

# **Fruits of the Forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka**

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## Abstract

Sri Lanka has yielded some of the earliest dated fossil evidence for *Homo sapiens* (~ 38–35,000 cal. years BP [calibrated years before present]) in South Asia, within a region that is today covered by tropical rainforest. Archaeozoological and archaeobotanical evidence indicate that these hunter-gatherers exploited tropical forest resources, yet the contribution of these resources to their overall subsistence strategies has, as in other Late Pleistocene rainforest settings, remained relatively unexplored. We build on previous work in this tropical region by applying both bulk and sequential stable carbon and oxygen isotope analysis to human and faunal tooth enamel from the sites of Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala. Tooth enamel preservation was assessed by means of Fourier Transform Infrared Spectroscopy. We use these data to produce a detailed stable isotope ecology for Late Pleistocene–Holocene foragers in Sri Lanka from ~36–29,000 cal. years BP, allowing us to test the degree of human tropical forest resource reliance over a considerable time period. Given that non-human primates dominate the mammalian assemblages at these sites, we also focus on the stable isotope composition of three monkey species in order to study their ecological preferences and, indirectly, human hunting strategies. The results confirm a strong human reliance on tropical forest resources from ~ 36–29,000 cal. years BP until the Iron Age ~3 cal. years BP, while sequential tooth data show that forest resources were exploited year-round. This strategy was maintained through periods of evident environmental change at the Last Glacial Maximum and upon the arrival of agriculture. Long-term tropical forest reliance was supported by the specialised capture of non-human primates, although the isotopic data revealed no evidence for niche distinction between the hunted species. We conclude that humans rapidly developed a specialisation in the exploitation of South Asia's tropical forests following their arrival in this region.

## Introduction

Tropical rainforests have often been ignored in discussions of the evolution and adaptations of our genus, *Homo* (Roberts et al., 2016), while open savannah environments, or mixed forest-open mosaics, have been a focus for the emergence and migration of hominins within and beyond Africa (Bird et al., 2005; Dennell and Roebrooks, 2005; Basell, 2008; Blome et al., 2012; Boivin et al., 2013; Domínguez-Rodrigo, 2014). Potential obstacles for human foragers in tropical forests are argued to include limited starch and protein-rich resources, navigational difficulties, seasonal resource fluctuations, and widely-spaced resources (Hutterer, 1983; Bailey et al., 1989; Bailey and Headland, 1991). In the last two decades, however, archaeological evidence has suggested that *Homo sapiens* utilised tropical rainforests from at least 45,000 years ago in Southeast Asia and Melanesia (Barker et al., 2007; Summerhayes et al., 2010, 2016; Barker, 2013), and possibly even 200,000 years ago in Africa (Mercader, 2002a,b).

Despite early evidence for rainforest use, poor organic preservation (Tappen, 1994) makes it difficult to test the extent of human reliance on these biomes. Indirect linkage of archaeological remains to ‘off-site’ pollen, microcharcoal, and geochemical studies from lake and marine settings is one common approach (Mercader, 2002a,b), yet the correlation of these records with human activity is problematic (Roberts and Petraglia, 2015). Where archaeological material is preserved within rare cave and rockshelter sequences, more direct insights into human rainforest resource use can be obtained from archaeobotanical and archaeozoological remains (Barker et al., 2007; Summerhayes et al., 2010), as well as typological and use-wear analysis of stone and bone tool technologies (Barker, 2013; O’Connor et al., 2014). Yet, these remains are frequently absent beyond the Holocene. Furthermore, it remains almost impossible to estimate overall dietary importance of tropical forest resources on the basis of archaeobotanical and archaeozoological snapshots alone.

Stable carbon and oxygen isotope analysis can, on the basis of a distinction between the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways at the base of tropical food webs, as well as the ‘canopy effect’, provide direct insight into long-term human forest reliance in tropical environments. This methodology has been widely applied to hominin fossil tooth enamel in Africa to determine when early hominins moved from C<sub>3</sub>-forest resources to open C<sub>4</sub> savannah reliance (White et al., 2009; Lee-Thorp et al 2010; Sponheimer et al., 2013; Levin et al., 2015). It has also been used to elucidate the forest adaptations of the early extinct apes *Gigantopithecus* and *Sivapithecus*, respectively (Nelson, 2003, 2007; Bocherens et al., 2014), as well as to discern forest niche distinctions in extant faunal communities (Cerling et al., 2004), including primates (Sandberg et al., 2012; Krigbaum et al., 2013).

The systematic application of this methodology to questions relating to rainforest adaptations in our own species, however, remains limited to just a few case studies (Krigbaum, 2003, 2005; Roberts et al., 2015a). Krigbaum (2001, 2003, 2005) first applied stable carbon and oxygen isotope analysis to questions of human diet following the onset of the Neolithic in a rainforest context in Southeast Asia. Sri Lanka has one of the richest human fossil records, spanning from ~38,000–3,000 years ago, in a modern rainforest setting worldwide (Deraniyagala, 1992; Perera et al., 2011). Recently, stable isotope analysis of human tooth enamel from this region provided the earliest direct evidence for human rainforest reliance anywhere in the world from 20,000–3,000 years ago (Roberts et al., 2015a). However, stable isotope methodologies are yet to be extended back to the earliest encounters of *H. sapiens* with tropical forests in Sri Lanka, as well as more globally, and there has been little attempt to explore, in detail, the stable isotope ecology of humans and their associated fauna in these settings.

*The Sri Lankan Microlithic tradition and primate specialisation*

Sri Lanka is divided into three broad climate-driven precipitation and vegetation zones. The ‘Wet Zone’ receives between 2,200–4,800 mm of annual rainfall and is home to wet deciduous and tropical evergreen rainforest (Ashton and Gunatilleke, 1987; Gunatilleke et al., 2005; Roberts et al., 2015b), while the ‘Intermediate Zone’ receives 1,700–2,200 mm and supports moist tropical deciduous and semi-evergreen ‘intermediate’ rainforest (Erdelen, 1988; Roberts et al., 2015b). The remaining ‘Dry Zone’ (still very wet by most standards) receives rainfall of ~1,000–1,700 mm and is characterised by open forest and large expanses of shrubs and grassland (Erdelen, 1988; Somaratne and Dhanapala, 1996) (Fig. 1). Although the majority of the rain in the ‘Wet Zone’ comes between May and October, as a result of the southwest monsoon, there is no real dry season. By contrast, the northern ‘Dry Zone’ of the island faces regular periods of drought between May and September (Mueller-Dombois, 1968; Dittus, 1977). The position of these boundaries in the past is relatively poorly understood, however, with well-dated palynological information coming from only the Horton Plains in the highlands of Sri Lanka (Premathilake and Risberg, 2003; Premathilake, 2012).

Fig. 1 about here

The ‘Microlithic’ characterizes a tradition of small, less than 2 cm long, stone tools found at sites in Sri Lanka from 38,000–35,000 cal. years BP (calibrated years before present) until the onset of the Iron Age ~3,000 cal. years BP (SU Deraniyagala, 1992; Lewis et al., 2014; Roberts et al., 2015b). Thus far no direct use-wear studies have been carried out on the microliths, although they have been associated with projectile weaponry (Perera et al., 2011; Roberts et al., 2015b). In contrast to many tropical regions of the world, the archaeological

sequences in which these tools are found are rich in organic material (Kennedy and Deraniyagala, 1989; Deraniyagala, 1992; Wijeyapala, 1997; Kennedy, 2000; Perera et al., 2011, 2017), potentially linked to the formation of gneiss rockshelter and cavesites out of the Precambrian Highland Complex of the island (Cooray, 1984). This facilitates the detailed construction of human subsistence choices at these tropical sites.

