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Of forests and grasslands: human, primate, and ungulate palaeoecology in Late Pleistocene-Holocene Sri Lanka

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The Wet Zone region of Sri Lanka has provided some of the earliest direct evidence of human utilization of rainforest resources anywhere in the world. Stable isotope analysis of human and animal remains, alongside detailed zooarchaeological analyses, have demonstrated reliance on rainforest resources as far back as 48,000 years ago. However, changes in human adaptations and the varying niches of exploited fauna, through major periods of climatic change such as during the Pleistocene-Holocene transition, remain relatively under-explored. Here, we present the results of stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotope analyses of dental enamel from 311 animal and eight human teeth recovered from recent excavations at Fa-Hien Lena and Kitulgala Beli-lena from contexts spanning the Late Pleistocene and Holocene. Our data for human teeth from the Terminal Pleistocene and Holocene layers of Fa-Hien Lena and the Holocene layers of Kitulgala Beli-lena show little departure from rainforest resource reliance between the Pleistocene and Holocene. Meanwhile, the most dominant faunal taxa, including cercopithecid monkeys, show a similar stability in canopied forest habitation across the different species. However, δ^{13}C data from ungulates found at Fa-Hien Lena indicate human populations did have access to forest edge and grassland habitats, suggesting either specific foraging trips or long-distance trade with other communities. In addition, our reporting of an Early Holocene presence of rhinoceros in the Wet Zone forest of Sri Lanka, the last fossil occurrence of this now regionally-extirpated taxon, highlights ongoing human interactions with large mammal communities on the island. We argue that our data demonstrate the benefits of detailed isotopic and zooarchaeological studies for detailed insights into the nature of tropical human adaptations through time.

1 Introduction

Sri Lanka has emerged as a key region for understanding human adaptations to tropical environments from the Late Pleistocene through into the Holocene. Archaeological sites on the island have provided some of the earliest direct evidence of human utilization of rainforest resources anywhere in the world, including targeted hunting of arboreal and semi-arboreal small bodied mammals using projectile technology as early as ~45,000 years ago (Wedage et al., 2019a), as well as gathering and processing of freshwater and terrestrial molluscs and fruits and nuts (i.e., breadfruit *Artocarpus* sp., and kekuna nut *Canarium* sp.) (Wedage et al., 2020). These activities were facilitated by microliths (Perera et al., 2011; Roberts et al., 2015a; Wedage et al., 2019b; Picin et al., 2022) and bone tools (Perera et al., 2016; Langley, 2016; Langley et al., 2020), including bow-and-arrow technology, the earliest found outside Africa so far, as well as implements for working skin and/or plant fibres (Langley et al., 2020). Archaeological investigations in the tropical rainforests of Sri Lanka have also produced the earliest *Homo sapiens* fossils found anywhere in South Asia (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989; Kennedy, 2000).

These findings have challenged the previously held notion that tropical rainforests were ecological barriers to Pleistocene human dispersals (Bailey et al., 1989; Gamble, 1993). Moreover, the association of the earliest clear evidence for human occupation in Sri Lanka with rainforest environments questioned prevailing assumptions of the predominance of coastal settings in supporting human migrations around the Indian Ocean rim (Mellars, 2005; Mellars, 2006; Bulbeck, 2007). Renewed multidisciplinary investigations of three caves sites in Sri Lanka's Wet Zone have continued to confirm the initial observations of Sri Lankan archaeologists from as early as the 1980s (Deraniyagala, 1992). Together, Batadomba-lena dated between~39,000 to ~10,000 years ago (Perera et al., 2011; Roberts et al., 2017b), Fa-Hien Lena dated ~45,000–~4,200 years ago (Wedage et al., 2019a) and Kitulgala Beli-lena dated ~45,000–~8,000 years ago (Wedage et al., 2020) provide a long-term record of human tropical forest interaction and records of early microlith and osseous technologies. Re-dating of early human occupational layers of Fa-Hien Lena and Kitulgala Beli-lena using methods that can address contamination in tropical environments (Higham et al., 2009), reassessment of the stratigraphy of the sites (Kourampas et al., 2009; Wedage et al., 2019a), detailed analyses of materials recovered from previous excavations and, in the case of Kitulgala Beli-lena, materials from new excavations, including lithic (Wedage et al., 2020) and osseous (Langley et al., 2020) artefacts, and faunal and botanical remains (Wedage et al., 2020), have been particularly important for developing more resolved insights into the specialized tropical adaptations of humans in this part of the world.

Stable isotope analyses of human and animal tooth enamel from Batadomba-lena and Fa-Hien Lena have also provided additional, clear evidence for the overall reliance of Late Pleistocene-Holocene human populations on resources from the rainforest (Roberts et al., 2015b; Roberts et al., 2017b). This approach, by looking at "bulk" dietary contributions of resources from different environments, is able to test between scenarios of seasonal rainforest use (Der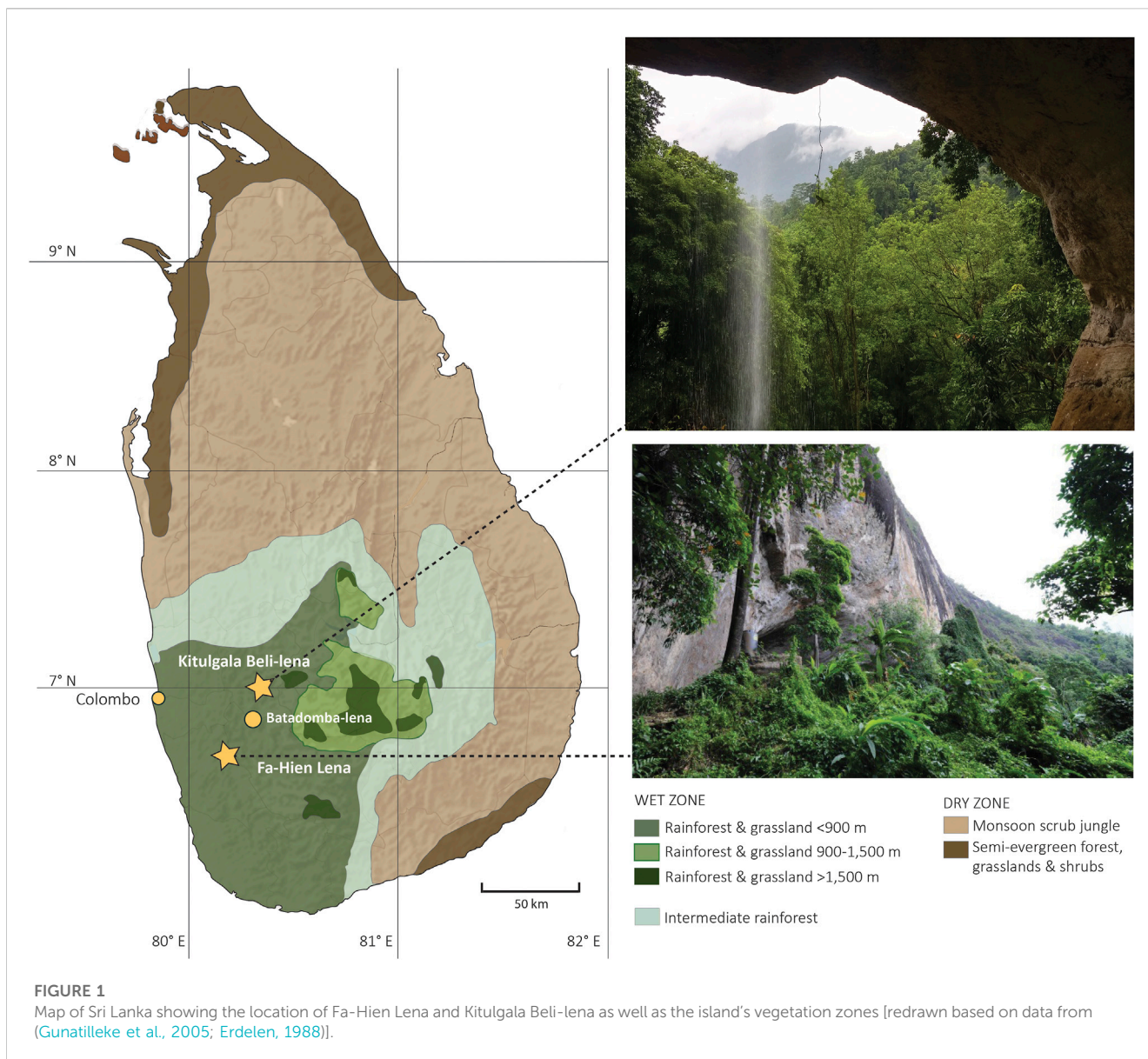aniyagala, 1992) or past rainforest fragmentation and long-term reliance of humans on these tropical habitats. Stable carbon isotope data from human teeth recovered from ~38–36,000 year old sedimentary layers in the site of Batadomba-lena (located ca. 25 km from Fa-Hien Lena and ca. 25 km from Kitulgala Beli-lena) showed year-long exploitation of rainforest resources (Roberts et al., 2017b). Reliance on rainforest resources apparently continued despite evidence for environmental fluctuations (i.e., development of more open forests and grasslands) during the Last Glacial Maximum up until the Mid-Holocene. The available isotope data from Batadomba-lena and Fa-Hien Lena suggest that forests were more open from ~36–29,000 years ago to 12,000, followed by an expansion of rainforests during the Pleistocene-Holocene transition, around the same time that the Wet Zone, Intermediate Zone and Dry Zone climatic and vegetation boundaries stabilized (Roberts et al., 2017b). This raises the question of the degree to which humans, and their associated prey species, adjusted their tropical foraging strategies across this period of major change.

