), The Archaeology of Crop Fields and Garden Archaeology. Edipuglia, Bari, pp. 251–270.

Mercuri, A.M., Accorsi, C.A., Mazzanti, M.B., Bosi, G., Cardarelli, A., Labate, D., Marchesini, M., Grandi, G.T., 2006a. Economy and environment of Bronze Age settlements – terramaras – on the Po Plain (Northern Italy): first results from the archaeobotanical research at the Terramara di Montale. Veg. Hist. Archaeobotany 16, 43–60. https://doi.org/10.1007/s00334-006-0034-1.

Mercuri, A.M., Bandini Mazzanti, M., Florenzano, A., Montecchi, M.C., Rattighieri, E., Torri, P., 2013. Anthropogenic pollen indicators (API) from archaeological sites as local evidence of human-induced environments in the Italian peninsula. Ann. Bot. (Rome) 3. https://doi.org/10.4462/annbotrm-10316.

Mercuri, A.M., Montecchi, M.C., Pellacani, G., Florenzano, A., Rattighieri, E., Cardarelli, A., 2015. Environment, human impact and the role of trees on the Po plain during the middle and recent Bronze Age: Pollen evidence from the local influence of the terramare of Baggiovara and Casinalbo. Rev. Palaeobot. Palynol. 218, 231–249. https://doi.org/10.1016/j.revpalbo.2014.08.009.

Mercuri, Anna Maria, Sadori, L., 2012. Climate changes and human settlements since the Bronze age period in central Italy. Rendiconti Online della Società Geologica Italiana 18, 32–34. https://doi.org/10.3301/ROL.2011.63.

Messana, C., Tornero, C., Madgwick, R., Lamb, A.L., Evans, J., Colominas, L., 2023. Between valleys, plateaus, and mountains: unveiling livestock altitudinal mobility in the Iron Age iberian peninsula (3rd c. BC) through a multi-isotope approach. Front. environ. archaeol. 2, 1245725. https://doi.org/10.3389/fearc.2023.1245725.

Migliavacca, M., 2014. Tracce di pastori protostorici negli alti Lessini: note etno-archeologiche e archeologiche per un'agenda futura, in: Antichi Pastori Sopravvivenze, Tradizione Orale, Storia, Tracce Nel Paesaggio e Archeologia, Atti Della Tavola Rotonda. Presented at the Tavola Rotonda Antichi Pastori Sopravvivenze, Tradizione Orale, Storia, Tracce Nel Paesaggio E Archeologia. MUSE Museo delle Scienze, Trento, pp. 157–168.

Migliavacca, M., Boscarol, C., Montagnari Kokelj, M., 2015. How to identify pastoralism in prehistory? Some hints from recent studies in Veneto and friuli Venezia Giulia. Il capitale culturale 597–620.

Müller, J., 2015. Eight million Neolithic Europeans : social demography and social archaeology on the scope of change, from the near East to Scandinavia. In: Kristiansen, K., Šmejda, L., Turek, J., Neustupný, E. (Eds.), Paradigm Found: Archaeological Theory Present, past and Future: Essays in Honour of Evžen Neustupný.

Motella De Carlo, S., 1997. Studio dei macroresti vegetali. In: Belemmi, L., Salzani, L., Squaranti, G. (Eds.), Povegliano: L'Abitato Dell'Età Del Bronzo Della Muraiola. Associazione Balladoro, Povegliano Veronese, pp. 67–76.

Nicosia, C., Dal Corso, M., D'Aquino, S., Baldan, M., Bortolini, M., Battistel, D., Polisca, F., 2025. Multiproxy analysis of stabling layers in four middle bronze age byre-houses from the site of Oppeano 4D (Verona, Italy). PLOS ONEe 20, e0323724. https://doi.org/10.1371/journal.pone.0323724.