The evidence uncovered to date indicates the use of tropical forest tree resources, such as *Canarium* sp. nuts, freshwater molluscs from fast-flowing rivers, and the exploitation of small-medium arboreal and semi-arboreal mammals (Perera, 2010; Perera et al., 2011). In particular, primate taxa consistently make up to 70–80% of the mammalian kill assemblage at the Microlithic sites of Fa Hien-lena and Batadomba-lena (Perera, 2010; Perera et al., 2011). This proportion is unprecedented, even with rifles in many parts of the African and Amazonian rainforests today (ProWildlife, 2007; Lu, 2010; Papworth et al., 2013), with perhaps one exception amongst the Raute of Nepal (Fortier, 2014). Ethnographies of hunter-gatherers highlight primates as a potentially valuable source of protein in tropical environments, extracted using a variety of techniques, including projectile hunting, trapping, or nets (Harako, 1982; Noss, 1997, 1998; Fortier, 2014). Clearly then, forest resources were an important component of hunter-gatherer subsistence at these sites. However, from technological, archaeobotanical and archaeozoological evidence alone it is not yet clear whether Late Pleistocene and Holocene human populations were reliant on these rainforest resources, or whether they were just one, seasonal strategy.

#### *Batadomba-lena rockshelter*

One of the most important sites to produce early human fossils associated with rainforest foraging in Sri Lanka is Batadomba-lena. This gneiss rockshelter (8°12'E, 6°46'N) is 10 x 15 m in area and lies near the banks of a stream in the Wet Zone rainforest of Sri Pada,

Ratnapura District (Fig. 1). It is currently surrounded by dense, lowland evergreen forest (Perera, 1975). Excavations in the 1980s indicated the presence of geometric microliths from the earliest horizon upwards, while bone tools, animal bones, archaeobotanical remains and human fossils were found throughout the sequence (Deraniyagala, 1992). Initial radiocarbon dates from wood charcoal indicated a period of occupation from ~28,000 to ~12,000 cal. years BP (Deraniyagala, 1992) but these dates were subsequently re-calibrated alongside additional AMS (Accelerator Mass Spectrometry) radiocarbon dates on wood charcoal to produce a stratigraphic sequence of Layers 7c to 1, dated from 36,000 cal. BP to 12,000 cal. BP (Perera, 2010; Perera et al., 2017). Perera et al. (2011) used a combination of one bulk (38,873–28,075 cal. years BP) and one AMS date (35,364–33,894 cal. years BP) to suggest that the most likely date for the lowermost stratum, Layer 7c, was ~36,000 cal. years BP.

Given that this date, in line with dates from Fa Hien-lena rockshelter (Wijeyapala, 1997; Roberts et al., 2015b), represents the earliest human presence in Sri Lanka, and indeed South Asia, as well as one of the earliest firm fossils of *H. sapiens* associated with rainforest environments (Roberts and Petraglia, 2015), further interrogation beyond simple averaging of the AMS and bulk charcoal dates for Layer 7c was deemed important. Building on our earlier work (Roberts et al. 2015b), here we provide a Bayesian model for published radiocarbon dates from 1980s and 2000s excavations of the Batadomba-lena sequence in order to provide a more refined chronology for rainforest foraging at the site. Given that all early radiocarbon dates for rainforest foraging in Sri Lanka come from charcoal, we also apply a new charcoal-based correction factor for the sequence for the first time (Dee and Bronk Ramsey, 2014). The results indicate that the start of Layer 7c spans 35,862 to 28,769 cal. years BP at 95% probability (Fig. 2; Supplementary Online Material [SOM] Table S1).

Layer 6b, which contains a wealth of human fossil material, and Layer 6a span the periods 19,497–17,238 cal. years BP and 17,809–15,883 cal. years BP, respectively, and indicate

occupation of the site around the time of the Last Glacial Maximum (LGM) (Fig. 2; SOM Table S1). Layers 5, 4b, and 4a indicate that the sequence then extends to ~12,000 cal. years BP. This dating provides a chronological constraint for a human tooth excavated from Layer 7c during the 1980s that potentially represents the oldest human fossil in South Asia, as well as abundant human teeth from the LGM layers. Given a similar Bayesian model for Fa Hien-lena (Roberts et al., 2015b), the date range for Layer 7c provided here potentially makes this human tooth the oldest human fossil in Sri Lanka. It is also worth noting that, as of yet, the Acid-Base-Oxidation (ABOX) protocol (Bird et al., 1999) has not been applied to the 1980s or 2000s charcoal samples from Batadomba-lena, nor at other rainforest forager sites in Sri Lanka. As a result, the chronology of Batadomba-lena presented here, its human fossils, as well as dates for rainforest foraging on the island more broadly, is likely composed of minimum ages that will be pushed further back in time with future re-analysis.

#### *Stable carbon and oxygen isotope analysis and human rainforest prehistory*

In a tropical context, the isotopic distinction between C<sub>3</sub> and C<sub>4</sub> biomass is useful for studying the relative proportion of C<sub>4</sub> grassland and C<sub>3</sub> woodland or forest in faunal and hominin diets and, indirectly, their associated environments (Sponheimer et al., 2006a; Codron et al., 2014; Crowley et al., 2014). Within tropical forests themselves, vegetation growing under a closed forest canopy is strongly depleted in <sup>13</sup>C, due to low light (Farquhar et al., 1989) and large amounts of respired CO<sub>2</sub>, especially near the forest floor (van der Merwe and Medina, 1991). This ‘canopy effect’ causes CO<sub>2</sub>, soils, leaves and fruits within a closed canopy to have low δ<sup>13</sup>C values that are also reflected in the tissues of animals feeding in the same environments (van der Merwe and Medina, 1991; Cerling et al., 2004). In faunal diets, prior to the impact of significant fossil fuel emission from the 18<sup>th</sup> and 19<sup>th</sup> centuries on atmospheric δ<sup>13</sup>C, tooth enamel with δ<sup>13</sup>C lower than -14‰ represents reliance on dense or closed canopy forest, while average herbivore values for C<sub>3</sub> and C<sub>4</sub> reliance are c. -12‰ and



~ 0‰, respectively (Lee-Thorp *et al.*, 1989a, b; Levin *et al.*, 2008).

It has also been suggested that stable carbon isotopes can be used to discern the niches of tropical forest-dwelling taxa, with most research here focusing on primates (see reviews by Schoeninger, 2009; Sandberg *et al.*, 2012). Researchers have argued that the proportion of fruits and leaves in primate diets can lead to significantly different stable carbon isotope values (Cerling *et al.*, 2004; Oelze *et al.*, 2014). Furthermore, it has been suggested that differential isotopic impacts of the ‘canopy effect’ may be used to discern niches in the canopy, sub-canopy and on the ground, with those animals living on the forest floor feeding on the most  $^{13}\text{C}$ -depleted vegetation as a result of low light and respired  $\text{CO}_2$  (Cerling *et al.*, 2004). However, although the vertical gradient in stable carbon isotopic ratios is visible in  $\text{CO}_2$  and foliage studies (van der Merwe and Medina, 1989, 1991), its presence and resolution in faunal communities remain equivocal (Schoeninger, 2009; Krigbaum *et al.*, 2013).

The oxygen isotope composition of animal tissues can provide additional palaeoecological information about water and food. In tropical ecosystems it has been shown that vegetation  $\delta^{18}\text{O}$  reflects either evaporative potential or the source-effect of rainfall (Buchmann *et al.*, 1997; Buchmann and Ehleringer, 1998; McCarroll and Loader, 2006). The relationship between plant  $\delta^{18}\text{O}$  and evaporative potential may be used to infer canopy density in a forest environment.  $\text{CO}_2$  and vegetation  $\delta^{18}\text{O}$  have also been shown to demonstrate differences depending on height within the canopy, and between different plant parts, given changing evaporative potentials (Sternberg *et al.*, 1989; Buchmann *et al.*, 1997; Buchmann and Ehleringer, 1998). Those animals, such as folivorous primates, which obtain the majority of their water requirements from plants will strongly reflect those environmental factors that influence plant transpiration and plant  $\delta^{18}\text{O}$  (Kohn *et al.*, 1996; Levin *et al.*, 2006; Carter and Bradbury, 2015).

