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Diet and habitat of the late Middle Pleistocene mammals from the Casal de' Pazzi site (Rome, Italy) using stable carbon and oxygen isotope ratios

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ABSTRACT

The late Middle Pleistocene archaeological site of Casal de' Pazzi (MIS 7, ~240–200 ka) in central Italy provided a complex of paleontological (both fauna and flora) and archaeological evidence, as well as a cranial fragment of *Homo heidelbergensis*.

Here, we investigated the stable carbon and oxygen isotopic ratios of tooth enamel from six herbivore species (*Palaeoloxodon antiquus*, *Hippopotamus amphibius*, *Bos primigenius*, *Stephanorhinus kirchbergensis*, *Equus ferus*, and *Dama Dama*) to contribute to the understanding of the paleoenvironment of the site through the reconstruction of the diet and habitat of Pleistocene mammals. Our results indicate that the analyzed taxa fed on C_3 plants and exploited both closed and open environments. This is consistent with the macro-botanical remains (leaf fossil impressions of *Zelkova* sp., *Laurus nobilis*, and *Cercis siliquastrum*) found at Casal de' Pazzi and pollen evidence from the nearby lake of Valle di Castiglione. The area around the site was characterized by diversified Mediterranean evergreen forest tree species, accompanied by mesophilic elements of the mixed deciduous oak and beach forest, alternating with diversified wooded/forested vegetation and xeric vegetation. This was the environmental context in which the late Middle Pleistocene *Homo* lived. Comparisons with published isotopic data from other European archaeological localities between ~600 and 125 ka evidenced considerable environmental differences through time and space, according to the general climate trends and local factors, such as latitude, temperature, and vegetation composition.

1. Introduction

The Chibanian (Middle Pleistocene, ~774–129 ka) (Suganuma et al., 2021) was a significant phase for the Earth System, characterized by the change in the periodicity and intensity of glacial-interglacial cycles from approximately 41 ka to 100 ka that occurred during the Early-Middle Pleistocene Transition (Clark et al., 2006; Head and Gibbard, 2015; Maslin and Brierley, 2015; Strani et al., 2021). During this phase, longer climatic oscillations determined relatively stable environmental conditions compared to previous phases, with changes in terms of habitat and vegetation composition, dispersal and evolutionary trends of mammalian communities, including hominins, in modern-day Europe (Palombo, 2009; Kahlke et al., 2011; Manzi et al., 2011; Magri and Palombo, 2013).

Tracking stable carbon and oxygen isotopes in tooth enamel is a common and powerful tool for investigating past habitats and environments by reconstructing the feeding behaviors of fossil species. This method is based on the principle that the carbonate fraction of teeth and bones reflects that of food and water ingested by an organism (Kohn, 1999). Tooth enamel is almost entirely inorganic, less susceptible to alteration owing to diagenesis, and is not remodeled throughout the lifetime of mammals (e.g., Lee-Thorp and Sponheimer, 2003; Bocherens et al., 2011; Bocherens and Drucker, 2013). Therefore, the original isotopic signal is more likely to be preserved than in dentine and bone (Kohn and Cerling, 2002).

Paleoenvironmental reconstruction of the European Middle Pleistocene contexts is one of the most studied issues in paleoecology, and it has often been addressed using stable isotope analysis in several archaeological sites (Filippi et al., 2001; Palombo et al., 2005; García et al., 2009; Grube et al., 2010; Ecker et al., 2013; Pushkina et al., 2014; Julien et al., 2015; Kuitems et al., 2015; Capalbo, 2018; Strani et al., 2019;

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Zanazzi et al., 2022).

Here, we present the stable carbon and oxygen isotope analysis of tooth enamel of six herbivore species (*Palaeoloxodon antiquus*, *Hippopotamus amphibius*, *Stephanorhinus kirchbergensis*, *Bos primigenius*, *Equus ferus*, and *Dama dama*) from the late Middle Pleistocene site of Casal de' Pazzi (MIS 7, ~240–200 ka) to reconstruct their dietary strategies and habitat and contribute to the understanding of the environmental context. Furthermore, we crosscheck our stable isotope data with macrobotanical evidence from the Casal de' Pazzi site and pollen analysis from the nearby lake of Valle di Castiglione to define better the paleoenvironment of the area around Casal de' Pazzi, where the late Middle Pleistocene *Homo* lived. Finally, we compare our isotopic results with those of other European archaeological localities between ~600 and 125 ka to test whether the same species displayed different feeding adaptations according to local environmental and climatic variability.

2. Archaeological background

The archaeological site of Casal de' Pazzi is located along the lower Aniene Valley, in the northeast suburbs of Rome (Italy) at 33 m above sea level (41°55′42.09″N; 12°33′49.83″E) (Fig. 1). The site was discovered in 1981 and investigated by Soprintendenza Archeologica di Roma until 1986 (Anzidei, 1983, 1984; Anzidei and Ruffo, 1984, 1985; Anzidei et al., 1999). The excavation involved an area of ~1.200 m^2, revealing part of a paleo-river channel, probably a small tributary of the Aniene River, according to the last stratigraphic excavation in 2013. Part of the paleosurface (~300 m^2) is still preserved and musealized (Gioia et al., 2014) (Supplementary A). The deposit is the result of various episodes of accumulation, erosion, and transportation of fluvial cycles. Numerous archaeological remains were transported and accumulated during flood episodes (Fig. S1). Subsequently, progressive infilling of the paleo-river contributed to the development of the overlying fluvial layers made of sand, gravel, and silt (Fig. S2) (Segre, 1983; Anzidei and Ruffo, 1984; Anzidei et al., 1984; Anzidei and Ruffo, 1985; Bietti, 1985; Anzidei and Morganti, 1988; Anzidei and Gioia, 1992). Also, the distribution of the archaeological materials is not uniform, which is consistent with a fluvial context (Anzidei et al., 1999). The deposit overlies a tuff bed, a pyroclastic deposit known as Pozzolane Superiori, dated by Villa (1992) at 355 ± 1 ka and by Karner and Renne (1998) at 357 ± 2 ka ($^{40}Ar/^{39}Ar$ dates) (Karner and Marra, 1998; Karner et al., 2001; Gioia et al., 2014). The archaeological complex is also correlated to the Vitinia Faunal Unit and the interglacial Marine Isotope Stage 7 (MIS 7) with a suggested age of ~240 - 200 ka (late Middle Pleistocene) (Conato et al., 1980; De Rita et al., 1991; Gliozzi et al., 1997; Anzidei and Cerilli, 2001; Choudhury et al., 2020).