Nicosia, C., Polisca, F., Miller, C., Ligouis, B., Mentzer, S., Mangani, C., Gonzato, F., 2022. High-resolution sediment analysis reveals middle Bronze Age byre-houses at the site of Oppeano (Verona province, NE Italy). PLoS One 17, e0272561. https://doi.org/10.1371/journal.pone.0272561.

Nier, A.O., 1938. The isotopic constitution of strontium, barium, bismuth, thallium and Mercury. Phys. Rev. 54, 275–278. https://doi.org/10.1103/PhysRev.54.275.

Nisbet, R., Rottoli, M., 1997. Le analisi dei macroresti vegetali dei siti dell'età del bronzo. In: Bernabò Brea, M., Cardarelli, A., Cremaschi, M. (Eds.), Le Terramare: La Più Antica Civiltà Padana. Electa, pp. 469–474.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. Bioscience 38, 328–336. https://doi.org/10.2307/1310735.

Olausson, M., 1999. Herding and stalling in Bronze Age Sweden. In: Fabech, C., Ringtved, J. (Eds.), Settlement and Landscape. Proceedings of a Conference in Aarhus, Denmark, May 4-7 1998, Jutland Archaeological Society Publications. Jutland Archaeological Society, Højbjerg, pp. 106–111.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals. J. Archaeol. Sci. 32, 1459–1470. https://doi.org/10.1016/j.jas.2005.03.015.

Payne, S., 1973. Kill-off patterns in sheep and goats: the mandibles from Aşvan Kale. Anatol. Stud. 23, 281–303. https://doi.org/10.2307/3642547.

Pederzani, S., Britton, K., 2019. Oxygen isotopes in bioarchaeology: principles and applications, challenges and opportunities. Earth Sci. Rev. 188, 77–107. https://doi.org/10.1016/j.earscirev.2018.11.005.

Perego, R., 2017. Contribution to the Development of the Bronze Age Plant Economy in the Surrounding of the Alps: an Archaeobotanical Case Study of Two Early and Middle Bronze Age Sites in Northern Italy (Lake Garda Region) (Phd Dissertation). Philosophisch-Naturwissenschaftliche Fakultät der Universität Basel.

Perego, R., Badino, F., Deaddis, M., Ravazzi, C., Vallè, F., Zanon, M., 2011. L'origine del paesaggio agro-pastorale in nord Italia: espansione di Orlaya grandiflora (L.) Hoffm. nella civiltà palafitticola dell'età del bronzo della regione del Garda. Notizie Archeologiche Bergomensi 19, 161–173.

Perego, R., Furlanetto, G., Rapi, M., Ravazzi, C., 2025. Plant-human interactions: from pristine forest to Bronze Age farming—vegetation history and depositional processes off-shore the lake dwelling of Lavagnone, N-Italy. Veg. Hist. Archaeobotany 34, 459–487. https://doi.org/10.1007/s00334-024-01027-2.

Perego, R., Rottoli, M., Castiglioni, E., 2022. Agricoltura e preferenze alimentari durante l'età del Bronzo e del Ferro in Lombardia, in Preistoria e Protostoria in Lombardia e nel Canton Ticino. In: De Marinis, R.C., Rapi, M. (Eds.), Atti Della LII Riunione Scientifica Dell. 'Istituto Italiano Di Preistoria e Protostoria, Rivista Di Scienze Preistoriche, pp. 63–76.

Pini, R., Ravazzi, C., Comolli, R., Perego, R., Castellano, L., Croci, C., De Amicis, M., Khair, D.A.E., Furlanetto, G., Marsetti, D., 2021. Life on a hilltop: vegetation history, plant husbandry and pastoralism at the dawn of Bergamo-Bergomum (northern Italy, 15th to 7th century bc). Veg. Hist. Archaeobotany 30, 525–553. https://doi.org/10.1007/s00334-020-00802-1.

Polisca, F., 2025. Exploring the impact of burial conditions and formation processes in intra-site contexts: a micromorphological comparison of waterlogged and well-drained Bronze Age deposits. Archaeol. Anthropol. Sci. 17, 153. https://doi.org/10.1007/s12520-025-02269-5.