In this paper, we add to the existing stable isotope data for the island of Sri Lanka by conducting novel stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope analyses of dental enamel from human and animal teeth recovered from recent excavations of Fa-Hien Lena and Kitulgala Beli-lena. Our goal is to look at the varying niches of fauna exploited by foragers that inhabited the cave sites as an indicator of changes in human adaptations, for instance the development of new hunting technologies as revealed by recent studies looking at the lithic and osseous materials from the sites (Wedage et al., 2019b; Langley et al., 2020; Picin et al., 2022). We also focus on the materials recovered from the Terminal Pleistocene and Holocene layers to investigate whether signatures for the expansion of rainforests during the Pleistocene-Holocene transition can be detected in the fauna from the cave sites. Although emphasis has often been placed on the utilization of the sites as early as ~45,000 years ago, the majority of the artefacts and faunal remains from both sites were recovered from archaeological layers dating to the Terminal Pleistocene and the Holocene. Whereas lithics and botanical remains were recorded in all stratigraphic units of Kitulgala Beli-lena, faunal remains were restricted to the Holocene layers, for example (Wedage et al., 2020). By focusing on these time periods, we hope to be able to shed further light on the nature of human tropical adaptations in Sri Lanka, during a time period where significant climatic and environmental changes impacted hunter-gatherer communities in different parts of tropical Asia and beyond.

2 Methods

2.1 The cave sites

We selected human and animal teeth recovered from the 2010–2012 excavations of Fa-Hien Lena and the 2017 excavations of Kitulgala Beli-lena. Both caves are located, ca. 45 km away from each other, in Sri Lanka's Wet Zone region (Figure 1), a vegetation zone characterized by wet deciduous and tropical evergreen forests which receives around 2,200 mm–4,800 mm of rainfall annually (in contrast to the grassland-dominated Dry Zone region which receives an annual rainfall of ~1,000 mm–1700 mm) (Ashton and Gunatilleke, 1987; Erdelen, 1988; Roberts et al., 2015b). The detailed stratigraphic

FIGURE 1
Map of Sri Lanka showing the location of Fa-Hien Lena and Kitulgala Beli-lena as well as the island's vegetation zones [redrawn based on data from (Gunatilleke et al., 2005; Erdelen, 1988)].

sequences of both sites have been published in previous papers (Wedage et al., 2019a; Wedage et al., 2020) and we therefore provide just a brief summary description here.

Fa-Hien Lena, located in the district of Kalutara in Sri Lanka's Western Province (6°36′6″N 80°13′6″E, ca. 180 mASL and ca. 30 km away from the nearest coast), was first excavated in 1986–1988 (Deraniyagala, 1992) and yielded the earliest *Homo sapiens* fossils in South Asia (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989). The rockshelter has an approximate surface area of 18 m². Initially dated to ca. 38,000 years ago (Wijeyapala, 1997), renewed excavations of 2009–2012 in 3 1 m × 1 m trenches (squares N3, O3 and P3, see Supplementary Figure S1) revealed undisturbed Late Pleistocene sedimentary layers dated between ~48,000 and ~37,000 cal years BP (Wedage et al., 2019a) (Supplementary Figure S1, Table S1). These deposits preserved numerous faunal remains (~30% of which showed evidence of burning), *Conus* shell beads, ochre fragments, quartz microliths and osseous points which

represent the earliest evidence for human presence in Sri Lanka so far. Overlying the clayey silt Late Pleistocene deposits is a series of organic-rich loam layers characterized by heavy ash and charcoal concentration which represents the site's Terminal Pleistocene occupational phase. Despite its relatively narrow temporal range (dated to 13,000–12,000 cal. BP), these deposits contained the densest concentration of artefacts and human occupational debris in the entire Fa-Hien stratigraphy. The Holocene occupational phase of the site is characterized by sandy silt and ash accumulation deposits representing undisturbed occupation floors dated between 8,000 and 4,500 years ago. Carbonized kekuna (*Canarium* sp.) nut endocarps were recovered in number from hearth features within these floors and some were directly dated to ca. 8,000–7,700 cal. BP (Wedage et al., 2020). The 2010–2012 excavation, which resolved the chronostratigraphy of the site, also yielded an estimated 150,000 bone fragments from which 14,485 fragments were sampled (from intact layers that can be

associated with ^{14}C dates) and analysed in detail. The number of lithic and osseous artefacts (both finished and unfinished) and the numerous faunal and botanical specimens recovered, in addition to the thick accumulations of ash and layers of occupational debris recorded, suggest that Fa Hien was utilized as a habitation site for ca., 40,000 years. We selected the human and faunal dental elements we analysed in this study from this sample so as to allow comparison of our results with those derived from the wider zooarchaeological analyses (Wedage et al., 2019a).

Kitulgala Beli-lena is located in Sabaragamuwa Province (7°0′8″N 80°26′8.8″E, ca., 380 mASL, and ca., 60 km away from the nearest coast) and was first excavated by PEP Deraniyagala in 1960–1961, and from the late 1970s to the early 2010s by Sri Lanka's Department of Archaeology (Wijeyapala, 1997). Kitulgala Beli-lena's main chamber has an estimated floor area of ca. 1,600 m², of which a total of 80 m² was previously excavated (see Supplementary Figure S2). These excavations exposed a 3 m cultural sequence dated between ca. 31,000–5,000 years BP along with human remains from at least ten individuals dating to ca. 13,000 years BP as well as a wealth of quartz lithic artefacts and osseous tools and a rich assemblage of faunal remains (Wijeyapala, 1997; Kourampas et al., 2009). In 2017, new excavations in Kitulgala Beli-lena were conducted with the aim of recovering new materials that would allow refinement of the chronology as well as improved understanding of the material culture, technology and subsistence economies of the humans that utilized the site. The excavation of two 1x1 m trenches revealed ca. 1.92 m of stratified detrital sediments deposited between 44,000 and 8,000 cal. BP representing four major phases of human occupation of the site (Wedage et al., 2020) (Supplementary Figure S2, Table S2). Although lithic artefacts and plant macrobotanical remains were recovered all throughout the sequence, faunal materials were only identified in the Holocene deposits (10,577–8,029 cal., BP). This was attributed to possible differential use of cave space by the Late Pleistocene and Holocene foragers occupying the site. The taxonomic composition of the faunal remains in Kitulgala Beli-lena is similar to that recovered from contemporaneous layers in Fa-Hien Lena (Wedage et al., 2020), with cercopithecid monkeys and squirrels dominating the assemblage (accounting for 32.4% and 21.2% of the identified remains respectively) in addition to a few large mammals (suids, bovids and cervids). Although detailed analyses of lithic artefacts and faunal materials recovered from the earlier excavations of the site are yet to be conducted, the current evidence we have suggests, that akin to Fa-Hien Lena, Kitulgala Beli-lena was utilized as a habitation site from the Late Pleistocene to the Early Holocene. We selected all unburnt faunal and human dental elements recovered from the 2017 excavation of the site and included them in the current study. In the case of complete mandibles and maxilla (or for fragmentary dental elements that showed association), we selected a single element to be sampled.

Although we tried to include as many taxa as possible, the taphonomy of certain specimens prohibited inclusion in the study. For instance, several canid and felid teeth exhibited evidence of burning and remineralization and were therefore excluded from the analyses. Likewise, numerous dental elements selected from ^{14}C-dated layers at Fa-Hien Lena were heavily covered in calcium carbonate making sampling difficult. As a result, we also included faunal dental elements recovered from undated sedimentary layers

that lie between or associated with dated archaeological deposits (Supplementary Figures S1, S2). We selected a total of 311 faunal and eight human teeth for analyses (detailed in Table 1). We divided the chronology of both sites into four phases: Late Pleistocene (ca. 45,000–16,000 BP), Terminal Pleistocene (16,000–11,600 BP), Holocene1 (11,6000–9000 BP) and Holocene2 (< 9000 BP). Samples from undated Holocene contexts were included in the Holocene2 phase as there is a lack of detailed resolution of archaeological layers dated to ca. 9,000 and younger at Fa-Hien Lena (i.e., undated archaeological layers cannot be assigned to either the Early or Mid-Holocene but they are overlying sediments dated to ca. 9,000 years BP).

2.2 Identification of dental elements

We build on previous zooarchaeological analyses of faunal remains recovered from Fa-Hien Lena and Kitulgala Beli-lena (Wedage et al., 2019a; Wedage et al., 2020) and identified sampled dental elements to genus whenever possible following published morphological criteria (e.g., Hillson, 1996; Swindler, 2002; Hillson, 2005; Hillson, 2016). Previously, we tried to identify the colobine teeth recovered from Fa-Hien Lena to species level (Wedage et al., 2019a). However, we acknowledge that it is not straightforward due to significant overlap in linear dental measurements and morphological features between the co-occurring grey langur (Semnopithecus priam) and purple-faced langur (Trachypithecus vetulus) (Amano et al., 2020). In contrast to Southeast Asia (Ki-Kydd and Piper, 2004; Piper et al., 2008; Ingicco et al., 2020; Amano et al., 2022), there is currently a lack of studies looking at morphological criteria for discriminating the colobines in South Asia (see Huffman et al., 2022). In a recent paper, we chose a more conservative identification method where we grouped the colobines together- and only discriminated them against macaques (Macaca sinica) (Wedage et al., 2020). We adopt the same approach here and, whenever possible, assigned the langurs as colobines and the macaques as cercopithecines. However due to the fragmentary nature, in addition to heavy wear, of the non-human primate teeth, the majority of the samples (71%) were just assigned as representing "Cercopithecidae". Lastly, we classified the identified taxa to size class based on live weight, large mammals being animals weighing 25 kg or more [modified from (Thomas, 1969; Grayson, 1978)].

2.3 Stable isotope analysis of dental enamel

Comparison of isotopic signatures between faunal and human tissues, such as bones and dental enamel, is useful for reconstructing past vegetation and environments. The majority of plants generally employ one of two photosynthetic pathways: a C_3 pathway utilized by dicots (bushes, herbs and trees) wherein a three-carbon compound is produced and the C_4 pathway used by most grasses wherein carbon dioxide is initially fixed into a four-carbon molecule during photosynthesis. The C_4 pathway allows for photosynthesis to proceed without significant water loss and is therefore advantageous in warm, open and dry environments (Pearcy and Ehleringer, 1984). The difference in the way carbon dioxide is fixed allows C_3 and C_4

TABLE 1 Human and animal teeth from Fa-Hien Lena and Kitulgala Beli-lena analysed in the current study (detailed list in Supplementary Table S3) (LP- Late Pleistocene, TP- Terminal Pleistocene, H1- Holocene1, H2- Holocene2).