The lithic artifacts comprise more than 1.500 Middle Palaeolithic tools (Mousterian), mostly on flakes from small siliceous pebbles, and only a retouched bone fragment (Fig. S3) (Anzidei and Ruffo, 1985; Anzidei and Gioia, 1992). The faunal assemblage (>2.000 remains) includes large herbivores, such as *Palaeoloxodon antiquus*, *Bos primigenius*, *Stephanorhinus kirchbergensis*, *Hippopotamus amphibius*, and other mammals (*Cervus elaphus*, *Equus* sp., *Dama dama*, *Sus scrofa*, *Canis lupus*, *Crocuta crocuta*), but also aquatic birds (*Anser albifrons*, *Anas penelope*, *Anas streptera*, *Anas crecca*), and tortoises (*Emys orbicularis*) (Gioia, 2020). In 1983, a human right parietal bone (CdP – H1) was discovered in the lowest layer, almost at the bottom of the sequence and directly in contact with the rocky riverbed (Figs. S4–S5). The fragment was generally attributed to an archaic *Homo*, then to *H. heidelbergensis* (Anzidei and Ruffo, 1985; Bietti, 1985; Manzi and Passarello, 1989, 1991; Passarello et al., 1987; Manzi et al., 1990; Di Vincenzo and Manzi, in press).

2.1. Palaeobotanical data

The Casal de' Pazzi deposit yielded leaf fossil impressions of *Zelkova* sp. (Fig. 2), a tree of the family Ulmaceae widespread in peninsular Italy during the Middle Pleistocene but later extinct in this country, *Laurus*

Fig. 2. Leaf fossil impressions of *Zelkova* sp. from Casal de' Pazzi (https://www.museocasaldepazzi.it/en, accessed 10th August 2022); scale bar = 2 cm.

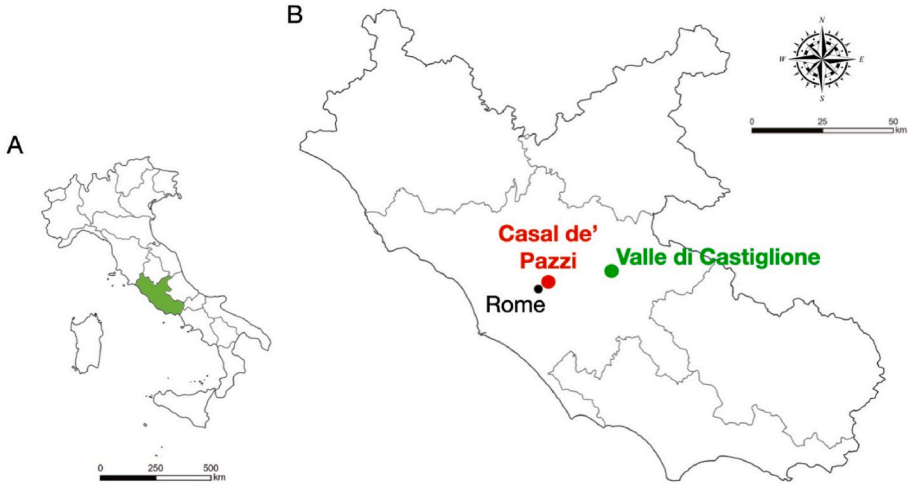

Fig. 1. Map of Italy with Lazio highlighted in green (A) and location of Casal de' Pazzi and Valle di Castiglione (B).

nobilis (laurel, an aromatic evergreen tree or large shrub), and *Cercis siliquastrum* (Judas tree), preserved by silt/clay layers (Magri, 2020). These macrofossils, which usually held close to their growth position, point to riparian habitats in a temperate and humid climate. Pollen analysis was unsuccessful at Casal de' Pazzi and did not provide evidence. However, palynological studies have been successfully carried out at the lake of Valle di Castiglione, located 12.5 km east of Casal de' Pazzi (Follieri et al., 1988). Pollen grains disperse at different distances, which has implications for reconstructing the past flora. Overall, the pollen data showed variations in the proportions of the forest tree species and herbaceous plants. For the period that is the focus of the present study (~240–200 ka), the pollen assemblages showed variations in the proportion of many Mediterranean evergreen forest tree species (*Fagus*, *Abies*, *Zelkova*, *Quercus*, and *Olea*), accompanied by mesophilic elements of the mixed deciduous oak and beach forest, indicating the development of diversified wooded/forest vegetation. However, the high percentage of herbaceous plants also pointed to the existence of open environments (Fig. 3). For more details on the sampling strategies, laboratory activities, and discussion, see Follieri et al. (1988).

3. Materials and methods

We measured the $^{13}C/^{12}C$ and $^{18}O/^{16}O$ isotopic ratios of enamel carbonates on 22 fossil teeth of *Palaeoloxodon antiquus*, *Hippopotamus amphibius*, *Stephanorhinus kirchbergensis*, *Bos primigenius*, *Equus ferus*, and *Dama* (Fig. 4). The enamel samples were collected in July 2020 at the Casal de' Pazzi Museum and then pretreated and analyzed at the Biogeology Research Group of the University of Tübingen (Germany), following the internal lab protocol (Koch et al., 1997). Fossil teeth were taxonomically identified by Dr Luca Pandolfi in 2017. The principles of the methods and techniques for tooth enamel bulk sampling, pretreatment, and analysis using an Isotope Ratio Mass Spectrometer (IRMS) are provided in Supplementary B and C. Briefly, 12–15 mg of enamel were pretreated with NaOCl followed by buffer acetic acid-calcium acetate. This pretreatment is the most used method for cleaning bioapatite samples, and it effectively removes organic matter and exogenous carbonate (Koch et al., 1997; Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). Then, 2.5–3 mg of powdered enamel were analyzed using a MultiFlow-Geo interface with the Elementar IsoPrime 100 IRMS. The stable isotopic results are typically expressed using the standard δ-notation: $X = [(R_{sample}/R_{standard}) - 1] * 1000$, where X is referred to as $\delta^{13}C$ and $\delta^{18}O$ values and R represents $^{13}C/^{12}C$ or $^{18}O/^{16}O$. Carbon and oxygen isotope compositions were expressed relative to Vienna PeeDee Belemnite (VPDB) and Vienna Standard Mean Ocean Water (VSMOW) standards, respectively. We applied the body-mass calibrated regression formulae (A and B) provided by Tejada-Lara et al. (2018) to calculate the enrichment factor (ε^*) of herbivorous mammals. Formula A is used for foregut fermenters, such as cervids and bovids:

$$\varepsilon^* = e\,[\,2.34 + 0.05\,(BM)\,] \quad (A)$$

Whereas formula B is used for hindgut fermenters, such as elephants, equids, and rhinos:

$$\varepsilon^* = e\,[\,2.42 + 0.032\,(BM)\,] \quad (B)$$

BM is the body mass in kg (Larramendi et al., 2017; Saarinen et al., 2016, 2021) and log-transformed (ln). The obtained ε^* needs to be inverted (e^x) to obtain the ‰ value to be applied to interpret the isotopic signature of the analyzed mammals (Tejada-Lara et al. (2018). Finally, we calculated the $\delta^{13}C_{ecosystem}$ by subtracting the obtained ε^* of each taxon from the $\delta^{13}C_{apatite}$ values (Cerling and Harris, 1999; Bocherens, 2014). $\delta^{13}C_{ecosystem}$ values higher than - 27 ‰ indicate open environments, such as grasslands and parklands, whereas $\delta^{13}C_{ecosystem}$ values lower than - 27 ‰ indicate closed environments, such as closed canopy and forests (Drucker et al., 2008; Bocherens, 2014; Pushkina et al., 2014).

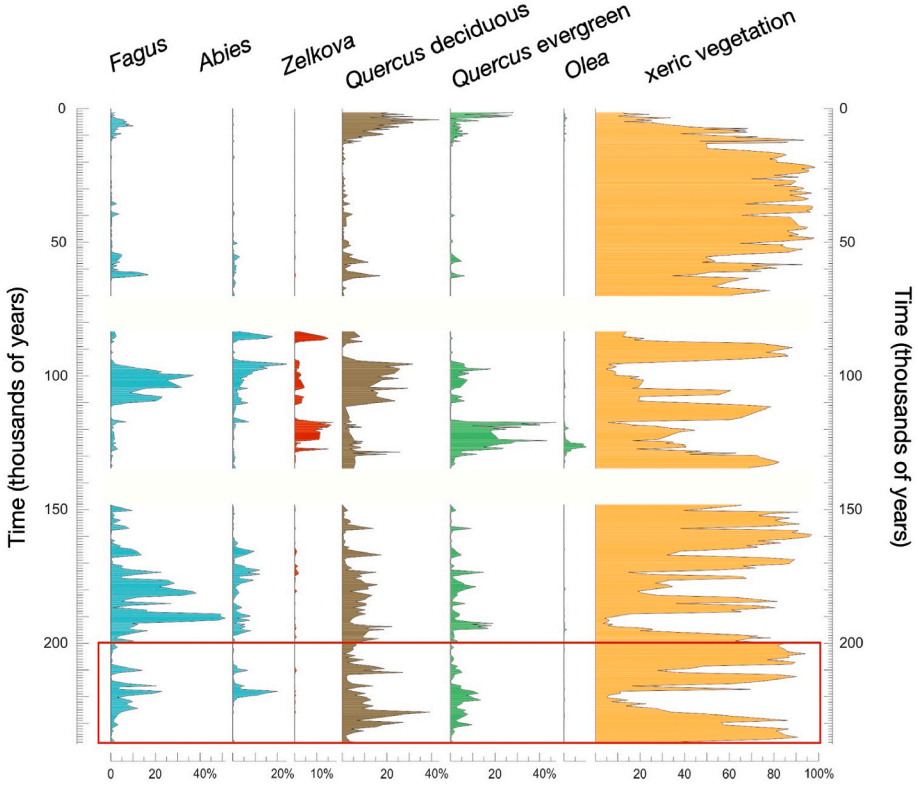

Fig. 3. Diagram showing the pollen percentage identified at the Valle di Castiglione sequence. The red rectangle indicates the chronological frame relevant to Casal de' Pazzi (modified after Magri, 2020).