Bone collagen is typically poorly preserved in tropical contexts so that tooth enamel is the archaeological material of choice (Krigbaum, 2005). The apatite of tooth enamel differs from that of bone and dentine in having fewer substitutions, less distortion and larger crystals (LeGeros, 1991), making it more resistant to post-mortem diagenetic substitution and degradation (Lee-Thorp et al., 1989b; Lee-Thorp, 2008). Tooth enamel will record an isotopic ‘whole-diet’ sequence for the period of enamel formation, a period that will vary depending on species and tooth sampled (Passey et al., 2005). The sequential nature of enamel mineralization and maturation allows chronologically-ordered, temporal isotopic changes to be studied (Balasse, 2002; Sponheimer et al., 2006b), even though some attenuation occurs as a result of ongoing mineralization beyond initial enamel deposition (Balasse, 2002; Passey et al., 2005).

Here, we build on the work of Roberts et al. (2015a) by extending the application of stable carbon and oxygen isotopes to questions of prehistoric human rainforest use in several new directions. We present new stable isotope data from the site of Batadomba-lena in order to determine the degree of tropical forest resource reliance exhibited by the earliest *H. sapiens* found in the Wet Zone of Sri Lanka ~36-29,000 cal. years BP, and enrich the sample size of human fossils available for the LGM at this site. We also undertake sequential stable carbon and oxygen isotope analysis of human and faunal tooth enamel from Fa Hien-lena, Balangoda Kuragala and Batadomba-lena to probe intra- and inter-annual variation in the reliance on tropical forest resources. Finally, we compare new, and existing, data from faunal and non-human primate enamel found at Sri Lankan Microlithic tradition archaeological sites in order to study intra-species niche variability and its relation to palaeoenvironmental change, as well as its potential impacts on human subsistence strategies. This paper also applies Fourier Transform Infrared Spectroscopy to study tooth enamel preservation in a rainforest environment.

Fig. 2 about here

## Material and methods

### *Fourier-Transform Infrared Spectroscopy (FTIR) and enamel preservation*

While reliable  $\delta^{13}\text{C}$ - and  $\delta^{18}\text{O}$ -based dietary and environmental indicators have been demonstrated across millions of years (Lee-Thorp et al., 1989a), protocols to check the structural preservation of fossil tooth enamel samples remain important. This is particularly the case in tropical forest environments with ion rich soils and high hydrological activity. One means to check enamel preservation is the application of Fourier Transform Infra-red Spectroscopy (FTIR), which absorbs radiation at discrete vibrational frequencies related to the presence and crystallographic environment of key functional groups. The polyatomic ions of interest are phosphates ( $\text{PO}_4^{3-}$ ), carbonates ( $\text{CO}_3^{2-}$ ), and hydroxyl groups ( $\text{OH}^-$ ). The observed absorbance bands of enamel can be ascribed to the internal vibrations of these molecular groups (Farmer, 1974; LeGeros, 1991) (SOM Table S2).

We use the empirical indices from Sponheimer and Lee-Thorp (1999), and Roche et al. (2010) to characterize the crystal-chemical properties of enamel bioapatite (SOM Table S3). The possible presence of calcite was assessed in all samples by checking for a peak at  $711\text{ cm}^{-1}$  (Lee-Thorp and van der Merwe, 1991; Sponheimer and Lee-Thorp, 1999). Fifteen fossil faunal samples compiled from the Microlithic tradition sites of Fa Hien-lena, Balangoda Kuragala, Bellan-bandipalassa, the 1980s collection from Batadomba-lena, and the 2005 collection from Batadomba-lena, and fifteen human fossil specimens, compiled from Fa Hien-lena, Balangoda Kuragala and Batadomba-lena, were subjected to FTIR analysis prior to any pre-treatment in order to determine the potential for diagenetic structural and compositional modification of enamel during burial (SOM Table S4). The fossil spectra were compared to those of 11 modern primate and cervid samples (SOM Table S4) and 15

historical (late 19<sup>th</sup> and early 20<sup>th</sup> century) human enamel samples from populations living in tropical forest environments (VAD) and urban (SL) areas in Sri Lanka, from the Duckworth Collection, University of Cambridge, and the Department of Anatomy, University of Edinburgh (SOM Table S4).

For all samples, powdered enamel was analysed between 400 and 4,000 cm<sup>-1</sup> by Fourier Transform Infrared spectroscopy with Attenuated Total Reflectance (FTIR-ATR – Agilent Technologies Cary 640 FTIR with GladiATR™ from Pike Technologies). Each sample was measured three times. The background was subtracted and a baseline correction was carried out using Agilent Resolution Pro software. The baselines of the spectra were normalised and all three spectra of each sample were averaged before calculation of the various infrared indices. To ensure better reproducibility of the measurements, only spectra with a minimum absorbance of 0.06 for the highest phosphate band at ~1035 cm<sup>-1</sup> were taken into account. The reproducibilities of the indices BPI, API, BAI, and PCI are  $\pm 0.01$ ,  $\pm 0.004$ ,  $\pm 0.1$  and  $\pm 0.1$ , respectively.

#### *Stable carbon and oxygen isotope analysis of human and faunal tooth enamel*

A single human tooth from Layer 7c was sampled, with associated fauna ( $n=17$ ), for stable carbon and oxygen isotope analysis (SOM Fig. S1, SOM Table S5). Sixteen further human teeth were sampled from Layers 7a/6b and 6b, alongside a further 21 faunal specimens from the 1980s excavations of Batadomba-lena that span Layers 7c, 7b, 7a, and 6 (SOM Table S5) (Deraniyagala, 1992; Perera, 2010). Two human teeth from Layers 7a/6b and three from Layer 6b were subjected to sequential analysis (SOM Tables S5 and S6). To avoid any possible influence of nursing effects, later-maturing teeth were preferred, with a focus on second or third molars (Hillson, 1996) (SOM Table S5).

These data complement previous bulk  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  faunal data from Layers 6, 5 and 4, and human  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from Layer 6b, at Batadomba-lena (Roberts et al., 2015a) (SOM Table S6). We also performed sequential analysis on human teeth previously bulk-sampled by Roberts et al. (2015a) from Fa Hien-lena (Wet Zone) ( $n=1$ ) and Balangoda Kuragala (Intermediate Zone) ( $n=2$ ) in order to assess intra-tooth variability during the Terminal-Pleistocene/Early Holocene period (SOM Table S6). Sequential analysis of two *Elephas* sp., two *Sus scrofa*, and three *Cervus unicolor* individuals from Balangoda Kuragala was also undertaken (SOM Table S6).

All faunal enamel specimens analysed from Batadomba-lena were identified to genus and species in previous publications and reports by Jude Perera using the substantial reference collections of the Natural History Museum, Sri Lanka, the Department of Archaeology, Government of Sri Lanka, the Postgraduate Institute of Archaeology, Sri Lanka, and personal collections of Jude Perera (Perera, 2010; Perera et al., 2011) (SOM Tables S5 and S6). The feeding and drinking preferences of these taxa are listed in SOM Table S7. Jude Perera and Jay Stock, University of Cambridge, identified the Batadomba-lena enamel specimens as human on the basis of fossil reference collections (per Roberts et al., 2015a) (SOM Table S5). All human and faunal teeth sampled are currently held by the Department of Archaeology, Government of Sri Lanka, Colombo.

Teeth or tooth fragments were cleaned using air-abrasion to remove any adhering external material. Enamel powder was obtained using gentle abrasion with a diamond-tipped drill along the full length of the buccal surface or fragment in order to maximize the period of formation represented by the resulting isotopic analysis for bulk samples. For sequential samples, each sample was a 1–2 mm-wide groove perpendicular to the tooth growth axis, through the thickness of the enamel layer. The distance of each sample from the enamel/root junction from the furthest sample margin was recorded. Given the smaller size of the human

teeth, four samples were taken along the buccal surface. While this resolution is low relative to laser-ablation studies (Sponheimer et al., 2006b; Lee-Thorp et al., 2010), this method should provide preliminary insight into potential dietary and drinking variability throughout the period of formation.