Taxonomic classification			Fa-hien Lena				Kitulgala beli-lena	Total
Family	Sub-Family	Genus	LP	TP	H1	MH	H2	
Cercopithecidae			10	34	23	29	31	127
Cercopithecidae	Cercopithecinae	*Macaca*	3	8	4	3	5	23
Cercopithecidae	Colobinae	*Trachypithecus + semnopithecus*	2	8	5	8	5	28
Herpestidae	Herpestinae	*Urva*	0	1	0	0	0	1
Hystricidae		*Hystrix*	0	2	2	0	1	5
Viverridae	Viverrinae	*Viverricula + paradoxurus*	5	11	11	3	24	54
Sciuridae	Sciurinae	*Petinomys + petaurista*	0	3	0	0	1	4
Sciuridae	Ratufinae	*Ratufa*	6	15	14	1	10	46
Rhinocerotidae			0	0	1	0	0	1
Suidae	Suinae	*Sus*	0	2	2	0	1	5
Tragulidae		*Moschiola*	0	1	0	0	4	5
Cervidae	Cervinae	*Muntiacus*	0	2	0	0	0	2
Cervidae	Cervinae	*Axis/Rusa*	0	8	0	0	0	8
Elephantidae		*Elephas*	0	1	0	1	0	2
Hominidae		*Homo*	0	6	1	0	1	8
			26	102	63	45	83	319

plants to be distinguished based on their $\delta^{13}C$ values which is in turn reflected in the tissues of the animals and humans that consume them. Considering stable carbon isotopes in the dental enamel, browsers usually have $\delta^{13}C$ values lower than −8‰, grazers have δ13C values higher than −2‰ (average ~0‰) and mixed feeders have values somewhere in between (Lee-Thorp et al., 1989; Cerling and Harris, 1999; Lee-Thorp et al., 2010). In tropical forest settings, the presence of thick canopy reduces the available carbon dioxide in the forest floor resulting in lower $\delta^{13}C$ values. This "canopy effect" is reflected in the tissues of animals and humans relying on resources in dense forests, with their tooth enamel having $\delta^{13}C$ values lower than −14‰ (Cerling et al., 2004) (though see (Tejada et al., 2020) for a note on baseline variation in this regard).

Stable oxygen isotope analyses of teeth can provide additional information on human and faunal paleoecology. $\delta^{18}O$ values of tooth enamel are influenced by a wide range of factors including habitat and climate, as well as the animal's drinking behavior, physiology and diet (Kohn, 1996; Pederzani and Britton, 2019). For example, the $\delta^{18}O$ values in teeth of mammals that are obligate drinkers have been shown to closely reflect the $\delta^{18}O$ values of the water they imbibe which is often strongly associated with precipitation $\delta^{18}O$. By contrast, non-obligate drinkers, which rely mostly on the plants they consume as their water source, have higher $\delta^{18}O$ values indicative of the high $\delta^{18}O$ values in leaves as a product of environmental factors influencing transpiration (Kohn, 1996). The $\delta^{18}O$ values of vegetation in tropical ecosystems have also been shown to reflect either the source-effect of rainfall or evaporative

potential, which can be used to infer canopy density and environmental change (Buchmann et al., 1997; Buchmann and Ehleringer, 1998).

The details of the archaeological animal and human teeth analysed in this study are presented in Supplementary Table S3, including the specimen number, excavation context, associated chronology, taxon identification, and element. Dental enamel records isotopic information related to diet and hydrological context over the period of enamel formation and therefore will vary depending on the species and the tooth sampled. For humans, the third molar, which develops between 7 and 13 years until the mid to late teenage years (Hillson, 1996) is an ideal representative of the late juvenile/adult diet. By contrast, first molars are generally avoided due to the temporal overlap between their formation and weaning (Wright and Schwarcz, 1998). For the current study, however, we were limited by the scarcity of human remains recovered from both sites (Fa-Hien Lena, $n = 7$; Kitulgala Beli-lena, $n = 1$) and no third molars were available (see Supplementary Table S3). Nonetheless, this does not hinder exploration of the significant δ13C differences between signatures of consumers relying on closed canopy C3, intermediate/open C3 and C4 resources, which is the primary focus of our study.

All selected samples were first cleaned using air abrasion to remove sediments and other minerals (i.e., manganese oxide and calcium carbonate) adhering to the tooth surface. We employed bulk sampling of dental enamel by gently and evenly abrading the full length of the buccal surface of the teeth with a diamond-tipped drill, ensuring a representative sample for the whole axis of enamel

mineralization. Organic and secondary contaminates were removed from the obtained enamel powder by pre-treatment following established protocols (Sponheimer et al., 2005; Lee-Thorp et al., 2012; Roberts et al., 2015b; Roberts et al., 2017b; Roberts et al., 2018; Ventresca Miller et al., 2018) which also allows for comparison between obtained isotopic measurements and those in the existing literature for Sri Lanka. This involved washing the samples with 1.5% NaOCl for 60 min followed by repeated rinsing with purified water. The samples were then washed with 0.1 M acetic acid for 10 min followed again by repeated rinsing with purified water, after which the samples were lyophilized for 24 h. Phosphoric acid (100%) was then added to ~2 mg of the lyophilized samples at 70°C and the resulting gasses were measured by stable carbon and oxygen isotope analysis using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Stable Isotopes Laboratory, Max Planck Institute for Geoanthropology (formerly for the Science of Human History). The obtained $\delta^{13}C$ and $\delta^{18}O$ values were compared against international standards [IAEA-603 ($\delta^{13}C$ = 2.5‰; $\delta^{18}O$ = −2.4‰); IAEA-CO-8 ($\delta^{13}C$ = 5.8‰; $\delta^{18}O$ = −22.7‰); USGS44 ($\delta^{13}C$ = −42.2‰)] and an in-house standard [MERCK ($\delta^{13}C$ = −41.3‰; $\delta^{18}O$ = −14.4‰)] using the Isodat 3.0 software from Thermo Electron Corporation. Machine measurement error is c. + 0.1‰ for $\delta13C$ and + 0.2‰ for $\delta^{18}O$, as determined by replicate analysis of MERCK carbonate standards.

All $\delta^{13}C$ and $\delta^{18}O$ measurements were tested for normality using the Shapiro-Wilk Test. Following observations of non-normality, the significance of $\delta^{13}C$ and $\delta^{18}O$ between different time periods and between different faunal groups was tested using Kruskal–Wallis tests and, if significant, the tests were followed by a *post hoc* Dunn test to determine which groups were significantly different from each other. The same approach was employed to make comparisons between different taxa in all time periods as well as between cercopithecids in different time periods. Analysis of variance (ANOVA) followed by *post hoc* Bonferroni/Tukey pairwise comparisons were conducted in cases where normality is observed. All statistical analyses were conducted using R (R Core Team, 2016).

3 Results

$\delta^{13}C$ of faunal teeth sampled from Late Pleistocene to Holocene layers of Fa-Hien Lena and the Holocene layers of Kitulgala Beli-lena showed the predominance of taxa with closed-canopy C_3 signatures (Figures 2–7). Considering all samples from both sites, cercopithecid monkeys (including both macaques and langurs) have a $\delta^{13}C$ range of −17.8‰ to −11.1‰ (n = 178, mean = −14.9‰) (Figures 4–6). Giant (*Ratufa macroura*) and flying (*Petinomys/Petaurista*) squirrels have a range of −16.3‰ to −10.9‰ $\delta^{13}C$ (n = 46, mean = −13.7‰) and −15.3‰ to −11‰ (n = 4, mean = −12.9‰), respectively (Figures 4, 7). Viverrids (including *Paradoxurus* and *Viverricula*) have $\delta^{13}C$ ranging from to −15.9‰ to −10.7‰ (n = 54, mean = −13.4‰) (Figures 4, 7). Similarly, smaller-bodied artiodactyls including mouse-deer (*Moschiola*) (−12.9‰ to −11.5‰, n = 5, mean = −12.2‰) and muntjac (*Muntiacus*) (n = 2, mean = −12.3‰) exhibited low $\delta^{13}C$ values (Figures 4, 8). By contrast, larger bodied artiodactyls such as suids (−12.9‰ to −5.8‰, n = 5, mean = −9.84‰), and elephants (n = 2,
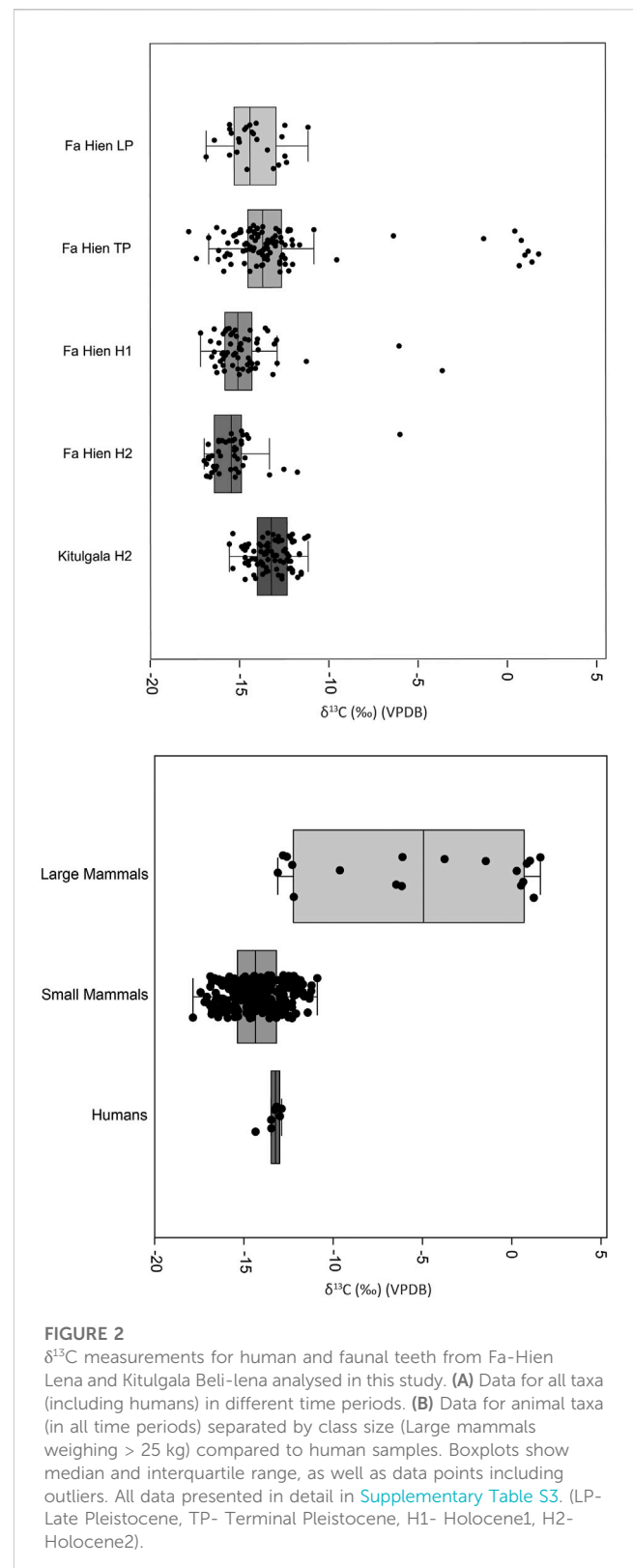