Polisca, F., Dal Corso, M., Baldan, M., Bortolini, M., Battistel, D., Dal Sasso, G., Gherardi, F., Canti, M., Piazzalunga, G., Nicosia, C., 2025. Phosphatic crusts as macroscopic and microscopic proxies for identifying archaeological animal penning areas. J. Archaeol. Sci. 177, 106207. https://doi.org/10.1016/j.jas.2025.106207.

Provenzano, N., 1997. Produzione in osso e corno delle terramare emiliane. In: Bernabò Brea, M., Cardarelli, A., Cremaschi, M. (Eds.), Le Terramare: La Più Antica Civiltà Padana. Electa, Milano, pp. 524–544.

Quattrocchi, U., 2006. CRC World Dictionary of Grasses: Common Names, Scientific Names, Eponyms, Synonyms, and Etymology - 3 Volume Set, 0 ed. CRC Press. https://doi.org/10.1201/9781420003222.

Ravazzi, C., Artioli, G., Badino, F., Baioni, M., Banino, R., Castellano, L., Castelletti, L., Chiesa, S., Colombaroli, D., Comolli, R., Cremaschi, M., Croce, E., Dal Corso, M., Dal Sasso, G., Deaddis, M., De Amicis, M., Ferrario, M.F., Fontana, F., Furlanetto, G., Garozzo, L., Livio, F., Mangani, C., Marchetti, M., Martinelli, E., Michetti, Motella De Carlo, S., Nicosia, C., Perego, R., Peresani, M., Pini, R., Poggiani Keller, R., Quirino, T., Rapi, M., Rottoli, M., Ruggiero, M.G., Tinner, W., Tramelli, A., Trentacoste, A., Vallè, F., Visentin, D., Wick, L., Zanon, M., Zerboni, A., 2022. Scenari Di Ricostruzione Delle Interazioni uomo-ambiente in Lombardia (N-Italia) Dal Paleolitico Medio All'Età Del Ferro, LXXII. Rivista di Scienze Preistoriche, pp. 9–36.

Ravazzi, C., Cremaschi, M., Forlani, 2004. Studio archeopalinologico della Terramara di S. Rosa di Poviglio (RE). Nuovi dati, analisi floristica e sintassonomica della vegetazione nell'età del Bronzo. In: Bernabò Brea, M., Cremaschi, M. (Eds.), Il

Villaggio Piccolo Della Terramara Santa Rosa Di Poviglio, pp. 703–736. Scavi 1987–1992, Origines. Firenze.

Ravazzi, C., Marchetti, M., Zanon, M., Perego, R., Quirino, T., Deaddis, M., De Amicis, M., Margaritora, D., 2013. Lake evolution and landscape history in the lower Mincio River valley, unravelling drainage changes in the central Po plain (N-Italy) since the Bronze Age. Quat. Int. 288, 195–205. https://doi.org/10.1016/j.quaint.2011.11.031.

Ravazzi, C., Pini, R., 2013. Clima, vegetazione forestale e alpeggio tra la fine del Neolitico e l'inizio dell'et a del Bronzo nelle Alpi e in Pianura Padana. In: De Marinis, R.C. (Ed.), L'Età Del Rame : La Pianura Padana E Le Alpi Al Tempo Di Ötzi. Compagnia Della Stampa Massetti Rodella, pp. 69–86. Roccafranca (Brescia).

Ravazzi, C., Valsecchi, V., 2001. Saggio di analisi pollinica nel sito di Castellaro del Vhò di Piadena. In: Frontini, P. (Ed.), Castellaro Del Vhò. Campagne Di Scavo 1996-1999. Scavi Delle Civiche Raccolte Archeologiche Di Milano, Milano, pp. 197–202.

Reed, K., 2024. Let me be fodder: unravelling human and animal derived plant remains recovered from Roman Mursa, Croatia. Quat. Int. 699, 23–34. https://doi.org/10.1016/j.quaint.2024.02.008.

