Fruits of the Forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene Sri Lanka

Volume 1: Thesis main text and references

Patrick Roberts
St Hugh's College, University of Oxford

Thesis submitted for the degree of Doctor of Philosophy in Archaeological Science

Trinity Term 2016

Abstract

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Despite ecological, anthropological, and archaeological debate surrounding their desirability as habitats for human occupation, tropical rainforests have received relatively little attention in discussions of *Homo sapiens'* Pleistocene dispersal. Sri Lanka has yielded some of the earliest dated fossil and material culture evidence (*c.* 38-35,000 cal. years BP) for our species in a modern rainforest context beyond Africa. Nevertheless, assertions in Sri Lanka, and elsewhere, regarding early human rainforest reliance have been largely based on coarse or 'off-site' palaeoenvironmental records, and the overall role of these environments in human subsistence strategies has remained uncertain.

This study applies stable carbon and oxygen isotope analysis to Sri Lankan human fossil, and associated faunal, tooth enamel dated to between 36-29,000 and 3,000 cal. years BP, in order to directly test human rainforest resource reliance, reconstruct a stable isotope ecology, and develop 'on-site' palaeoenvironmental records for Late Pleistocene-Holocene Sri Lankan rainforest foragers. Stable carbon and oxygen isotope analysis of modern Sri Lankan primates, and stable carbon, oxygen, and nitrogen isotope analysis of modern plant samples from the Polonnaruwa Nature Sanctuary, are also performed to investigate the ecology of Sri Lankan primates on which Late Pleistocene-Holocene forager subsistence strategies were focused.

The results demonstrate that *Homo sapiens* relied on rainforest resources in Sri Lanka from *c.* 36-29,000 cal. years BP until the Iron Age *c.* 3 cal. years BP, even when open environments, and their corresponding resources, were available. This remains the case through periods of evident environmental change at the Last Glacial Maximum and even upon the arrival of agriculture in the island's tropical forests. The primate stable isotope data prove difficult to interpret as ecological niche separation in the absence of observation data. Nonetheless, humans were evidently able to not only use but also rapidly *specialise* in the exploitation of South Asia's rainforests.

Preface and acknowledgments

This thesis was borne out of a general interest in the adaptation of our species to novel climatic and environmental challenges beyond Africa during the Late Pleistocene. My supervisor, Michael Petraglia, must take the credit for introducing me to Sri Lankan archaeology. The arrival of *Homo sapiens* on this island attracted me specifically given that it potentially represents one of the earliest interactions of our species with a rainforest ecosystem. Ongoing discussion with colleagues, including Nuría Sanz, Robin Dennell, Ryan Rabett, Glenn Summerhayes, and Graeme Barker, heightened my interest regarding the place of Sri Lanka in the broader archaeological literature of human rainforest adaptations (Glenn and Graeme also provided photographs used in Chapter 3, and Glenn read the portions of this thesis touching on human tropical adaptations in Sahul). This interest led to the writing of Chapter 2 and the publication of reviews (Roberts and Petraglia, 2015; Roberts *et al.,* 2015a) of Late Pleistocene *Homo sapiens* rainforest adaptations and Sri Lankan Microlithic tradition archaeology in *World Archaeology* and the *Journal of World Prehistory*, respectively.

Increasing evidence had demonstrated the presence of *Homo sapiens* in rainforest environments in Southeast Asia and Melanesia, *c.* 45,000 years ago, and, more controversially, in Africa, *c.* 200,000 years ago. However, preservation issues made it difficult to pinpoint whether rainforest resources were being used as part of a dedicated specialisation by our species, or as part of seasonal exploitation of various environments. My other supervisor, Julia Lee-Thorp, who must be acknowledged for turning me from an 'essay-writing' undergraduate student to something resembling a scientist, pointed me to the work of John Krigbaum as a means of addressing this question. Further discussion with Julia developed my use of stable carbon and oxygen isotope analysis of human tooth enamel as a means of directly assessing Late Pleistocene and Holocene human rainforest resource reliance. The first set of isotope data for human and faunal tooth enamel from the Sri Lankan sites discussed in Chapter 5 was published as Roberts *et al.* (2015b) in *Science*. Further samples were subsequently analysed and the complete dataset is reported in Chapter 6.

The application of this methodology to Sri Lanka's rich human and faunal fossil record would not have been possible without the generous support of my Sri Lankan colleagues. For granting access to the Sri Lankan archaeological materials and coordinating my research on the 'Resplendent Island' I remain indebted to the Department of Archaeology, Government of Sri Lanka, and especially Senarath Dissanayake, Siran Deraniyagala, Oshan Wedage, Jude Perera and Nimal Perera. I would also like to thank Nimal and his family for their hospitality during my first stay in Sri Lanka, while Oshan Wedage has repeatedly taken great effort to show me some of the greatest wonders this island has to offer. From day one of this project, the people of Sri Lanka have shown me nothing but friendliness and warmth, and for that I am truly grateful. Analysis of the fossil enamel samples presented in this thesis took place in the University of Bradford, under the kind and patient guidance of Andrew Gledhill. Marta Lahr, Duckworth Collection, University of Cambridge and Malcolm MacCallum, Department of Anatomy, University of Edinburgh also provided access to ethnographic samples used as comparative material in the FTIR studies reported in Chapter 6.

Upon visiting Sri Lanka and analysing the existing archaeological literature for the region, it became clear that the archaeological record of the Wet Zone rainforests of the

island was also remarkable for the apparent human focus on semi-arboreal and arboreal monkey taxa in the mammalian kill assemblages. Julia Lee-Thorp therefore also encouraged me to develop an additional isotopic focus on these species, using a modern primate and modern plant stable isotope baseline to help interpret fossil primate niche distinctions and corresponding human hunting strategies. For this part of the project I must extend my heartfelt thanks to Wolfgang Dittus and Vatsala Dittus, as well as their research assistants at the Polonnaruwa Nature Sanctuary and Archaeological Reserve, for helping me obtain and process the modern primate and vegetation samples. The modern vegetation samples were analysed at the University of Oxford with the help of Peter Ditchfield, while Scott Blumenthal generously read sections of this thesis pertaining to these samples.

From conception to completion, both of my supervisors, Julia Lee-Thorp and Michael Petraglia, have offered continued support, advice, guidance, and patience in developing not only my final thesis, but also my ideas, project planning, and writing style more broadly, for which I am most thankful. I would also like to thank my Transfer and Confirmation assessors, Peter Mitchell and Peter Ditchfield, for stimulating discussion and for suggesting future research directions. I must also extend a further personal thanks to these two individuals. While Peter Ditchfield has helped me from the first moment I stepped foot in a stable isotope laboratory, Peter Mitchell has shown an ongoing personal and academic interest in me from the day he encouraged me to apply to Oxford and, without him, I am sure I would not be where I am today. As ever, he has read every word of this thesis, despite its spurious relationship to southern Africa, horses, or donkeys!

The University of Oxford has always offered me an incredible support network of colleagues and friends. John Pouncett, Erika Nitsch, and Maciej Wencel gave significant GIS, R statistical software, and OxCal Bayesian modelling support, respectively, throughout the completion of my studies. I would like to thank Laura, Margaret, Tom, Katerina, and Mike for their company on the various trips to Sri Lanka, Tom, Jonny, Sol, Luíseach, Ed, Abi, Vince, Nora, Adam, Olly, Maciej, Danielle, Ray, Steve, Fran, Amy, Emma, Michaela and Petra for their friendship and for keeping me sane through their participation in numerous pub discussions and DPhil room antics, and Liam for putting up with all of the ‘Archaeology-chat’. On a more intimate note, my thanks go out to Elisabeth, my parents, grandparents, aunty and brother, for their unrelenting support, encouragement and patience. Without them none of my academic progress would be possible.

Table of Contents

Volume 1: Thesis main text and references

Abstract ..... **i**

Preface and acknowledgements ..... **iii**

Table of contents ..... **v**

List of figures ..... **ix**

List of tables ..... **xxi**

Chapter 1: Introduction **1**

1.1 Stable isotope analysis in tropical rainforest and the reconstruction of human and faunal ecology 6

1.2 Stable isotopic reconstruction of human diet, ecology, environment, and subsistence for the Sri Lankan Microlithic tradition 10

1.3 Thesis structure 13

Chapter 2: Early human encounters with tropical forest environments **17**

2.1 Late Pleistocene human rainforest occupation in Africa, Southeast Asia, Melanesia and Australasia 17

2.2 Late Pleistocene human occupation of Sri Lankan tropical forest 30

2.3 Archaeological evidence for the nature of rainforest hunting and gathering: issues and approaches 45

2.4 Early human rainforest resource reliance: why should we care? 49

2.5 Remaining questions regarding Late Pleistocene and Holocene human rainforest use 51

Chapter 3: Prehistoric and ethnographic rainforests: the ecological, climatic, and human context **55**

3.1 Tropical rainforests: an introduction 55

3.2 Rainforest palaeoenvironmental reconstruction across the Late Pleistocene and Holocene 68

3.3 Global (and Sri Lankan) rain forest diversity and its impact on early human occupation and adaptation 75

3.4 Ethnographic evidence for the nature of rainforest hunting and gathering: a review 82

3.5 Rainforest *prehistories* and the search for new methods 95

Chapter 4: Reconstructing early human rainforest adaptations: stable carbon and oxygen isotope analysis of human and faunal tooth enamel 97

4.1 Stable carbon and oxygen isotopes in tropical environments 97

4.2 Stable isotope analysis of hominin and human tooth enamel in a tropical context 114

4.3 Stable isotope analysis of tropical primate niches and the importance of a modern reference 128

4.4 Stable isotope analysis and the Sri Lankan Microlithic tradition 134

Chapter 5: Sites, samples, and methods 145

5.1 Archaeological sites analysed in this thesis 145

5.2 Faunal and human archaeological samples 167

5.3 Enamel pre-treatment and diagensis 184

5.4 Modern plant and primate study at the Polonnaruwa Nature Sanctuary 193

5.5 Mass spectrometry and statistical analysis 200

Chapter 6: Human stable isotope ecology during the Sri Lankan Microlithic tradition 207

6.1 Results of FTIR and SEM studies 207

6.2 Human and faunal stable carbon and oxygen isotope measurements from the Wet, Intermediate, and Dry Zones of Sri Lanka across the Terminal Pleistocene/Holocene transition 217

6.3 Human rainforest resource reliance during the Terminal Pleistocene/Holocene transition 241

6.4 Human and faunal stable carbon and oxygen isotope measurements from Batadomba-lena: the early Microlithic tradition of the Wet Zone 246

6.5 Human isotopic niches and ecology in Late Pleistocene/Holocene Sri Lanka 255

Chapter 7: Late Pleistocene-Holocene and modern primate stable isotope ecology in Sri Lanka 261

7.1 Stable isotope ecology of Late Pleistocene-Holocene Sri Lankan primates 261

7.2 Modern vegetation baseline results from the Polonnaruwa Nature Sanctuary 282

7.3 Modelling modern primate diet $\delta^{13}C$ and $\delta^{18}O$ at the Polonnaruwa Nature Sanctuary 317

7.4 Sri Lankan primate isotopes, past and present 323

7.5 Stable isotopes and primate ecology 327

Chapter 8: Conclusions **331**

8.1 Stable carbon and oxygen isotope analysis of fossil humans and fauna as a direct test of human rainforest resource reliance in Late Pleistocene-Holocene Sri Lanka 333

8.2 Stable carbon and oxygen isotope analysis of fossil fauna as a palaeoenvironmental proxy for rainforest environments in Late Pleistocene-Holocene Sri Lanka 337

8.3 Stable carbon and oxygen isotope analysis of fossil and modern primate tooth enamel as an indirect indicator of human hunting strategies in Late Pleistocene-Holocene Sri Lanka 341

8.4 A Sri Lankan 'rainforest prehistory' 345

8.5 Forests of plenty or 'green deserts': the desirability of rainforests for long-term human subsistence 347

References **351**

Volume 2: Catalogues A, B and C

Table of catalogue contents **397**

List of catalogue figures **399**

List of catalogue tables **403**

Catalogue A – Figures and tables associated with "Chapter 5: Sites, samples and methodology **413**

Figures A1-A2 413

Tables A1-A11 415

Catalogue B - Figures and tables associated with "Chapter 6: Human stable isotope ecology during the Sri Lankan Microlithic tradition" **463**

Figure B1-B33 463

Tables B1-B100 493

Catalogue C – Tables associated with "Chapter 7 – Late Pleistocene and modern primate stable isotope ecologies in Sri Lanka" **585**

Tables C1-C100 585

List of Figures

Chapter 1

Figure 1.1. The location of the archaeological sites sampled (1. Batadomba-lena, 2. Fa Hien-lena, 3. Balangoda Kuragala and 4. Bellan-bandi Palassa) relative to A) elevation map of Sri Lanka based on Digital Elevation Model, data divided geometrically into six categories on the basis of the number of spatial cells covered. Elevation (source CGIAR SRTM [3s resolution]) B) precipitation modelled using Worldclim 1.3 records of international precipitation and shown in three arithmetic groups discussed here as the Wet Zone, Intermediate Zone, and Dry Zone and C) map of the vegetation redrawn using data from Dittus (1977a), Ashton and Gunatilleke (1987), and Erdelen (1988). 11

Chapter 2

Figure 2.1. Schematic illustration of evidence for Late Pleistocene human forager rainforest occupation in Africa, Southeast Asia, Australasia and Sri Lanka with focus on the last 50,000 years. 18

Figure 2.2. Sites postulated as having evidence for pre-Terminal Pleistocene (c. 18 ka) human rainforest occupation and exploitation plotted in relation to the current distribution of tropical forest determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the U.S. Geological Survey Earth Resources Observation System (EROS) Data Center (EDC). 1. Bete 2. Guabuo 3. Médoumane 4. Kango 5. Okala 6. Okanda 7. Ogooué basin 8. Mosumu 9. Kalambo Falls 10. Mufo 11. Panxian Dadong 12. Tam Pa Ling 13. The Niah Caves 14. Matja Kuru 2 15. Lang Rongrien and Moh Khiew 16. Nguòm 17. Punung Cave sites 18. Luzon 19. Palawan 20. Ivane Valley sites 21. West New Britain sites (Yombon region) 22. New Ireland sites (Buang Merabek, Mapenkupkum and Matenbek) 23. Nombe 24. Bird's Head Peninsula, Western Papua New Guinea 25. Northeastern Queensland sites (Walkunder Arch, Fern Cave, Nguarrabullgan, and Lake Euramoo) 26. Sri Lanka sites: Batadomba-lena, Fa Hien-lena, Kitulgala Beli-lena 27. Fuyan Cave.. 19

Figure 2.3. Bathymetry model for Sri Lanka and Southern India using the GEBCO.08. 30Arcsecond dataset. Red and black lines show the position of the coastline following drops in sea-level of 10 and 50 metres, respectively. 33

Figure 2.4. Elevation map of Sri Lanka based on Digital Elevation Model data. Source CGIAR SRTM (3 seconds resolution). Divided geometrically into six categories on the basis of the number of spatial cells covered. 34

Figure 2.5. Precipitation map of Sri Lanka. Source Worldclim 1.3. Annual precipitation is geometrically divided into three categories on the basis of number of spatial cells covered. The result broadly correlates with designations of 'Wet', 'Dry' and 'Intermediate' zones followed in previous studies of vegetation, elevation, and precipitation. 35

Figure 2.6. Vegetation map of Sri Lankabased on Dittus (1977a), Ashton and Gunatilleke (1987), and Erdelen (1988). Pink (A1) and orange (A2)= monsoon scrub jungle ('arid zone forest'- Dittus, 1977a); Yellow (A3)= semi-evergreen forest, grassland, and shrubs; Green-brown (A4)= Intermediate rainforest; Light green (B) = rainforest and grassland below 900m; Green (C) = rainforest and grassland between 900 and 1500m; Dark green (D) = rainforest and grassland above 1500m. Comparison with Figure 2.5 shows that border between Zone A4 and B broadly characterises the boundary between the Wet and Intermediate Zones, with the border between A3 and A4 characterising the Dry Zone and Intermediate Zone boundary. 37

Figure 2.7. Map showing the location of all archaeological and palaeoenvironmental sites discussed in the text: 1. Batadomba-lena, 2. Fa Hien-lena, 3. Kitulgala Beli-lena, 4. Bellan-bandi Palassa, 5. Nilgala Caves, 6. Galge Caves, 7. Bandarawela, 8. Alu-lena Attangoda, 9. Beli-lena Athula, 10. Site 43, 11. Site 49, 12. Site 50, 13. Matota (Mantai), 14. Patirajawela Site 50, 15. Henagahapulgala Site 57, 156. Arnakallu, Site 30, 17. Udamalala, 18. Hungama Mini-athiliya, 19. Pallemalla, 20. Karagan Lewaya, 21. Ravanalla, 22. Anuradhapura, 23. Pomparippu, 24. Horton Plains..... 39

Chapter 3

Figure 3.1. The current distribution of tropical forests in the Old World as determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the U.S. Geological Survey Earth Resources Observation System (EROS) Data Center (EDC)..... 60

Figure 3.2. The distribution of plant and animal resources, and conditions, relevant to human subsistence in a rainforest ecosystem 61

Figure 3.3. Rainforest formations discussed in the text (see also Whitmore, 1998): Tropical lowland evergreen forest (Brazilian Amazon, Source: Harris, 2001), Tropical semi-evergreen forest (Brazil, Source: Oliveira-Filho, 2014), Montane rainforest (Ecuadorean Andes, Source: Read, 2016), Heath forest (Malaysia, Source: Dupont, 2007), Peat swamp forest (Borneo, Source: Department of Forest Sciences, University of Helsinki, 2008), Freshwater swamp forest (Amazon, Source: Mlinaric, 2008)..... 63

Figure 3.4. Annual precipitation anomalies associated with ENSO (pink = drought, blue= flooding). From Dai and Wigley (2000: 1284 – Figure 1c). 73

Figure 3.5. Photographs of rainforest from A) 2,000m in the Ivane Valley, Melanesia (courtesy of Glenn Summerhayes), B) View from the Niah Caves, Sarawak, Borneo (courtesy of Graeme Barker), C) the Congo-Kinshasa (Source: Wilson Center Staff, 2012), D) lowland rainforest of the Sri Lankan Wet Zone (photograph: Patrick Roberts). 76

Figure 3.6. The distribution of certain and uncertain Lupemban sites after J.G.D. Clark (1967), shown with the main river basins of Africa and the contemporary extent of rainforest ecosystems as presented by Mayaux *et al.* (2004) for the year 2000. From Taylor (2011: 9 – Figure 6)..... 77

Chapter 4

Figure 4.1. Histogram of $\delta^{13}C$ values of East and Central African plants collected between 1997 and 2006 (data from Cerling *et al.,* 2010). 101

Figure 4.2. Diagram representing C_3 plant $\delta^{13}C$ variation in a tropical forest context. Low irradiance and recycled CO_2 result in lower $\delta^{13}C$ values in air, soil, and vegetation growing under a closed canopy relative to more open areas. In closed areas, understory vegetation is significantly depleted in ^{13}C, and vegetation has more negative $\delta^{13}C$ values, compared to that growing higher in the canopy. Adapted from Jackson *et al.* (1993), Quade *et al.* (1995), and Krigbaum (2003). 105

Figure 4.3. Plot of faunal tooth enamel $\delta^{13}C$ from extant herbivores in East Africa plotted by location: Ituri Forest, Congo-Kishasa (Cerling *et al.,* 2004), Kenya Mountains and Athi Plains (Cerling *et al.,* 1999; Harris and Cerling, 2002; Cerling *et al.,* 2003a, 2003b), Kahuzi-Biega, Bale and Simien, Nechisar, Awash, and Turkana (Levin *et al.,* 2008). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, and C_4 diets are shown based on Lee-Thorp *et al.* (1989a), Cerling *et al.* (2004) and Levin *et al.* (2008). 111