FIGURE 2
$\delta^{13}C$ measurements for human and faunal teeth from Fa-Hien Lena and Kitulgala Beli-lena analysed in this study. **(A)** Data for all taxa (including humans) in different time periods. **(B)** Data for animal taxa (in all time periods) separated by class size (Large mammals weighing > 25 kg) compared to human samples. Boxplots show median and interquartile range, as well as data points including outliers. All data presented in detail in Supplementary Table S3. (LP- Late Pleistocene, TP- Terminal Pleistocene, H1- Holocene1, H2- Holocene2).

mean = −7.5‰) exhibited higher $\delta^{13}C$ values (Figures 2, 4, 8). The same is the case for the single rhinoceros specimen having a δ^{13} of −3.3‰. Cervids (*Rusa/Axis*) have the highest $\delta^{13}C$ observed, with values ranging from −0.96‰ to 2.2‰ (n = 9, mean = 1.13) (Figures 4, 8).

FIGURE 3
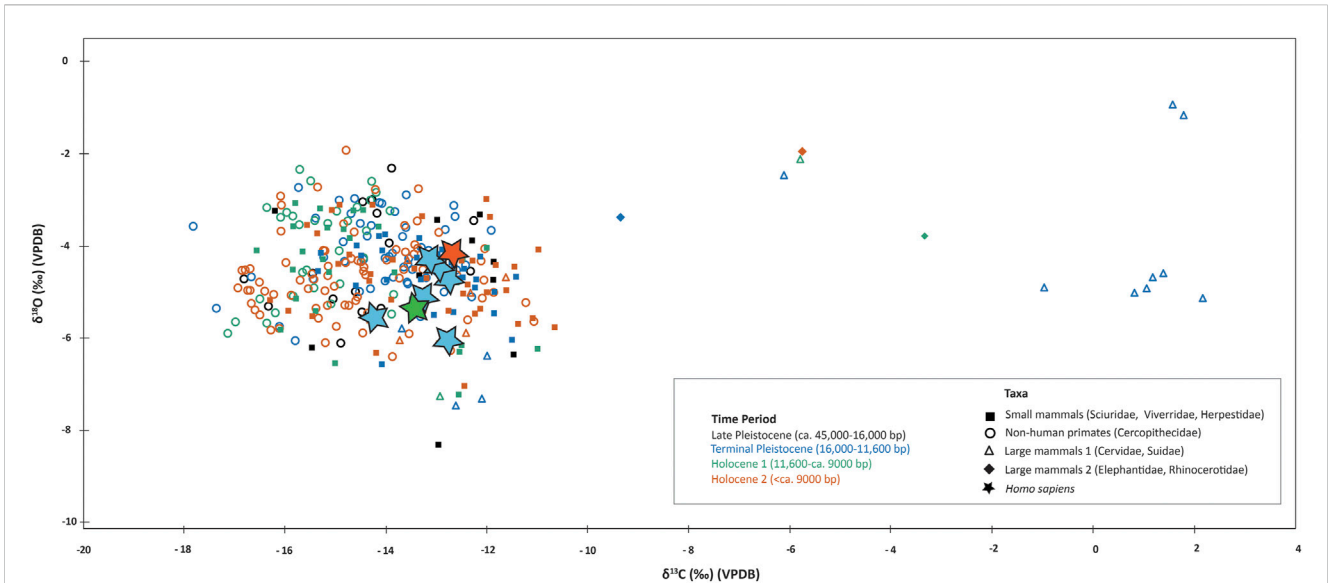Stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotope data for human and animal tooth enamel samples from Fa-Hien Lena and Kitulgala Beli-lena.
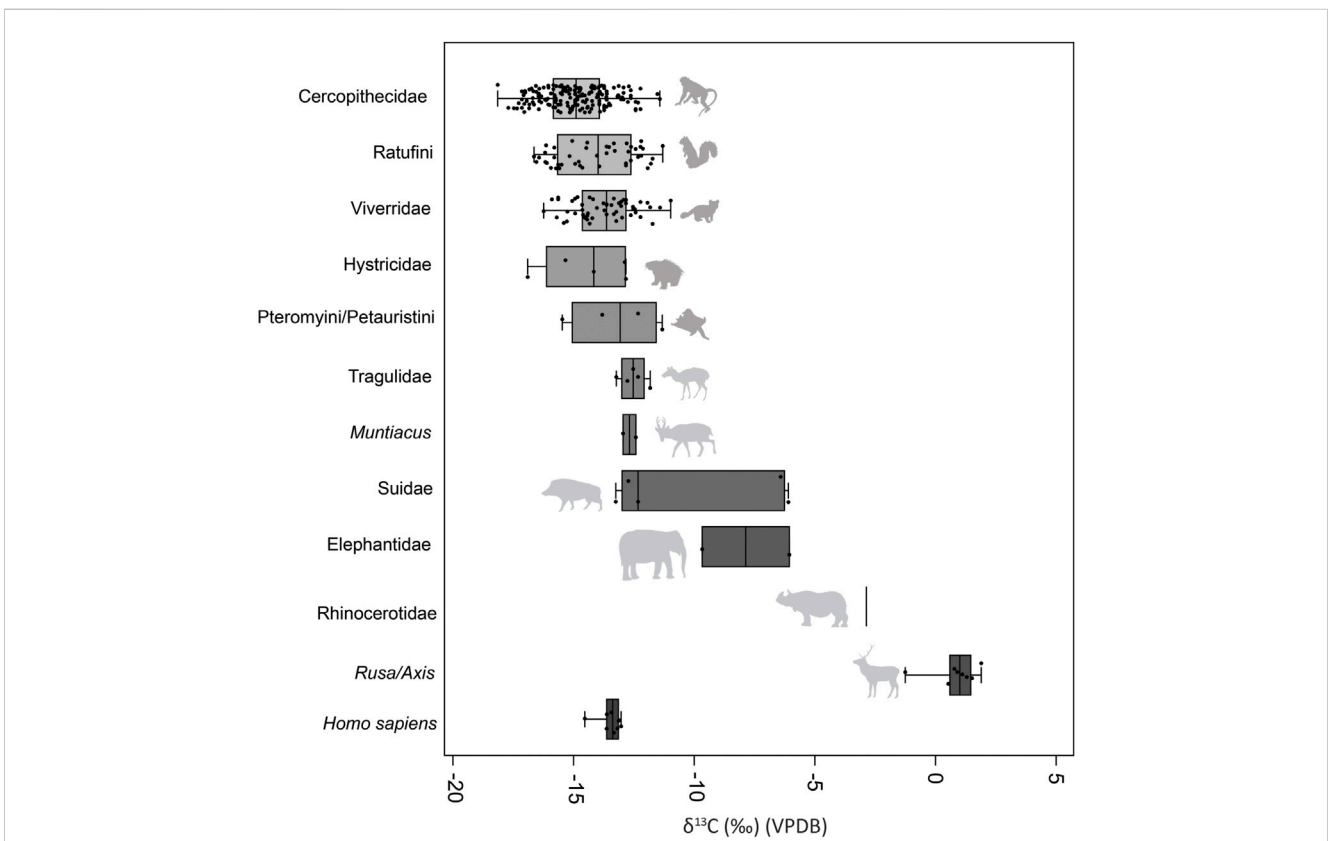