Emilia-Romagna, Regione, 2016. Acqua dalle rocce, una ricchezza della montagna. Percorsi Interdisciplinari Nell'Affascinante Mondo Delle Sorgenti. Eliofototecnicabarbieri, Parma.

Riedel, A., 1997. La fauna di Muraiola. In: Belemmi, L., Salzani, L., Squaranti, G. (Eds.), Povegliano: L'Abitato Dell'Età Del Bronzo Della Muraiola, pp. 77–89.

Riedel, A., Tecchiati, U., 2003. La capra e la pecora in Italia tra il Neolitico e l'età del Bronzo. In: Bazzanella, M., Mayr, A., Moser, L., Rast-Eicher, A. (Eds.), Textiles. Intrecci E Tessuti Della Preistoria Europea. Provincia Autonoma di Trento, Trento, pp. 73–78.

Robbins, C.T., Felicetti, L.A., Sponheimer, M., 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. Oecologia 144, 534–540. https://doi.org/10.1007/s00442-005-0021-8.

Rottoli, M., 1999. I resti vegetali di Sammardenchia-Cûeis (Udine), insediamento del Neolitico antico. In: Ferrari, A., Pessina, A. (Eds.), Sammardenchia, Cûeis: Contributi per La Conoscenza Di Una Comunità Del Primo Neolitico, 41. Pubblicazioni Del Museo Friulano Di Storia Naturale, Udine, pp. 307–326. Museo Friulano di Storia Naturale.

Rottoli, M., 2001. Analisi archeobotaniche al Castellaro del Vhò: i macroresti vegetali. In: Frontini, P. (Ed.), Castellaro Del Vhò. Campagne Di Scavo 1996-1999. Scavi Delle Civiche Raccolte Archeologiche Di Milano, Milano, pp. 175–195.

Rottoli, M., 2024. Le specie vegetali alimentari nelle palafitte del lago di Garda e della pianura veronese: uno sguardo d'insieme. In: Migliavacca, M., Martinelli, N., Salzani, P., Saracino, M. (Eds.), Food and Wine in Ancient Verona - Cibo E Vino Nella Verona Antica. Quasar, Roma, pp. 64–78.

Rottoli, M., Castiglioni, E., 2009a. Indagini Sui resti vegetali macroscopici. In: Bernabò Brea, M., Cremaschi, M. (Eds.), Acqua E Civiltà Nelle Terramare: La Vasca Votiva Di Noceto. Skira, Milano, pp. 152–163.

Rottoli, M., Castiglioni, E., 2009b. Prehistory of plant growing and collecting in northern Italy, based on seed remains from the early Neolithic to the chalcolithic (c. 5600–2100 cal b.c. Veg. Hist. Archaeobotany 18, 91–103. https://doi.org/10.1007/s00334-007-0139-1.

Rottoli, M., Motella De Carlo, S., 2004. I resti antracologici e lignei della terramara Santa Rosa di Poviglio. In: Bernabò Brea, M., Cremaschi, M. (Eds.), Il Villaggio Piccolo Della Terramara Santa Rosa Di Poviglio, pp. 737–742. Scavi 1987–1992, Origines. Firenze.

Rösch, M., 2018. Evidence for rare crop weeds of the Caucalidion group in Southwestern Germany since the Bronze Age: palaeoecological implications. Veg. Hist. Archaeobotany 27 (1), 75–84. https://doi.org/10.1007/s00334-017-0615-1.

Ryder, M.L., 1994. Observations on Vlach sheep-milking and milk-processing in south-east Europe. Anthropozoologica 3–10.

Sabatini, S., Bergerbrant, S., Brandt, L.Ø., Margaryan, A., Allentoft, M.E., 2019. Approaching sheep herds origins and the emergence of the wool economy in continental Europe during the Bronze Age. Archaeol. Anthropol. Sci. 11, 4909–4925. https://doi.org/10.1007/s12520-019-00856-x.