Figure 4.4. A) $\delta^{13}C$ and $\delta^{15}N$ of modern plants from the Ituri Forest, Congo-Kinshasa showing the vertical and horizontal $\delta^{13}C$ 'canopy effect' (data from Cerling *et al.,* 2004). B) $\delta^{13}C$ and $\delta^{18}O$ of modern animals from the Ituri Forest and corresponding niche distinctions. The two primates with highest $\delta^{18}O$ are the colobines discussed in the text (data from Cerling *et al.,* 2004). 114

Figure 4.5. $\delta^{13}C$ of hominin tooth enamel from southern, eastern, and central Africa plotted by genus/species (as per. Levin *et al.,* 2015). Hominin taxa are arranged from oldest (bottom) to youngest (top) (as per. Levin *et al.,* 2015). Data from Lee-Thorp *et al.* (1994), Sponheimer and Lee-Thorp (1999), Lee-Thorp *et al.* (2000), van der Merwe *et al.* (2003), Sponheimer *et al.* (2005, 2006b), van der Merwe *et al.* (2008), White *et al.* (2009), Cerling *et al.* (2011), Henry *et al.* (2012), Lee-Thorp *et al.* (2012), Cerling *et al.* (2013), Sponheimer *et al.* (2013), Wynn *et al.* (2013), Levin *et al.* (2015). 118

Figure 4.6. $\delta^{13}C$ and $\delta^{18}O$ values for tooth enamel from Ardipithecus ramidus and associated fauna from the Lower Aramis Member of the Sagantole Formation in the Middle Awash Valley, Ethiopia: A) Individual $\delta^{13}C$ and $\delta^{18}O$ values plotted by taxon, B) bivariate means ±1 standard deviation. Data from White et al. (2009). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, C_3/C_4 mixed, and C_4 diets are shown based on Lee-Thorp *et al.* (1989a), Cerling *et al.* (2004) and Levin *et al.* (2008). 119

Figure 4.7. $\delta^{13}C$ and $\delta^{18}O$ values for tooth enamel from the hominoid *Sivapithecus* and associated fauna within the S-Level (9.3-9.3 million years ago) of the Miocene Siwalik Group of Pakistan. A) Individual $\delta^{13}C$ and $\delta^{18}O$ values plotted by taxon, B) bivariate means ±1 standard deviation Data from Nelson (2007). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, C_3/C_4 mixed, and C_4 diets are shown based on Lee-Thorp *et al.* (1989a), Cerling *et al.* (2004) and Levin *et al.* (2008). 122

Figure 4.8. $\delta^{13}C$ and $\delta^{18}O$ values of tooth enamel for orang-utans (*Pongo*) and the giant ape *Gigantopithecus blacki* from the Plio-Pleistocene of Southern China and the

Pleistocene of Thailand. Adapted from Bocherens *et al.* (2015) that incorporates data from Pushkina *et al.* (2010), Nelson (2014), Qu *et al.* (2014) and Bocherens *et al.* (2015)..... 123

Figure 4.9. $\delta^{13}C$ and $\delta^{18}O$ values of tooth enamel from Pre-Neolithic and Neolithic human skeletons from Gua Sireh, Lubang Angin, Gua Cha, and the Niah Caves, Sarawak. Data from Krigbaum (2001, 2003, 2005). 125

Figure 4.10. Bivariate mean $\delta^{13}C$ and $\delta^{15}N$ measurements from the hair of four monkey species from Central and South America ± 1 standard deviation. Data from Schoeninger *et al.* (1997)..... 129

Figure 4.11. $\delta^{13}C$ and $\delta^{15}N$ measurements of lemur hair from Madagascar plotted by 'group'. Data from Loudon *et al.* (2007). 130

Figure 4.12. $\delta^{13}C$ and $\delta^{15}N$ measurements of A) food plants of chimpanzees and gorillas plotted with bivariate mean ± standard deviation of chimpanzee and gorilla hair from Loango National Park, Gabon. Data from Oelze *et al.* (2014) and B) bivariate mean ± standard deviation of modern chimpanzee and gorilla hair from Loango National Park, Gabon measured by Oelze *et al.* (2014) and historic chimpanzee and gorilla hair from central Cameroon measured by Macho and Lee-Thorp (2014). 132

Figure 4.13. Average $\delta^{13}C$coll (collagen), $\delta^{13}C$ap (apatite) and $\delta^{18}O$ap for modern primate species living in the Taï Forest, Ivory Coast alongside observed average feeding heights. Data from (Krigbaum *et al.* 2013). 133

Figure 4.14. *Macaca sinica* – Toque macaque (photograph: Patrick Roberts). 140

Figure 4.15. *Semnopithecus priam thersites* – Grey crested langur (photograph: Patrick Roberts). 141

Figure 4.16. *Trachypithecus vetulus* – Purple-faced leaf monkey (photograph: Patrick Roberts). 142

Figure 4.17. Expected feeding positions of *Macaca sinica*, *Semnopithecus entellus priam*, and *Trachypithecus vetulus* in the canopy and the expected corresponding effects on enamel $\delta^{13}C$ and $\delta^{18}O$ values. 144

Chapter 5

Figure 5.1. South-facing view of the 2011-2012 excavation section at Fa Hien-lena Shelter B (photograph: Oshan Wedage). 148

Figure 5.2. Stratigraphic diagram of 2011-2012 excavations at Fa Hien-lena (adapted from Roberts *et al.,* 2015b) (Oshan Wedage, pers. comm.). 149

Figure 5.3. The Bayesian date model for the site of Fa Hien-lena treats Layers 247 and 174 as 'Phase 1', Layers 237, 141, and 139 and 'Phase 2' and Layer 136 as 'Phase 3'. These phases are, in turn, treated as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer *et al.,* 2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014). 150

Figure 5.4. Photograph taken from the site of Balangoda Kuragala in the Intermediate Zone of Sri Lanka, showing the steep gradient in elevation and vegetation from mountainous rainforest and intermediate hilly rainforest in Sri Lanka's Wet and Intermediate Zones to open grassland in the Dry Zone (photograph: Patrick Roberts). 152

Figure 5.5. Stratigraphic diagram of 2013 excavations at Balangoda Kuragala (courtesy of Nimal Perera) (see also Roberts *et al.,* 2015b). 153

Figure 5.6. The Bayesian date model for the site of Balangoda Kuragala treats each layer as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer *et al.,* 2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014). 154

Figure 5.7. Stratigraphic diagram of 2005 excavations at Bellan-bandi Palassa, See also Perera (2010). 158

Figure 5.8. Available radiocarbon determinations from 2005 excavations at Bellan-bandi Palassa (Perera, 2010 calibrated using the OxCal 4.2 software and the IntCal13 calibration curve (Reimer *et al.,* 2013) with the latest Charcoal Outlier Model applied (Dee and Bronk Ramsey, 2014). Both dates were modelled as part of a single contiguous phase. 158

Figure 5.9. View into Batadomba-lena rockshelter. The sides of the 2005 excavation trench (Figure 5.8) have been supported by bricks (centre-left of shot) (photograph: Patrick Roberts). 160

Figure 5.10. Stratigraphic diagram of 2005 excavations at Batadomba-lena. See also Perera *et al.* (2011). * denote layers with radiocarbon dates (Table 5.4, Figure 5.9). 161

Figure 5.11. The Bayesian date model for the site of Batadomba-lena based on available dates from S.U. Deraniyagala (1992) and Perera *et al.* (2011) that treats each archaeologically-identified layer (e.g. 7c, 7b, 7a) as contiguous, bounded units (Roberts *et al.,* 2015a) (see also Table 5.4). Models were run using OxCal4.2 and the calibration curve IntCal13 (Reimer *et al.,* 2013). The latest Charcoal Outlier Model was also applied (Dee and Bronk Ramsey, 2014). 163

Figure 5.12. Human incisor from Batadomba-lena 7c examined in this study (photograph: Ian Cartwright). 165

Figure 5.13. *Axis axis* (*ceylonensis*) – Ceylon spotted deer (Source: Aravinda, 2014). 169

Figure 5.14. *Cervus unicolor* (*unicolor*) - Ceylon sambhur (Source: Drriss and Marrionn, 2013). 170

Figure 5.15. *Elephas maximus maximus* – Sri Lankan elephant (photograph: Patrick Roberts). 171

Figure 5.16. *Herpestes* sp. – Mongoose (Source: Issadeen, 2012). 172

Figure 5.17. *Hystrix indica* – Indian crested porcupine (Source: Souza, 2011). 173

Figure 5.18. *Lepus nigricollis* (*singhala*) – Ceylon black-naped hare (Source: Wijeratne, 2013). 174

Figure 5.19. *Muntiacus muntjak* (*malabaricus*) – South Indian muntjac or Barking deer (Source: Sani, 2010). 175

Figure 5.20. *Paradoxurus* sp. – Palm cat or Palm civet (Source: Dupont, 2003). 176

Figure 5.21. *Petaurista philippensis* – Indian giant flying squirrel (Source: Francey, 2015). 177

Figure 5.22. *Pteropus giganteus* (*giganteus*) – Common flying fox (Source: Mennerich, 2013). 178

Figure 5.23. *Ratufa macroura* – Giant squirrel (Source: Garvie, 2009). 179

Figure 5.24. *Sus scrofa* – Wild boar (Source: Garvie, 2009). 180

Figure 5.25. *Tragulus meminna* (*Moschiola meminna*) – The Indian spotted chevrotain or mouse-deer (Source: Dupont, 1994). 181

Figure 5.26. Viverricula indica – Sri Lankan small civet cat (Source: Abad, 2013). 182

Figure 5.27. FTIR spectra of five fossilised faunal enamel sample analysed by Roche *et al.* (2010). The chemical groups causing the absorption bands (as per Table 5.7) are indicated. From Roche *et al.* (2010: 1692 – Fig. 1). 188

Figure 5.28. The Polonnaruwa Nature Sanctuary and Archaeological Reserve. The irrigation channel (solid) line delimits the southern portion of the study area. The main road and the railway lines are marked by dashed and dotted lines, respectively. Adapted from Dittus (1975). 195

Chapter 6

Figure 6.1. FTIR spectra for samples from the Modern Human Group (SL2), Modern Fauna Group (MOP1), Fossil Human Group (BDH1), and Fossil Fauna Group (BD12). 209

Figure 6.2. Box plots of the infrared indices (A=API, B=BPI, C=WAMPI, D=PCI, E=BAI) for the investigated groups (as per Roche *et al.,* 2010). 212

Figure 6.3. Box plots of the infrared indices (A=API, B=BPI, C=WAMPI, D=PCI, E=BAI) for groups studied in pretreatment screening (as per Roche *et al.,* 2010). 215

Figure 6.4. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna and B) fauna over-plotted by the human specimen from Layer 248 from Fa Hien-lena. 219

Figure 6.5. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Fa Hien-lena plotted by stratigraphic layer. Available radiocarbon dates from Table 5.1 are shown. 221

Figure 6.6. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Fa Hien-lena by stratigraphic layer. 223

Figure 6.7. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human sample FHH 1 (Layer 248) from Fa Hien-lena. 225

Figure 6.8. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna and B) fauna over-plotted by human samples from Balangoda Kuragala. 226

Figure 6.9. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of *Elephas* sp. samples BK 144 (Layer 16) and BK 130 (Layer 32) from Balangoda Kuragala. 230

Figure 6.10. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of *Sus scrofa* samples BK 121 (Layer 7) and BK 97 (Layer 8) from Balangoda Kuragala. 231

Figure 6.11. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of Cervus unicolor samples BK 35 (Layer 14), BK 37 (Layer 15) and BK 94 (Layer 15) from Balangoda Kuragala. 232

Figure 6.12. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Balangoda Kuragala plotted by stratigraphic layer. Available radiocarbon dates from Table 5.2 are shown. 234

Figure 6.13. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Balangoda Kuragala by stratigraphic layer. 236

Figure 6.14. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BKH 19 (Layer 6) and BKH 21 (Layer 7) from Balangoda Kuragala. 238

Figure 6.15. $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from Bellan-bandi Palassa. 239

Figure 6.16. Boxplots of faunal A) $\delta^{13}C$ and B) $\delta^{18}O$ used to form the 'Wet Zone', 'Intermediate Zone', and 'Open' zone ellipses in Figure 6.17. 243

Figure 6.17. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa. The isotopic values from characteristic rainforest fauna from Fa Hien-lena and forest and open grassland fauna from Balangoda Kuragala have been used to construct 90% confidence ellipses [using the R software dataEllipse function] indicative of closed 'Wet Zone' rainforest, 'Intermediate' rainforest, and 'Open' conditions (Roberts *et al.,* 2015b), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Late Holocene deposits at Balangoda Kuragala, C) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Terminal Pleistocene/Early Holocene deposits from Fa Hien-lena and Balangoda Kuragala. 244

Figure 6.18. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna from Layers 4, 5, 6, 7a, 7b, and 7c and B) fauna over-plotted by the human specimens from Layers 6b, 6b/7a, and 7c from Batadomba-lena. 246

Figure 6.19. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Batadomba-lena plotted by stratigraphic layer. Available radiocarbon dates from Table 5.4 are shown. For the purposes of this plot the three human samples labelled 6b/7a have been shown in Layer 6. 248

Figure 6.20. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Batadomba-lena by stratigraphic layer. 249

Figure 6.21. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa with 90% confidence ellipses representing Wet Zone rainforest, Intermediate rainforest, and Open conditions (see Figures 6.16 and 6.17), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Layer 6b and 6b/7a of Batadomba-lena, C) $\delta^{13}C$ and $\delta^{18}O$ values of the human specimen from Layer 7c of Batadomba-lena. 251

Figure 6.22. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BDH 5, BDH 6, BDH 17 (all Layer 6b) from Batadomba-lena. 253

Figure 6.23. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BDH 21 and BDH 22 (both Layer 6b/7a) from Batadomba-lena. 254

Figure 6.24. 90% confidence ellipses of Wet Zone rainforest, Intermediate rainforest, and Open conditions from Figures 6.16 and 6.17 with A) Late Holocene human $\delta^{13}C$ and $\delta^{18}O$ measurements from Balangoda Kuragala, B) Terminal Pleistocene/Early Holocene human $\delta^{13}C$ and $\delta^{18}O$ measurements from Balangoda Kuragala and Fa Hien-lena, C) Layer 6b and 6b/7a human $\delta^{13}C$ and $\delta^{18}O$ measurements from Batadomba-lena (*c.* 20,000-17,000 cal. years BP), and D) Layer 7c human $\delta^{13}C$ and $\delta^{18}O$ measurements from Batadomba-lena (*c.* 36,000-29,000 cal. years BP) over-plotted. 256

Figure 6.25. Boxplots of A) $\delta^{13}C$ and B) $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena (FH), Balangoda Kuragala (BK), and Bellan-bandi Palassa (BBP) and the Late Pleistocene deposits of Batadomba-lena (BDL). 258

Figure 6.26. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa with 90% confidence ellipses representing Wet Zone rainforest, Intermediate rainforest, and Open conditions (see Figures 6.16 and 6.17), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Layers 6b and 6b/7a and faunal specimens from Layer 6 at Batadomba-lena, C) $\delta^{13}C$ and $\delta^{18}O$ values of human and faunal specimens from Layer 7c at Batadomba-lena. 259

Chapter 7

Figure 7.1. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena. 262

Figure 7.2. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer. 263

Figure 7.3. Boxplots of *Macaca sinica* A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer. 266

Figure 7.4. Boxplots of *Trachypithecus vetulus* A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer. 267

Figure 7.5. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala. 268

Figure 7.6. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer. 269

Figure 7.7. Boxplots of *Macaca sinica* A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer. 271

Figure 7.8. Boxplots of Semnopithecus priam thersites A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer. 272

Figure 7.9. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Layer 10 (*c.* 12-11,000 cal. years BP) of Bellan-bandi Palassa. 273

Figure 7.10. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Late Pleistocene site of Batadomba-lena 275

Figure 7.11. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Batadomba-lena shown by stratigraphic layer. 276

Figure 7.12. Boxplots of *Macaca sinica* A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Late Pleistocene sequence of Batadomba-lena shown by stratigraphic layer. 278

Figure 7.13. Boxplots of *Trachypithecus vetulus* A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Late Pleistocene sequence of Batadomba-lena shown by stratigraphic layer. 279

Figure 7.14. Plot of the first two components of PCA analysis, and the observation location of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$, of modern plant samples (with Cyperaceae spp. included). 285

Figure 7.15. Plot of the first two components of PCA analysis, and the observation location of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$, of modern plant samples (with Cyperaceae spp. excluded). 286

Figure 7.16. A) Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ values from the Polonnaruwa Nature Sanctuary shown by the season in which they were collected B) the means and standard deviations of wet and dry season $\delta^{13}C$ and $\delta^{18}O$ excluding Cyperaceae spp. 290

Figure 7.17. Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ plotted by species for A) the dry season and B) the wet season. 292

Figure 7.18. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for each modern plant species sampled during A) the dry season and B) the wet season. 293

Figure 7.19. Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ plotted by plant part for A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 295

Figure 7.20. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for modern plant parts sampled during A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 296

Figure 7.21. $\delta^{13}C$ by $\delta^{18}O$ of modern plant samples collected in the dry season plotted by species and plant part (Cyperaceae spp. are excluded). 298

Figure 7.22. $\delta^{13}C$ by $\delta^{18}O$ of modern plant samples collected in the wet season plotted by species and plant part (Cyperaceae spp. are excluded). 299

Figure 7.23. Modern plant sample $\delta^{13}C$ and $\delta^{18}O$ plotted by qualitatively assigned insolation groupings (low, medium or high) for A) the dry season and B) the wet season (Cyperaceae spp. are excluded).. 301

Figure 7.24. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of qualitatively assigned insolation groupings (low, medium or high) (Cyperaceae spp. are excluded). .. 302

Figure 7.25 Modern plant sample $\delta^{13}C$ and $\delta^{18}O$ plotted by canopy height groupings (floor, low, middle or upper) for A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 303

Figure 7.26. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of canopy height groupings (floor, low, middle or upper) for A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 304

Figure 7.27. A) Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ values from the Polonnaura Nature Sanctuary shown by the season in which they were collected B) the means and standard deviations of wet and dry season $\delta^{13}C$ and $\delta^{15}N$ excluding Cyperaceae spp..... 307

Figure 7.28. Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ plotted by plant part for A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 308

Figure 7.29. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for modern plant part sampled during A) the dry season and B) the wet season (Cyperaceae spp. are excluded). 309

Figure 7.30. $\delta^{13}C$ by $\delta^{15}N$ of modern plant samples collected in the dry season plotted by species and plant part (Cyperaceae spp. are excluded). 310

Figure 7.31. $\delta^{13}C$ by $\delta^{15}N$ of modern plant samples collected in the wet season plotted by species and plant part (Cyperaceae spp. are excluded). 311

Figure 7.32. Mean and standard deviations for $\delta^{13}C$ and $\delta^{15}N$ of qualitatively assigned insolation groupings (low, medium or high) (Cyperaceae spp. are excluded). .. 312

Figure 7.33. Mean and standard deviations for $\delta^{13}C$ and $\delta^{15}N$ of canopy height groupings (floor, low, middle or upper) (Cyperaceae spp. are excluded). 313

Figure 7.34. Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ plotted by species for A) the dry season and B) the wet season. 315

Figure 7.35. Mean and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for each modern plant species sampled during A) the dry season and B) the wet season..... 316