FIGURE 4
δ^{13}C measurements for human and faunal tooth from Fa-Hien Lena and Kitulgala Beli-lena analysed in this study grouped by taxon. Boxplots show median and interquartile range, as well as data points including outliers. All data presented in detail in Supplementary Table S3. (LP- Late Pleistocene, TP- Terminal Pleistocene, H1- Holocene1, H2- Holocene2) (Animal silhouettes from phylopic.org, modified under Creative Commons license).
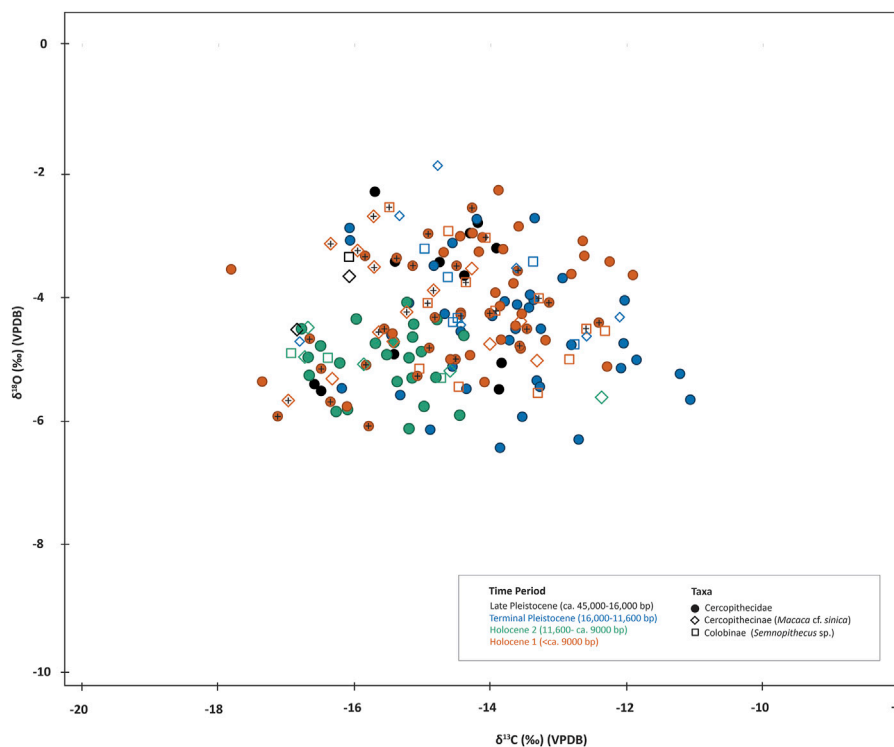
FIGURE 5
Stable carbon (δ¹³C) and oxygen (δ¹⁸O) isotope data from tooth samples of non-human primates from Fa-Hien Lena and Kitulgala Beli-lena (datapoints with cross +).

FIGURE 6
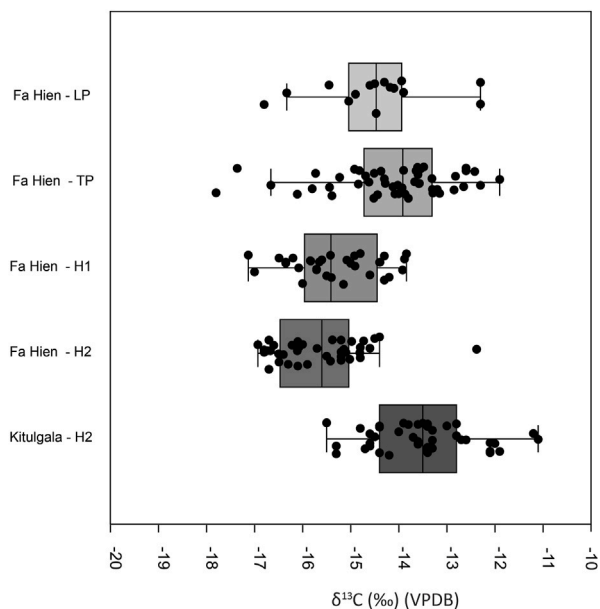δ¹³C measurements for cercopithecid monkey (including both langurs and macaques) teeth from Fa-Hien Lena and Kitulgala Beli-lena grouped based on time period. Boxplots show median and interquartile range, as well as data points including outliers. All data presented in detail in Supplementary Table S3. (LP- Late Pleistocene, TP- Terminal Pleistocene, H1- Holocene1, H2- Holocene2).

In terms of δ¹⁸O values, cercopithecid monkeys exhibited values ranging from of −6.4‰ to −1.9‰ ($n = 178$, mean = −4.4‰), giant squirrels between −8.3‰ and −3.0‰ δ¹³O ($n = 46$, mean = −4.6‰), flying squirrels between −6.3‰ and −4.1‰ ($n = 4$, mean = −5‰), civet cats and porcupines between −7.3‰ and −4.1‰ ($n = 54$, mean = −4.7‰) and −6.6‰ to −3.1‰ ($n = 5$, mean =−5.8‰) respectively and mouse-deer between −7.5‰ and −4.5‰ ($n = 5$, mean = −5.6‰). With the exception of muntjacs, which have the lowest δ¹⁸O values in the sample set analyzed (mean = −7.4‰, $n = 2$), larger bodied taxa exhibited higher δ¹⁸O values. Suids exhibited a wide range of δ¹⁸O values ranging from −7.3‰ to −2.1‰ ($n = 5$, mean = −4.8‰). The two elephant samples have an average δ¹⁸O values of −2.7‰ while the single rhinoceros specimen yielded a value of −3.8‰. In comparison, the larger cervids have δ¹⁸O between −5.2‰ and −0.9‰ ($n = 8$, mean = 3.9‰).

The six human specimens from the Terminal Pleistocene of Fa-Hien Lena have δ¹³C values ranging from −14.2‰ to −12.8‰ (mean = −13.6‰) and δ¹⁸O values between −6.0‰ and −4.4‰ (mean = −5.1‰). By comparison, the single specimen from the Early Holocene phase of the site has a δ¹³C of −13.3‰ and δ¹⁸O of −5.3‰. The δ¹³C and δ¹⁸O values of the human molar fragment from the Holocene layers of Kitulgala Beli-lena fall within the range of the values of obtained from the Fa-Hien specimens (δ¹³C= 12.7‰ and δ¹⁸O= −4.2‰).

A Shapiro-Wilk test for normality indicates that the δ¹³C ($p = <0.05$) of the dataset when grouped according to taxon follows a normal distribution (Supplementary Table S4). An ANOVA test shows that taxonomic grouping significantly
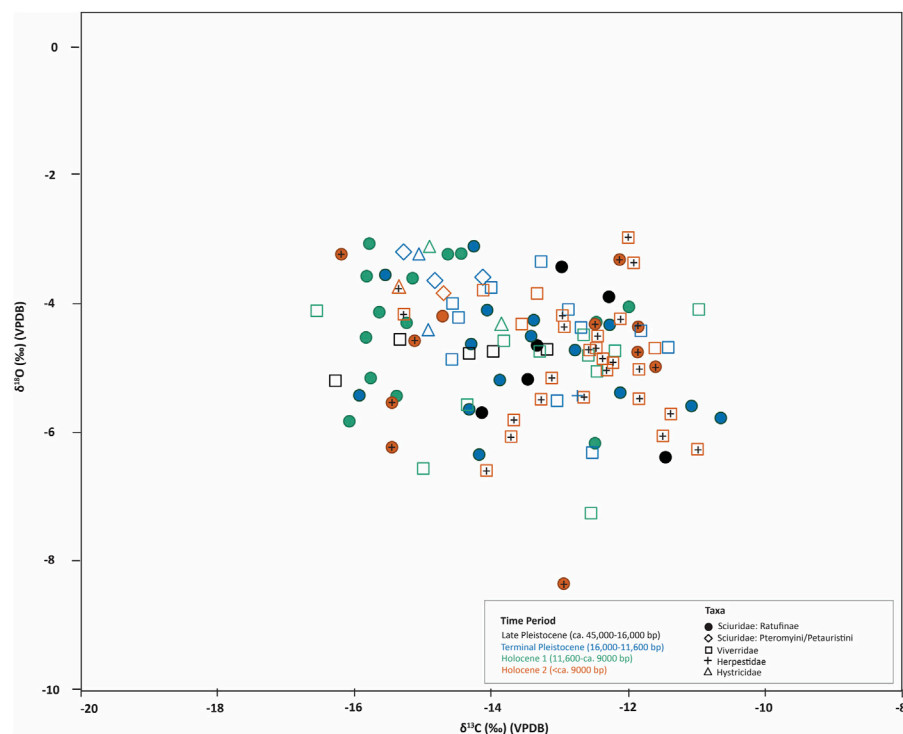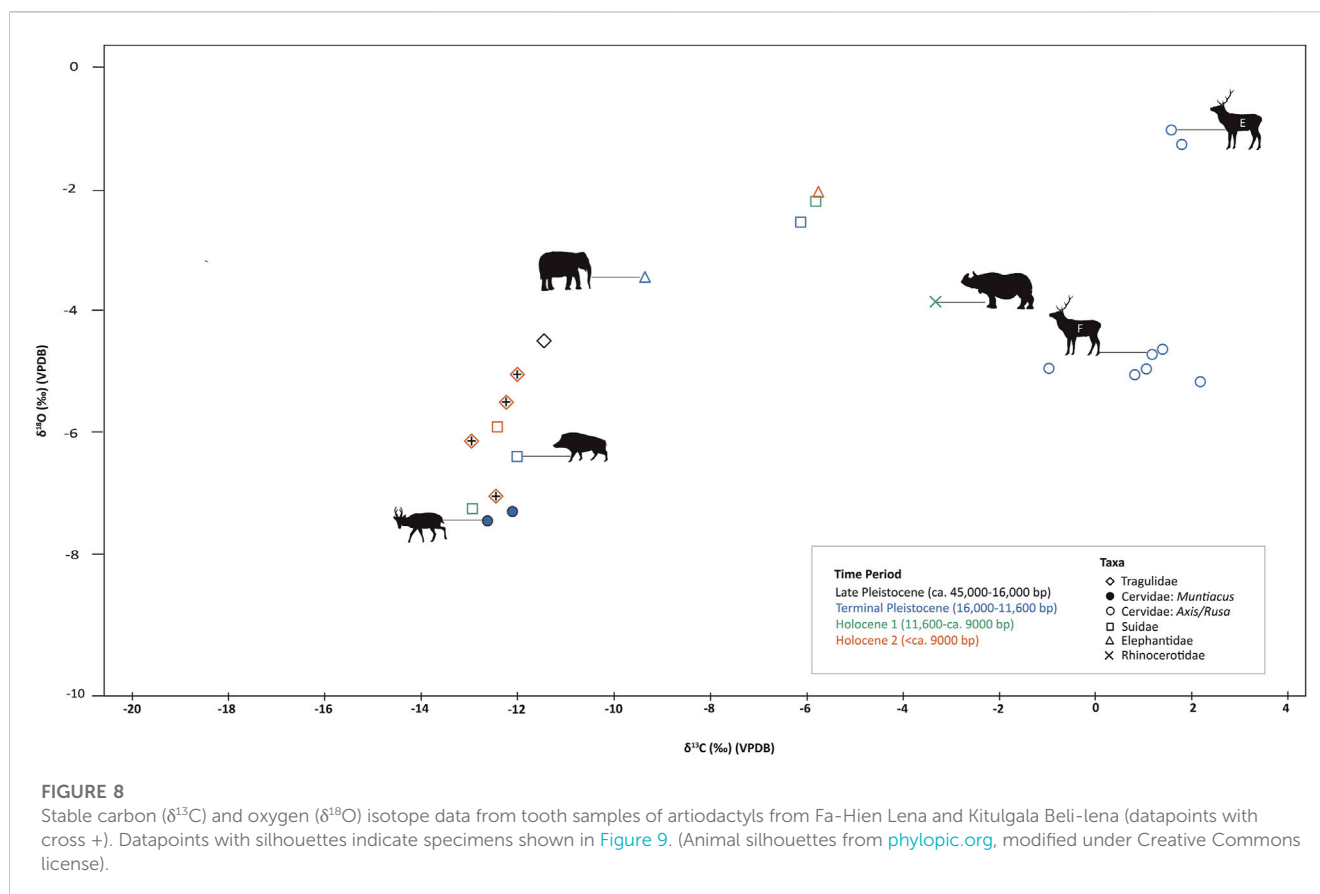
FIGURE 7
Stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotope data from tooth samples of small mammals (live weight < 25 kg) from Fa-Hien Lena and Kitulgala Beli-lena (datapoints with cross +).