Sabatini, S., Earle, T., Cardarelli, A., 2018. Bronze Age textile & wool economy: the case of the terramare site of montale, Italy. Proc. Prehist. Soc. 84, 359–385. https://doi.org/10.1017/ppr.2018.11.

Sabatini, S., Frei, K.M., De Grossi Mazzorin, J., Cardarelli, A., Pellacani, G., Frei, R., 2022. Investigating sheep mobility at Montale, Italy, through strontium isotope analyses. J. Archaeol. Sci.: Report 41, 103298. https://doi.org/10.1016/j.jasrep.2021.103298.

Salzani, L., 1997. Indagini archeologiche alla Muraiola. In: Belemmi, L., Salzani, L., Squaranti, G. (Eds.), Povegliano: L'Abitato Dell'Età Del Bronzo Della Muraiola, pp. 17–27.

Sauro, U., 2018. Lessinia. Montagna Teatro E Montagna Laboratorio. Cierre Edizioni, Verona.

Schepers, M., Van Haaster, H., 2015. Dung matters: an experimental study into the effectiveness of using dung from hay-fed livestock to reconstruct local vegetation. Environ. Archaeol. 20, 66–81. https://doi.org/10.1179/1749631414Y.0000000030.

Schlütz, F., Hofmann, R., Dal Corso, M., Pashkevych, G., Dreibrodt, S., Shatilo, M., Ţerna, A., Fuchs, K., Filipović, D., Flohra, P., Makarewicza, C.A., Ţernaa, S., Videiko, M., Rud, V., Müller, J., Kirleis, W., 2023. Isotopes prove advanced, integral crop production, and stockbreeding strategies nourished Trypillia mega-populations. Proc. Natl. Acad. Sci. USA 120, e2312962120. https://doi.org/10.1073/pnas.2312962120.

Scorrer, J., Faillace, K.E., Hildred, A., Nederbragt, A.J., Andersen, M.B., Millet, M.-A., Lamb, A.L., Madgwick, R., 2021. Diversity aboard a Tudor warship: investigating the origins of the *Mary Rose* crew using multi-isotope analysis. R. Soc. Open Sci. 8, rsos.202106. https://doi.org/10.1098/rsos.202106, 202106.

Shahack-Gross, R., 2017. Animal gathering enclosures. In: Nicosia, C., Stoops, G. (Eds.), Archaeological Soil and Sediment Micromorphology. Wiley, pp. 265–280. https://doi.org/10.1002/9781118941065.ch29.

Sherratt, A., 1981. Plough and pastoralism: aspects of the secondary products revolution. In: Hodder, I., Isaac, G., Hammond, N. (Eds.), Pattern of the Past: Studies in Honour of David Clarke. Cambridge University Press, Cambridge, pp. 261–305.

Shillito, L.-M., Blong, J.C., Green, E.J., Van Asperen, E.N., 2020. The what, how and why of archaeological coprolite analysis. Earth Sci. Rev. 207, 103196. https://doi.org/10.1016/j.earscirev.2020.103196.

Smerdel, I., 2014. Art of a mower: skills with a scent of sexuality. In: van Gijn, A., Whittaker, J.C., Anderson, P.C. (Eds.), Exploring and Explaining Diversity in Agricultural Technology. Oxbow Books, Oxford & Philadelphia, pp. 269–275.

Sonsini, A., Angelucci, S., 2012. La morra. Memorie Ed Eredità Della Pastorizia Non Transumante. Libri Edizioni Menabò, Pescara.

Sorbini, L., Gandini, F., Meneghel, M., Rigoni, A., Sommaruga, M., 1984. Geologia e geomorfologia di una porzione della pianura a sud-est di Verona. In: Memorie Del Museo Civico Di Storia Naturale Di Verona (Iia Serie), 2.