Enamel powders were pre-treated using a protocol to remove any organic or secondary carbonate contaminants. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H<sub>2</sub>O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H<sub>2</sub>O (per Sponheimer et al., 2005; Lee-Thorp et al., 2012). Following reaction with 100% phosphoric acid, gases evolved from the samples were analysed to stable carbon and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Division of Archaeological, Geographic and Environmental Sciences Bradford University. Carbon and oxygen isotope values were compared against an International Atomic Energy Agency (NBS 19) and in-house standard (MERCK). Replicate analysis of OES standards suggests that machine measurement error is *c.*  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.2\text{‰}$  for  $\delta^{18}\text{O}$ .

### *Statistical analysis*

Analysis of variance (ANOVA) followed by post-hoc Tukey pair-wise comparisons were performed for each of the main FTIR indexes of enamel apatite (PCI, PO<sub>4</sub>RF, BPI, API, and WAMPI –per Roche et al., 2010 and defined in SOM Table S3) across the sample groups (i.e. fossil fauna, modern fauna, fossil humans, modern humans) in order to determine statistical differences in enamel crystallinity and structure between fossil and modern samples.

The ANOVAs were performed on the new, and existing, faunal enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from Batadomba-lena, as well as the bulk data obtained from the Terminal Pleistocene-Holocene sites of Fa Hien-lena and Balangoda Kuragala by Roberts et al. (2015a), to determine the influence of species and stratigraphic layer on isotopic variation at each site. Where variance was found to be significant, this was combined with a post-hoc Tukey pair-wise comparison to determine which taxa or stratigraphic layers were significantly different from each other in terms of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ . At each site, at least two of the three Sri Lankan primate species – toque macaque (*Macaca sinica*), grey crested langur (*Semnopithecus priam thersites*) and the purple-faced leaf monkey (*Trachypithecus vetulus*) were identified. The ANOVAs and post-hoc Tukey pair-wise comparisons were repeated separately on new and existing (SOM Tables S5 and S6)  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  for each monkey species by layer in order to study differences in the responses of these primate taxa to potential environmental changes through time at Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala.

The significance of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  variation between the Late Pleistocene faunal dataset from Batadomba-lena and the Terminal Pleistocene and Holocene faunal datasets from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa (Dry Zone), was determined using ANOVA comparative tests, followed by post-hoc Tukey pair-wise comparisons to determine which sites were significantly different from each other in terms of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ . The relationship between faunal and human  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  at Batadomba-lena was assessed using paired t-tests.

The statistical validity of the ecological distinction between fauna from Balangoda Kuragala with  $\delta^{13}\text{C}$  values above and below -10.0‰, observed during ANOVA testing, was further tested using a quadratic Discriminant Function analysis with Jackknifed reclassification in the free Software R, to check the predictive power and accuracy of dividing the Balangoda

Kuragala dataset into an ‘Intermediate’ forest group and an ‘Open’ group on the basis of both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ .

All  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  datasets were tested for normality using the Shapiro-Wilk test and histogram observations. Where found to be non-normal, a Mann-Whitney U or Kruskal-Wallis test was applied in addition to the tests listed above. In all cases the results of the parametric and non-parametric tests supported each other. We consequently report only the results of the t-tests, ANOVAs and, where relevant, post-hoc Tukey pair-wise comparisons for consistency across the datasets. All statistical analyses were conducted using the free program R software (R Core Team, 2013).

## **Results**

### *FTIR*

Full results of the infrared indices of samples subjected to FTIR analysis are shown in SOM Table S8. All of the fossil and modern enamel samples displayed classic enamel FTIR spectra (SOM Fig. S2). No additional bands from secondary carbonate (e.g. calcite at  $710\text{cm}^{-1}$  – Farmer, 1974) were observed in the spectra of the fossil samples. ANOVA and post-hoc Tukey pair-wise comparison showed no significant difference in B-site carbonation between modern faunal and fossil faunal groups, with the exception of fauna from the 1980s Batadomba-lena excavations ( $p < 0.05$ ) (SOM Fig. S3; SOM Tables S9–S10). The same is true of PCI, with the exception of the Bellan-bandī Palassa sample ( $p < 0.05$ ) (SOM Tables S11–S12). Fossil human enamel demonstrates increased PCI relative to the modern human group ( $p < 0.05$ ), but no significant differences in terms of A-site carbonation ( $p > 0.05$ ) (SOM Tables S13–S14), B-site carbonation ( $p > 0.05$ ), dehydration/organic decay (WAMPI) ( $p > 0.05$ ) (SOM Tables S15–S16), or B-site/A-site carbonation ratio (BAI) ( $p > 0.05$ ) (SOM Tables S17–S18).



Some significant crystal-chemical variations are present among the sample groups, however (SOM Fig. S3). Fossil mammalian enamel demonstrates A-site de-carbonation ( $p<0.05$ ) (SOM Tables S13–14), dehydration and organic decay (lower WAMPI) ( $p<0.05$ ) (SOM Tables S15–S16), and higher BAI ( $p<0.05$ ) (SOM Tables S17–18) relative to modern mammal samples, as observed elsewhere (Sponheimer, 1999; Roche et al. 2010). A loss of water organic content (as indicated by WAMPI) is expected over multi-millennial time-scales, particularly in tropical areas with limited organic preservation. Given API and WAMPI reduction, alongside BPI stability, in fossil mammal samples, the primary mechanism of BAI change in this instance is likely endogenous carbonate loss at A-sites linked to organic degradation (Sponheimer, 1999; Roche et al., 2010).

Poor preservation of skeletal material has been highlighted elsewhere for tropical rainforest environments, though primarily in terms of organic bone material (Tappen, 1994). The fossil enamel FTIR spectra produced here are virtually indistinguishable from modern spectra (SOM Fig. S4). The precipitation of carbonate minerals is likely to be more of a problem in the context of more porous materials such as dentine and bone (Lee-Thorp and van der Merwe, 1991; Michel et al., 1996; Sponheimer, 1999). Subtle differences noted in faunal enamel apatite during fossilization, including increased BAI, decreased WAMPI, and decreased A-carbonate on phosphate index, appear to be linked to the reduction in organic material within the apatite matrix through time. Such change is not considered to have major impacts on overall enamel apatite structure or stable carbon and oxygen isotope measurements from enamel (Sponheimer, 1999; Roche et al., 2010).

#### *Stable carbon and oxygen isotope results from Batadomba-lena*

The full dataset of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements of humans and fauna from Batadomba-lena is shown in Fig. 3, Table 1 and SOM Table S19. The fauna identified at Batadomba-lena is

characteristic of the Wet Zone rainforest of Sri Lanka (Table 1, SOM Table S7). The  $\delta^{13}\text{C}$  range of the measured samples (-17.8 to -9.5‰) (mean=-14.1‰) supports this and, when compared to published modern faunal data (Cerling et al., 2004; Levin et al., 2008), is indicative of closed-canopy forest conditions with some elements of open  $\text{C}_3$  vegetation or  $\text{C}_3$  open/forest mosaics. The mean  $\delta^{13}\text{C}$  values of *T. vetulus* ( $-14.6 \pm 1.2\text{‰}$ ) and *Hystrix indica* ( $-14.9 \pm 1.3\text{‰}$ ) occupy the lower end of this spectrum, while *Parradoxurus* sp. ( $-12.4 \pm 0.4\text{‰}$ ), *Tragulus meminna* ( $-11.7\text{‰} \pm 0.2\text{‰}$ ), and the *Petinomys fuscocapillus* ( $-10.6\text{‰}$ ) and *Muntiacus muntjak* ( $-12.0\text{‰}$ ) individuals, demonstrate relatively higher  $\delta^{13}\text{C}$  values. The generalist *Ratufa macroura* also has higher mean  $\delta^{13}\text{C}$  ( $-12.3 \pm 2.5\text{‰}$ ), while the primate dietary generalist *M. sinica* sits towards the lower end of the site's range ( $-14.1 \pm 0.9\text{‰}$ ).