Figure 7.36. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of modelled monkey diets (for *Trachypithecus vetulus*, *Semnopithecus priam thersites*, and *Macaca sinica*) for A) the dry season and B) the wet season when species and plant parts of importance '1' are included (see Catalogue Tables A8 and A9). To remove the impact of different sample sizes an average $\delta^{13}C$ and $\delta^{18}O$ value was obtained for each species/plant prior to inclusion in an overall calculation of the mean and standard deviation for the whole 'diet'..... 318

Figure 7.37. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of modelled monkey diets (for *Trachypithecus vetulus*, *Semnopithecus priam thersites*, and *Macaca sinica*) for A) the dry season and B) the wet season when species and plant parts of importance '1' and '2' are included (see Catalogue Tables A8 and A9). To remove the impact of different sample sizes an average $\delta^{13}C$ and $\delta^{18}O$ value was obtained for

each species/plant prior to inclusion in an overall calculation of the mean and standard deviation for the whole 'diet'. 320

Figure 7.38. $\delta^{13}C$ and $\delta^{18}O$ values of modern monkey and Cervus sp. samples from a collection of Wolfgang Dittus collected at the Polonnaruwa Nature Sanctuary during the 1980s. 322

Chapter 8

Figure 8.1. Inferred stable carbon isotope data of vegetation for a) modern chimpanzees and gorillas in western-central Africa (Oelze *et al.,* 2014; Macho and Lee-Thorp, 2014), extinct apes (Sivapithecus-Nelson, 2007; *Gigantopithecus* - Nelson, 2014; Bocherens *et al.,* 2016), b) African hominin species (from data compiled in Sponheimer *et al.,* 2013) and c) *Homo sapiens* in Late Pleistocene/Holocene Sri Lanka (this thesis) and Holocene Southeast Asia (Krigbaum, 2001). A correction of -13‰ (shown in Cerling and Harris, 1999 for non-ruminant ungulates) has been applied to the fossil enamel data, while a correction of -4.5‰ has been applied to modern ape hair data. This latter value includes a correction of -3‰ for diet-hair enrichment (as in Sponheimer *et al.,* 2003) and a further -1.5‰ in order to correct for the fossil fuel effect. 348

List of Tables

Chapter 3

Table 3.1. Tropical rainforest formations (after Whitmore, 1998 – Table 2.1). Those in bold are briefly summarised in the text. 67

Chapter 5

Table 5.1. Dates available from the 2011-2012 excavation at Fa Hien-lena associated with the faunal samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Fa Hien-lena treats Layers 247 and 174 as 'Phase 1', Layers 237, 141, and 139 and 'Phase 2' and Layer 136 as 'Phase 3'. These phases are, in turn, treated as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer *et al.,* 2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014). .. 151

Table 5.2. Dates available from the 2013 excavation at Balangoda Kuragala associated with the faunal samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Balangoda Kuragala treats each layer as contiguous, bounded units. The model was run using OxCal4.1 (Bronk Ramsey, 2009) and the calibration curve IntCal13 (Reimer *et al.,* 2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014). 155

Table 5.3. Dates available from 2005 excavations at Bellan-bandi Palassa (Perera, 2010) associated with the faunal samples analysed in this study. All radiocarbon determinations have been calibrated using the OxCal 4.2 software and the IntCal13 calibration curve (Reimer *et al.,* 2013) with the latest Charcoal Outlier Model applied (Dee and Bronk Ramsey, 2014). Both dates were modelled as part of a single contiguous phase. 159

Table 5.4. Dates available from 1980s and 2005 excavations at Batadomba-lena (S.U. Deraniyagala, 1992; Perera, 2010; Perera *et al.,* 2011) associated with the faunal and human samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Batadomba-lena treats each layer as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer *et al.,* 2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014). 166

Table 5.5. Description of the FTIR spectrum of bioapatite (based on LeGeros, 1991; Michel *et al.,* 1995; Sponheimer and Lee-Thorp, 1999; Trueman *et al.,* 2008; and Roche *et al.,* 2010) (adapted from Roche *et al.* 2010) 189

Table 5.6. Description of the FTIR indices of enamel bioapatite. 'B' and 'V' denote the height of the bands and the valleys, respectively. Numbers in parentheses represent the approximate positions of the apparent bands (adapted from Roche *et al.* 2010). 190

Chapter 6

Table 6.1. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample FH 54 from Fa-Hien lena. 218

Table 6.2. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample BK 129 from Balangoda Kuragala. 218

Table 6.3. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample BBP 5 from Bellan-bandi Palassa. 218

Chapter 7

Table 7.1. $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ measurements of ten subsamples taken from PL 183 (*Ficus benghalensis* fruits). 283

Table 7.2. $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ measurements of ten subsamples taken from PL 178 (*Manilkara hexandra* leaves)..... 283

Trees are sanctuaries. Whoever knows how to speak to them, whoever knows how to listen to them, can learn the truth. They do not preach learning and precepts, they preach, undeterred by particulars, the ancient law of life.

— Hermann Hesse, *Bäume. Betrachtungen und Gedichte* (1984).

Chapter 1 - Introduction

The novel environmental challenges faced by hominin populations expanding throughout Africa and into Europe, the Middle East, equatorial Asia, Melanesia, and Australia during the Late Pleistocene have long been a focus for archaeological investigation (Gamble *et al.,* 2004; Rabett, 2012). Given its unprecedented global expansion, much attention has been focused on the climatic and environmental thresholds of our own species, *Homo sapiens*, in this context (Mellars, 2006; Rabett, 2012; Boivin *et al.,* 2013). Certain environments have traditionally been seen as 'barriers' to human migration and occupation until the Holocene (Gamble, 1993). Nevertheless, recent research into the arid regions of the Middle East and equatorial Asia has suggested that environments previously assumed to have been unattractive for human occupation were successfully inhabited at various points in time (Groucutt and Petraglia, 2012; Petraglia *et al.,* 2012; Blinkhorn *et al.,* 2013; Boivin *et al.,* 2013 Crassard *et al.,* 2013). One of the other more dramatic global environments, tropical rainforests, has also been given relatively little attention in discussions of Pleistocene dispersal until recently (Barker *et al.,* 2007; Gosden, 2010; Barton *et al.,* 2012; Barker, 2013), despite ecological, anthropological, and archaeological debate surrounding their desirability as sustained habitats for human occupation (Hutterer, 1983; Bailey *et al.,* 1989; Gamble, 1993; Mercader, 2002a, 2002b; Roberts and Petraglia, 2015).

Since Lamarck in 1809, tropical forests have tended to be perceived as the archaic, untouched preserve of the earliest ape-like hominoids, left behind as the hominin clade gained increasingly 'human' traits of tool use, medium-large game hunting, and upright locomotion on open savannah landscapes (Dart, 1925; Potts, 1998; Klein, 1999;

Domínguez-Rodrigo, 2014). Today, tropical forests are home to our closest extant great ape relatives that have frequently formed the basis of ancestral analogies for our earliest common ancestors (Clutton-Brock and Harvey, 1977; Goodall, 1986; Foley and Lewin, 2004; Tuttle, 2014). Perhaps unsurprisingly, as a consequence, rainforests have tended to be somewhat neglected in discussions of human evolution and adaptation (though see Mercader, 2002a, Barton *et al.,* 2012). Moreover, in the late 1980s, human ecologists and sociocultural anthropologists argued that long-term human foraging, in the absence of agricultural support, is both undocumented and inconceivable in the tropical rainforests of the modern world and the recent past (Hutterer, 1983; Bailey *et al.,* 1989; Headland and Reid, 1989). This perspective has seen rainforests discussed as major navigational, and nutritionally-poor, obstacles to the migration of hominins, including our own species, beyond Africa (Gamble, 1993; Dennell and Roebroeks, 2005; Boivin *et al.,* 2013), as well as the expansion of agriculture and social complexity during the Holocene (Grollemund *et al.,* 2015).

The perception of rainforests as treacherous human environments has been challenged from ecological, anthropological and archaeological standpoints (Carneiro, 1988; Ellen, 1988; Colinvaux and Bush, 1991; Ichikawa, 1992; Bellwood, 1993; Balée, 1994; Willis *et al.* 2004; Barton *et al.* 2012). Indeed, archaeological and palaeoenvironmental research in tropical forest regions of Africa (Mercader, 2002a), Southeast Asia (Barker *et al.,* 2007), and Melanesia (Gosden, 2010; Summerhayes *et al.*, 2010) has suggested that *Homo sapiens* was able to exploit and manipulate a variety of faunal and floral taxa available in rainforest environments at least as early as 45,000 years ago, and, more controversially, 200,000 years ago (Mercader, 2002a, 2002b). Nevertheless, with some notable exceptions (Barker *et al.,* 2007; Barker, 2013), thus far little attempt has been made to analyse the specific rainforest niche filled by humans in these regions due, in

part, to the considerable preservation issues facing archaeological remains in such humid environments. Existing research has often associated human fossil and technological sequences with indirect pollen, archaeobotanical, and archaeozoological palaeoenvironmental records of unknown resolution and catchment. Without a direct measure of human tropical rainforest resource reliance, the nature, longevity, and potentially seasonal role of these ecologies in early human subsistence continues to elude us (Mercader, 2002a).

Sri Lanka provides a rare opportunity to study, in detail, Late Pleistocene human adaptations to rainforest environments. Sri Lankan rockshelter and cave sites dating from *c.* 38,000-35,000 to 3,000 cal. years BP have yielded the earliest *Homo sapiens* fossils, microlithic technologies, bone toolkits, and some of the earliest evidence for shell beads and other articles of personal ornamentation, in South Asia, all within a modern-day rainforest environment (Kennedy and Deraniyagala, 1989; S.U. Deraniyagala, 1992; Wijeyapala, 1997; Kennedy, 2000; Perera *et al.,* 2011; Roberts *et al.,* 2015a). Unlike many regions of Late Pleistocene human rainforest research, the existence of a wealth of mammalian faunal evidence of small arboreal and semi-arboreal fauna, including forest primates, archaeobotanical traces of *Canarium* sp. nuts, and molluscan indicators, directly-associated with the archaeological record, suggests that similar rainforest conditions existed during occupation *c.* 38,000-35,000 to 3,000 cal. years BP (S.U. Deraniyagala, 1992; Perera, 2010; Perera *et al.,* 2011). Nevertheless, palaeoenvironmental evidence from molluscan and faunal remains, and reconstructed taxa habitat preferences, can be relatively coarse. As a result, the overall role of rainforest resources, and whether they provided seasonal or dedicated dietary contributions, to human subsistence during this period, remain unexplored.

This issue is exacerbated by the fact that the span of the Sri Lankan record of human skeletons and complex material culture, from *c.* 38-35,000 to 3,000 cal. years BP, encompasses climatic periods, including the Last Glacial Maximum (LGM) and the Terminal Pleistocene/Holocene transition, during which rainforest extent and structure is known to have changed considerably in other regions of the world (Chapter 3 – Section 3.2) (Colinvaux *et al.,* 1996; Dupont *et al.,* 2000; Mercader, 2002a; Haberle *et al.,* 2012). Indian Ocean palaeoenvironmental proxies (Prabhu *et al.,* 2004; Caley *et al.,* 2011; Rashid *et al.,* 2011; Deplazes *et al.,* 2014), as well as pollen evidence from the Horton Plains in the Highlands of Sri Lanka (Premathilake and Risberg, 2003; Premathilake, 2006, 2012; Premathilake and Gunatilaka, 2013), suggest that changes in climate and vegetation structure may also have occurred in Sri Lanka from the LGM onwards. Nonetheless, these records remain spatially disconnected from the main sites of human rainforest occupation in Sri Lanka and detailed 'on-site' palaeoenvironmental data are currently limited to a single site, Batadomba-lena (Perera *et al.,* 2011). Consequently, palaeoenvironmental perspectives of immediate relevance to human activities in Sri Lanka, as well as our knowledge of human responses to these changes, are currently limited.

Finally, the available faunal records indicate that early and persistent human rainforest foraging in Sri Lanka may have been facilitated by specialised primate hunting. Forest-dwelling, semi-arboreal and arboreal primates consistently make up between 70 and 80% of the mammalian assemblage over the period of occupation at Batadomba-lena and Fa Hien-lena (Perera, 2010; Perera *et al.,* 2011). Such a high proportion is unprecedented in both the archaeological and anthropological literature, even with the modern-day availability of rifle technologies in many parts of the Amazon rainforest (ProWildlife, 2007; Lu, 2010; Papworth *et al.,* 2013), with perhaps the sole exception of

the Raute of Nepal (Fortier, 2009). Although modern ecological information exists for these Sri Lankan primate species, and suggests that they exploit different parts of the forest ecosystem and feed at different heights in the canopy (Hladik and Hladik, 1972; Hladik, 1977; Dittus, 1974, 1977a, 1985a; Fooden, 1979; Phillips, 1926, 1980; Vandercone *et al.,* 2012) (Chapter 4 – Section 4.4), the relevance of these observations to their behaviour in the past is unknown, making it difficult to reconstruct human exploitation strategies with confidence. There has also been little work done thus far on functional analysis of the microlithic and bone tool technologies likely used in primate capture (Perera *et al.,* in press).

In this thesis I apply stable isotope analysis to Late Pleistocene and Holocene human and faunal remains, alongside modern vegetation and primate samples, in order to reconstruct a detailed environmental and ecological context for the early rainforest hunter-gatherers of Sri Lanka. This currently represents the only means of *directly* evaluating human rainforest resource reliance across the considerable span of the Sri Lankan archaeological record, and across periods of significant palaeoenvironmental change. The comparison of stable isotope measurements of faunal samples from the Sri Lankan Wet Zone dated to the LGM and across the Terminal Pleistocene and Holocene transition should also enable the testing of whether the nature and extent of the rainforest of this region has changed significantly in the past. Finally, stable isotope analysis of different Sri Lankan primate species may provide further insights into the forest niches (e.g. low, mid, and high canopy) humans were exploiting to subsist on consistently large numbers of these primate taxa during periods of occupation. The application of these methods, in association with *Homo sapiens* fossils and material culture in Sri Lanka, has the potential to inform wider debates regarding the

anthropological viability and desirability of rainforests for long-term human exploitation and occupation.

1.1 – Stable isotope analysis in tropical rainforests and the reconstruction of human and faunal ecology

Stable isotope analysis of faunal tissues in tropical, or subtropical, regions has frequently been used to track the proportion of C_3 or C_4 biomass in their diets. In a tropical context, this has been used to provide an indirect assessment of the relative availability of C_4 grassland savannah and C_3 woodland or forest habitats (Sponheimer *et al.,* 2006a; Codron *et al.,* 2014; Crowley *et al.,* 2014). In the context of tropical forest isotope ecology, variation within the C_3 photosynthetic pathway itself, and of the resulting biomass, is of greatest interest. Vegetation growing under a closed, dense forest canopy is strongly depleted in ^{13}C, due to low light (Farquhar *et al.,* 1989) and the presence of large amounts of respired CO_2, especially near the forest floor (van der Merwe and Medina, 1989; 1991). As a result of the 'canopy effect', CO_2, soils, and plants under the canopy have lower $\delta^{13}C$ values (van der Merwe and Medina, 1991; Bowman and Cook, 2002; Yonekura *et al.,* 2012; Pietsch and Gautam, 2013) that are also reflected in the tissues of animals living in the same environments (Cerling *et al.,* 2004; Levin *et al.,* 2008) (Chapter 4 – Sections 4.1 and 4.3). The tissues of forest-dwelling animals have significantly lower $\delta^{13}C$ values (by at least 3‰), than those spending some, or all, of their time consuming open-habitat foodstuffs (Cerling *et al.,* 2004; Oelze *et al.,* 2014, Macho and Lee-Thorp, 2014).

It has also been suggested that stable carbon isotopes can be used to discern, in detail, the niches of tropical forest-dwelling taxa, with most research here focusing on primates (van der Merwe and Medina, 1991; Cerling *et al.,* 2004; Sponheimer *et al.,* 2009).

Researchers have argued that the proportion of fruits and leaves in primate diet can lead to significantly different stable carbon isotope values (Cerling *et al.,* 2004; Sandberg *et al.,* 2012; Oelze *et al.,* 2014). Furthermore, it has been argued that differential isotopic impacts of the 'canopy effect' may be used to discern niches at different heights within the canopy itself, with those animals living on the forest floor being more influenced by low light, respired CO_2 and the isotopic 'canopy effect' (van der Merwe and Medina, 1989, 1991; Cerling *et al.,* 2004) compared to those feeding at higher positions or within canopy openings (Cerling *et al.,* 2004; Macho and Lee-Thorp, 2014). However, although the vertical gradient in stable carbon isotopic ratios is clearly visible in CO_2 and leaf studies (van der Merwe and Medina, 1989, 1991), its presence and resolution amongst differentially feeding faunal communities remains equivocal (Schoeninger, 2009; Krigbaum *et al.,* 2013) (Chapter 4 – Sections 4.1 and 4.3).

While $\delta^{13}C$ has been considered the main indicator of the 'canopy effect', stable oxygen isotope measurements from animal tissues can provide additional palaeoecological information about water and food (Koch, 2007; Krigbaum *et al.,* 2013). In tropical ecosystems, it has been shown that stable oxygen isotope analysis of CO_2 and vegetation 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 stable oxygen isotope ratios and evaporative potential means that, like stable carbon isotopes, they can hypothetically be used to indirectly infer canopy density in a rainforest environment (Chapter 4 – Section 4.1). Furthermore, stable oxygen isotopes of CO_2 and vegetation have been shown to demonstrate differences depending on height within the canopy, and between different plant parts, as a result of changing evaporative potentials (Sternberg *et al.,* 1989; Buchmann *et al.,* 1997; Buchmann and Ehleringer, 1998; Carter and Bradbury, 2015). In the tissues of

animals that obtain most of their water from drinking surface water, $\delta^{18}O$ measurements will reflect that source. However, those animals that obtain the majority of their water requirements from plants and plant sugars will reflect most strongly the environmental factors that influence plant transpiration and plant $\delta^{18}O$ (Kohn *et al.,* 1996; Levin *et al.,* 2006).

The above principles provide a firm methodological basis for the discernment of prehistoric faunal and hominin forest occupation and ecological niches. In tropical rainforest contexts, tooth enamel is the archaeological material of choice as a result of issues in bone collagen and hydroxyapatite preservation (Chapter 4 – Section 4.2) (Ambrose, 1990; Ambrose and Norr, 1992; Krigbaum, 2005). Tooth enamel consists primarily of inorganic biological calcium phosphate apatite that is extremely resistant to post-mortem diagenesis, even in the humid and hydrologically active environments of the tropics (Lee-Thorp *et al.,* 1987, 1991; Wang and Cerling, 1994; Krigbaum, 2003; Cerling *et al.,* 2011; Sponheimer *et al.,* 2013). Tooth enamel records an isotopic dietary signature for the period of enamel formation, a period that will vary depending on species and tooth sampled. For humans, the longest isotopic signature comes from third molars which may form anywhere between 7-13 years old and mid to late teenage years (Hillson, 1996). Although providing a 'sub-adult' diet, tooth enamel provides the best fossil material in tropical rainforest regions of the globe for dietary reconstruction (Krigbaum, 2005).

In the context of discussions of early human tropical forest occupation and adaptation, stable $\delta^{13}C$ and $\delta^{18}O$ isotopic analysis of human tissues preserved in tropical forest archaeological contexts can provide the only existing *direct* information regarding long-term human reliance on rainforest resources. Other methods, such as residue analysis

(Barton, 2005; Fullager, 2006), typological considerations of material artefacts (Mercader, 2002a, 2002b; Rabett and Piper, 2012; Perera *et al.,* in press), faunal assemblages (Barker *et al.,* 2007; Perera *et al.,* 2011), and macrobotanical assemblages (Barker *et al.,* 2007; Perera *et al.,* 2011), provide indirect inferences regarding contributions of different tropical resources to human diet. More direct evidence from bioanthropological studies of tooth wear patterns provides coarse records of diet at best (Forshaw, 2009), while direct evidence seen in the stomach contents of ice or bog 'mummies' (Rollo *et al.,* 2002) is virtually impossible to obtain in the environments and timespan of interest here. Even phytoliths from dental calculus, which can provide direct insight into plant species consumed (Henry and Piperno, 2008; Henry *et al.,* 2011), provide but transient, short-term perspectives of relative contributions to human subsistence.