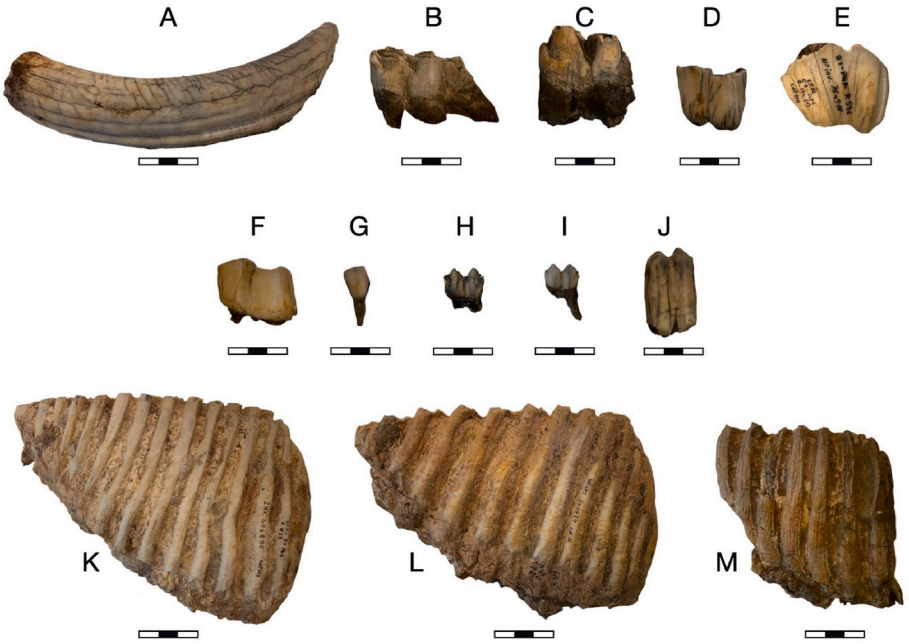

Fig. 4. Examples of teeth sampled for the isotopic analyses: A *Hippopotamus amphibius* upper right canine (CDP 107); B *Hippopotamus amphibius* lower left third molar (CDP 110); C *Hippopotamus amphibius* lower right third molar (CDP 109); D *Stephanorhinus kirchbergensis* lower left premolar (CDP 105); E *Stephanorhinus kirchbergensis* upper left third molar (CDP 104); F *Stephanorhinus kirchbergensis* lower left fourth molar (CDP 106); G *Bos primigenius* lower incisor (CDP 82); H, I *Dama dama* lower right molars (CDP 125; CDP 124); J *Bos primigenius* upper third molar (CDP 84); K, L *Palaeoloxodon antiquus* upper right molars (CDP 97; CDP 101); M *Palaeoloxodon antiquus* upper molar fragment (CDP 99); scale bar = 3 cm.

4. Results

The $\delta^{13}C$ and $\delta^{18}O$ values are reported in Table 1 and plotted in Fig. 5. Overall, the $\delta^{13}C$ values ranged from - 15.8 ‰ to - 9.4 ‰. Hippo (n = 4; average: 14.7 ‰), deer (n = 2; average: 13.4 ‰), rhinos (n = 3; average: 12.5 ‰), and elephants (n = 9; average: 12.5 ‰) had lower δ13C values than those of a single equid specimen (-12 ‰) and bovids (n = 3; average: 11.2 ‰). Elephant (n = 9) is the only taxon that showed a wide range of δ13C values, spanning from - 14.7 ‰ to - 9.4 ‰ (average: 12.5 ‰). However, two deciduous teeth of elephants had lower δ13C values (-14.7 ‰ and - 14.6 ‰) than the adult specimens (n = 7; average: 11.9 ‰) (Fig. 6). The statistics indicate a normal distribution of $\delta^{13}C$ and $\delta^{18}O$ values (Shapiro-Wilk Tests: p = 0.9891; p = 0.9931, respectively), which was also confirmed by visual Kernel density and Normal Quantile Plot observations. Statistically significant differences in $\delta^{13}C$ values of semi-aquatic and terrestrial herbivores were observed (*t*-Test: p = 0.0045). The $\delta^{18}O$ values ranged between +21.3 ‰ and +26.9 ‰, with lower $\delta^{18}O$ values for hippos (average: +22.3 ‰) than for fully terrestrial animals such as rhinos (average: +23.7 ‰), elephants (average: +24.2 ‰), deer (average: +25.5 ‰), bovids (average: +25.6 ‰), and

Table 1
Faunal specimen information and stable carbon and oxygen isotopic results from Casal de' Pazzi (Rome, Italy).

	Sample ID	Fauna ID	Element	Order	Family	Species	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (SMOW)	CO3 (%)
1	CDP 1	CDP 108	lower right canine fragment	Artiodactyla	Hippopotamidae	*Hippopotamus amphibius*	−14.4	22	3.9
2	CDP 2	CDP 107	upper right canine	Artiodactyla	Hippopotamidae	*Hippopotamus amphibius*	−14.9	21.3	4.3
3	CDP 3	CDP 110	lower left third molar	Artiodactyla	Hippopotamidae	*Hippopotamus amphibius*	−13.7	22.8	4.4
4	CDP 4	CDP 109	lower right third molar	Artiodactyla	Hippopotamidae	*Hippopotamus amphibius*	−15.8	23.2	3.7
5	CDP 5	CDP 105	lower left premolar	Perissodactyla	Rhinocerotidae	*Stephanorhinus kirchbergensis*	−12.6	24.3	3.2
6	CDP 6	CDP 104	upper left third molar	Perissodactyla	Rhinocerotidae	*Stephanorhinus kirchbergensis*	−12.5	24.2	4
7	CDP 7	CDP 106	lower left fourth premolar	Perissodactyla	Rhinocerotidae	*Stephanorhinus kirchbergensis*	−12.6	22.8	3
8	CDP 8	CDP 82	lower incisor	Artiodactyla	Bovidae	*Bos primigenius*	−11.6	25.8	3.9
9	CDP 9	CDP 84	upper third molar	Artiodactyla	Bovidae	*Bos primigenius*	−10.7	25.7	4.4
10	CDP 10	CDP 83	lower third molar	Artiodactyla	Bovidae	*Bos primigenius*	−11.4	25.3	4.9
11	CDP 11	CDP 124	lower right molar	Artiodactyla	Cervidae	*Dama*	−12.9	24.2	4.8
12	CDP 14	CDP 125	lower right molar	Artiodactyla	Cervidae	*Dama*	−14	26.9	5.1
13	CDP 15	CDP 113	upper left molar	Perissodactyla	Equidae	*Equus ferus*	−12	26	4.7
14	CDP 12	CDP 103	upper left molar	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−13.2	23.9	4.4
15	CDP 13	CDP 101	upper right molar	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−13.3	24.6	4.2
16	CDP 16	CDP 82bis	molar fragment	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−11.5	23.5	4.5
17	CDP 17	CDP 95	upper deciduous	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−14.6	24.9	5.3
18	CDP 18	CDP 96	lower left fourth deciduous	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−14.7	24.7	4.9
19	CDP 19	CDP 97	upper right molar	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−12.9	23.9	6.9
20	CDP 20	CDP 98	lower right molar	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−10.9	25.2	6.9
21	CDP 21	CDP 99	upper molar fragment	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−12.6	22.8	5.6
22	CDP 22	CDP 100	upper molar fragment	Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	−9.4	24.8	6.5