influences δ^{13}C [F (10,306)= 1.86, p<0.05], Supplementary Table S5) and *post hoc* Bonferroni and Tukey pairwise comparisons suggest that larger ungulates, specifically cervids, suids and elephants have significantly different δ^{13}C from the smaller-bodied taxa (Supplementary Tables S6, S7). The *post hoc* tests likewise show that the δ^{13}C of the human specimens are distinct from cercopithecid monkeys, mouse-deer, suids and larger cervids (Supplementary Tables S6, S7; Figures 3, 4). Like the δ^{13}C values, the δ^{18}O values are also different between taxonomic groups as shown by an ANOVA test [F (10,306)= 4.76, p<0.05], Supplementary Table S7). Post hoc pairwise comparisons point to the δ^{18}O of muntjacs and elephants being different from some of the other taxa, though this could be an artifact of the small sample size for both group (Supplementary Tables S9, S10).

In terms of the difference of δ^{13}C and δ^{18}O datasets between different occupational phases within Fa-Hien Lena and Kitulgala Beli-lena, a Shapiro-Wilk test indicated that the values, when grouped according to chronology, do not follow a normal distribution. Kruskal–Wallis analyses indicate there to be significant δ^{13}C (Hchi^2: 94.83, df= 4, p<0.05) differences between chronological phases within the sites. Post hoc Dunn tests suggest that there is a significant difference in the δ^{13}C between the Late Pleistocene and the later Holocene (H2) phase of Fa-Hien Lena (Supplementary Table S11). The tests also indicate significant δ^{13}C differences between the Terminal Pleistocene and the Holocene (both H1 and H2) phases of site occupation. The difference appears to be driven by the lower δ^{13}C values for H1 and H2 (Figure 2A). Interestingly, the *post hoc* Dunn tests indicate that the Holocene

phase of Kitulgala (H2) has distinct δ^{13}C values from the Late Pleistocene and Holocene (H1 and H2) phases of Fa-Hien Lena. Visually (Figure 2A), it appears that this is driven by the higher δ^{13}C values for Kitulgala Beli-lena, which is within the range of values for the Terminal Pleistocene of Fa-Hien. Kruskal–Wallis analyses also indicate significant differences (Hchi^2: 10.22, df= 4, p<0.05) in δ^{18}O values between the different chronological phases of the sites. Post hoc Dunn tests suggest that the δ^{18}O values for the later Holocene (H2) phase of Fa-Hien Lena are distinct from the earlier Holocene and Terminal Pleistocene phases with the box plot (Supplementary Figure S4) showing lower δ^{18}O values for the former. Likewise, the Holocene phase (H2) in Kitulgala Beli-lena has significantly lower δ^{18}O values compared to the earlier Holocene (H1) phase of Fa-Hien (Supplementary Table S12, Figure S4).

The δ^{13}C and δ^{18}O values for cercopithecid monkeys are good indicator of the types of environments exploited by the forager communities that inhabited Fa-Hien Lena and Kitulgala Beli-lena as they were the most common animals exploited in all phases of occupation in both sites. Shapiro-Wilk tests indicate that the δ^{13}C (p<0.05) and δ^{18}O (p<0.05) values for monkeys, when grouped according to chronology, do not follow a normal distribution. Kruskal–Wallis analyses indicate there to be significant δ^{13}C (Hchi^2: 71.97, df = 4, p<0.05) and δ^{18}O (Hchi^2: 16.95, df = 4, p<0.05) differences between chronological phases within the sites. Post hoc Dunn tests suggest that there is a significant difference in δ^{13}C values of monkeys from Late Pleistocene compared to the Holocene phases of Fa-Hien Lena. Similarly, the cercopithecid samples from the Terminal Pleistocene phase have distinct δ^{13}C

FIGURE 8
Stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotope data from tooth samples of artiodactyls from Fa-Hien Lena and Kitulgala Beli-lena (datapoints with cross +). Datapoints with silhouettes indicate specimens shown in Figure 9. (Animal silhouettes from phylopic.org, modified under Creative Commons license).

values compared to those from H1 and H2. The δ^{13}C values of monkey teeth from the Holocene phase (H2) of Kitulgala Beli-lena are significantly different from the values from all occupational phases of Fa-Hien Lena except for the Terminal Pleistocene (p= 0.072) (Supplementary Table S13). This mirrors the results obtained when all taxa are grouped according to chronological phase, which the scatter (Figure 5) and box (Figure 6) plots suggest is due to lower δ^{13}C values of monkey teeth in the Holocene levels of Fa-Hien Lena. By contrast, the monkey teeth from the Holocene layers of Kitulgala Beli-lena have higher δ^{13}C values (−15.1‰ to −11.1‰, mean= −13.5‰) compared to those from the early (−17.1‰ to −13.8‰, ave= −15.3‰) and later (−16.9‰ to −12.4‰, mean= −15.6‰) Holocene phases of Fa-Hien Lena.

In terms of differences in δ^{18}O values of the primate samples analysed, *post hoc* Dunn pairwise comparison only draws out the later Holocene phase (H2) as being significantly different from the earlier Holocene (H1) and Terminal Pleistocene phases (Supplementary Figure S5, Table S12). Previously, it was shown that *T. vetulus* has lower δ^{13}C than *M. sinica* in Fa-Hien Lena (Roberts et al., 2017a). We originally aimed to evaluate if this is the case with the new samples from the site as well as in Kitulgala Beli-lena, but our adoption of stricter identification methods reduced our sample size significantly. Of the 178 cercopithecid dental elements selected for the study, only 51 can be identified as either langur (*T. vetulus/S. priam*) or macaque (*M. sinica*). Grouping langur (−17‰ to 12.1‰, ave= −15.08) and macaque (−16.93 to −12.3‰, ave= −14.36) specimens together without consideration of the sites' occupational phases, T-tests showed that there is no

significant difference between their δ^{13}C (df= 49, t= −1.92, p>0.05) and δ^{18}O (df= 49, t= 0.01, p>0.05) values.