In contrast, stable carbon and oxygen isotope analysis of hominin tooth enamel in tropical or subtropical regions of Africa has been shown to provide direct indication of the dietary adaptations and niches of our ancestors and their associated fauna, mostly focusing on the distinction between the C_3- or C_4-photosynthetic pathways at the base of African foodwebs (Lee-Thorp *et al.,* 1994, 2000; Sponheimer and Lee-Thorp, 1999; White *et al.,* 2009; Cerling *et al.,* 2011; Sponheimer *et al.,* 2013). Isotopic approaches to early hominin and human ecological reconstruction have, however, thus far been restricted to Africa (Chapter 4 – Section 4.2), with no attempt to develop a stable isotope ecology or a direct stable isotopic record of human subsistence in any of the regions where early human rainforest occupation and exploitation has been inferred (Barker *et al.,* 2007; Summerhayes *et al.,* 2010). One exception is the use of stable carbon and oxygen isotopes from Early to Middle Holocene human tooth enamel to elucidate dietary changes between Neolithic human groups entering the tropical forests

of Southeast Asia and those foraging within forested environments during the pre-Neolithic phase (Krigbaum, 2003, 2005) (Chapter 4 – Section 4.2). Nonetheless, these principles are yet to be applied further back in the rainforest prehistory of our species.

1.2 – Stable isotopic reconstruction of human diet, ecology, environment, and subsistence strategies for the Sri Lankan Microlithic tradition

In this thesis, I apply stable isotope analysis to faunal and human tooth enamel from Late Pleistocene and Holocene Microlithic tradition sites in Sri Lanka to address three main research areas and hypotheses.

Firstly, I test the extent of Late Pleistocene and Holocene human rainforest resource reliance in Sri Lanka by comparing the stable carbon and oxygen isotope results of fossil *Homo sapiens* tooth enamel with associated fauna of known ecological preferences. This is achieved by sampling fauna from Terminal Pleistocene/ Holocene sites from the modern-day Wet Zone (Fa Hien-lena), Dry Zone (Bellan-bandi Palassa), and Intermediate Zone (Balangoda Kuragala) of Sri Lanka (Figure 1.1) to characterise rainforest extent and dynamics across this interesting climatic period. I then compare *Homo sapiens* fossils from Fa Hien-lena and Balangoda Kuragala to this faunal baseline in order to directly determine the place of human foragers in Sri Lankan rainforest environments during this period. I also apply this methodology further back in time to the site sequence of Batadomba-lena, spanning from *c.* 36,000-29,000 to *c.* 12,000 cal. years BP (Roberts *et al.,* 2015a), in an attempt to investigate the degree of rainforest reliance practiced by some of the earliest *Homo sapiens* yet known in Sri Lanka. Use of this methodology will facilitate testing of the hypothesis that:

1. *Sri Lankan human foragers relied on rainforest resources back to at least c. 36-29,000 years ago, well beyond the Holocene, and through periods of climatic and environmental flux when the productivity, stability and spatial organisation of global forest environments are known to have changed dramatically.*

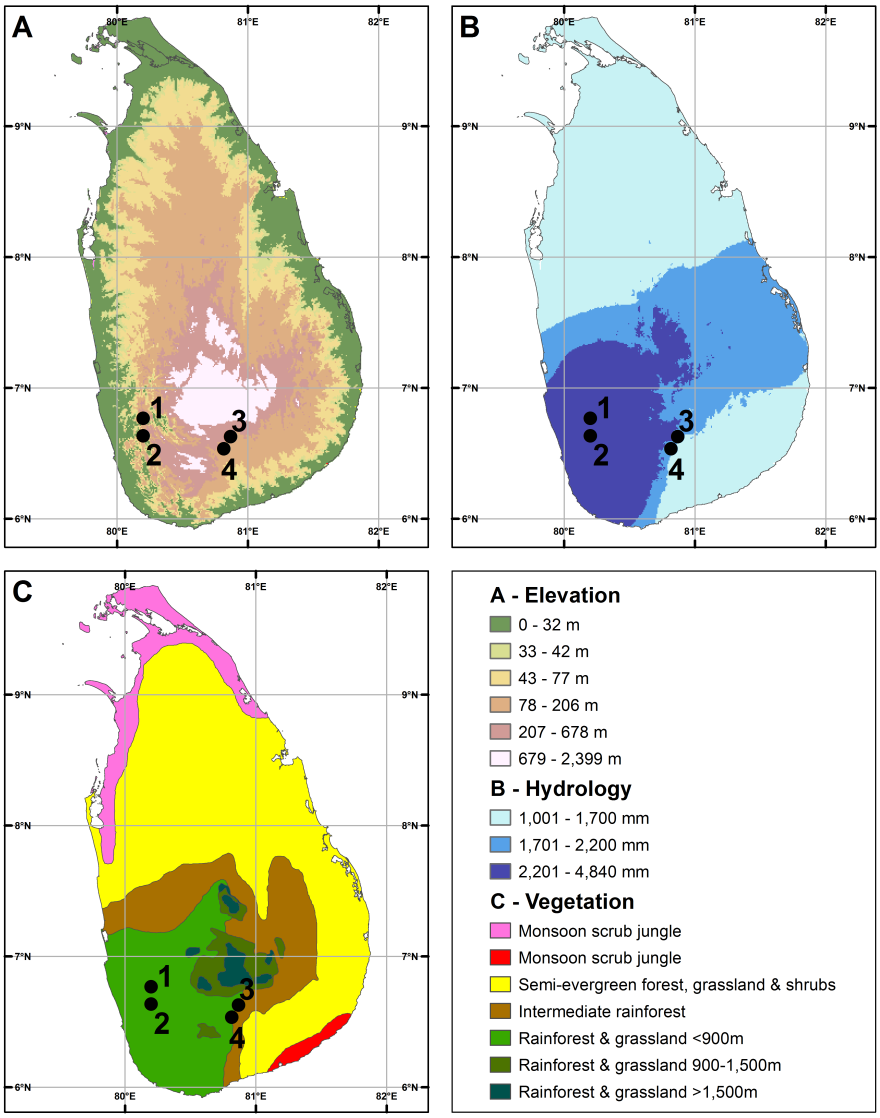


Figure 1.1. The location of the archaeological sites sampled (1. Batadomba-lena, 2. Fa Hien-lena, 3. Balangoda Kuragala and 4. Bellan-bandi Palassa) relative to A) elevation map of Sri Lanka based on Digital Elevation Model, data divided geometrically into six categories on the basis of the number of spatial cells covered. Elevation (source CGIAR SRTM [3s resolution]) B) precipitation modelled using Worldclim 1.3 records of international precipitation and shown in three arithmetic groups discussed here as the Wet Zone, Intermediate Zone, and Dry Zone and C) map of the vegetation redrawn using data from Dittus (1977a), Ashton and Gunatilleke (1987), and Erdelen (1988).

Within this approach, the stable carbon and oxygen isotopic data from fossil fauna not only provide a useful ecological baseline with which to test human rainforest resource reliance, but can also be used to reconstruct 'on-site' palaeoecological and palaeoenvironmental sequences in their own right. $\delta^{13}C$ and $\delta^{18}O$ measurements from fauna from different sites, with known ecological preferences, will provide isotopic reference values for different 'forest' and 'open' habitats and habitat structures in Sri Lanka. This is all the more important in Sri Lanka, where division of the island into three climatic zones on the basis of precipitation parameters, has resulted in corresponding vegetation and tropical forest zonation today (Figure 1.1) (Chapter 2 – Section 2.2). The stable isotopic analysis of fossil faunal tooth enamel from well-dated sites in these different zones, and across different time periods, will therefore also enable testing of the hypothesis that:

2. *The extent of the closed 'Wet Zone' rainforest of Sri Lanka waxed and waned in the past, especially across the significant climatic transitions of the LGM (c. 20,000 years ago) and the Terminal Pleistocene/Holocene boundary (c. 12,000-8,000 years ago).*

Within the prehistoric faunal assemblages of Late Pleistocene and Holocene Sri Lanka, it is the proportion of primate specimens that is perhaps of greatest interest from the perspective of human subsistence strategies, with human populations seemingly placing particular importance in the hunting and utilisation of these fauna (Chapter 2 – Section 2.2). Importantly, across the climatic and vegetation zones covered by the samples obtained for this thesis, all three existing Sri Lankan primate species – grey crested langur (*Semnopithecus priam thersites*), toque macaque (*Macaca sinica*), and purple leaf monkey (*Trachypithecus vetulus*) (Phillips, 1926, 1980) – are available. These species have their own distinct ecological niches in modern Sri Lanka (Chapter 4 –

Section 4.4). The tracking of these niche distinctions further back in time, using stable carbon and oxygen isotope analysis of fossil tooth enamel, and modern enamel and vegetation reference datasets, should enable the testing of the hypothesis that:

3. *Late Pleistocene and Early Holocene forest-dwelling humans in Sri Lanka practised diverse primate hunting strategies to capture the different primate species present at associated archaeological sites.*

1.3 – Thesis structure

This thesis is divided into eight chapters. Chapter Two presents and critically evaluates existing Late Pleistocene archaeological evidence for early human rainforest use in Africa, Southeast Asia, and Melanesia. This chapter presents and describes Sri Lanka as a key case study in the context of Late Pleistocene rainforest adaptations. Issues of preservation, visibility of sites, and reconstruction of rainforest resource use in 'rainforest archaeology' are also discussed (Krigbaum, 2005). Chapter Two ends by highlighting areas of research that have currently been largely neglected in studies of early human 'rainforest prehistory' worldwide.

Chapter Three explores the ecological category of 'rainforest', evaluating how it has been applied in both anthropological and archaeological studies. This includes a global review of Late Pleistocene-Early Holocene climatic impacts on rainforest environments, with a particular focus on Sri Lanka. Following this is a more specific archaeological and ethnographic exploration of the subsistence strategies human hunter-gatherers have implemented across the world's rainforests, both past and present, with particular attention paid to the capture of rainforest primate species.

Chapter Four presents stable isotope analysis of tooth enamel as a tool for assessing prehistoric human rainforest resource reliance and subsistence strategies. Stable carbon and stable oxygen isotope tropical rainforest dynamics are discussed, with particular attention paid to stable isotope studies of tropical primates and hominins. Issues of diagenetic alteration of enamel, and possible means to test and subvert this, are evaluated. Chapter Four also discusses the necessity of a modern isotopic reference collection to facilitate interpretation of archaeological primate stable isotope datasets.

In Chapter Five, the stratigraphies, chronologies and samples from the Microlithic tradition sites analysed in this thesis (Fa Hien-lena, Balangoda Kuragala, Bellan-bandi Palassa, and Batadomba-lena) are discussed in detail. The Polonnaruwa Nature Sanctuary and Archaeological Reserve, from which modern vegetation and primate enamel samples have been obtained, is also introduced as an important modern baseline for the interpretation of Sri Lankan primate niches. Chapter Five ends with a detailed discussion of the exact methods of diagenetic control, stable isotope sampling and analysis, and statistical evaluation employed in this thesis.

Chapter Six reports the results of studies designed to assess preservation (or diagenesis), followed by the stable isotope measurements of fauna and humans from the four Late Pleistocene and Holocene sites sampled in this thesis. The results from Fa Hien-lena, Bellan-bandi Palassa and Balangoda Kuragala are then discussed in the context of tracking the potential presence of modern Sri Lankan Wet, Dry and Intermediate Zone vegetation into the Terminal Pleistocene/Early Holocene. The results from Batadomba-Lena are discussed in terms of earlier, Late Pleistocene human isotopic niches and ecology in the modern-day Wet Zone of Sri Lanka.

Chapter Seven focuses on the stable isotope results from the archaeological primates sampled at all four sites. These results are interpreted in light of stable carbon, oxygen and nitrogen isotope results analysed from the modern vegetation, and stable carbon and oxygen isotope measurements of modern primate enamel, samples from the Polonnaruwa Nature Sanctuary and Archaeological Reserve. Niche distinctions between *Macaca sinica*, *Tracypithecus vetulus*, and *Semnopithecus priam thersites*, past and present, are discussed, alongside the potential importance of these different niches in the context of prehistoric human rainforest subsistence in Sri Lanka.

Chapter Eight concludes this thesis by bringing together the isotopic results to address the three main hypotheses developed in Section 1.2. This includes an assessment of the ability of the stable carbon and oxygen isotope analysis of human tooth enamel to test the nature and extent of Late Pleistocene human reliance on rainforest resources. The complications and potential in the use of archaeological primate enamel to shed light on Microlithic tradition subsistence strategies are also highlighted. Chapter Eight also relates the stable isotope data presented in this thesis to broader theoretical questions regarding whether adaptation to tropical rainforest environments in general is fundamentally a 'risk' or an 'opportunity' for our species.

Chapter 2 - Early human encounters with tropical forest environments

This chapter presents a review of the earliest evidence for human presence within the tropical forest environments of Africa, Southeast Asia, Melanesia and Australia before focusing in on Sri Lanka as a particularly interesting example of Late Pleistocene human-rainforest interaction. The nature of the evidence that has been used to infer human rainforest use, as well as the anthropological and ecological debate surrounding the possibility of human rainforest resource reliance, is critically evaluated. This discussion, as well as the current lack of detailed investigation into specific rainforest ecologies occupied by Late Pleistocene humans (Chapter 3), presents a series of questions, about the nature, longevity, and intensity of *Homo sapiens'* initial rainforest subsistence and adaptations, that have yet to be systematically investigated in the context of the Late Pleistocene archaeological record.

2.1 – Late Pleistocene human rainforest occupation in Africa, Southeast Asia, Melanesia and Australasia

Although there is evidence for their early presence in tropical forest environments during the Pleistocene (Bonnefille, 1994; Swisher *et al.,* 1994; Mercader, 2002a, 2002b; Brumm *et al.,* 2010), no hominin species has been shown to be exclusively adapted to closed forest environments (Mercader, 2002a, 2002b). It has been argued that *Homo erectus* reached Southeast Asia, 1.2 million years ago, at a time of widespread tropical forest (Sémah *et al.,* 2002). Association of this early member of our genus with rainforest fauna in the region potentially confirms this (Huang *et al.,* 1995; Brumm *et al.,* 2010; Sémah and Sémah 2012). While it has also been suggested that *Homo erectus* actually avoided rainforest environments (Ciochon 2009), finds of *Homo floresiensis* at

Liang Bua, Flores, Indonesia, *c.* 100-60,000 cal. years BP (Sutikna *et al.,* 2016), in an environment at least partially characterised by tropical forest (Westaway *et al.,* 2009), may provide a further indication of long-term hominin rainforest presence and evolution (Morwood and Jungers 2009; Brumm *et al.,* 2010; Sutikna *et al.,* 2016). Nonetheless, direct evidence for the use and consumption of rainforest resources by these hominin species is thus far completely absent and it is only with the emergence of our own species, *Homo sapiens*, *c.* 200 ka, that clear, detailed evidence has emerged, in multiple regions, of rainforest colonisation and exploitation (Figures 2.1 and 2.2).

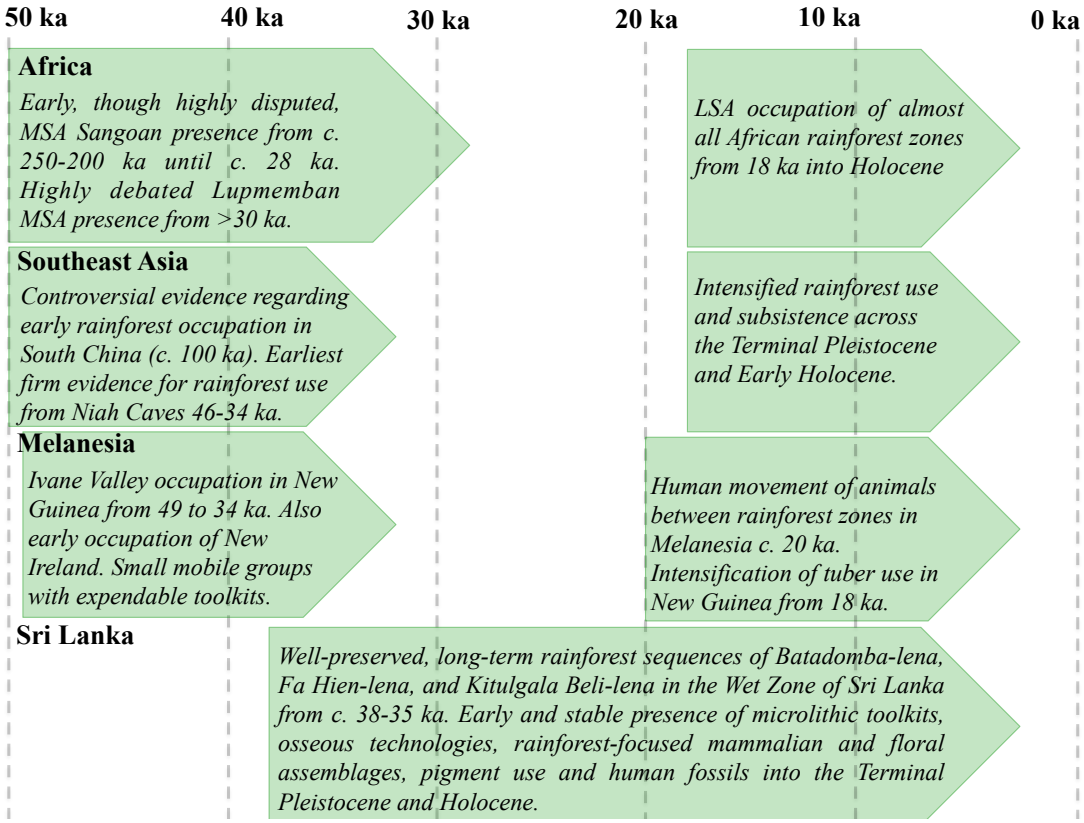


Figure 2.1. Schematic illustration of evidence for Late Pleistocene human forager rainforest occupation in Africa, Southeast Asia, Australasia and Sri Lanka with focus on the last 50,000 years.