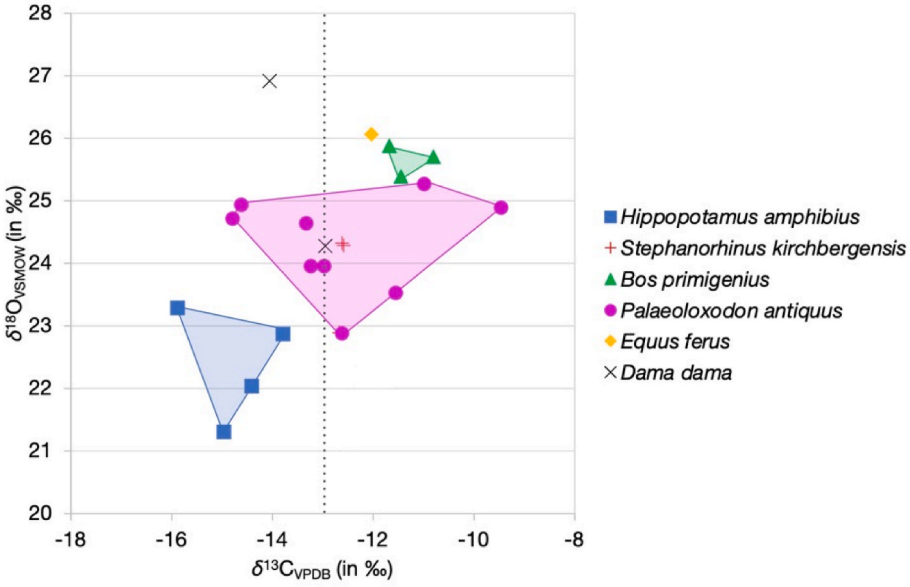

Fig. 5. $\delta^{13}C$ and $\delta^{18}O$ values of fauna tooth enamel from Casal de' Pazzi. The $\delta^{13}C$ value - 13 ‰ (vertical dotted line) is fixed to distinguish closed vs. open vegetation, following Bocherens (2014).

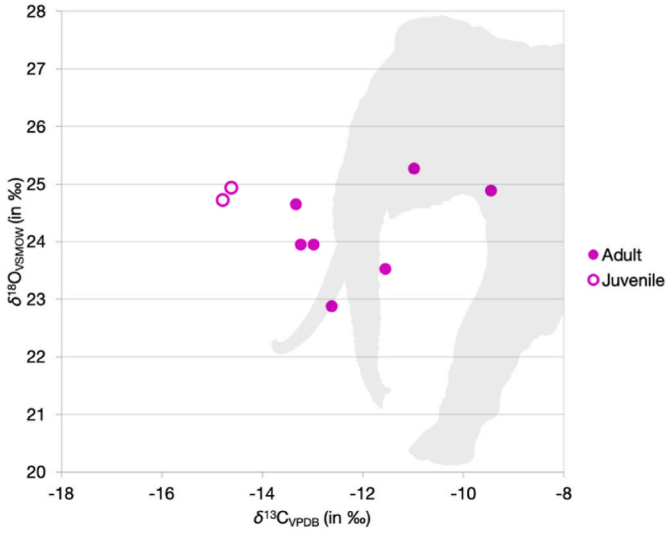

Fig. 6. Pre- and post-weaning elephant samples from Casal de' Pazzi. Animal silhouette: http://phylopic.org.

equids (+26 ‰) (*t*-Test: p = 0.0043).

5. Discussion

5.1. Dietary and environmental reconstruction

The $\delta^{13}C$ values from Casal de' Pazzi indicate that the fauna foraged in a mosaic C_3-plant-dominated ecosystem with no evidence of the consumption of C_4 plants at ~240–200 ka (late Middle Pleistocene). Among the analyzed taxa, deer, rhinos, and some elephants have $\delta^{13}C$ values that indicate the consumption of C_3 plants in a closed environment. Hippopotamids possibly fed on C_3 wetland plants, C_3 browse, fruits, aquatic vegetation, or a combination of them (Ansell, 1965; Mugangu and Hunter, 1992; Boisserie et al., 2005; Cerling et al., 2008; Souron et al., 2012). In contrast, bovids and equids ate C_3 plants in a slightly more open environment. *Palaeoloxodon antiquus* is the only taxon with a wide range of $\delta^{13}C$ values, indicating a mix of diets in both closed and open environments (Fig. 5). In addition, the analysis of deciduous specimens allowed us to distinguish pre- and post-weaning elephant samples (Fig. 6) (e.g., Balasse, 2002; Boisserie et al., 2005). Our isotopic results are consistent with previous isotopic studies on other elephant specimens from Casal de' Pazzi that suggested a C_3 diet in forested and open environments for this taxon (Filippi et al., 2001; Palombo et al., 2005). Filippi et al. (2001) and Palombo et al. (2005) also conducted microwear and strontium isotope ($^{87}Sr/^{86}Sr$) analyses. Microwear results indicated that elephants ate grass or plants containing a relatively large amount of phytoliths. This behavior is also attested in extant elephants (Eltringham, 1992). Strontium isotope composition ($^{87}Sr/^{86}Sr$) defined the volcanic province of Latium as the geographical area where they lived. The $\delta^{18}O$ values reflect distinct physiologies, behaviors, and habitats. For example, hippopotamids, due to their semiaquatic habitat , have lower $\delta^{18}O$ values than terrestrial animals such as rhinos, bovids, deer, equids, and elephants (Bocherens et al., 1996; Clementz et al., 2008). Moreover, the high $\delta^{18}O$ values of deer agree with the fact that these animals rarely drink and obtain most of their water from leaves, as high $\delta^{18}O$ values are expected for non-obligate drinkers (Sponheimer and Lee-Thorp, 1999).

Isotopic evidence indicates that even during more densely forested episodes, closed environments were interspersed by locally open spaces at Casal de' Pazzi (Fig. 7). This is consistent with leaf fossil impressions from Casal de' Pazzi and pollen analysis of the nearby lake of Valle di Castiglione (~12.5 km east), which indicated variations in the propositions of forest tree species and herbaceous plants (Follieri et al., 1988; Magri, 2020). Based on this evidence, we speculate that the late Middle Pleistocene *Homo* from Casal de' Pazzi possibly exploited the same mosaic C_3-plant-dominated landscape that would have provided abundant potential prey species of large mammals and diverse edible plant resources (e.g., Miras et al., 2020).