4 Discussion

The fauna recovered from the different occupational phases of Fa-Hien Lena and the Holocene layers of Kitulgala Beli-lena can be broadly divided into three different groups based on their δ^{13}C signatures: taxa with low δ^{13}C values suggestive of high proportion of C$_3$ biomass in their diets and therefore dependence on forests or closed environments which include small bodied mammals such as monkeys, squirrels, civet cats and porcupines as well as smaller ungulates such as mouse-deer and muntjacs (between −17.5‰ and −12‰); taxa including pigs, elephants and rhinos, with higher δ^{13}C values (between −12‰ and −3‰) which is indicative of feeding on a slightly more mixed C$_3$/C$_4$ biomass and therefore representative of animals inhabiting mixed closed-canopy to intermediate open environments; and taxa with high δ^{13}C (> −3‰), which include larger cervids (*Axis/Rusa*), indicative of high proportion of C$_4$ in their diet, and therefore representing animals in grasslands/open environments. A similar distribution of habitats for prey animals was observed at the site of Balangoda Kuragala (Roberts et al., 2015b) which today sits within the Intermediate Rainforest Zone of the island (Roberts et al., 2015a). Isotope data at this site highlighted human access to forest dwelling primates and squirrels as well as open dwelling elephants and lagomorphs (Roberts et al., 2015b), with a clear preference for
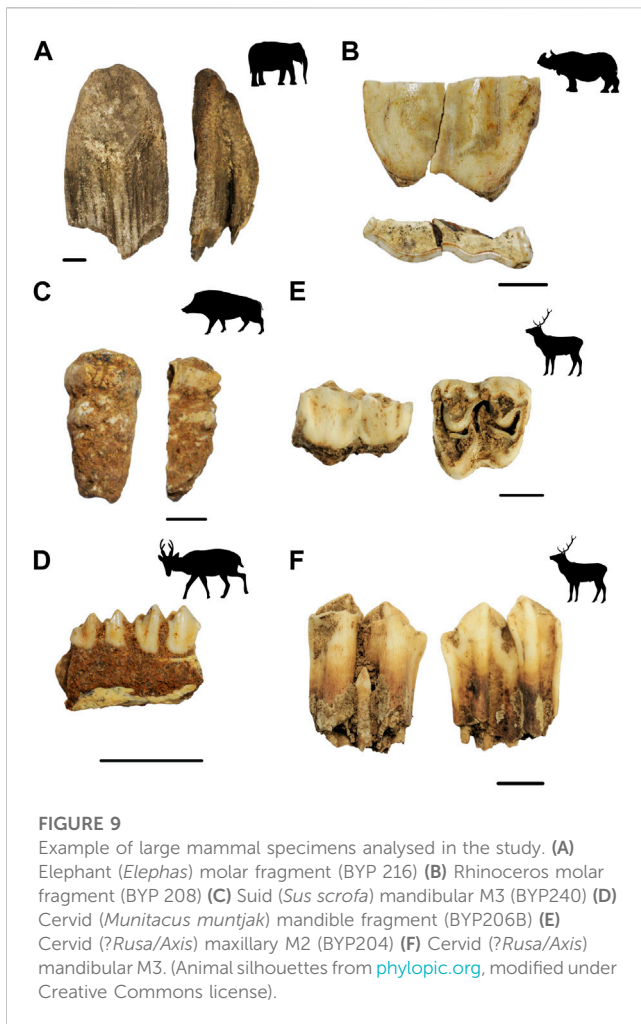
FIGURE 9
Example of large mammal specimens analysed in the study. **(A)** Elephant (*Elephas*) molar fragment (BYP 216) **(B)** Rhinoceros molar fragment (BYP 208) **(C)** Suid (*Sus scrofa*) mandibular M3 (BYP240) **(D)** Cervid (*Munitacus muntjak*) mandible fragment (BYP206B) **(E)** Cervid (?*Rusa/Axis*) maxillary M2 (BYP204) **(F)** Cervid (?*Rusa/Axis*) mandibular M3. (Animal silhouettes from phylopic.org, modified under Creative Commons license).
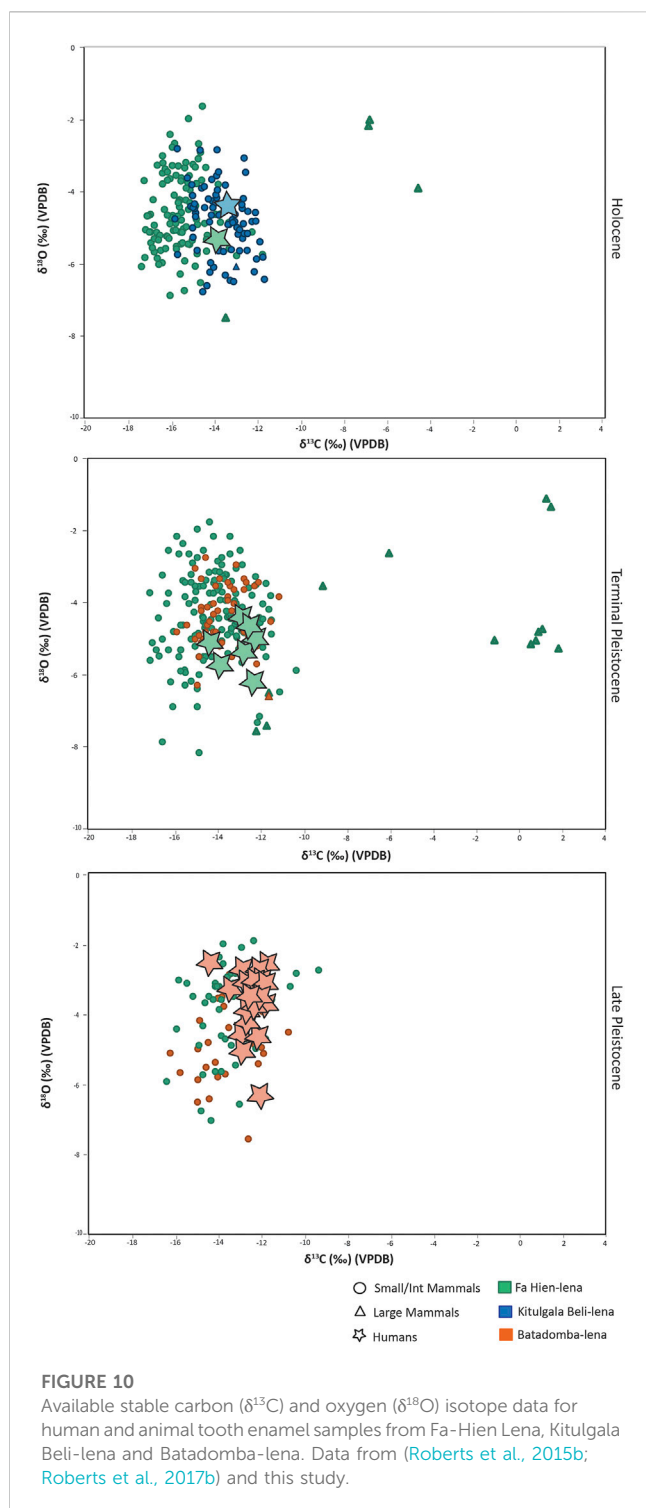
the former and forested habitats. Interestingly, while Balangoda Kuragala is located at the edge of a forest-grassland ecotone today, our new data demonstrate that the access to open-dwelling animals was even maintained by Wet Zone rainforest communities across the Terminal Pleistocene and Holocene.

A single rhinoceros specimen, a broken piece of an upper premolar/molar (buccal side), too fragmented to be confidently assigned to element (Figure 9B), from the Early Holocene layers of Fa-Hien Lena has a $\delta^{13}C$ of −3.3‰ ± 0.1‰, suggesting mixed forest/open environment foraging. Previously, isolated teeth identified as representing "*Rhinoceros sivalensis sinhaleyus*" were reported from the Ratnapura beds of Western Sri Lanka, associated with hippopotamus (*Hexaprotodon sivalensis*) and elephant fossils and presumed to be from the Upper Pleistocene, although no dates are available (Deraniyagala, 1938; Deraniyagala, 1965). To our knowledge, there are no other reported occurrences of rhinoceros in any Pleistocene/Holocene archaeological sites in the island and the tooth fragment we recorded at Fa-Hien Lena is the evidence for the last appearance of the taxon in Sri Lanka. Although there are no direct dates for the specimen, the archaeological layer where it was recovered (c. 168) is sandwiched by layers dated between 7,955 and 7,791/8,595−8,430 cal. BP., (c. 153/138) and 12,575−12,150 cal. BP. (c. 174) [see (Wedage et al., 2019a) for details]. The $\delta^{13}C$ value for

the Fa-Hien Lena rhino is slightly higher compared to the range of reported Indian rhino (*R. unicornis*) $\delta^{13}C$ values from the Late Middle Pleistocene of Thailand (Suraprasit et al., 2018) and lines up with known diets of modern Indian rhino populations which include mostly grasses but also leaves, shrubs, tree branches and fruits (Laurie, 1982; Nowak and Walker, 1999). By contrast, the $\delta^{13}C$ values for the more forest-adapted Javan rhinoceros (*R. sondaicus*) from the Middle Pleistocene to Early Late Pleistocene of Thailand ranged from −17.8‰ to −12.0‰ (Suraprasit et al., 2018). Overall, the presence of the rhinoceros remain in the site highlights the longevity of human interactions with large mammals in Sri Lanka, even as they focused primarily on small-bodied arboreal and semi-arboreal prey.

Similarly, cervids identified as belonging to the genus *Rusa* or *Axis* exhibited distinct open/grassland C_4 signatures with $\delta^{13}C$ ranging from −1.0 to 2.2 (*n* = 9, mean = 1.13) (Figures 4, 8). On-going work (Amano et al., In Prep) aims to identify the dental element to specific taxon but the current lack of comparative data for Sri Lanka in addition to the fragmentary nature of the Fa-Hien Lena specimens limits our current identification. Three species of deer (in addition to muntjacs), the sambar (*Rusa unicolor*), the chital (*Axis axis*) and the hog deer (*Axis porcinus*) are currently present in Sri Lanka, albeit it is still uncertain whether the hog deer is native to the island (Vishvanath et al., 2014; Timmins et al., 2015). Throughout its wide distribution range, the sambar is known for its highly adaptive ecology and diets that consists of grasses, foliage, fruits and submerged water plants (Geist, 1998). In Sri Lanka, sambar deer from the Horton Plains National Park were found to be more dependent on graminoid grasses, though food compositions varied heavily depending on the season (Padmalal et al., 2003). By contrast, the chital is known to be more of a grazer, feeding mostly on grasses, although it is also known to feed on flowers and fruits and will occasionally browse when necessary (Moe and Wegge, 1994). In Sri Lanka, the chital is currently inhabiting the shrubby areas in the Dry Zone (Balasubramanian et al., 1980).

The $\delta^{13}C$ values of the large cervids from the Terminal Pleistocene and Holocene layers of Fa-Hien Lena are much higher than the $\delta^{13}C$ values for *R. unicolor* (−12‰ to −4.1‰, ave= −7.74‰) and *A. axis* (−12.1‰ to −11.7‰, ave= −11.9‰) reported from contemporaneous archaeological layers in Balangoda Kuragala mentioned above (Roberts et al., 2015b). The high $\delta^{13}C$ values of these animals suggest that the people that utilized Fa-Hien Lena during the Terminal Pleistocene/Early Holocene had access to forest edges or grassland environments where they hunted cervids in presumably long expedition trips. Given the overall forest reliance recorded in human $\delta^{13}C$ values at these rainforest sites, it is possible that the foragers that inhabited Fa-Hien Lena employed a mobility organization and/or hunting strategy wherby small groups undertook some specialized long-distance (ca. >60 km) hunting trips. Alternatively, it is also possible that the deer skeletal elements were sourced from other groups which had access to more open environments though contact and trade networks. Interestingly, cervid specimens were present in very low frequencies (< 1.5%) in Fa-Hien indicating that they did not play a significant role in the subsistence of the people that settled the site. The cervids (and all other large ungulates for that matter) were mostly represented by tooth or long bone fragments, suggesting that they were not butchered on-site (Wedage et al., 2019a). Instead,

FIGURE 10
Available stable carbon (δ¹³C) and oxygen (δ¹⁸O) isotope data for human and animal tooth enamel samples from Fa-Hien Lena, Kitulgala Beli-lena and Batadomba-lena. Data from (Roberts et al., 2015b; Roberts et al., 2017b) and this study.

ecologies is also supported by the presence of shell beads manufactured from marine taxa as well as isolated shark teeth which were hypothesized to have been traded or exchanged with groups living in the coast (Langley et al., 2020). It is possible that coastal resources were sourced through expedition trips as Fa-Hien is only ca., 30 km away from the nearest coast, though, as noted above, human δ¹³C implies rainforest residence (Roberts et al., 2015b; Roberts et al., 2017b). Future work and discovery of coastal sites contemporaneous to Fa-Hien would be necessary to investigate these hypotheses.