Fig. 3 about here

Table 1 about here

An ANOVA test confirms that species significantly influences  $\delta^{13}\text{C}$  but a post-Hoc Tukey pair-wise comparison fails to draw out any species as significantly different from each other ( $F(8,84)=5.160, p<0.05$ ) (SOM Tables S20 and S21). *Rattus* sp., which may be indicative of local cave conditions rather than a focus of human hunting, has a mean  $\delta^{13}\text{C}$  of  $-15.0 \pm 0.6\text{‰}$ . The range of  $\delta^{18}\text{O}$  at Batadomba-lena (-6.8 to -1.3‰) (Fig. 3) is smaller than that reported at Sri Lankan Terminal Pleistocene and Holocene sites (Roberts et al., 2015a) and ANOVA testing followed by post-Hoc Tukey suggest that species differences do not impact  $\delta^{18}\text{O}$  variation at the site ( $F(8,84)=1.501, p>0.05$ ) (SOM Tables S22 and S23).

The ANOVA indicates that stratigraphic layer plays a role in  $\delta^{13}\text{C}$  variation at Batadomba-lena. When  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  are plotted by stratigraphic layer, variation is visually greater in Layer 7c (Fig. 4). However, post-hoc Tukey pair-wise comparison fails to draw out any

layers as distinctively different from each other in terms of  $\delta^{13}\text{C}$  ( $F(5,84)=2.456$ ,  $p>0.05$ ) (SOM Tables S20–S21). By contrast, ANOVA testing and post-Hoc Tukey pair-wise comparisons in  $\delta^{18}\text{O}$  demonstrate that Layer 7c is distinct from Layers 7b, 5 and 4 ( $F(5,84)=6.356$ ,  $p<0.05$ ) (SOM Tables S22 and S23).

Fig. 4 about here

T-tests demonstrate that *H. sapiens* samples from Batadomba-lena have higher  $\delta^{13}\text{C}$  (mean  $-12.7 \pm 0.5\text{‰}$ ) ( $df=119$ ,  $t=-5.012$ ,  $p<0.05$ ) and  $\delta^{18}\text{O}$  (mean  $-3.1 \pm 0.9\text{‰}$ ) ( $df=119$ ,  $t=-2.707$ ,  $p<0.05$ ) than the associated fauna. Sequential analysis shows no perceptible shift in either  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$  during the period of enamel formation for individuals from Layer 6b (Fig. 5) ( $c.$  20-17,000 cal. years BP) (SOM Table S24). When compared to modern and fossil primate datasets (Lee-Thorp et al., 1989a; Nelson, 2003, 2007, 2013; Sponheimer et al., 2006a; Bocherens et al., 2015), the Batadomba-lena human  $\delta^{13}\text{C}$  range ( $-14.9$  to  $-12.2\text{‰}$ ) is indicative of reliance on closed-canopy  $\text{C}_3$  resources and  $\text{C}_3$  forest resources/forest-open  $\text{C}_3$  mosaics. However, given that hominins tend to utilise  $\text{C}_4$  grassland resources where they are available (and the presence of more open vegetation is indicated by  $\delta^{13}\text{C}$  as low as  $-9\text{‰}$  in Layer 7c – Fig. 4) their restriction here to the lower end of the  $\text{C}_3$  scale suggests a reliance on closed and slightly open forest environments, akin to those found in the ‘Wet’ and ‘Intermediate’ rainforests of Sri Lanka today. The earliest human fossil in this study, from Layer 7c  $c.$  36-29,000 cal. years BP, has a  $\delta^{13}\text{C}$  value ( $-14.9\text{‰}$ ) that documents reliance on resources influenced by the “canopy effect”.

Fig. 5 about here

*Statistical analyses and human and faunal sequential analyses from Fa Hien-lena and Balangoda Kuragala*

The fauna identified at Fa Hien-lena (~12,000–8,000 cal. years BP) is characteristic of the modern day ‘Wet Zone’ rainforests of Sri Lanka (SOM Tables S4 and S7) (Roberts et al., 2015a). This is supported by the  $\delta^{13}\text{C}$  range of the faunal tooth enamel at this site (-17.8 to -13.2‰) that demonstrates the influence of the “canopy effect” (SOM Figure S4). An ANOVA of  $\delta^{13}\text{C}$  by layer and species, followed by post-Hoc Tukey pair-wise comparison, suggests that species does impact on  $\delta^{13}\text{C}$ , but draws out only *T. vetulus* as being distinct from *M. sinica* and *Paradoxurus* sp. ( $F(9,66)=6.191$ ,  $p<0.05$ ) (SOM Tables S25 and S26). No distinctions were found in terms of  $\delta^{18}\text{O}$  (SOM Table S27 and S28) ( $p>0.05$ ).

The fauna identified at Balangoda Kuragala (~15,000–3,000 cal. years BP) is characteristic of a range of habitats, from closed forest to more open grassland and shrubland (SOM Table S7) (Roberts et al., 2015a). The range in  $\delta^{13}\text{C}$  of the fauna (-15.7 to -3.3‰) is consistent with this habitat variability (SOM Fig. S5). When compared to modern faunal datasets (Cerling and Harris, 1999; Cerling et al., 2004; Sponheimer et al., 2006a; Levin et al., 2008), the lowest end of the Balangoda Kuragala faunal range, with  $\delta^{13}\text{C}$  values c. -15.7 to -14.0‰ and dominated by primate taxa, is indicative of the influence of closed forest conditions. Fauna from -14.0 to -11.0‰ either represent dietary reliance on more open forest conditions, akin to that of the modern ‘intermediate’ rainforest, or the use of a mosaic of closed and open  $\text{C}_3$  environments. Values from -10.0 to -3.0‰ likely represent variable contributions of  $\text{C}_4$  plants, from open tropical grasslands, to animal diets. The large range of  $\delta^{18}\text{O}$  at Balangoda Kuragala (-9.0 to -1.7‰) seems to follow this dietary variability, with fauna consuming  $\text{C}_4$  foodstuffs having  $\delta^{18}\text{O}$  towards the higher end of the range, perhaps as a result of feeding and drinking in more open settings.

$\delta^{13}\text{C}$  values between -12.0 to -11.0‰ would not be out of place in a mixed forest/woodland/‘savannah’  $\text{C}_3$  environment (e.g. Sponheimer et al., 2006a; Levin et al.,

2008). However, on the basis of individuals identified to species with  $\delta^{13}\text{C}$  values between -15.7 and -11.0‰, the most parsimonious interpretation is that they represent a forest structure similar to the ‘intermediate’ rainforest observed in modern Sri Lanka. The taxa with values between -10.0 and -3.0‰, by contrast, include solely *Elephas* sp., *C. unicolor*, *S. scrofa* and *L. nigricollis* that are known to prefer feeding in more open settings. While *C. unicolor* and *S. scrofa* also occur in the -15.7 and -11.0‰ range, here they are accompanied by primates, rodents, semi-arboreal small mammals, and small ungulates all known to prefer forest foraging. The ‘Intermediate rainforest and ‘Open’ division is also visible in the quadratic Discriminant Function Analysis that correctly predicted the placement of all 120 Balangoda Kuragala individuals into a ‘Forest’ and ‘Open’ group (SOM Table S29). However, it should be borne in mind that such an analysis is biased by the categories placed into the model.