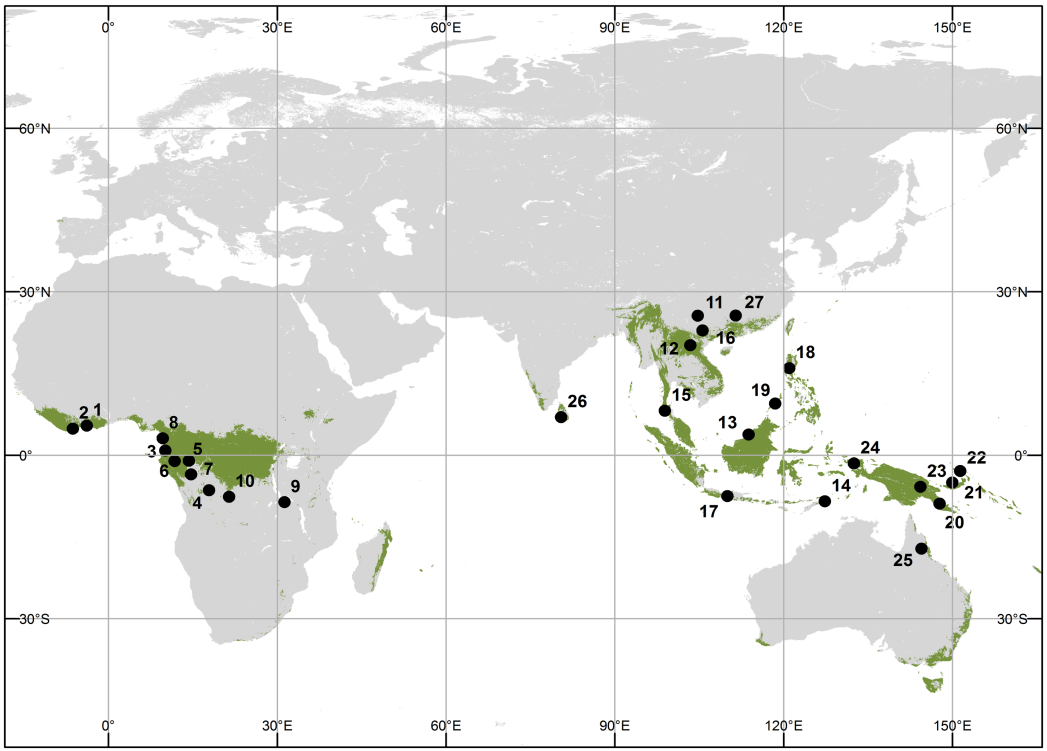


Figure 2.2. Sites postulated as having evidence for pre-Terminal Pleistocene (c. 18 ka) human rainforest occupation and exploitation plotted in relation to the current distribution of tropical forest determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the U.S. Geological Survey Earth Resources Observation System (EROS) Data Center (EDC). 1. Bete 2. Guabuo 3. Médoumane 4. Kango 5. Okala 6. Okanda 7. Ogooué basin 8. Mosumu 9. Kalambo Falls 10. Mufo 11. Panxian Dadong 12. Tam Pa Ling 13. The Niah Caves 14. Matja Kuru 2 15. Lang Rongrien and Moh Khiew 16. Nguòm 17. Punung Cave sites 18. Luzon 19. Palawan 20. Ivane Valley sites 21. West New Britain sites (Yombon region) 22. New Ireland sites (Buang Merabek, Matenkupkum and Matenbek) 23. Nombe 24. Bird's Head Peninsula, Western Papua New Guinea 25. Northeastern Queensland sites (Walkunder Arch, Fern Cave, Nguarrabullgan, and Lake Euramoo) 26. Sri Lanka sites: Batadomba-lena, Fa Hien-lena, Kitulgala Beli-lena 27. Fuyan Cave.

Africa

Julio Mercader's work in Africa provided the first real stimulus behind recent archaeological investigations of early human rainforest exploitation. In his analysis of the Middle Stone Age (MSA) Sangoan technocomplex, found throughout the equatorial regions of Central Africa, West Africa, western East Africa, and South-Central Africa, Mercader (2002a, 2002b) suggested the possibility that some of the earliest members of our species flourished in rainforest environments rather than avoiding them. The heavy duty elements of this industry, including large bifacial sub-triangular 'pick' forms, massive core-scrapers, and coarse Acheulean-like bifaces, have led some authors to suggest that this is an archaic complex (Lioubine and Guede, 2000; McBrearty and Brooks, 2000). Indeed, its age and technological affinities, although strongly debated, potentially reach back to 250 ka, placing it at the limits of the oldest fossil appearance of our species (Barham, 2000). Although some archaeologists question the existence of this technocomplex as a distinct entity altogether, or whether it can be associated with MSA humans, the archaeological evidence of the Sangoan, supported by palynological and geological inference (Jahns *et al.,* 1998; Dupont *et al.,* 2000), potentially hints at the very early movement of our species into tropical forest environments (Barham, 2000; Mercader, 2002a; Basell, 2008).

The Sangoan has been reported from the rainforest region of Ivory Coast, at Bete and Guabuo, dated by thermoluminescence to as early as *c.* 254 ka (Lioubine and Guede, 2000; Mercader, 2002a). Palynological records from 'neighbouring' marine cores have indicated open forest conditions at Bete and closed forest at Guabuo (Mercader, 2002a). However, Mercader (2002a) reports these dates without error margins. Furthermore, the marine cores used to reconstruct local palaeoenvironments are up to *c.* 200 km away

(Jahns *et al.,* 1998; Dupont *et al.,* 2000), inherently 'off-site', of unknown relevance to site-specific habitats, and difficult to correlate chronologically with West and Central African Sangoan archaeological records that have been subject to considerable depositional re-working that prohibits the development of detailed chronological frameworks (Basell, 2008; Blome *et al.,* 2012). The Sangoan has also been documented from the lowland forests of Gabon at Médoumane, Kango, Okala and Okanda, as well as in southern Cameroon (Mercader and Martí, 1999). Sparse palaeoenvironmental evidence has been argued to indicate proximate rainforest (Bayles des Hermens *et al.,* 1987; Clist, 1993, 1995) but this evidence is again indirect and difficult to compare both chronologically and spatially with periods of MSA activity and occupation. Modern rainforest distributions, or indirect, off-site marine cores, cannot be used as a reliable proxy for local rainforest extent in Pleistocene Africa, where rainforests have been argued to be vulnerable to reduction during glacial periods with cooler temperatures, decreased rainfall, and lower atmospheric CO_2 concentration (Maley and Brenac, 1998; Malhi and Wright, 2004; Blome *et al.,* 2012) (Chapter 3 – Sections 3.2 and 3.3).

The Lupemban industry, characterised by bifacially flaked lanceolate points has also been argued by Mercader, among others, to provide evidence for MSA tropical forest colonisation (J.D. Clark, 1963, 1971, 1988; Barham, 2000, 2001; Mercader, 2002a). Core-axes have been associated with heavy-duty digging activities for tropical roots and tubers (Ichikawa, 1996), while Lupemban lanceolates, points, backed blades, and tranchets have been linked to the hunting of terrestrial and arboreal fauna (Barham, 2001). The distribution of Lupemban sites, focused around the Congo Basin and its eastern and southern margins (J.D. Clark, 1967; Cole, 1967) has been superimposed onto contemporary distributions of rainforest and woodland ecosystems (Mayaux *et al.,* 2004) to suggest a close relationship between this technocomplex and the southern edge

of the Central African rainforest zone (Bayles des Hermens, 1975; Taylor, 2011). Similarly, pollen records have been used to associate sites of Lupemban finds, such as those within the Ogooué Basin and Mosumu in Equatorial Guinea, dated to as old as *c.* 30-20,000 cal. years BP, with modern tropical forest or reconstructed tropical forest for the recent past (Mercader and Martí, 2002).

There is currently, however, scant empirical evidence linking Lupemban stone tools to the exploitation of rainforest resources (Cornelissen, 2002). Post-depositional disturbance of the majority of Lupemban sites has led to considerable difficulties in dating the technocomplex, with estimated dates converging on the range 40-12 ka, resulting in coarse palaeoenvironmental correlations (J.D. Clark and Brown, 2001; Cornelissen, 2002; Taylor, 2011). Contractions in the Central African rainforest during the last glacial period would have resulted in an advance and admixture of seasonal, semi-deciduous forests and savannah grasslands at its fringes (Thomas, 2000; Basell, 2008; Blome *et al.,* 2012) (Chapter 3 – Sections 3.2 and 3.3). Consequently, the main distribution of Lupemban sites, sitting on the current border of the region's rainforests (Taylor, 2011), may not have been located in rainforest during periods of occupation. Where on-site palaeoenvironmental records are available for the Lupemban, deposits tend to be disturbed, leaving palaeoenvironmental reconstruction limited to modern contexts or the more recent past (Mercader and Martí, 2002; Mercader *et al.,* 2003). At those sites where well-stratified archaeological sequences are associated with palaeoenvironmental records, including Kalambo Falls, northern Zambia (J.D. Clark, 1969; J.D. Clark and Brown, 2001; Taylor *et al.,* 2001) and Mufo, Angola (J.D. Clark, 1963), pollen and faunal sequences indicate that the tool industry corresponds with deciduous woodland and open savannah ecosystems.

Therefore, while both the Sangoan and Lupemban hint at potentially early human encounters with tropical forests in Africa, poor palaeoenvironmental resolution, chronological correlation, and a considerable lack of direct subsistence or technological use information, has meant that there has been little understanding regarding the local environments of *Homo sapiens* at these MSA sites as well as human behaviours that may have enabled them to exploit the tropical forests of Central Africa. More systematic palaeoenvironmental analyses, at resolutions of both region and site, are now being undertaken in tropical Africa. These records increasingly suggest that MSA human groups tracked the formation of forest, woodland, and open mosaics during periods of increased climatic aridity (Basell, 2008; Blome *et al.,* 2012), albeit with potentially increased specialisation in forest and woodland biomes during wetter periods (Mercader *et al.,* 2013). This fits earlier suggestions that both the Lupemban and Sangoan industries demonstrate strong technological continuity across postulated forest habitats and open environments (Van Noten *et al.,* 1972; McBrearty, 1988).

It is only in the Later Stone Age (*c.* < 40 ka) that more extensive and specialised human settlement of the African rainforests occurred (Mercader, 2002a, 2002b), with many of the Central African forest regions being settled prior to the Holocene (Mercader *et al.,* 2003). In the Ituri region, three phytolith sequences indicate high percentages of arboreal rainforest taxa in association with cultural remains, dating across the last 18,000 years, indicating sustained hunter-gatherer settlement of the lowland forests of the northeast Congo Basin (Mercader *et al.,* 2000). Almost all twelve countries that make up the African rainforest demonstrate dense evidence for Later Stone Age occupation. The sites of Bosumpra (Ghana) and Yengema Cave (Sierra Leone), as well as 50 sites characterised as Later Stone Age in Central Africa, yield archaeological evidence in lowland evergreen, seasonal, dry, and mosaic forest contexts prior to the

Holocene (Coon *et al.,* 1968; Smith, 1975; Mercader and Martí, 2002). Furthermore, palynological sequences from Atlantic Central Africa and West Africa, as well as phytolith data from the eastern Congo-Kinshasa, indicate that Later Stone Age hunter-gatherers continued to inhabit rainforests throughout the climatic and vegetation changes of the Terminal Pleistocene/ Early Holocene (Mercader, 2002a, 2002b).

Southeast Asia

Alongside possible evidence for early hominin interaction with rainforest environments, Southeast Asia is also potentially home to some of the earliest fossils of our species in tropical forest contexts. Four teeth at Panxian Dadong in South China, dated to between 300-130 ka, based on biostratigraphy, U-series, and Electron Spin Resonance dating (Shen *et al.,* 1997; Rink *et al.,* 2003; Schepartz and Miller-Antonio, 2004), have been identified as *Homo sapiens* (Schepartz *et al.,* 2000), and associated with fauna indicative of mixed woodland, bamboo forest, and grassland (Schepartz *et al.,* 2000). However, the species attribution of the teeth, and their chronological association, remains debatable (Liu *et al.,* 2013). Confirmed early *Homo sapiens* have been found at Fuyan Cave, in Daoxian, South China, dated to *c.* 100 ka and in association with mixed tropical rainforest, woodland, and grassland fauna (Liu *et al.,* 2015), though their relationship to the dated flowstone remains disputed (Maxime Aubert, pers. comm.). A premolar possibly dating to earlier than *c.* 100 ka on the island of Java, associated with Punung tropical rainforest fauna, has been argued to represent early human rainforest presence in Indonesia (Storm *et al.,* 2005; Storm and De Vos, 2006; Westaway *et al.,* 2007). However, only one tooth was found and its identification and dating remains provisional (Storm *et al.,* 2005; Barker *et al.,* 2007; Bacon *et al.,* 2008). The recent find of *Homo sapiens* fossils at Tam Pa Ling, Laos, dated to between *c.* 60 and 46 ka, though

lacking palaeoenvironmental information, represents another potentially early human fossil presence in the tropical ecologies of this region (Demeter *et al.,* 2012).

It is at the Niah Caves, Borneo, however, where significant advances have been made in the study of early interactions of our species with tropical rainforests, and where the earliest firm evidence for tropical forest exploitation by *Homo sapiens* in Southeast Asia exists (Barker *et al.,* 2007; Barker, 2013). Located in Sarawak, the Niah Caves have yielded another early human fossil in this region (*c.* 44,000-40,000 cal. years BP) (Higham *et al.,* 2009) associated with human activity dated to between 46,000 and 34,000 cal. years BP (Barker *et al.,* 2007). Multidisciplinary analysis of sedimentology, pollen, phytoliths, macrobotanical remains, starch grains, and vertebrate remains has indicated that human foraging activities were tailored to a tropical forest environment, including the collection and processing of toxic plants, potential alteration of forest edges, and the hunting of arboreal taxa (Rabett *et al.,* 2006; Barker *et al.,* 2007; Rabett and Barker, 2007; Barton *et al.,* 2009; Hunt *et al.,* 2012; Piper and Rabett, 2014). These datasets, alongside detailed studies of the earliest record of bone technology in Southeast Asia, dated to *c.* 45,000 cal. years BP (Rabett *et al.,* 2006; Barker *et al.,* 2007), make the Niah Caves one of the best examples of detailed Late Pleistocene human rainforest subsistence reconstruction.

Nonetheless, vegetation in the immediate vicinity of the Niah Caves has been shown to vary significantly over time, including wet lowland forest, montane forest, mangrove forest, savannah and grassland (Barker *et al.,* 2007; Hunt *et al.,* 2012). While large numbers (16% of the number of identified vertebrate specimens) of arboreal tropical forest primates were likely exploited through projectile hunting (Barker *et al.,* 2007), the faunal assemblage has generally been argued to be representative of the human

exploitation of mosaic habitats, of which tropical rainforest was one (Cranbrook, 2000). Moreover, Hunt *et al.* (2012) suggest that during periods of maximum forest extent, human groups at the Niah Caves deliberately practised vegetation burning and disturbance in order to promote the presence of open habitats. Indeed, from the evidence available at present, most early human occupation in both Mainland and Island Southeast Asia appears to have focused on open mosaic habitats (Rabett, 2012; Pawlik *et al.,* 2014). For example, the earliest layers of occupation at the Lang Rongrien rockshelter on the Thai side of the Thai-Malay Peninsula, dated to between *c.* 44,000 and 32,000 cal. years BP, are associated with open savannah-like conditions, with the presence of some open-canopy forest on the basis of molluscan and mammalian assemblages (Anderson, 1997; Mudar and Anderson, 2007). Similarly, although the nearby site of Moh Khiew shows increased exploitation of arboreal taxa *c.* 30,000 cal. years BP, the palaeoenvironmental and faunal data are indicative of a mosaic of open and forest habitats immediately surrounding the rockshelter (Pookajorn, 1996).

Mosaic and shifting environments have also been inferred for the Punung Cave sites in central and eastern Java from 45,000 years ago (Sémah *et al.,* 2002), as well as pre-27,000 cal. years BP and 27,000 cal. years BP layers at the Nguòm rockshelter (Reynolds, 1990). While caves in the Philippines (Détroit *et al.,* 2004; Mijares *et al.,* 2010) have been argued to show Late Pleistocene human presence in rainforest environments, palaeoenvironmental evidence suggests changeable mosaic ecologies on the islands of Palawan and northern Luzon (Pawlik *et al.,* 2014). It is also worth noting that although early bone technologies date from 45 and 35 ka at the Niah Caves and the site of Matja Kuru 2, Timor, Wallacea (O'Connor *et al.,* 2014), respectively, Rabett (2012) has argued that complex bone technologies and a diversification of lithic assemblages only occur during the Terminal Pleistocene and Early Holocene. Indeed,

even at the Niah Caves, it is only in the Terminal Pleistocene layers that complex bone technologies and hunting of arboreal taxa become widespread (Barker *et al.,* 2007). Rabett (2012) links this to increased precipitation and expanding forests, and increased selective exploitation of arboreal and semi-arboreal fauna, at this time (Piper and Rabett, 2009; Rabett *et al.,* 2009; Rabett and Piper, 2012) (though other researchers have suggested rainforest fragmentation – Cannon *et al.,* 2009).

Melanesia and Australia

The earliest evidence for human tropical forest occupation in Australasia comes from the Ivane Valley region of Papua New Guinea. Here, at an elevation of 2,000 metres, archaeological sites have been radiocarbon dated to between 49,000 and 43,000 cal. years BP at the site of Vilukuav (Summerhayes *et al.,* 2010). Waisted stone axes from the early layers of Airstrip Mound, South Kov, and Kosipe (dated to *c.* 40,000 cal. years BP) have been interpreted as implements used to modify forest environments (Groube, 1989). Starch grains of *Dioscorea* yam species and charred *Pandanus* nuts from radiocarbon-dated Ivane Valley sites also indicate the exploitation of forest products from as early as 49,000-43,000 cal. years BP (Summerhayes *et al.,* 2010). Comparably early evidence for the human occupation of modern-day tropical forests on the Late Pleistocene continent of Sahul has been found elsewhere in Papua New Guinea (Summerhayes *et al.,* in press) and the Yombon region of West New Britain in the Bismarck Archipelago where the organised utilisation of tropical forest resources is seen *c.* 35,500 cal. years BP (Pavlides and Gosden, 1994; Pavlides, 2004; Summerhayes *et al.,* in press). Late Pleistocene evidence for human occupation in the tropics of this region has also been documented in New Ireland back to *c.* 40,000 cal. years BP (Leavesley, 2002, 2004, 2005).

In the Ivane Valley of New Guinea, as well as at Late Pleistocene sites in New Ireland such as Buang Merabek, tropical forest foragers have been argued to be small, highly mobile groups, flexibly exploiting local raw materials as part of a seasonal subsistence strategy that made use of a wide variety of environments and ecologies (Pavlides, 2004; Leavseley, 2007; Gosden, 2010; Summerhayes and Ford, 2014; Summerhayes *et al.,* in press). Indeed, the cold temperatures of the Ivane Valley, in particular, make it unlikely that humans lived there permanently (Gosden, 2010) and human activity ceased there almost entirely during the LGM (Summerhayes *et al.,* 2010). While there is evidence for the exploitation of montane tropical forest resources at the Ivane Valley, limited forest-specific subsistence evidence is available from the mosaic tropical ecologies of West New Britain and New Ireland. Furthermore, detailed reconstruction of local ecological and environmental contexts is almost completely lacking across West New Britain, New Ireland, and the Ivane Valley. Overall, there is currently limited indication that humans were able to specialise in the occupation of Melanesia's rainforests at this time.

It is arguably not until after *c.* 26 ka and into the Terminal Pleistocene (*c.* 18 ka) that Melanesia began to witness intensive human occupation and manipulation of tropical rainforests. Two long-term cave sequences in the Bird's Head region of western New Guinea have been argued to provide evidence for rainforest hunting strategies during the last 26,000 years (albeit with these behaviours only really intensifying during the Middle Holocene) (Pasveer, 2004). Further sites across the rest of New Ireland (including Buang Merabek, Panakiwuk and Balof) and mainland Papua New Guinea (Nombe, NFX, and Wañelek) also show increasing evidence for human tropical forest presence at this time (Pavlides, 2004; Leavesley, 2007). Evidence from the site of Matenkupkum, New Ireland, indicates that post-LGM (*c.* 20-18 ka) people began to

introduce wild animals into forest ecosystems, naturally poor in animal protein, that they were now persistently inhabiting over the long-term (Gosden and Robertson, 1991; Gosden, 1995). Ecological manipulation culminates in the emergence of horticulture in Papua New Guinea during the Early Holocene *c.* 9 ka, with intensive clearance and the progressively specialised exploitation of endemic plants and animals (Golson, 1977; Gosden, 2010).