Sucholas, J., Molnár, Z., Łuczaj, Ł., Poschlod, P., 2022. Local traditional ecological knowledge about hay management practices in wetlands of the Biebrza Valley, Poland. J. Ethnobiol. Ethnomed. 18, 9. https://doi.org/10.1186/s13002-022-00509-9.

Tafuri, M.A., Craig, O.E., Canci, A., 2009. Stable isotope evidence for the consumption of millet and other plants in Bronze Age Italy. Am. J. Phys. Anthropol. 139, 146–153. https://doi.org/10.1002/ajpa.20955.

Tafuri, M.A., Rottoli, M., Cupitò, M., Pulcini, M.L., Tasca, G., Carrara, N., Bonfanti, F., Salzani, L., Canci, A., 2018. Estimating C_4 plant consumption in Bronze Age Northeastern Italy through stable carbon and nitrogen isotopes in bone collagen. Int. J. Osteoarchaeol. 28, 131–142. https://doi.org/10.1002/oa.2639.

Taguchi, T., Lopez, M.J., 2021. An overview of de novo bone generation in animal models. J. Orthop. Res. 39, 7–21. https://doi.org/10.1002/jor.24852.

Tecchiati, U., Salzani, P., Putzolu, C., Fapanni, F., Gulino, F., Orsi, M., Perolfi, L., Proserpio, B., Reggio, C., Simonini, G., 2024. Ambiente, economia e alimentazione nel sito preistorico delle Colombare di Villa (Negrar di Valpolicella – VR). Nuovi dati 2019-2023. In: Migliavacca, M., Martinelli, N., Salzani, P., Saracino, M. (Eds.), Food and Wine in Ancient Verona = Cibo E Vino Nella Verona Antica. 2: Mangiare E Bere Nella Preistoria E Protostoria. Edizioni Quasar, Roma, pp. 46–63.

Tieszen, L.L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. J. Archaeol. Sci. 18, 227–248. https://doi.org/10.1016/0305-4403(91)90063-U.

Tinley, N.L., 1949. Good Sheep Farming. The English Universities Press Ltd.

Tornero, C., Aguilera, M., Ferrio, J.P., Arcusa, H., Moreno-García, M., Garcia-Reig, S., Rojo-Guerra, M., 2018. Vertical sheep mobility along the altitudinal gradient through stable isotope analyses in tooth molar bioapatite, meteoric water and pastures: a reference from the Ebro valley to the Central Pyrenees. Quat. Int. 484, 94–106. https://doi.org/10.1016/j.quaint.2016.11.042.

Tornero, C., Bălăşescu, A., Ughetto-Monfrin, J., Voinea, V., Balasse, M., 2013. Seasonality and season of birth in early eneolithic sheep from Cheia (Romania): methodological advances and implications for animal economy. J. Archaeol. Sci. 40, 4039–4055. https://doi.org/10.1016/j.jas.2013.05.013.

Tosco, U., 1958. Stazioni Floristiche Che Scompaiono: Le Dune Della Bassa Veronese. Memorie del Museo Civico di Storia Naturale di Verona VI, pp. 253–260.

Vaiglova, P., Halstead, P., Pappa, M., Triantaphyllou, S., Valamoti, S.M., Evans, J., Fraser, R., Karkanas, P., Kay, A., Lee-Thorp, J., Bogaard, A., 2018. Of cattle and feasts: multi-isotope investigation of animal husbandry and communal feasting at Neolithic Makriyalos, northern Greece. PLoS One 13, e0194474. https://doi.org/10.1371/journal.pone.0194474.

van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. J. Archaeol. Sci. 26 (6), 687–695. https://doi.org/10.1006/jasc.1998.0385. https://linkinghub.elsevier.com/retrieve/pii/S0305440398903855.

Varalli, A., Moggi-Cecchi, J., Dori, I., Boccone, S., Bortoluzzi, S., Salzani, P., Tafuri, M.A., 2016. Dietary continuity vs. discontinuity in Bronze Age Italy. The isotopic evidence from Arano di Cellore (Illasi, Verona, Italy). J. Archaeol. Sci.: Report 7, 104–113. https://doi.org/10.1016/j.jasrep.2016.03.047.