Further supporting this distinction, ANOVA and post-hoc Tukey pair-wise comparison of  $\delta^{13}\text{C}$  by species at Balangoda Kuragala draws out species present in this ‘Open’ group, including *Elephas* sp., *C. unicolor*, *L. nigricollis* and *S. scrofa*, as distinct from other taxa ( $F(16,94)=16.272$ ,  $p<0.05$ ), though not for  $\delta^{18}\text{O}$  ( $F(16,94)=1.975$ ,  $p>0.05$ ) (SOM Tables S30-S33). Similarly, sequential analysis indicates that in no case do members of the ‘Open’ group (based on bulk analysis in Roberts et al., 2015a) cross into the ‘Forest’ group. (SOM Table S34) (Fig. 6). *Elephas* sp. sample BK 130  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values ( $\delta^{13}\text{C}=-8.8$  to  $-5.7$ ‰;  $\delta^{18}\text{O}=-4.2$  to  $-2.5$ ‰) indicate varied diet and water sources over the period of enamel formation. *Elephas* sp. sample BK 144 by contrast demonstrates relatively consistent ‘Open’  $\delta^{13}\text{C}$  ( $-8.0$  to  $-7.0$ ‰) and  $\delta^{18}\text{O}$  ( $-3.2$  to  $-2.1$ ‰) values. The *S. scrofa* specimens have relatively stable  $\delta^{13}\text{C}$  values (BK 121= $-12.3$  to  $-11.6$ ‰; BK 97= $-11.5$  to  $-9.3$ ‰), although BK 97 shows a trend towards lower  $\delta^{13}\text{C}$  through time. Two *C. unicolor* individuals from the ‘Open’ group demonstrate variable  $\delta^{13}\text{C}$  sequences (BK 37= $-6.8$  to  $-4.1$ ‰; BK 94= $-7.5$  to  $-1.0$ ‰). By contrast the ‘Forest’ *C. unicolor* demonstrates a more stable  $\delta^{13}\text{C}$  signal.

Fig. 6 about here

Statistical analyses of the Fa Hien-lena and Balangoda Kuragala faunal isotope data indicate stability in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  across the Terminal Pleistocene-Holocene boundary. At Fa Hien-lena, ANOVA testing and post-hoc Tukey pair-wise comparison draws out only Layers 248 and 247 as being distinct in  $\delta^{13}\text{C}$  ( $F(9,66)=4.620$ ,  $p<0.05$ ) and  $\delta^{18}\text{O}$  ( $F(9,66)=73.429$ ,  $p<0.05$ ) (SOM Tables S25-28). Similarly, ANOVA testing and post-hoc Tukey comparison draws out Layer 32 as distinct in  $\delta^{13}\text{C}$  ( $F(9, 94)=7.582$ ,  $p<0.05$ ) and Layer 16 in  $\delta^{18}\text{O}$  ( $F(9,94)=4.121$ ,  $p<0.05$ ) compared to all layers at Balangoda Kuragala (SOM Tables S30-33).

Sequential analysis of the human tooth (~12,000 cal. years BP) from Fa Hien-lena shows no fluctuation in  $\delta^{13}\text{C}$  (-15.7 to -14.6‰) and  $\delta^{18}\text{O}$  (-5.6 to -4.2‰) during formation, indicating a uniform reliance on closed canopy resources (Fig. 5) (SOM Table S35). At Balangoda Kuragala, individuals BKH 19 and BKH 21 from Layers 6 and 7 (c. 6,000-5,000 cal. years BP) show no fluctuations in  $\delta^{13}\text{C}$  (BKH 19= -14.4 to -13.3‰; BKH 21= -14.8 to -13.4‰) and  $\delta^{18}\text{O}$  (BKH 19= -8.6 to -8.1‰; BKH 21= -5.3 to -4.7‰) during the period of tooth formation, despite  $\text{C}_4$  resources from open settings being evident in the high  $\delta^{13}\text{C}$  for the *Elephas* sp., *L. nigricollis* and *C. unicolor* individuals in the ‘Open’ group (SOM Table S35). As at Batadomba-lena, human  $\delta^{13}\text{C}$  values at Balangoda Kuragala (-14.0 to -12.0‰) most likely reflect a reliance on more open tropical forest resources akin to those found in the Intermediate Zone of Sri Lanka today.

#### *Fossil primate $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$*

At Fa Hien-Lena, Balangoda Kuragala, Bellan-bandī Palassa (c. 12,000 cal. years BP – Roberts et al., 2015a) and Batadomba-lena there is consistently more than one of the primate

species, *M. sinica*, *S. priam thersites*, and *T. vetulus*, present (Fig. 7). Only in one instance, however, is a statistically significant distinction observed between taxa in either  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$ . Fig. 7 shows that at Fa Hien-lena *T. vetulus* has lower  $\delta^{13}\text{C}$  values (mean=  $-16.3 \pm 0.9\text{‰}$ ) than *M. sinica* (mean=  $-14.9 \pm 0.8\text{‰}$ ). This was confirmed by an ANOVA test and post-hoc Tukey pair-wise comparison ( $F(9,74)=6.191$ ,  $p<0.05$ ) (SOM Tables S25 and S26). By contrast, no obvious  $\delta^{18}\text{O}$  distinction is observable between the species, as confirmed by ANOVA testing (SOM Tables S27 and 28) ( $p>0.05$ ).

Fig. 7 about here

At Balangoda Kuragala, where *M. sinica* and *S. priam thersites* were present, no distinction in either  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$  was found during ANOVA testing (SOM Tables S30-33) ( $p>0.05$ ). No  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$  distinctions were found between *M. sinica*, *S. priam thersites*, and *T. vetulus*, at Bellan-bandi Palassa (SOM Tables S31 and S33) ( $p>0.05$ ), nor between *M. sinica* and *T. vetulus* in the Late Pleistocene sequence at Batadomba-lena (SOM Tables S20-S23) ( $p>0.05$ ). The  $\delta^{13}\text{C}$  values of *T. vetulus* individuals at Bellan-bandi Palassa ( $-14.8$  to  $-9.5\text{‰}$ ) and Batadomba-lena (range=  $-17.0$  to  $-10.9\text{‰}$ ) are, however, consistently higher and more variable, respectively, compared to individuals of the same species at Fa Hien-lena ( $-17.8$  to  $-14.1\text{‰}$ ).

At Fa Hien-lena, ANOVA and subsequent post-hoc Tukey pair-wise comparison indicates statistical differences among stratigraphic layers for *T. vetulus*  $\delta^{18}\text{O}$  ( $F(8,17)=5.748$ ,  $p<0.05$ ) (SOM Tables S38-39), but not  $\delta^{13}\text{C}$  ( $p>0.05$ ) (SOM Table S40). Lower  $\delta^{18}\text{O}$  values in the oldest part of the Fa Hien-lena sequence are also observed in the faunal assemblage as a whole. Similarly, *S. priam thersites*  $\delta^{18}\text{O}$  demonstrates some structuring by stratigraphic layer ( $F(8,18)=4.198$ ,  $p<0.05$ ), with members of this primate species from Layers 16 and 8 being distinct from each other (SOM Tables S41–S42), as was also indicated in the overall faunal

dataset from Balangoda Kuragala ( $F(9,94)=4.121, p<0.05$ ). These trends were not observed for *M. sinica* at the same sites (SOM Tables S44–S47) ( $p>0.05$ ).

## ***Discussion***

### *Human tropical forest resource reliance in Sri Lanka 36,000-3,000 cal. years BP*

$\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of fauna from the sites of Fa Hien-lena and Balangoda Kurgala (and Bellan-bandī Palassa) indicate that an environmental spectrum persisted across the Wet, Intermediate, and Dry Zones of Sri Lanka during the Terminal Pleistocene and Holocene (Fig. 8). Low faunal  $\delta^{13}\text{C}$  at Fa Hien-lena is indicative of a predominance of closed canopy tropical forest in the Wet Zone, while varied  $\delta^{13}\text{C}$  at Balangoda Kuragala and Bellan-bandī Palassa (Roberts et al., 2015a) indicates a mixture of closed  $\text{C}_3$  forest, open  $\text{C}_3$  forest, open  $\text{C}_3$  environments and varying presence of  $\text{C}_4$  resources in the vicinity of the Intermediate and Dry Zone sites. On the basis of faunal ecological preferences and comparison of the  $\delta^{13}\text{C}$  with existing modern stable isotope datasets, these data likely indicate the presence of ‘Wet Zone’ closed rainforest and more open ‘intermediate’ rainforest, seen in these two zones today, during the Terminal Pleistocene–Holocene.