Finally, it should be noted that stable isotopes, leaf fossil impressions, and pollen data provide information on the past environment according to different temporal and spatial resolutions. Fossil impressions provide snapshot evidence of the context at the time of deposition; stable isotopes of tooth enamel record an averaged diet during tooth formation, spanning from several months to years, which is related to the animal feeding strategies and behavior; and pollen data record local flora located at some distance from the deposit. In addition, the fossil teeth from Casal de' Pazzi used for isotopic analyses were unearthed in a

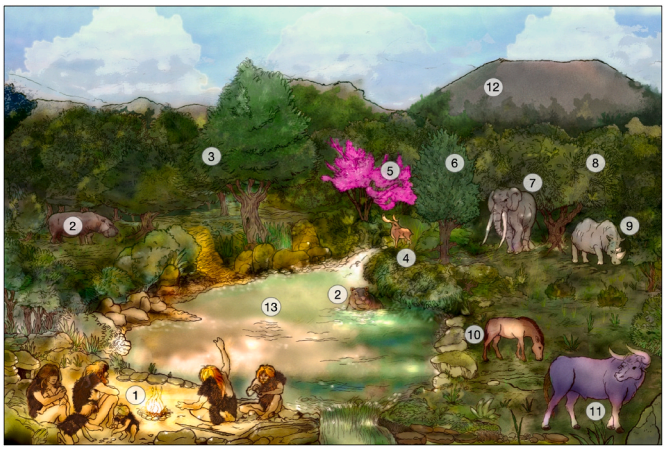

Fig. 7. Artistic reconstruction of the ecological and environmental context of Casal de' Pazzi: 1 *Homo heidelbergensis*; 2 *Hippopotamus amphibius*; 3 *Quercus* sp.; 4 *Dama*; 5 *Cercis siliquastrum*; 6 *Zelkova* sp.; 7 *Palaeoloxodon antiquus*; 8 *Olea* sp.; 9 *Stephanorhinus kirchbergensis*; 10 *Equus ferus*; 11 *Bos primigenius*; 12 volcano; 13 river. Artwork by S. Sanna Magrini.

fluvial context. This implies that the archaeological remains were naturally selected, transported, and accumulated along the water stream. Accordingly, isotopic data on tooth enamel could reflect environments close to the site area and/or the vegetation located several kilometers apart along the course of the paleo-Aniene River (or its tributary).

5.2. Isotopic comparison of fauna tooth enamel

In order to compare our isotopic results and test whether the same species displayed different adaptations according to local environmental and climatic variability, we gathered 274 isotopic values ($\delta^{13}C$ and $\delta^{18}O$) from other European archaeological sites between ~600 and 125 ka. Previously, only comparative isotopic evidence related to Italian archaeological localities have been discussed in Briatico and Bocherens (in press). Here, we present a more comprehensive isotopic dataset which pertains to the following archaeological sites:

- Mauer, Schöningen, Neumark-Nord 1, and Steinheim an der Murr (hereafter Steinheim) in Germany (Grube et al., 2010; Pushkina et al., 2014; Julien et al., 2015; Kuitems et al., 2015);
- Atapuerca in Spain (García et al., 2009);
- Payre in France (Ecker et al., 2013);
- Casal de' Pazzi, La Polledrara, Poggetti Vecchi, Isernia La Pineta, Guado San Nicola, and Fontana Ranuccio in Italy (Filippi et al., 2001; Palombo et al., 2005; Capalbo, 2018; Strani et al., 2019; Zanazzi et al., 2022).

Overall, we discuss 296 isotopic data from five faunal families (Elephantidae, Equidae, Cervidae, Bovidae, and Rhinocerotidae), which are represented in each selected site (Tables S1–S5).

Elephantidae. Elephants (n = 66) from Mauer, Schöningen, La Polledrara, Steinheim, Casal de' Pazzi, Poggetti Vecchi, and Neumark-Nord 1 belong to *Palaeoloxodon antiquus*. The $\delta^{13}C_{ecosystem}$ values indicate dominant closed canopy and forested environments, as evidenced in Steinheim, Schöningen, Neumark-Nord 1, Mauer, and Casal de' Pazzi. However, Casal de' Pazzi and Neumark-Nord 1 showed a wider range of $\delta^{13}C_{ecosystem}$ values than the other localities, which also suggests open space in the vegetation. In contrast, the $\delta^{13}C_{ecosystem}$ values from La Polledrara and Poggetti Vecchi exclusively indicate open C_3-environments, such as grasslands (Table S1, Fig. 8A). The $\delta^{18}O$ values showed a median of +26.7 ‰ with a range of +20.3 ‰ to +27.9 ‰ (Table S1,