Despite Australia being joined to New Guinea, and the rest of Sahul, until the end of the last glacial cycle (Allen *et al.,* 1977), firm evidence for the early human occupation of its rainforests has yet to be established. A thin strip of fragmented rainforest in the far north of Queensland is buffered from fire-prone sclerophyll vegetation by wet sclerophyll forests, characterised by a sclerophyll overstory and fire tolerant rainforest species underneath (Head, 1996; Hilbert *et al.,* 2001). It has been argued that frequencies of charcoal and pollen in sediment sequences, including those from Lake Euramoo, can be associated with the onset of anthropogenic exploitation of the fire-prone sclerophyll vegetation from *c.* 30,000 years ago (Kershaw, 1985, 1986; Haberle, 2005; Haberle *et al.,* 2010). However, inferences of early human presence in these forests are based on indirect association of burning with human action (Cosgrove *et al.,* 2007). No archaeological evidence for Pleistocene human occupation has been found where excavation has been attempted (Cosgrove and Raymont, 2002). Human occupation of the rainforests themselves is evident only with the Holocene expansion of rainforest from *c.* 8,000 years ago (Cosgrove *et al.,* 2007; Haberle *et al.,* 2010). From this point in time, peaks in rainforest and sclerophyll burning, and archaeological traces in Australia, occur alongside potential Middle-Late Holocene use of domesticated plantain and taro (Denham *et al.,* 2009).

2.2 – Late Pleistocene human occupation of Sri Lankan tropical forest

Compared to the regions discussed in Section 2.1, early human encounters with South Asia's rainforests have remained relatively little-explored (Mercader, 2002b), despite the fact that the earliest human fossils from this region (dated to as early as *c.* 38-35,000 cal. years BP) were found within the lowland tropical rainforest contexts of Sri Lanka (Wijeyapala, 1997; Kennedy, 2000; Perera, 2010; Roberts *et al.,* 2015a). In contrast to the limited density of occupation and relative paucity of technological change apparently demonstrated by the earliest human inhabitants of tropical forests in Africa, Melanesia and, to a lesser extent, Southeast Asia (Section 2.1), *Homo sapiens* fossils found in modern-day Sri Lankan rainforest are accompanied by early and persistent microlith toolkits, bone technologies, and evidence for the exploitation rainforest flora and fauna from *c.* 38,000-35,000 to 3,000 cal. years BP (Wijeyapala, 1997; Perera, 2010; Perera *et al.,* 2011, in press; Lewis *et al.,* 2014). This long-lasting human fossil, technological, and cultural florescence, as well as a series of well-preserved tropical forest rockshelter sites, makes Sri Lanka an important case study in the context of appraisals of the nature of early human encounters with tropical forests.

Geology, climate, and environment

The island of Sri Lanka lies *c.* 48 km off the southern tip of the Indian subcontinent, with an overall area of approximately 65,610 km^2. Geologically, 90% of the island consists of crystalline rocks formed during granulite and amphibolite metamorphism. The remainder of the island is composed of sedimentary Jurassic, Tertiary and Quaternary age formations (Cooray, 1967; 1994). Prior to 130 million years ago (Ma), Sri Lanka formed a bridge linking east Gondwana (Australia, Antarctica, India, and Madagascar) and west Gondwana (Africa and South America). At 130 Ma, Sri Lanka

and India separated from this landmass to move in a northeasterly direction. Fossil reef data indicate that Sri Lanka was intermittently connected to mainland India throughout the Pleistocene period (Rohling *et al.,* 1998), until sea level rise led to its complete separation during the Early-Middle Holocene (Vaz, 2000).

Although historical records refer to 'Adam's Bridge', a navigable land bridge connecting Sri Lanka and India up until the 15th century AD (Ganga Ram, 1992), Remote Sensing Satellite data suggest that this is composed of a number of small patch reefs that are unlikely to have resulted in any sustained above-water contact, given the current data available for Sri Lankan sea-level, during the Holocene (Bahuguna *et al.,* 2003). Modelling of GEBCO.08 bathymetry data indicates that decreases in sea-level of just 10 m in the past would have lead to substantial connections between Sri Lanka and India, with a land bridge >100 km wide becoming visible with a 50 m drop (Figure 2.3). However, neither mark was apparently reached during the Middle-Late Holocene (Ranasinghe *et al.,* 2013).

The majority of Sri Lanka is made up of low-lying plains, between 30 and 200 m above mean sea level (a.s.l.), though the central highlands of the island reach to above 2,500 m a.s.l. (Figure 2.4). This leads to a temperature gradient from *c.* 27°C in the Sri Lankan lowlands to 18°C across the central highlands of the island (Erdelen, 1988; Ashton *et al.,* 2001). The major climatic parameter of Sri Lanka, however, is rainfall, with the seasonality and amount of precipitation being predominantly governed by the major Asian monsoonal forces (Wang *et al.,* 2005). During the months of May and October, the 'wet season' of the southwestern regions of Sri Lanka is brought by the tropical southwest monsoon. By contrast, the northeast of the island receives the majority of its precipitation between the months of December and March.

These monsoonal forces result in wide annual precipitation ranges across Sri Lanka, from *c.* 635 mm to well over 4,000 mm (Puvaneswaran and Smithson, 1993). This has led to the division of Sri Lanka into climatically defined 'zones'. These have often been characterised by subject-specific definitions utilising various criteria including isohyets, effective rainfall (Cooray, 1948), and vegetation (Gaussen *et al.,* 1965) rather than objective precipitation data. Here, I model annual precipitation across Sri Lanka using Worldclim 1.3 records of international precipitation (Figure 2.5). Although coarser than the locality-based, inter-seasonal studies of Puvaneswaran (1992) and Puvaneswaran and Smithson (1993), the results broadly correlate with these studies, as well as those defined on the basis of vegetation and relief (Dittus, 1977a; Gunatilleke and Gunatilleke, 1985; Ashton and Gunatilleke, 1987).

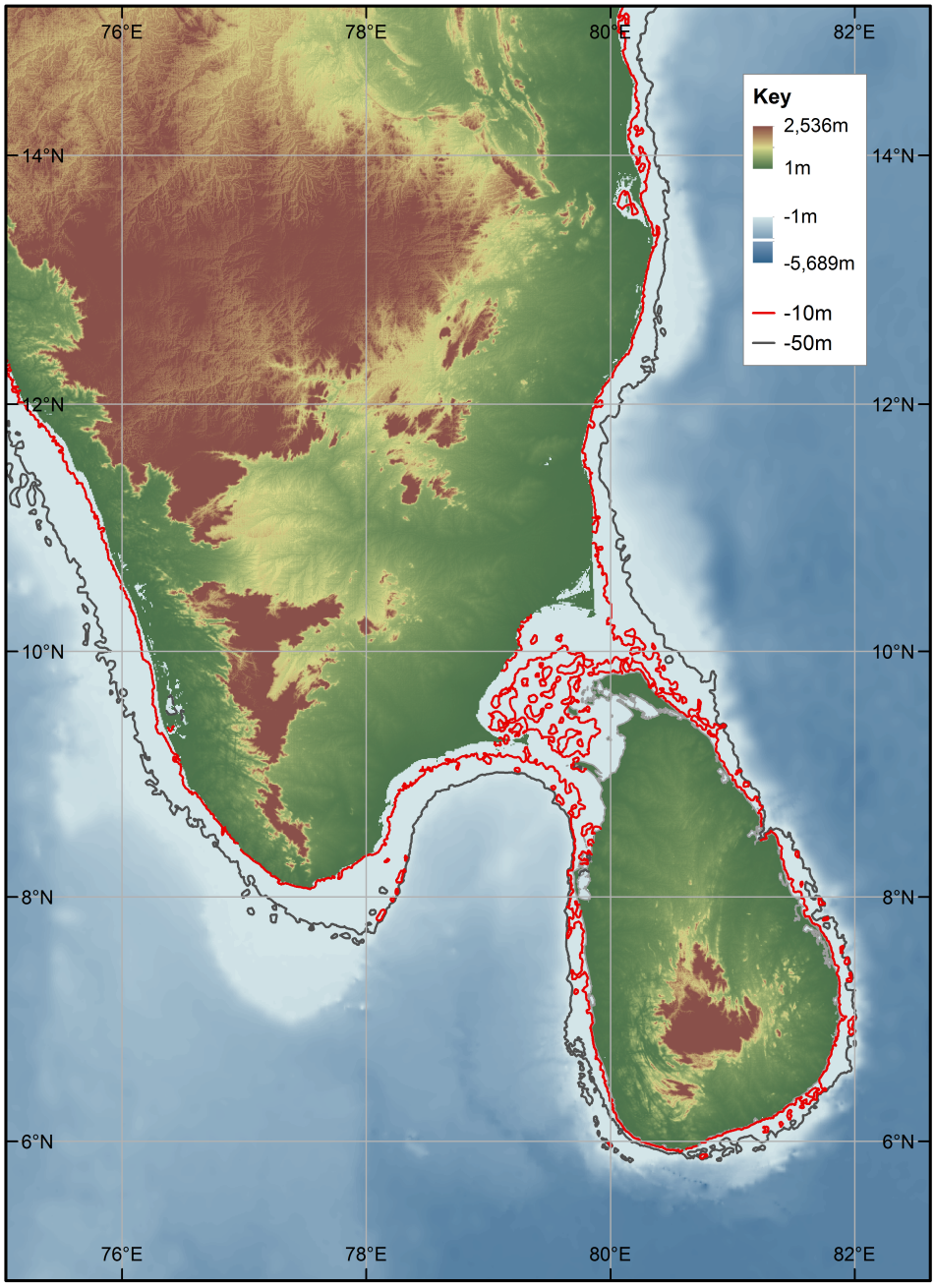


Figure 2.3. Bathymetry model for Sri Lanka and Southern India using the GEBCO.08. 30Arcsecond dataset. Red and black lines show the position of the coastline following drops in sea-level of 10 and 50 metres, respectively.

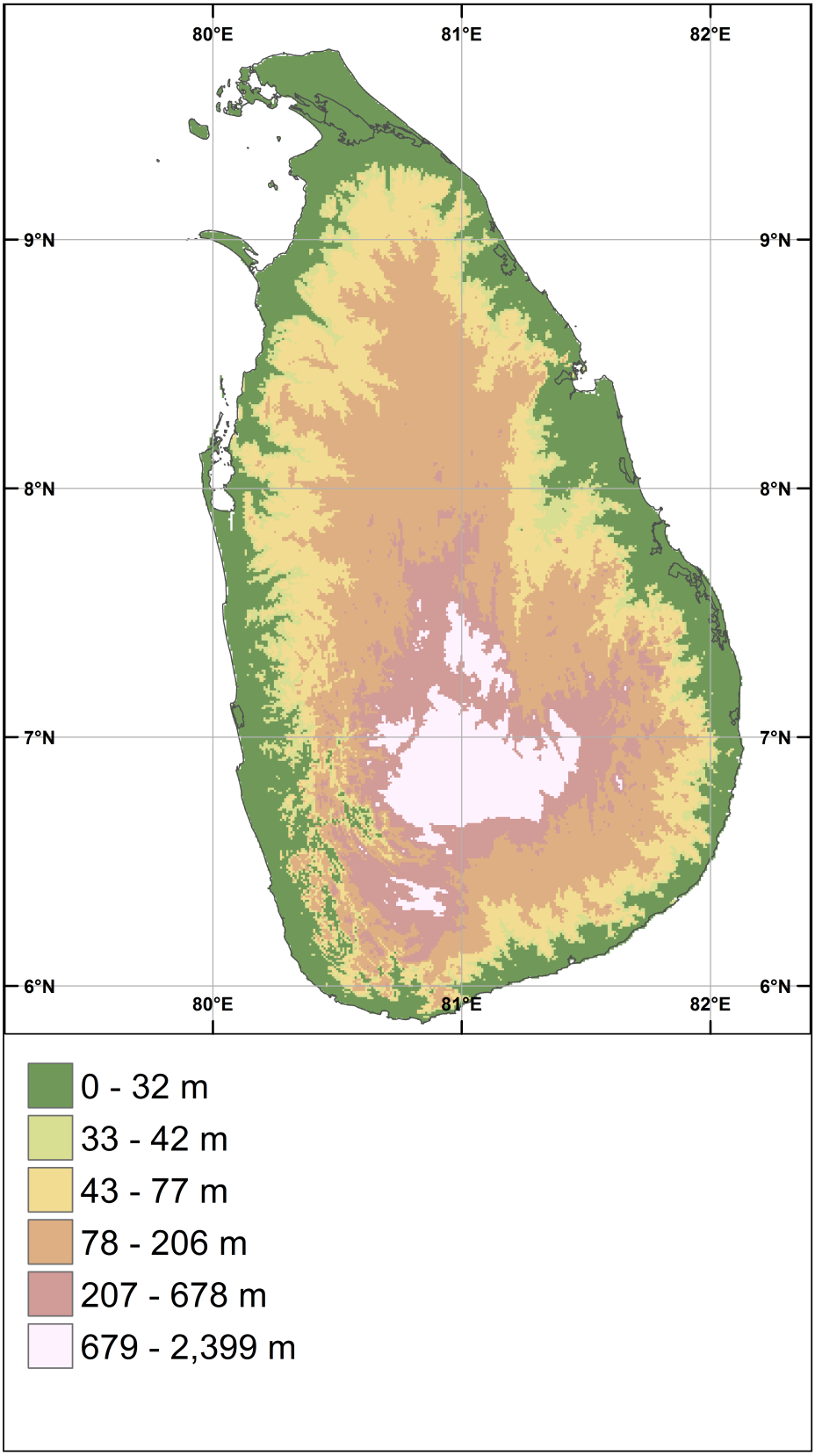


Figure 2.4. Elevation map of Sri Lanka based on Digital Elevation Model data. Source CGIAR SRTM (3 seconds resolution). Divided geometrically into six categories on the basis of the number of spatial cells covered.

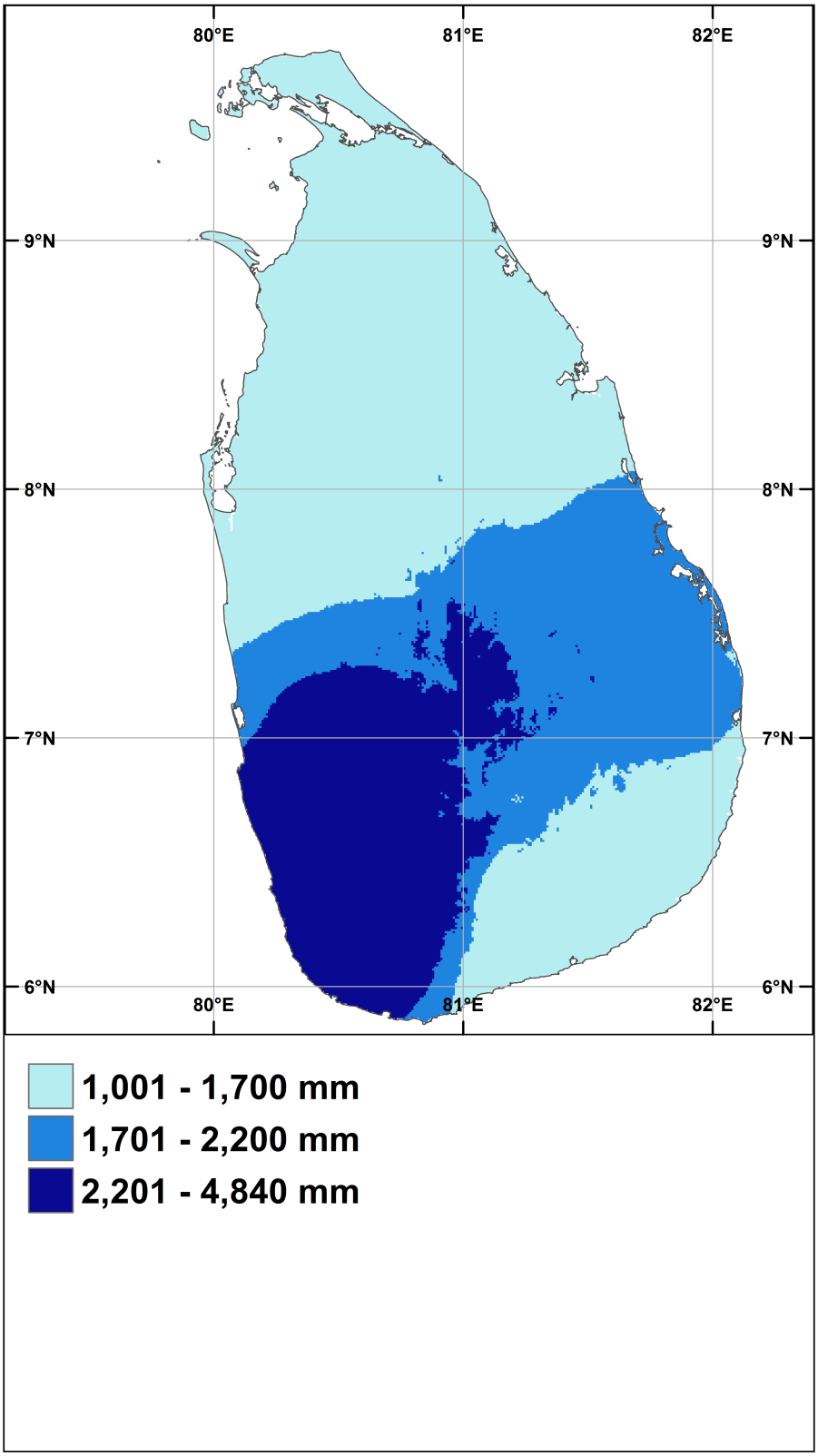


Figure 2.5. Precipitation map of Sri Lanka. Source Worldclim 1.3. Annual precipitation is geometrically divided into three categories on the basis of number of spatial cells covered. The result broadly correlates with designations of 'Wet', 'Dry' and 'Intermediate' zones followed in previous studies of vegetation, elevation, and precipitation.

The highest annual precipitation within Sri Lanka occurs at the altitudinal gradient between the southwestern coastal plain and the central highlands, where the mountainous terrain captures warm, moist air prevailing from the Indian Ocean. This 'Wet Zone' receives between 4,840 and 2,201 mm of annual rainfall (Figure 2.5). The semi-arid and arid 'Dry Zone' of Sri Lanka makes up the majority of the rest of Sri Lanka's landmass, covering the northern and southeastern coastlines, as well as the majority of the northern interior, with mean annual rainfall between 1,001 and 1,700 mm. There is considerable rainfall variability within this larger Dry Zone with the potential for prolonged periods of drought especially at its northernmost reach. Finally, the 'Intermediate Zone' of Sri Lanka lies geographically and altitudinally between the Wet and Dry Zones of the island, in an arc from the centre of its western coast to the southern tip, with mean annual rainfall of between 1,701 and 2,200 mm (Figure 2.5).

These climate zones, as well as broadly corresponding altitudinal features, have an impact on the vegetation distributions of Sri Lanka, leading to corresponding vegetation 'zones' (Dittus, 1977a; Erdelen, 1988) (Figure 2.6). Although heavily curtailed by the urban and industrial expansion of Colombo today, the higher rainfall of the Wet Zone of Sri Lanka has made it home to the island's tropical rainforest flora of closed-canopy wet deciduous, and tropical evergreen mixed dipterocarp forests (Ashton and Gunatilleke, 1987; Gunatilleke *et al.,* 2005) (Zone B-up to 900 m, Zone C- between 900 and 1500 m, Zone D- above 1500 m – Dittus, 1977a; Erdelen, 1988). Tropical moist deciduous rainforest and tropical semi-evergreen forest extend into the Intermediate Zone of the island (Ashton and Gunatilleke, 1987; Gunatilleke and Gunatilleke, 1991) (Zone A4- 'Intermediate rainforest'). However, while patches of tropical evergreen forest exist in the Sri Lankan Dry Zone, these tend to be more open, dry-adapted forest (Somaratne and Dhanapala, 1996)(Zone A3). Large expanses of arid-adapted shrubs and grasslands,

with some ‘monsoon scrub jungle’ or ‘arid zone forest’ along the northern and southern coasts (Zone A1, A2) (Erdelen, 1988), characterise the remainder of this climatic zone.