Fig. 8 about here

When the whole Batadomba-lena Wet Zone dataset is compared to the Wet Zone record from Fa Hien-lena, it is clear that fauna excavated from the Wet Zone has higher  $\delta^{13}\text{C}$  ( $F(3,326)=48.848, p<0.05$ ) and  $\delta^{18}\text{O}$  ( $F(3,326)=15.406, p<0.05$ ) between ~36-29,000 to 12,000 cal. years BP than it does during the Terminal Pleistocene-Holocene (SOM Tables S48–S51). In Layer 7c, at 36–29,000 cal. years BP, there is variation in faunal  $\delta^{13}\text{C}$  exploited by humans at this site, suggesting the presence of some open clearings or open habitats in the vicinity. Nevertheless, the oldest human individual sampled for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from this layer



indicates a reliance on closed tropical forest resources (Fig. 8) despite open habitats being available. Human specimens from Layers 6b and 6b/7a sampled in this study, and by Roberts et al. (2015a), indicate a persistence of this reliance through the LGM, with an increasing preference for slightly more open tropical forest resources similar to those seen in the ‘intermediate’ rainforests of Sri Lanka today.

This reliance on closed and more open (‘intermediate’) tropical forest resources continues in the Terminal Pleistocene–Holocene sequences of Fa Hien-lena and Balangoda Kuragala, right up until the onset of the Iron Age in Sri Lanka c. 3,000 cal. years BP (Deraniyagala, 1992, 2007; Roberts et al., 2015a). As at Batadomba-lena, Fa Hien-lena and Balangoda Kuragala, the stability of this reliance is evident from intra-tooth  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  of human teeth sampled sequentially. The only two human individuals to show an ‘open’/C<sub>4</sub>  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  signature come from ~3,000 cal. years BP, suggesting the contribution of open resources, perhaps in the form of C<sub>4</sub> crops, with the emergence of agriculture in the region. However, even then, a number of human individuals from the same period maintain a reliance on C<sub>3</sub> rainforest resources (Fig. 8), implying a complex shift to farming in this rainforest ecology, as has been documented elsewhere in South Asia (Roy, 2009, 2011, 2012) and Southeast Asia (Krigbaum, 2003, 2005).

*Climate and vegetation change in Sri Lanka at the LGM and across the Terminal Pleistocene-Holocene boundary*

Batadomba-lena faunal  $\delta^{13}\text{C}$  indicates more variable faunal diets in the Wet Zone at 36–29,000 cal. years BP including use of open habitats or forest clearings. Batadomba-lena faunal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  is higher across the period 36–29,000 to 12,000 cal. years BP than Fa Hien-lena faunal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from the Terminal Pleistocene–Holocene transition (Fig. 8). This elevated  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  suggests that the tropical forests of the Wet Zone of Sri Lanka

were more open during this period. Decreased canopy coverage and changes in tropical forest structure have been noted in Africa, Melanesia, and Southeast Asia at this time, and has been linked to decreased precipitation, decreased temperature, and increased atmospheric CO<sub>2</sub> concentrations during the LGM (e.g. Mercader et al., 2000; Thompson et al., 2000; Dupont et al., 2000; Denham and Haberle, 2008; Haberle et al., 2012). The data presented here confirm previous suggestions that the extent and nature of Sri Lanka's rainforests fluctuated during the Late Pleistocene (Boivin et al., 2013).

By contrast, statistical analyses of faunal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from the Terminal Pleistocene-Holocene sequences of the Wet Zone site of Fa Hien-lena and Intermediate Zone site of Balangoda Kuragala suggest that the extent of these boundaries may have changed little over the past 12,000 years. While there may have been some subtle changes within the sequences, for the most part the extent and vegetation structure of the Wet Zone, Intermediate Zone, and Dry Zone, or at least closed canopy C<sub>3</sub> tropical forest to more open C<sub>3</sub> tropical forest-open C<sub>3</sub> habitat mosaics, remained remarkably stable across this period. This may suggest that the extent of the 'Wet Zone' rainforest in Sri Lanka recovered following the LGM, at around 12,000 cal. years BP, at the same time as has been argued in Southeast Asia (Bird et al., 2005; Rabett, 2012), Africa (Dupont et al., 2000; Mercader et al., 2000), and certain parts of Australasia (Fairbairn et al., 2006).

The stable isotope evidence presented here is consistent with existing palaeoenvironmental records from Sri Lanka. The pollen record from the Horton Plains highlands, although greatly separated from the locales of relevance to human occupation discussed here, characterises the period of the LGM (24,000–18,500 cal. years BP) as progressively cooler and drier with significant grassland encroachment (Premathilake and Risberg, 2003; Premathilake, 2006, 2012; Premathilake and Gunatilaka, 2013). Relatively stable forest expansion occurs between 16,000 and 8,700 cal. years BP prior to a slow trend towards semi-arid conditions in this

high-altitude region into the Middle Holocene. It has been suggested that changes in vegetation during these periods, as a result of changes in the Indian Ocean Monsoon would have greatly affected the resources available to human populations in Sri Lanka (Premathilake, 2012). Micromorphological analysis from the Wet Zone rockshelter site of Kitulgala Beli-lena also demonstrates broadly corresponding trends of precipitation intensity (Kourampas et al., 2009). Therefore, although archaeological faunal assemblages can represent anthropogenic influence, in this instance their enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  signatures seem to provide a reliable indicator of regional vegetation and climate.

*Primate niches and human hunting strategies in the Sri Lankan Microlithic tradition*

*Trachypithecus vetulus* has lower  $\delta^{13}\text{C}$  values than *M. sinica* at the site of Fa Hien-lena. Given what we know about the digestive tract of the former (Hladik, 1977) and generalist diet of the latter (Dittus, 1977), this could be linked to an increased focus on leaf consumption in *T. vetulus* versus *M. sinica* (SOM Table S7). At the Polonnaruwa Nature Sanctuary and Archaeological Reserve in northern Sri Lanka, where all three species are sympatric, long-term observational data demonstrate that *T. vetulus* is a specialised folivore, obtaining 70% of its food from the mature leaves of three species (Hladik, 1977). *Semnopithecus priam thersites*, in contrast, obtains ~ 70% of its food from 10 tree species, including in its diet 48% leaves, 7% flowers, and 45% fruits by wet weight (Hladik, 1977). The generalist *M. sinica* exploited 89% of the 46 species of trees within the Reserve, with fruits constituting over 70% of their diet, alongside flowers, leaves, mushrooms, fungi, grasses, roots, tubers, resins and invertebrates (Dittus, 1977).

The fact that the  $\delta^{18}\text{O}$  of *T. vetulus* tracks the overall faunal trends in  $\delta^{18}\text{O}$  at this site may provide further confirmation of its folivorous niche. Nevertheless, the isotope distinction between *T. vetulus* and *M. sinica* in  $\delta^{13}\text{C}$  at Fa Hien-lena could also be the result of the

former feeding in more shaded forest areas/parts of the canopy. Where both species are present at Bellan-bandī Palassa and Batadomba-lena, there is no distinction between them in  $\delta^{13}\text{C}$ . What is of greater interest is the fact that this supposedly specialised folivore, *T. vetulus*, is making use of more varied and more open habitats at Batadomba-lena ( $\delta^{13}\text{C}$  range= -17.0 to -10.9‰) and Bellan-bandī Palassa (( $\delta^{13}\text{C}$  range= -14.8 to -9.5‰), respectively, relative to the apparently focused, closed canopy diets of this species at Fa Hien-lena (-17.8 to -14.1‰ (-16.3 $\pm$ 1.0‰)). This suggests Late and Terminal Pleistocene dietary flexibility in this primate species that is also evident now among its subspecies in modern contexts of agricultural expansion (Dela, 2012).