Varalli, A., Moggi-Cecchi, J., Goude, G., 2022. A multi-proxy bioarchaeological approach reveals new trends in Bronze Age diet in Italy. Sci. Rep. 12, 12203. https://doi.org/10.1038/s41598-022-15581-0.

Varkuleviciute, K., Gron, K.J., Patterson, W.P., Panelli, C., Rossi, S., Timsic, S., Gröcke, D. R., Maggi, R., Rowley-Conwy, P., 2021. Transhumance in the Early Neolithic? Carbon and oxygen isotope insights into sheep husbandry at Arene Candide, Northern Italy. J. Archaeol. Sci.: Report 40, 103240. https://doi.org/10.1016/j.jasrep.2021.103240.

Webb, E.C., Stewart, A., Miller, B., Tarlton, J., Evershed, R.P., 2016. Age effects and the influence of varying proportions of terrestrial and marine dietary protein on the stable nitrogen-isotope compositions of pig bone collagen and soft tissues from a controlled feeding experiment. Star: Science & Technology of Archaeological Research 2, 54–66. https://doi.org/10.1080/20548923.2015.1133121.

Wick, L., 1996. Late-glacial and early-holocene palaeoenvironments in Brianza, N Italy. Il Quat. 9, 653–660.

Witzel, C., Kierdorf, U., Frölich, K., Kierdorf, H., 2018. The pay-off of hypsodonty - timing and dynamics of crown growth and wear in molars of Soay sheep. BMC Evol. Biol. 18, 207. https://doi.org/10.1186/s12862-018-1332-9.

Zanon, M., Davis, B.A.S., Marquer, L., Brewer, S., Kaplan, J.O., 2018. European forest cover during the past 12,000 years: a palynological reconstruction based on modern analogs and remote sensing. Front. Plant Sci. 9, 253. https://doi.org/10.3389/fpls.2018.00253.

Zanon, M., Unkel, I., Andersen, N., Kirleis, W., 2019. Palaeoenvironmental dynamics at the southern Alpine foothills between the Neolithic and the Bronze Age onset. A multi-proxy study from Bande di Cavriana (Mantua, Italy). Quat. Sci. Rev. 221, 105891. https://doi.org/10.1016/j.quascirev.2019.105891.

Zazzo, A., Balasse, M., Passey, B.H., Moloney, A.P., Monahan, F.J., Schmidt, O., 2010. The isotope record of short- and long-term dietary changes in sheep tooth enamel: implications for quantitative reconstruction of paleodiets. Geochem. Cosmochim. Acta 74, 3571–3586. https://doi.org/10.1016/j.gca.2010.03.017.

Zeder, M.A., Pilaar, S.E., 2010. Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, Ovis, and goats, Capra. J. Archaeol. Sci. 37, 225–242. https://doi.org/10.1016/j.jas.2009.10.002.

Ziliotto, U., Andrich, O., Lasen, C., Ramanzin, M., 2004. Tratti essenziali della tipologia veneta dei pascoli di monte e dintorni. Regione del Veneto. Accademia Italiana Di Scienze Forestali.

Zimmerman, W.H., 1999. Why was cattle-stalling introduced in prehistory? The significance of byre and stable and of outwintering. In: Fabech, C., Ringtved, J. (Eds.), Settlement and Landscape. Proceedings of a Conference in Aarhus, Denmark, May 4-7 1998, Jutland Archaeological Society Publications. Jutland Archaeological Society, Højbjerg, pp. 301–318.

Zorzin, R., 1997. Appunti di geologia. In: Belemmi, L., Salzani, L., Squaranti, G. (Eds.), Povegliano: L'Abitato Dell'Età Del Bronzo Della Muraiola. Associazione Balladoro, Povegliano Veronese, pp. 11–15.