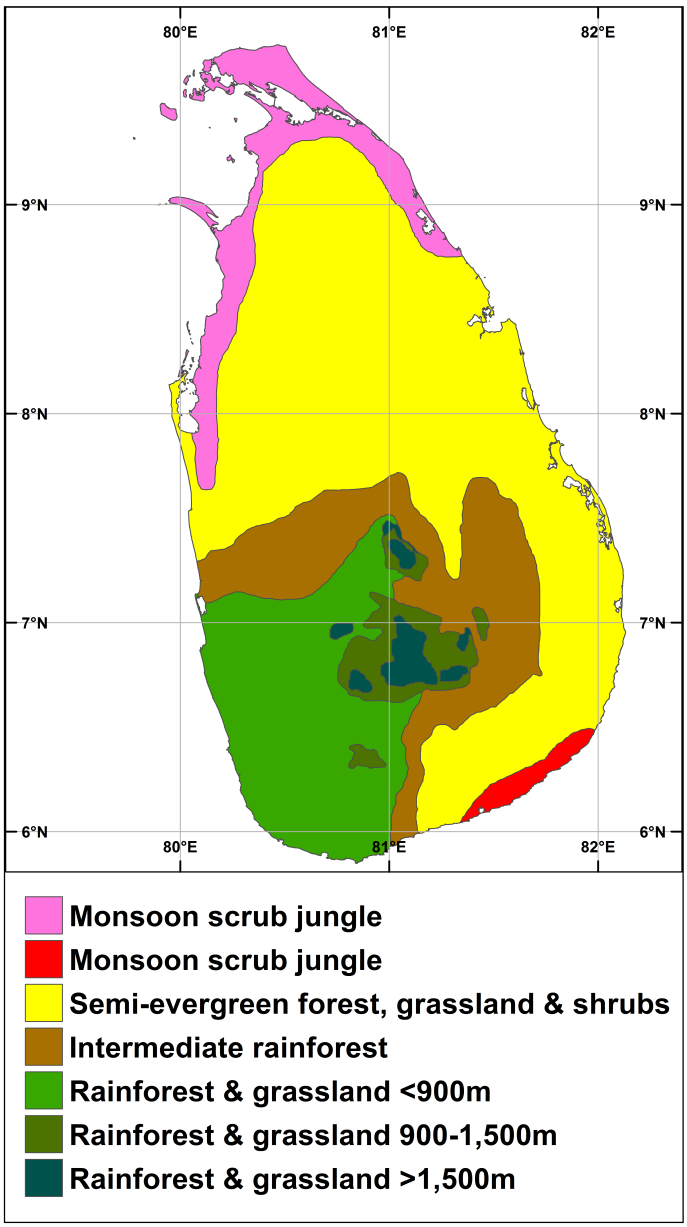


Figure 2.6. Vegetation map of Sri Lankabased on Dittus (1977a), Ashton and Gunatilleke (1987), and Erdelen (1988). Pink (A1) and orange (A2)= monsoon scrub jungle (‘arid zone forest’- Dittus, 1977a); Yellow (A3)= semi-evergreen forest, grassland, and shrubs; Green-brown (A4)= Intermediate rainforest; Light green (B) = rainforest and grassland below 900m; Green (C) = rainforest and grassland between 900 and 1500m; Dark green (D) = rainforest and grassland above 1500m. Comparison with Figure 2.5 shows that border between Zone A4 and B broadly characterises the boundary between the Wet and Intermediate Zones, with the border between A3 and A4 characterising the Dry Zone and Intermediate Zone boundary.

The Sri Lankan Microlithic tradition: chronologies, sites, and material culture

The Late Pleistocene record of Sri Lanka is broadly synonymous with the so-called 'Microlithic' tradition, characterised by very small quartz stone tools, less than 2 cm-long, fashioned into geometric microliths (cf. Mode 5 *sensu* G. Clark, 1969; S.U. Deraniyagala, 1992; Lewis *et al.,* 2014). Unlike many areas of the Old World, the fully-developed microblade assemblages of the Microlithic tradition dominate the Sri Lankan archaeological record following tentative evidence for an earlier Middle Palaeolithic period, with no evidence for what has been termed an Upper Palaeolithic elsewhere (Mellars, 2006) or transitional industries like those described for India (James and Petraglia, 2005). The first appearance of these microlithic toolkits, dated to *c.* 36-29,000 cal. years BP (Perera *et al.,* 2011; Lewis *et al.* 2014; Roberts *et al.,* 2015a), and possibly *c.* 38-35,000 cal. years BP (Wijeyapala, 1997; Perera *et al.,* 2011; Roberts *et al.,* 2015a), is also associated with the earliest confirmed fossil remains of *Homo sapiens* in Sri Lanka (Kennedy and Deraniyagala, 1989; S.U. Deraniyagala, 1992; Wijeyapala, 1997; Perera *et al.,* 2011). This suggests that they can be firmly associated with our species, alongside some of the earliest evidence for osseous technologies and long-distance exchange found anywhere in South Asia (Perera, 2010; Perera *et al.,* in press).

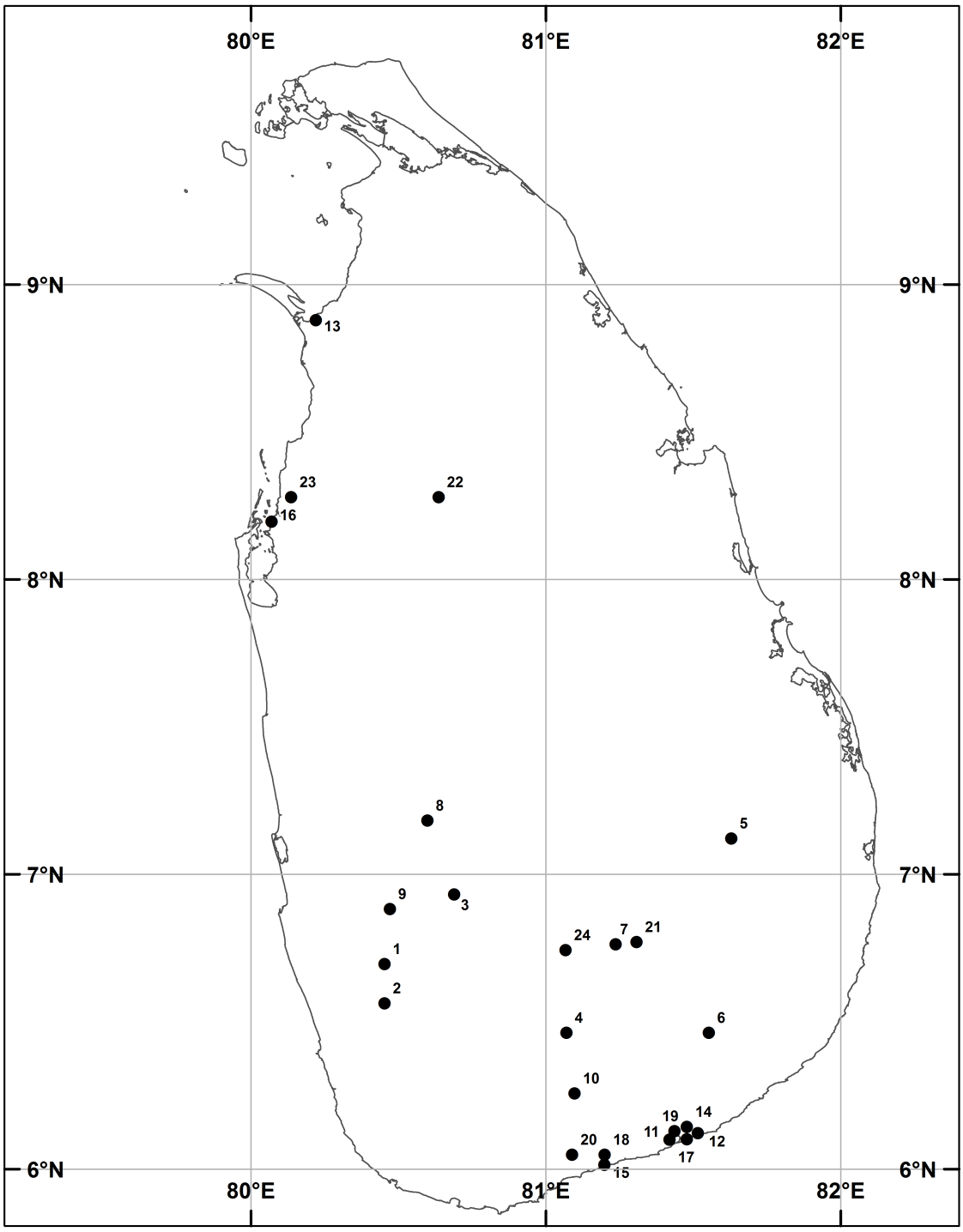


Figure 2.7. Map showing the location of all archaeological and palaeoenvironmental sites discussed in the text: 1. Batadomba-lena, 2. Fa Hien-lena, 3. Kitulgala Beli-lena, 4. Bellan-bandi Palassa, 5. Nilgala Caves, 6. Galge Caves, 7. Bandarawela, 8. Alu-lena Attangoda, 9. Beli-lena Athula, 10. Site 43, 11. Site 49, 12. Site 50, 13. Matota (Mantai), 14. Patirajawela Site 50, 15. Henagahapulgala Site 57, 156. Arnakallu, Site 30, 17. Udamalala, 18. Hungama Mini-athiliya, 19. Pallemalla, 20. Karagan Lewaya, 21. Ravanalla, 22. Anuradhapura, 23. Pomparippu, 24. Horton Plains.

Figure 2.7 plots the prehistoric and palaeoenvironmental sequences of Sri Lanka discussed here. Evidence for the Lower Palaeolithic and Middle Palaeolithic in Sri Lanka comes from three coastal sites on the southern tip of the island (Sites 43, 49, and 50). The earliest confirmed appearance of the Microlithic tradition, however, is at the Batadomba-lena and Fa Hien-lena rockshelters, deep within the Sri Lankan Wet Zone. In the 1990s the microlithic industries and human fossils at these sites had already been dated to 28,500 years BP (S.U. Deraniyagala, 1992) and 33,000 years BP (Wijeyapala, 1997), respectively. Recent additional dates and re-calibration of existing radiocarbon dates now indicate that Batadomba-lena has a sequence of microliths and bone tools that ranges from *c.* 36-29,000 cal. years BP down to *c.* 12,000 cal. years BP (Perera *et al.,* 2011, in press; Lewis et *al.,* 2014; Roberts *et al.,* 2015a) (Chapter 5 – Section 5.1), while Fa Hien-lena has a sequence of human occupation that reaches from 38,000-35,000 cal. years BP to 5,000 cal. years BP (Roberts *et al.,* 2015a). The Wet Zone cave site of Kitulgala Beli-lena provides an additional Microlithic tradition sequence from 31,000 to 2,700 cal. years BP (S.U. Deraniyagala, 1992; Roberts *et al.,* 2015a).

The Microlithic tradition appears to have taken until the Terminal Pleistocene and Early Holocene to spread into the current Intermediate and Dry Zones of Sri Lanka, though it should be borne in mind that prehistoric archaeological research has intensively focused on the rockshelters of the Wet Zone rainforest over the last two decades, perhaps to the neglect of these regions. Re-excavation at the site of Bellan-bandi Palassa, located on the edge of the Intermediate-Dry Zone transition, has dated a series of human burials, microlithic toolkits and faunal remains to *c.* 12,000 cal. years BP (Perera, 2010), while ongoing excavation at the recently discovered site of Balangoda Kuragala in Sri Lanka's Intermediate Zone has also yielded Terminal Pleistocene occupation layers (Perera, pers. comm.; Roberts *et al.,* 2015b) (Chapter 5 – Section 5.1). It is not until *c.* 6,500

years ago that radiocarbon dates suggest a Microlithic tradition presence deep into Sri Lanka's modern-day Dry Zone at a series of shell midden and coastal sites, and the semi-arid lowland Dry Zone sites of Ravanalla and Alu-galge (P.E.P Deraniyagala, 1955, 1956, 1963; S.U. Deraniyagala, 1992) (Figure 2.7). None of these sites have yielded records of continuous occupation remotely comparable to the extent and longevity of those found in the Wet Zone. Although there are huge gaps in archaeological knowledge across the Mid-Holocene of Sri Lanka, microlithic toolkits appear to remain present across Sri Lanka until the appearance of the Sri Lankan Iron Age *c.* 3,200-2,800 cal. years BP (S.U. Deraniyagala, 1972, 1992, 2007). Tentative evidence for the transition from the Microlithic tradition to the Iron Age has been suggested at the sites of Anuradhapura and Pomparippu, though little is known regarding its eventual disappearance (S.U. Deraniyagala, 1992, 2007) (Figure 2.7).

The origins and stability of the Microlithic tradition therefore appear to be tied primarily to the modern-day tropical forests of the Wet Zone of Sri Lanka, though precipitation and vegetation boundaries may have shifted in the past (Chapter 3 – Section 3.3). In Africa, microlithic technologies first appear in savannah and grassland settings (Ambrose, 2002). Yet, in Sri Lanka, these formalised, refined toolkits apparently first appear in a tropical rainforest context (S.U. Deraniyagala, 1992; Perera, 2010; Perera, *et al.,* 2011; Lewis *et al.,* 2014). Whereas osseous technologies appear sparsely and briefly during the earliest signs of potential human occupation of rainforest environments in Southeast Asia (Rabett, 2012), the Sri Lankan Microlithic tradition is associated with remarkably stable and abundant bone toolkits from its first appearance *c.* 38-35,000 cal. years BP (Wijeyapala, 1997; Perera *et al.,* 2011, in press). Further human material investment in the tropical forests of Sri Lanka is suggested by the presence of ochre from *c.* 38-35,000 cal. years BP, and the presence of marine shell beads and shark teeth,

that must have been transported distances of over 80 km from the coast, from *c.* 36,000-29,000 cal. years BP (Wijeyapala, 1997; Perera, 2010; Perera *et al.,* 2011; Lewis *et al.,* 2014). Yet it is only with detailed palaeoenvironmental and palaeoecological data, associated with these material records, that the nature of early human rainforest adaptations in Sri Lanka can be thoroughly investigated.

A rainforest specialisation?

Unlike many rainforest environments where early human presence has been sought, the rockshelter and cave sites of Sri Lanka's Wet Zone provide long, well-dated, well-preserved records of material culture directly associated with ecological evidence from molluscan, faunal, and floral remains. However, until now, systematic multidisciplinary work has only been attempted at Batadomba-lena (Perera *et al.,* 2011). The available faunal records from this site suggest that forest-dwelling, semi-arboreal and arboreal primates consistently make-up between 70 and 80% of the mammalian assemblage over the period of occupation (Perera, 2010; Perera *et al.,* 2011). Similar numbers have been documented at the site of Fa Hien-lena (Wijeyapala, 1997; Perera, 2010). As noted in Chapter 1, this proportion is unheard of elsewhere, even with the modern-day availability of rifles in many parts of the African and Amazonian rainforests (ProWildlife, 2007; Lu, 2010; Papworth *et al.,* 2013), and implies a complex, specialised exploitation strategy. Other resources exploited at Batadomba-lena include mouse deer, porcupine, giant squirrel, mongoose, jungle cat, and civet, abundant freshwater mollusc remains, as well as *Canarium* sp. nuts and other starchy forest plants (Perera *et al.,* 2011).

The focused rainforest subsistence picture indicated at Batadomba-lena is supported by on-site palaeoenvironmental information from molluscan and macrobotanical evidence that indicates the consistent presence of tropical forest in the immediate vicinity of the site through the LGM and into the Terminal Pleistocene (Perera *et al.,* 2011). Similar environmental contexts appear to be demonstrated at the cave and rockshelter sequences of Fa Hien-lena (Wijeyapala, 1997; Perera, 2010) and Kitulgala Beli-lena (Kourampas *et al.,* 2009), though systematic multidisciplinary work at these sites remains limited. Together, the available information is so far indicative of an early and sustained human occupation of rockshelters located within the tropical rainforests of the island's Wet Zone from *c.* 38-35,000 cal. years BP until well into the Terminal Pleistocene and Holocene. When combined with the material records above, the early and stable presence of microlithic toolkits, bone technologies, ochre, and exotic items of symbolic ornamentation, within a tropical forest context, appears to set Sri Lanka apart from other regions of the world where early human rainforest occupation has been suggested.

Nevertheless, there still remain some questions with regard to the extent and nature of human rainforest adaptations in Sri Lanka. Detailed Microlithic tradition 'on-site' palaeoenvironmental data is currently limited to Batadomba-lena. Furthermore, palaeoenvironmental evidence from molluscan and faunal remains, and reconstructed taxa habitat preferences, can be relatively coarse. For example, although three primate species are represented at the Wet Zone sites, at least two (sub) species of these primates can today be found across the Wet Zone, Intermediate Zone, and Dry Zone of the island (Phillips, 1980) (Chapter 4 – Section 4.4). It is possible that faunal and molluscan remains could have been transported to the site from more distant ecologies. There has also been very little work thus far done in terms of functional analysis of the microlithic and bone tool technologies. Perera *et al.* (in press) recently compared the

proportion of osseous technologies at Batadomba-lena to associated faunal records to suggest that these toolkits were potentially correlated with the number of molluscan shells (perhaps suggestive of use as mollusc extractors) and small, terrestrial game, such as civets (perhaps indicative of use within traps). Nonetheless, systematic use-wear studies, such as those from the Niah Caves (Rabett, 2005; Barton *et al.,* 2009), remain to be undertaken, making associations of microlithic and osseous toolkits with rainforest subsistence difficult.

Finally, as will be seen in Chapter 3, 'off-site' palaeoenvironmental and palaeoclimatic data across Sri Lanka currently remains sparse and fragmented. Premathilake and Risberg (2003) have used a pollen sequence from the Highland Plateau to demonstrate fluctuations in forest extent through the Late Pleistocene and Early Holocene (Chapter 3 – Section 3.3). However, this record is both spatially and stratigraphically disconnected from Microlithic tradition sequences of human behaviour. There are also no proximate marine cores to the island of Sri Lanka, leaving assumptions of climatic and environmental change to be based on broad-scale global models (Boivin *et al.,* 2013). Without greater palaeoenvironmental resolution it is difficult to reconstruct the composition, nature, and density of tropical rainforest in the vicinity of Sri Lankan Microlithic tradition sites through time (Perera *et al.,* 2011). Therefore, although there is limited evidence for Late Pleistocene occupation elsewhere on the island, given Sri Lanka's relatively small size, it could be argued that humans were occupying and utilising the Wet Zone rainforest as part of mobile, seasonal subsistence strategies, with long-distance marine item exchange in Late Pleistocene sequences indicative of mobility rather than exchange (Holt, 2003; Lovis *et al.,* 2006).

2.3 – Archaeological evidence for the nature of rainforest hunting and gathering: issues and approaches

A number of issues have made it difficult to investigate past human-rainforest subsistence strategies in detail, both in Sri Lanka and more widely. Tropical rainforests are poor taphonomic environments for archaeological preservation, especially with respect to organic remains likely to provide insights about human subsistence or prevailing environmental conditions (Tappen, 1994). Archaeologists working in such zones are therefore often forced to compare their results with 'off-site' information, using indirect archaeobotanical, archeaozoological and palaeoenvironmental records. Well-preserved stratigraphic archaeological sequences in these tropical environments are limited, and often confined to cave or rockshelter sites, resulting in snapshots of human adaptations and behaviours (Mercader *et al.,* 2000, 2003; Barker *et al.,* 2007; Perera *et al.,* 2011). Furthermore, the high water flow in rainforest ecosystems means that many of these site sequences are sometimes disturbed, as seen in Section 2.1 for Africa, making chronological and palaeoenvironmental reconstruction difficult (Mercader *et al.,* 2003), and detailed micromorphological study key (Kourmapas *et al.,* 2009). Finally, landscape or satellite surveying data that provide useful knowledge regarding the spatial extent and diverse nature of human landscape use in many other environments, are rarely available in rainforest regions, in part due to incredibly low site visibility, especially in the case of open-air sites, and navigational difficulties involved in survey by foot or vehicle. This is exacerbated by the fact that some regions of Central Africa, where the earliest evidence for human rainforest occupation is likely to be found, are frequently inaccessible as a result of political concerns (Roberts and Petraglia, 2015).