The δ¹⁸O values we observed for the different taxa in Fa-Hien Lena and Kitulgala Beli-lena generally track their feeding position in the forest (i.e., "vertical stratification" (Cerling et al., 2004; Krigbaum et al., 2013; Carter and Bradbury, 2016), with animals feeding in the canopy having higher δ¹⁸O than animals such as mouse-deer and muntjacs which forage in the forest floor (Supplementary Figure S3). Specifically, *post hoc* Tukey pairwise comparisons point to muntjacs having significantly lower δ¹⁸O values compared to canopy-dwelling taxa such as monkeys, civet cats and squirrels. However, as with the δ¹³C, we do not see any difference with the δ¹⁸O between langurs and macaques. We presume that this is brought about by our failure to discriminate between the obligate-drinker, canopy-dwelling *T. vetulus* which is expected to have higher δ¹⁸O than the semi-terrestrial, also obligate-drinking *S. priam*. But as pointed out by Roberts et al. (Roberts et al., 2017b), this could also be an issue of equifinality, with the elevated δ¹⁸O values in *T. vetulus* resulting from them feeding up high in the canopy and in *S. priam* (and *M. sinica*) possibly resulting from them drinking from open, ¹⁸O-enriched water sources in the ground. The latter could also explain the high δ¹⁸O values we observed for taxa in mixed/open environments including elephants and larger cervids. It would also fit with observations that the primate isotopic values track overall environmental changes through the occupation sequences of the site.

The δ¹³C values from the different occupational phases within Fa-Hien Lena hint at slight differences in the local environment in the site at different time periods. The difference appears to be driven by the lower δ¹³C values for the Holocene (H1 and H2), which is consistent with the previously reported increase in the canopy cover in/or around the site following the onset of the Holocene (Roberts et al., 2017b). This can be seen in the box plot considering all taxa (Figure 2A) and in the plot for δ¹³C of cercopithecid monkeys (Figure 6). By contrast, the δ¹³C values for human and fauna in the Holocene (H2) layers of Kitulgala Beli-lena is higher compared to contemporaneous layers in Fa-Hien Lena. This suggests that environment in/or around (or at least where the foragers hunted the fauna) Kitulgala Beli-lena is more open than in Fa-Hien Lena during the Early to Mid-Holocene (i.e., 9,000 years BP and later). This is consistent with existing, albeit sparse, paleoenvironmental proxy records in Sri Lanka. Pollen record from the Horton Plains, although distantly located from both Fa-Hien Lena and Kitulgala Beli-lena, indicate forest expansion from around 16,000–8,700 cal years BP (Premathilake and Risberg, 2003; Premathilake, 2012). An alternative explanation for the higher δ¹³C of fauna from the Holocene layers of Kitulgala Beli-lena could relate to the site's location and environmental setting. Kitulgala is located closer to higher altitude rainforest and grassland environments as well to intermediate rainforests. The higher δ¹³C could be brought about by foragers exploiting more

cervid skeletal and dental elements were most likely brought to the site as finished tools or as materials for tool production as evidenced by the high proportion of worked fragments (Langley et al., 2020). Of the 72 deer skeletal and dental elements, 25% were worked metapodial and antler fragments. This suggests that certain parts of the deer carcass, the skull with the antler and the metapodials, were transported or traded over long distance. Although this remains to be ascertained, contact between groups focusing on different

diverse ecological niches, including more open environments. Further research, perhaps looking at forager and prey mobility through strontium isotopes, would help shed light on this question.

Focusing on the primate data, the $\delta^{13}C$ signatures of cercopithecid monkeys in the assemblage is consistent with previously published values for the three species that occur in Sri Lanka (Roberts et al., 2017b). We initially aimed to describe in detail the difference in the $\delta^{13}C$ signatures among these species. We were able to confidently discriminate isolated langur teeth from macaque teeth based on well documented colobine dental features (e.g., high, pointed molar cusps linked by ridges but separated by deep lingual notches) (Delson, 1973; Kay, 1975; Swindler, 1976). However, our application of a strict identification criteria fails to discriminate the different langur species from each other which resulted to a small sample size. We are currently looking at morphological/geometric morphometric features that could discriminate *T. vetulus* dental elements from those of *S. priam* (building on (Kay and Hylander, 1978; Wright and Willis, 2012)). As these species were previously shown to have slightly different $\delta^{13}C$ values (Roberts et al., 2017b), and are known to currently exploit slightly different habitats (Hladik, 1977; Dittus, 1984) differentiating them from each other would be important in reconstructing the different ecological niches exploited by monkeys and if/how they change through time. We observed no significant difference in the $\delta^{13}C$ values between the langurs and the macaques when grouped without consideration of the sites' occupational layers. This is expected as previous research (Roberts et al., 2017b) has shown that the $\delta^{13}C$ values for *S. priam* sit between the values for heavily folivorous *T. vetulus* (Hladik, 1977) and the generalist *M. sinica* (Dittus, 1984). Interestingly, the $\delta^{13}C$ values for the monkeys track the observed $\delta^{13}C$ difference in the different occupational layers of Fa-Hien Lena, with both langurs and macaques in the Holocene layers of Kitulgala Beli-lena having higher $\delta^{13}C$ values compared to contemporaneous layers in Fa-Hien Lena (see Supplementary Figure S6 and discussion below). This shows that the langurs during the Holocene in Kitulgala were making use of more open habitats, indicating some dietary flexibility, which has also been suggested by colobine $\delta^{13}C$ values from Terminal and Late Pleistocene layers of Batadomba-lena (Roberts et al., 2017b) and studies looking at current langur populations (Dela, 2007; Amato et al., 2020).

Finally, moving to our human data, our study aligns well with previously published isotopic data (Roberts et al., 2017b) in suggesting reliance on rainforest resources by humans that inhabited Fa-Hien Lena from the Terminal Pleistocene (mean = −13.2‰, n = 6) to the Holocene (a single specimen with $\delta^{13}C$ of −13.2‰ ± 0.1‰). The human specimen (a fragment of an isolated molar) from the Holocene layers of Kitulgala Beli-lena ($\delta^{13}C$ of −12.7‰) also showed a C_3 forest signature (Figures 2–4), albeit the $\delta^{13}C$ value suggests a reliance on slightly more open forests (i.e. forest-open mosaics) similar to those found currently in Sri Lanka's Wet and Intermediate Zones and in line with the slightly more open environment suggested by the $\delta^{13}C$ from faunal dental enamel (see below). Interestingly, comparison with published data show that the $\delta^{13}C$ of Terminal Pleistocene humans in Fa-Hien Lena (mean = −13.5‰, n = 7, df = 29, t = −2.88, p < 0.05) is lower than those from the Late Pleistocene of Batadomba-lena (mean = −12.7‰, n = 23) [(Roberts et al., 2017b) see Supplementary Figure S7], suggesting reliance on resources from more closed forest in Fa-Hien. In terms of $\delta^{18}O$, the human specimens from Fa-Hien Lena had values ranging

between −6.5‰ and −4.4‰. Post hoc Tukey pairwise comparison show no significant difference between the $\delta^{18}O$ values of the human specimens compared to cercopithecids and other small mammalian taxa (Supplementary Figure S3, Table S10). As humans are obligate drinkers, these values suggest humans mainly sourced their drinking water from with the local forest setting. Comparison with published data indicates that the Terminal Pleistocene specimens from Fa-Hien Lena (mean = −5.11‰, n = 8, df = 29, t = 5.59, p<0.0001) had lower $\delta^{18}O$ than those from the Late Pleistocene of Batadomba-lena (mean = −3.11‰, n = 23). This may indicate denser forest conditions, and less evaporative impacts on water sources, in the vicinity of Terminal Pleistocene than at Late Pleistocene Batadomba-lena, something that has also been suggested in previous studies on the basis of faunal isotopes from these different contexts (Roberts et al., 2015b; Roberts et al., 2017a).

Figure 10, summarizes all the available dental enamel stable isotopes data for the island of Sri Lanka. Our data adds to the already huge dataset for the island, which overall shows continued human utilization of rainforest resources over the past ca. 48,000 years. Our results show that although humans in Sri Lanka's Wet Zone region were reliant on forest resources, they had access to grassland and more open environments or had contact with groups exploiting different kinds of ecosystems. More research is required to understand these prehistoric mobility patterns or exchange networks, perhaps by employing strontium stable isotopes. Meanwhile, the sampling more animal taxa, and resolving taxonomy of closely related groups, could further enhance the understanding in the adaptations, not only of humans but also of other animal taxa to different ecological niches at different times. For example, the expansion of rainforests revealed by isotopic data during the Holocene in Fa-Hien Lena coincided with increased frequency of taxa usually associated with more open environments, including the Indian hare (*Lepus nigricollis*), jackal (*Canis aureus*) and cervids (*Rusa/Axis*) (Wedage et al., 2019a). Whether the presence of these taxa represent their adaptation to changing environments (i.e., Amano et al., 2016) or human foraging of different ecological niches remains to be fully explored.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

Author contributions

NA and PR designed the study with supervision from NB and MP. NA conducted the zooarchaeological analyses as well as the identification of dental elements. NA, JI, and PR conducted the stable isotopes analyses and analyzed the data. The excavations of Fa-Hien Lena and Kitulgala Beli-lena was conducted by OW with supervision from NB and MP. OW and NA are responsible for the curation and sampling of the finds from the excavations. NA and PR wrote the original draft and all coauthors contributed to the review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2023.1133281/full#supplementary-material

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