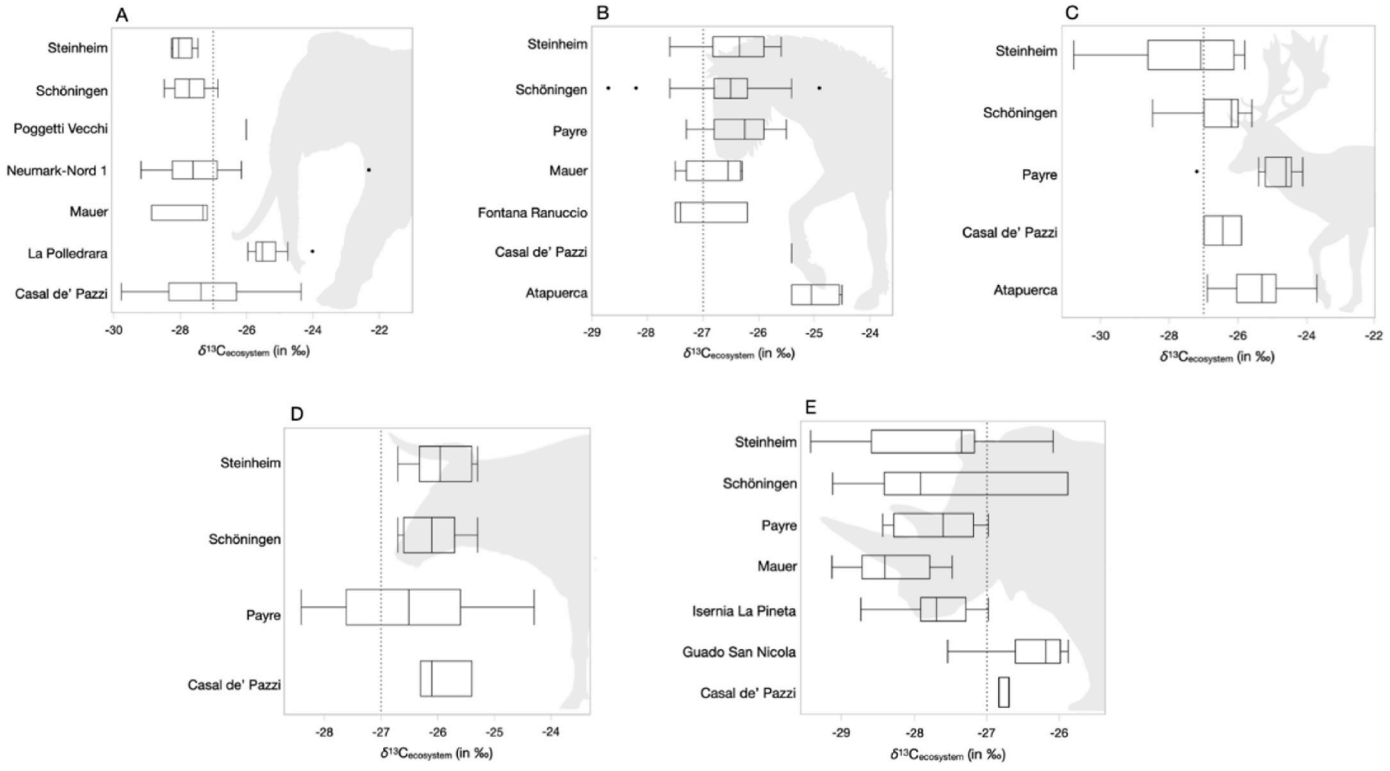

Fig. 8. Box and whisker plots of $\delta^{13}C_{ecosystem}$ of Elephantidae (A), Equidae (B), Cervidae (C), Bovidae (D), and Rhinocerotidae (E) from European archaeological sites between ~600 and 125 ka. The $\delta^{13}C$ value - 27 ‰ (vertical dotted line) is fixed to distinguish closed canopy and forests vs. grasslands, following Drucker et al. (2008). The vertical line in the boxes marks the median values, the box ends are the lower and upper quartiles, and the lines define the range of data except for outliers. Animal silhouettes: http://phylopic.org.

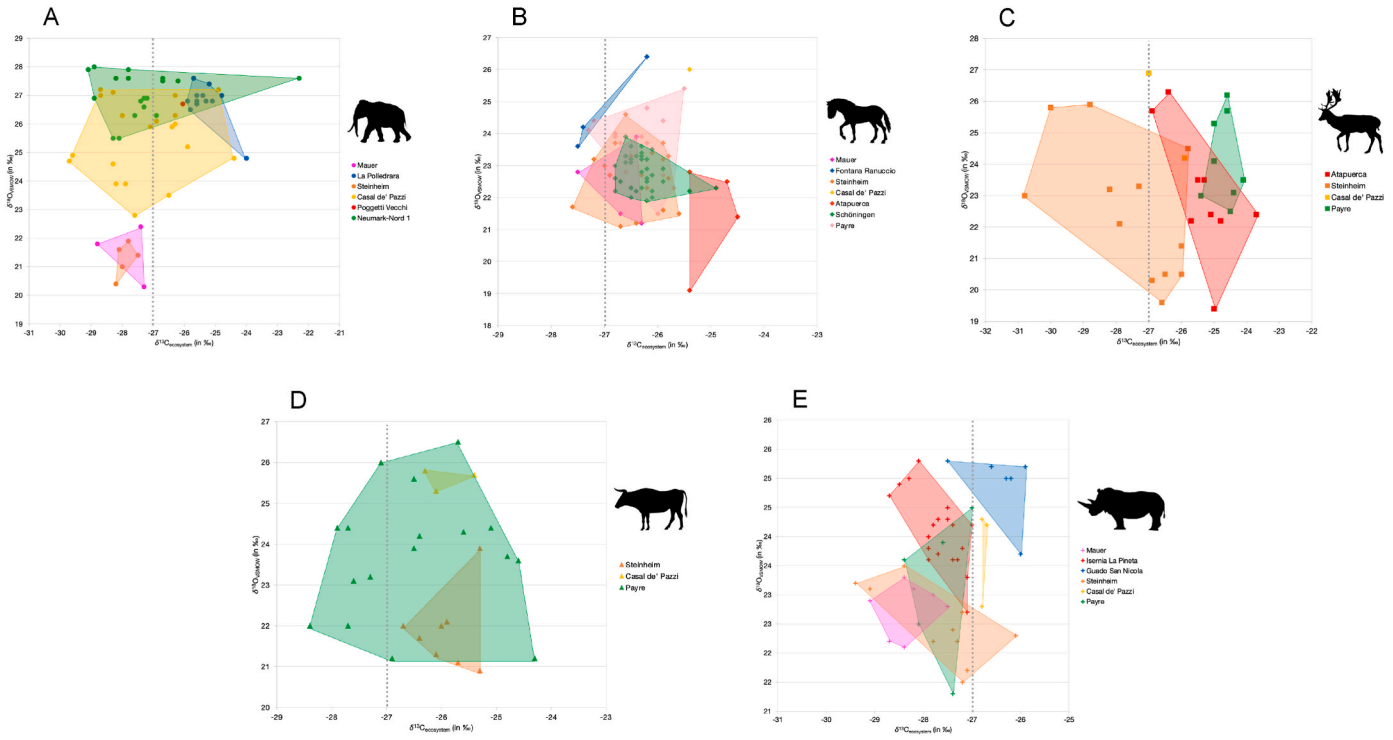

Fig. 9. $\delta^{13}C_{ecosystem}$ and $\delta^{18}O$ values of Elephantidae (A), Equidae (B), Cervidae (C), Bovidae (D), and Rhinocerotidae (E) from European archaeological sites between ~600 and 125 ka. Animal silhouettes: http://phylopic.org.