On the basis of existing primate isotope literature, it would have been expected that *T. vetulus*, a non-obligate drinker that feeds high in the canopy (Hladik, 1977), would have higher  $\delta^{18}\text{O}$  values than the semi-terrestrial non-obligate drinker *S. priam thersites* and the semi-terrestrial obligate drinker *M. sinica* (Dittus, 1977; Fooden, 1979; Cerling et al., 2004; Krigbaum et al., 2013; Carter and Bradbury, 2015). However, we see no distinction between primate taxa at any of the sites in  $\delta^{18}\text{O}$ . At Fa Hien-lena, *M. sinica* and *T. vetulus* have very similar  $\delta^{18}\text{O}$  ranges. This, and the above interpretation of  $\delta^{13}\text{C}$ , highlights the main problem – equifinality –with detailed primate niche reconstructions on the basis of stable isotope analysis, in the absence of modern observation data. Elevated  $\delta^{18}\text{O}$  could simultaneously result from *M. sinica* drinking from open, evaporative water sources on the ground (Fooden, 1979; Dittus, 1984) and *T. vetulus* being a non-obligate drinker obtaining the majority of its water from foliage (Cerling et al., 2004; Krigbaum et al., 2013).

In the case of the Sri Lankan Microlithic tradition, the basic zooarchaeological identification of these monkey species, with known ecological distinctions in the present, provides a better indication of human hunting strategies. Modern observations suggest that the capture of *T.*

*vetulus* would necessitate projectile technologies to shoot this species from high in the canopy and traps to capture the semi-arboreal and highly mobile *M. sinica*. Interestingly, preliminary contextual analyses of the Microlithic tradition bone tool points suggest that they may have been used as part of traps for small-medium, semi-arboreal prey (Perera et al., 2017) while the presence of the nocturnal *H. indica* and *Paradoxurus* sp. in the assemblages may also imply some form of virtual trapping technique. Although no direct use-wear analysis has been undertaken on the Sri Lankan specimens, microlith stone technologies have been linked with projectile hunting (Shea and Sisk, 2010), likely necessary for the frequent capture of *T. vetulus*.

## **Conclusion**

Late Pleistocene evidence for human exploitation of Sri Lanka's tropical forests adds to the growing body of evidence for early occupation and adaptation to the world's rainforests by at least 45,000 years ago (Mercader, 2002a; Barker et al., 2007; Summerhayes et al., 2010; Roberts and Petraglia, 2015). Thus far, evidence from Southeast Asia and Melanesia has demonstrated that human groups used rainforest resources (Barker et al., 2007; Summerhayes et al., 2010) but zooarchaeological, archaeobotanical, and technological snapshots have so far been unable to determine the overall reliance of these populations on rainforest habitats. The stable carbon and oxygen isotope data from the rich human, and associated faunal, fossil sequences in Sri Lanka demonstrate that humans here not only used tropical forest resources between 36–29,000 and 3,000 cal. years BP, but they also specialised in the exploitation of these resources for their subsistence. The presentation of stable isotope sequences from humans, rather than just bulk data, confirms this by highlighting a persistent use of forest resources, rather than a mixture of deep forest and open resource usage.

Tropical forest specialisation appears to have been aided by relatively limited fluctuation in the extent and nature of Sri Lanka's tropical forests over the past ~ 36–29,000 years.

Although stable isotope evidence from faunal tooth enamel suggests that the forests in the Wet Zone of the island were more open ~36–29,000 to 12,000 cal. years BP, humans maintained a reliance on tropical forest resources at this time, despite the existence of open habitats, albeit with a focus on more open ‘intermediate’ tropical forest resources. Following an expansion of the dense forest between ~12,000 cal. years BP, the Wet Zone, Intermediate Zone, and Dry Zone climatic and vegetation boundaries appear to have then remained stable across the Terminal Pleistocene–Holocene transition. Although the arrival of agriculture in the rainforest of Sri Lanka, during the Iron Age, ~3,000 cal. years BP, brought with it the first significant human use of resources from more open areas, many foragers retained a reliance on tropical forest resources at this time.

The stable isotope data align with existing archaeological evidence for early and stable microlith technologies, bone toolkits, and rainforest animal and plant use in Sri Lanka, from the earliest arrival of humans in the Wet Zone of the island. In particular, a focus on three primate taxa, *M. sinica*, *S. priam thersites* and *T. vetulus*, appears to have provided a consistent source of protein from these tropical forest environments. Although stable isotope analysis has not been able to refine the past niches of these species, it is highly likely that diverse hunting strategies would have been necessary in order to obtain large numbers of these taxa, perhaps including trapping and projectiles (Perera et al., 2017). Future systematic use-wear analyses of these technologies should provide further insight into their function. Regardless, it is clear that the Microlithic tradition of Sri Lanka represents an early and stable specialisation of our species in the exploitation of the fauna and flora of South Asia’s tropical forests. Future research, using the approaches outlined here, should hopefully also be able to clarify when humans first became specialised users of rainforests in Africa as well as Island and Mainland Southeast Asia.

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## Figure captions

Fig. 1. The location of key archaeological sites (1. Batadomba-lena, 2. Fa Hien-lena, 3. Balangoda Kuragala, 4. Bellan-bandi Palassa) relative to a) elevation and b) precipitation (modelled using Worldclim 1.3 records of international precipitation, and shown in the three arithmetic groups discussed here, ‘Wet’ Zone, ‘Intermediate’ Zone, and ‘Dry’ Zone –per Roberts et al., 2015b) and c) map of vegetation redrawn using data from Dittus (1977) and Erdelen (1988).

Fig. 2. The site of Batadomba-lena. a) stratigraphic profile, and b) Bayesian model using available dates from the site (Deraniyagala, 1992; Perera et al., 2011). The model treats each archaeologically-identified layer (e.g. 7c, 7b, 7a) as contiguous, bounded units. Models were run using OxCal4.2 and the calibration curve IntCal13 (Reimer et al., 2013). The most recent Charcoal Outlier Model was applied (Dee and Bronk Ramsey, 2014) (SOM Table S1). BP = before present.

Fig. 3.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements of Batadomba-lena a) fauna from Layers 4, 5, 6, 7a, 7b, and 7c and b) the human specimens from Layers 6 and 7c plotted over them. VPDB = Vienna Pee Dee Belemnite.

Fig. 4.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements of human and faunal fossil tooth enamel from Batadomba-lena plotted by stratigraphic layer. Available radiocarbon dates from the Bayesian model in Fig. 2 and SOM Table S1 are shown. VPDB = Vienna Pee Dee Belemnite; cal. years BP = calibrated years before present.

Fig. 5. Sequential human tooth enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measured in this study from a) Layer 7a/6b from Batadomba-lena, b) Layer 6b from Batadomba-lena, c) Layer 248 from Fa Hien-lena, and d) Layers 6 and 7 of Balangoda Kuragala. VPDB = Vienna Pee Dee Belemnite. Details of the samples shown (e.g. BDH 21) can be found in Table 1.

Fig. 6. Sequential tooth enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measured in this study of *Cervus unicolor*, *Elephas* sp., and *Sus scrofa* from Balangoda Kuragala. VPDB = Vienna Pee Dee Belemnite. Details of the samples shown (e.g. BK 35) can be found in Table 1.

Fig. 7.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements of primates from: a) Fa Hien-lena, b) Balangoda Kuragala, c) Bellan-bandu Palassa, and d) Batadomba-lena. Data come from this study (Table 1) and Roberts et al. (2015a). VPDB = Vienna Pee Dee Belemnite.

Fig. 8. a)  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandu Palassa with 90% confidence ellipses representing ‘Wet Zone’ tropical forest, ‘Intermediate’ tropical forest, and ‘Open’, b) Late Holocene human  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements from Balangoda Kuragala, c) Terminal Pleistocene/Early Holocene human  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements from Balangoda Kuragala and Fa Hien-lena, d)  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of human and faunal specimens from Layer 6 at Batadomba-lena, e)  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of human and faunal specimens from Layer 7c. Data come from this study (Table 1) and Roberts et al. (2015a). VPDB = Vienna Pee Dee Belemnite.