Fig. 9A). Variations in $\delta^{18}O$ values can be affected by the water sources and other factors such as precipitation, continentality, seasonality, latitude, and altitude. We note that the elephants from Mauer and Steinheim (Germany) had lower $\delta^{18}O$ values (median: +21.5 ‰) than the Italian localities (La Polledrara, Casal de' Pazzi, and Poggetti Vecchi; median: +26.5 ‰). This could suggest differences in temperature and humidity: during the Middle Pleistocene, colder climate and environmental conditions could have characterized Mauer and Steinheim localities; in contrast, despite the different latitudes, warmer temperatures could be experienced at La Polledrara, Casal de' Pazzi, and Poggetti Vecchi. Unexpectedly, elephants from Neumark-Nord 1 showed higher $\delta^{18}O$ values with a median of +26.9 ‰ and did not follow latitude and temperature patterns. At ~125 ka, the lake near Neumark-Nord 1 was subjected to different degrees of evaporation during the year, and it was possibly the main elephant drinking water source (Grube et al., 2010).

Equidae. Equids (n = 94) from Mauer, Atapuerca, Fontana Ranuccio, Schöningen, Steinheim, Payre, and Casal de' Pazzi were *Equus mosbachensis*, *Equus ferus*, *Equus hydruntinus*, *Equus* sp. (*ferus*) *germanicus*, and other equids. The $\delta^{13}C_{ecosystem}$ values indicate environments marked by grasslands, although a few values from Steinheim, Schöningen, Payre, Mauer, and Fontana Ranuccio point to slightly more wooded environments than in Atapuerca and Casal de' Pazzi (Table S2, Fig. 8B). The $\delta^{18}O$ values showed a median of +23.3 ‰ with a range of +19.1 ‰ to +26.4 ‰ (Table S2, Fig. 9B).

Cervidae. The cervid group (n = 41) consists of *Cervus elaphus* and *Dama dama* from Atapuerca, Schöningen, Steinheim, Payre, and Casal de' Pazzi. The $\delta^{13}C_{ecosystem}$ values of Steinheim and Schöningen indicate a more closed environment than those from Payre, Casal de' Pazzi, and Atapuerca (Table S3, Fig. 8C). The $\delta^{18}O$ values showed a median of +23.2 ‰ with a range of +19.4 ‰ to +29.7 ‰ (Table S3, Fig. 9C).

Bovidae. This group comprises samples (n = 37) of *Bos primigenius*, *Bison priscus*, *Bison* sp., and other bovids from Schöningen, Steinheim, Payre, and Casal de' Pazzi. The $\delta^{13}C_{ecosystem}$ values point to extensive grasslands at Steinheim, Schöningen, and Casal de' Pazzi. In contrast, bovids from Payre suggest the presence of both closed and open vegetation (Table S4, Fig. 8D). The $\delta^{18}O$ values showed a median of +25.7 ‰ with a range of +20.9 ‰ to +26.5 ‰. Bovids from Steinheim had lower $\delta^{18}O$ values (median: +21.8 ‰) than Casal de' Pazzi and Payre (median: +25.7 ‰). This could be interpreted as evidence of colder conditions at Steinheim than at Casal de' Pazzi and Payre (Table S4, Fig. 9D).

Rhinocerotidae. Rhinos (n = 58) from Mauer, Isernia La Pineta, Guado San Nicola, Schöningen, Steinheim, Payre, and Casal de' Pazzi included *Stephanorhinus kirchbergensis*, *Stephanorhinus hundsheimensis*, *Stephanorhinus* cf. *hemitoechus*, and other rhinos. All $\delta^{13}C_{ecosystem}$ values indicate densely forested environments, with the most depleted $\delta^{13}C_{ecosystem}$ values reported at Steinheim, Schöningen, and Mauer. In contrast, $\delta^{13}C_{ecosystem}$ values from Casal de' Pazzi and Guado San Nicola suggest open environments (Table S5, Fig. 8E). The $\delta^{18}O$ values showed a median of +22.7 ‰ with a range of +21.3 ‰ to +25.3 ‰. As observed with other taxa, the German locality of Mauer and Steinheim had lower $\delta^{18}O$ values than Casal de' Pazzi, Isernia La Pineta, and Guado San Nicola, possibly suggesting colder and warmer contexts, according to the latitude effect (Table S5, Fig. 9E). We compared isotopic data from several European archaeological sites with different chronologies (between ~600 and 125 ka) and geographic locations (Fig. 9), which reflect diverse feeding behaviors according to the vegetation composition, as well as global and local climate trends over time (Manzi et al., 2011; Magri and Palombo, 2013; Head and Gibbard, 2015). This seems to be also evidenced by comparing $\delta^{18}O$ values: colder climate and environmental conditions could have characterized the German localities, whereas warmer conditions could have been experienced at the southern European sites. Nevertheless, $\delta^{18}O$ values were affected by water sources and other factors such as precipitation, continentality, seasonality, latitude, and altitude. Therefore, it is difficult to establish a clear and direct link with climatic conditions (e.g., Bocherens et al., 2016).

6. Conclusion

This study provides information on the paleoecology of the late Middle Pleistocene site of Casal de' Pazzi (central Italy), with implications for environmental reconstruction in European archaeological contexts. Carbon isotopic data indicate that the analyzed mammals fed in a C_3-plant-dominated ecosystem characterized by closed and open environments. Our results are consistent with the vegetation recorded by leaf fossil impressions of *Zelkova* sp., *Laurus nobilis*, and *Cercis siliquastrum* found at Casal de' Pazzi and pollen analyses of the nearby lake of Valle di Castiglione (~12.5 km east). The area around the site inhabited by the late Middle Pleistocene *Homo* was characterized by diversified Mediterranean evergreen forest tree species, accompanied by mesophilic elements of the mixed deciduous oak and beach forest, alternating with diversified wooded/forested and xeric vegetation. Comparisons with published isotopic results from other European archaeological sites between ~600 and 125 ka showed that mammals exploited both C_3-closed and open environments, according to animal feeding habits and considerable environmental differences through time and space. Furthermore, based on stable oxygen stable isotopic values, we possibly observed cold and warm conditions depending on the latitude of the archaeological localities. Still, in many cases, local factors play a significant role, making paleoclimatic inferences difficult.

Data availability

Data can be found in the supplementary materials.

CRediT authorship contribution statement

Giuseppe Briatico: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Patrizia Gioia:** Resources, Writing – review & editing, Supervision. **Hervé Bocherens:** Resources, Writing – review & editing, Supervision.

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.quaint.2023.11.002.

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