Increasingly refined multidisciplinary methodological approaches are providing information regarding Late Pleistocene human rainforest adaptations around the world. As a result of preservation issues, the most common methodology used to reconstruct human impacts on palaeoforests has been pollen, microcharcoal, and geochemical analysis of sequences from lake cores, marine cores, or site sequences themselves. For example, the human use of fire to alter New Guinea's montane tropical forests has been argued, on the basis of microcharcoal and pollen evidence for forest burning and clearance, to date to as early as 36 ka in the Ivane Valley and Balim regions of New Guinea (Hope, 1998; Fairbairn *et al.,* 2006). However, one issue with these studies is the equifinality of climatic and anthropogenic impacts on forests, with natural fires, especially during dry periods, being potentially as likely as human burning. In this instance, the presence of a moist mid to upper montane forest at Kosipe in the Ivane Valley is thought to indicate human agency (Fairbairn *et al.,* 2006). Such records are most fruitfully used when directly associated with archaeological sequences. For example, pollen, phytolith, and charcoal records from the Kuk Swamp can be linked to archaeological evidence for landscape use and plant exploitation in the locality. Short-term patchy forest clearance and burning throughout the Early Holocene is evident prior to more persistent and widespread forest loss in the mid-Holocene when the human transplanting of plantains becomes increasingly intensive (Golson, 1989; Denham *et al.,* 2004; Haberle *et al.,* 2012).

In Australia, by contrast, the interpretation of evidence for forest burning in northeastern Queensland and beyond from off-site pollen records is the *only* evidence for early human presence in these regions, and is therefore completely disconnected from the archaeological record (Kershaw, 1985; 1986; Kershaw *et al.,* 2002). Given the potential for natural fires, especially in the dry forest fringes of this region, and the lack

of archaeological evidence in the region at this time (albeit with evidence for human occupation elsewhere in Australia at 45 ka) (Cosgrove and Raymont 2002), such evidence should be treated with caution (Cosgrove *et al.,* 2007). In Central Africa, Bayon *et al.* (2012) have used geochemical evidence for soil weathering from a marine sediment record to argue for increased human landscape modification contemporaneous with the migration of Bantu-speaking farmers (*c.* 2,500 cal years BP). The use of marine cores to track highly local or regional human forest modification is, however, highly problematic in terms of issues of palaeoenvironmental catchments of relevance to past human behaviour, particularly for the Late Pleistocene. Finally, in the Solomon Islands, a combination of historical ecology, mapping, ethnobotany, oral traditions, and archaeological observations have been used to argue that the current forest is a product of substantial regeneration following modification by large human populations in the 1800s (Bayliss-Smith *et al.,* 2003). Nonetheless, such methodologies are again not so useful for evaluating human forest modification at the timescales considered here.

Information relating to past human use of rainforest resources can also be obtained from archaeobotanical remains preserved at a given archaeological site. At the Niah Caves, Sarawak, fragments of fruits, nuts, and plant tissue, and starch grains have indicated that the collection of rainforest tuberous plants such as aroids, taro, yam, and sago palm occurred as early as 45 ka (Barker, 2005; Barton, 2005; Paz, 2005; Barker *et al.,* 2007). Many of these tubers require extensive processing to make them digestible, suggesting that the early human occupants were experienced in rainforest manipulation (Barker *et al.,* 2007). Charred *Pandanus* nutshells at the early Ivane Valley sites in Papua New Guinea provide a similar record of rainforest exploitation. The composition of archaeozoological remains can provide a further indication of human rainforest strategies. For example, at the Niah Caves, pig seems to have formed the primary source

of protein, alongside primates, porcupines, and monitor lizards (Barker *et al.,* 2007). A particularly interesting rainforest zooarchaeological case study comes in the form of *Phalanger orientalis*, an exotic marsupial, at sites in New Ireland at 20 ka, apparently as a transplanted protein source (Allen *et al.,* 1989; Gosden and Robertson, 1991; Leavesley, 2006). Nevertheless, the broad ranges of many fauna (and their human hunters), and the differential preservation of organic remains in tropical environments, mean that the relative contributions and degree of reliance on different resources are difficult to assess.

Specific studies of certain stone or bone technologies in archaeological sequences can provide more direct insights into the strategies followed in human rainforest use. For example, waisted axes found at Late Pleistocene sites in Melanesia have been associated with the modification and clearance of forest environments (Groube, 1989). Reconstruction of raw material source and stone artefact production has also been used to argue for highly mobile foragers in Late Pleistocene Melanesia, moving between lowland rainforest, sub-montane forest and grassland, and potentially coastal areas (Pavlides, 2004; Torrence *et al.,* 2004 Leavesley, 2006; Summerhayes *et al.,* 2010). Further detail can be gained from use-wear and residue studies of tools, where such indicators are preserved. Summerhayes *et al.* (2010), for example, have noted the presence of tuber-like starch grains on stone tools from the Ivane Valley sites dated to *c.* 40 ka. At the Niah Caves the detailed use-wear analysis of a subset of bone tools was used to argue for their use as plant digging equipment in the procurement of underground storage organs (Rabett, 2005), while use-wear and residue analysis of bone points and stingray spines, here and at Matja Kuru 2, Timor, have suggested their hafting and use as projectile points (Barton *et al.,* 2009; O'Connor *et al.,* 2014). Yet, while the latter studies are more convincing, ancient starch residue preservation in a

tropical rainforest environment is rare and difficult to document as a definitive trace of past human activity.

2.4 – Early human rainforest resource reliance: why should we care?

As discussed in Sections 2.1, 2.2 and 2.3 it has become apparent over the last decade that our species both occupied, and also exploited, rainforest environments as early as *c.* 38-35,000 cal. years BP in Sri Lanka (Wijeyapala, 1997; Perera, 2010; Roberts *et al.,* 2015a), *c.* 45,000 cal. years BP in Southeast Asia and Melanesia (Higham *et al.,* 2009; Summerhayes *et al.,* 2010), and, more controversially, as early as *c.* 200,000 years ago in Africa (Mercader, 2002a). However, as mentioned in Sections 2.1 and 2.2, archaeological evidence for the longevity and nature of human rainforest occupation and adaptation remains surprisingly limited, even in Sri Lanka, and even during the Terminal Pleistocene and Holocene periods, when, as suggested in Section 2.1, human occupation and exploitation of rainforest environments intensified. Section 2.3 demonstrates how evidence for the specialised hunting or processing of rainforest resources (Barton, 2005; Barker *et al.,* 2007), the movement of endemic fauna for protein into rainforest locales (Gosden, 1995), and the burning of forest settings (Fairbairn *et al.,* 2006; Summerhayes *et al.,* 2010), can be obtained. Nevertheless, evidence for habitat mosaics, indirect and poorly dated 'off-site' palaeoenvironmental records, and snapshots of rainforest plant and animal use does not preclude the use of rainforests as part of mobile, diverse foraging strategies (Pavlides, 2004; Leavesley, 2006). Consequently, while archaeology may have conclusively demonstrated that humans could occupy and use rainforest environments back well into the Pleistocene (Barton *et al.,* 2012), it has not yet indicated that they could do so without recourse to other environmental biomes.

Rainforests: risk or reward?

During the 1970s and 1980s rainforests were seen as 'pristine' habitats, home to some of the last groups of hunter-gatherer societies, untouched by agriculture and capitalism, left anywhere in the world (Stiles, 1992). To counter this simplistic perception, Headland and Reid (1989) surveyed a series of ethnographic communities inhabiting rainforest environments that were frequently argued to be 'pristine'. They demonstrated that these groups had, in fact, been in consistent contact and exchange with agricultural societies. Furthermore, they suggested that human forager inhabitation of rainforest environments was virtually impossible without this contact (Headland and Reid, 1989; Bailey *et al.,* 1989). Hutterer (1983) indicated that human hunter-gatherers would face difficulties in the procurement of secure foodstuffs as a result of highly spaced resources, seasonal flux, and issues of navigation through dense rainforest vegetation. Meanwhile, Headland (1987) and Bailey *et al.* (1989) argued that subsistence based purely on foraging is difficult in tropical rainforest because of the scarcity, and seasonal availability, of energy-rich wild foods, such as fat-rich animals, oilseeds, and carbohydrate-rich tubers and tuberous roots such as those of wild yams (Hart and Hart, 1986). This, combined with knowledge of the dangers of many rainforest plant and animal species, led to a conclusion that rainforests presented a somewhat undesirable habitat for human foragers rather than refugia of plenty.

Headland and Reid's (1989) argument about the supposed undesirability of rainforests for human foragers was based on the fact that the extant rainforest foraging groups they reviewed maintained long-term relationships with neighbouring agricultural societies that provided a large proportion of their subsistence requirements. However, this does not mean that purely foraging lifestyles in rainforests are a) impossible now or b) were

impossible in the past (Bahuchet *et al.,* 1991; Bellwood, 1993). Bahuchet *et al.* (1991) used direct assessments of the ecological and nutritional availability of wild yams in the western Congo Basin to demonstrate, among others (Brosius, 1991; Dwyer and Minnegal, 1991; Endicott and Bellwood, 1991; Bellwood, 1993), that it *is* nutritionally possible for ethnographic foragers to live off wild resources alone in a rainforest. As will be seen in Chapter 3, it is clear that hunter-gatherers make use of a huge diversity plant and animal resources from rainforest micro-habitats (Chapter 3 – Section 3.4) (Dentan, 1991). The capacity of ethnographic humans to survive tropical rainforest environments therefore does not appear to be in doubt. That said possibility does not necessarily provide evidence for sustainable rainforest subsistence in a modern context where it is difficult to abstract hunter-gatherers from surrounding trade networks and economies (Headland and Reid, 1989). Indeed, Bailey and Headland (1991: 279) argued that it was always archaeology that would provide the 'definitive test' to whether humans can live in tropical rainforests independently of cultivated foods.

2.5 – Remaining questions regarding Late Pleistocene and Holocene human rainforest use

If the nature and extent of early human adaptations to tropical rainforests is to be further advanced beyond indirect assumptions of occupation and exploitation, three main areas need to be addressed:

i) Given the evidence discussed in Section 2.1 for early ephemeral occupation of rainforest environments, followed by an intensification of Terminal Pleistocene and Holocene rainforest colonisation, there remains a need to develop more contextual understandings of human rainforest occupation at different sites and at different points in time. The use of the term 'rainforest' in the anthropological literature has often

created dichotomous standpoints regarding its suitability for human existence (Bahuchet *et al.,* 1991; Dentan, 1991). As will be seen in Chapter 3 (Section 3.1), however, it can cover a variety of different floristic communities, climates, ecologies, and environments (Whitmore, 1998; Cosgrove *et al.,* 2007), making generalisation simplistic and unhelpful. More research is required as to how human populations adapted to rainforests at different times, in different climatic situations, in different regions of the globe, and how far differences in past rainforest ecologies affected human life-ways within them.

ii) To understand human-environment interactions, well-dated, 'on-site' palaeoenvironmental and palaeoecological records, associated directly with records of human rainforest occupation, are required. Such records will move away from reliance on coarse-resolution, 'off-site' sequences of surrounding environments and enable human relationships to forest habitats through time to be investigated. Multidisciplinary pollen, geomorphological, macrobotanical, and faunal records have now been developed at a number of sites (e.g. the Niah Caves - Barker *et al.,* 2007, Batadomba-lena - Perera *et al.,* 2011). Furthermore, at the Niah Caves, and to some extent in Melanesia, researchers have been able to reconstruct human relationships to certain rainforest plants (Barker *et al.,* 2007; Summerhayes *et al.,* 2010) and animals (Barton *et al.,* 2009; Rabett, 2012). However, these studies remain exceptions in a growing literature of rainforest prehistory, leaving the specific rainforest niches of early humans little understood at most sites.

iii) Finally, as emphasised here, virtually all investigations of early human occupation and subsistence within rainforests have thus far relied on indirect records to infer human rainforest adaptation. For archaeology, it has so far been enough simply to demonstrate humans occupied a site when it was surrounded by rainforest or that humans practised

one form of tailored rainforest resource exploitation. However, while such information can get us some way in describing the ways in which humans could support themselves in such an environment, it completely neglects the questions as to whether humans remained specialised in rainforest occupation and where human subsistence was positioned within the local rainforest ecology. If archaeology is to truly to get to grips with the question as to whether humans can forage in rainforests independently of agriculturalists [or other environments] (Bailey and Headland, 1991- [my addition]), then *direct* records of human subsistence and resource reliance are crucial.

Chapter 3 - Prehistoric and ethnographic rainforests: the ecological, climatic, and human context

In this chapter I define tropical rainforests and outline their natural history, tracking the susceptibility of rainforests to climatic and human impact through the Late Pleistocene and into the Holocene. This chapter then interrogates methods used to reconstruct the natural history of tropical rainforests worldwide, with a particular focus on Sri Lanka's palaeoenvironmental record. It finishes with a reappraisal of ethnographic evidence that provides more specific insight into the potential subsistence strategies employed by rainforest hunter-gatherer groups to harness the faunal and floral diversity found between and within the world's rainforest formations. In the context of evidence for specialised monkey hunting by users of the Sri Lankan Microlithic tradition, this includes a particular focus on ethnographic evidence for forest primate exploitation (Chapter 2 – Section 2.2).

3.1 – Tropical rainforests: an introduction

"The edge of a colossal jungle, so dark-green as to be almost black, fringed with white surf, ran straight, like a ruled line, far, far away along a blue sea whose glitter was blurred by a creeping mist … Settlements some centuries old, and still no bigger than pinheads on the untouched expanse of their background" (Conrad, 1999: 80).

In many cultures, tropical rainforests are synonymous with a static vision of 'mystery' and 'wilderness'. In perhaps the most vivid of Victorian colonial dramas, a 'Heart of Darkness', it is the Congolese tropical rainforest that forms the oppressive, dark, maddening background to one man's grappling with the concept of 'civilisation'. The

term jungle, often used in common reference to tropical forests, comes from the Hindi word *jangal* which has long been used in reference to untouched, impenetrable forests surrounding human settlements (Whitmore, 1998). It is perhaps perspectives such as these that have led to a relative reluctance in archaeology, until recently (Barton *et al.,* 2012), to delve into the climatic, ecological, and human histories of tropical rainforests, considering them relatively uninteresting from the perspective of dynamic environmental and cultural changes.

As shown in Chapter 2, not only is the time-depth of human-rainforest interactions being dramatically extended, it is now evident that our species has, itself, influenced a wide variety of forest niches and elements, on prehistoric, historic, and ethnographic timescales (Willis *et al.,* 2004; Barton *et al.,* 2012). Ecological and palaeoenvironmental research has increasingly demonstrated that the flora, fauna, and ecosystem dynamics of the globe's tropical rainforests are the regionally-diverse product of multiple anthropogenic, evolutionary, ecological, and climatic forces still operating today (Whitmore, 1998; Bermingham *et al.,* 2014). As a result, if we are to understand early human-rainforest interactions we need to examine the regional and local impacts of climate change on different tropical rainforest regions and formations, as well as the different human subsistence strategies practiced in these environments today. These topics have thus far received little systematic review in an archaeological context, despite popular interest in them in the face of the increasing disappearance of these habitats (Moritz *et al.,* 2014).

What is a tropical rainforest?

The term 'tropical rainforest', first used by the botanist A.F.W. Schimper in 1898 (*tropische Regenwald* – Allaby, 2010), is used to separate forests of the *permanently* wet regions of the tropics from the monsoon forests, savannah forests, and thorn forests that form in progressively drier and more seasonal areas. Indeed, while ecologists have defined tropical rainforests on the basis of their composition (warmth-loving botanical formations dominated by broad-leaf angiosperms; White, 1983), precipitation (an annual precipitation in excess of 1,400 mm, and often around 2,000 mm or more; Grainger, 1996a, 1996b), and even temperature (mean temperature of coldest month >18°C, annual temperature >24°C; Holdridge, 1947), it is actually low seasonality, in both temperature and rainfall, that is the key climatic parameter behind the presence and sustenance of tropical rainforests (Whitmore, 1998; Sternberg, 2001; Barboni *et al.,* 2003). This is because for plants and animals, especially those living in areas of rich species diversity, extremes are more important than means. For rainforests, unusually prolonged dry periods are of particular significance as triggers for flowering or because drought can kill plants or encourage forest burning (Whitmore, 1998). Rainforests develop, and persist, where every month is wet (with 100 mm rainfall or more), or where there are only short dry spells lasting only a few days or weeks (Whitmore, 1998; Sternberg, 2001). Regions with pronounced seasonality and dry periods of more than two months support seasonal forests with deciduous species, open forest structures, and mosaics (Grainger, 1996a, 1996b).

Tropical rainforests occur in all three of the tropical continents (Sayer *et al.,* 1992; Harcourt and Sayer, 1996; Blasco *et al.,* 1996; Malhi and Wright, 2004) (Figure 3.1). Most extensive are the Neotropical rainforests that occur in the Amazon and Orinoco

Basins, on the eastern slopes of the Andes, along the Pacific coasts of Ecuador and Colombia, in Mesoamerica, and on the Atlantic coast of Brazil. The second largest rainforest region is the Eastern tropics. Centred on the Malay Archipelago, these forests extend into the Pacific and form a narrow coastal strip in Queensland, northeast Australia. They also extend up the Malay Peninsula into continental Southeast Asia, Burma, Thailand, and Indo-China. Smaller again is Africa's rainforest zone, centred on the Congo Basin. Other African 'outliers' can be found on the east coast of Madagascar and in the Mascarenes. As seen in Chapter 2, small blocks of rainforest exist in southwest Sri Lanka and along the Western Ghats of India. Importantly for our purposes here, these 'blocks' are not neat. In South America and Southeast Asia there is often an ill-defined boundary with subtropical forests as one moves away from the Equator, while in South Asia various layers of rainforest persist through strong monsoonal seasonality in precipitation (Whitmore, 1998; Barboni *et al.,* 2003). In Australia, where rainforests reach their temperate limit, tropical rainforest becomes increasingly restricted to the wettest areas and deepest, most fertile soils (Webb, 1968).

In forest ecology, the canopy refers to the habitat zone formed by mature tree crowns, and canopy structure (its organisation or spatial arrangement) is often a key parameter in the definition of forest types (Parker, 1995). In tropical rainforests, low climatic seasonality encourages the formation of closed canopies, whereby the crowns of individual trees overlap to form a virtually continuous layer. This characteristic canopy layer intercepts around 95% of sunlight (Whitmore, 1998) and has resulted in the classification of rainforests into different abstract strata, or layers, with vegetation organised into a vertical pattern from the top of the soil to the canopy (Bourgeron, 1983; Denslow, 1987) (Figure 3.2). Each stratum is home to a unique biotic community adapted to life within a particular microclimate and of different relevance to human

activity. For example, the forest floor is home to a few plants adapted to low light conditions and, away from disturbances such as riverbanks, swamps, and clearings, it is relatively clear, facilitating the movement of large mammals, reptiles, and amphibians (Bourgeron, 1983). The understory and canopy contain a larger variety of usable plants and plant parts (including herbs, climbers, mosses, and tree fruits) and are home to diverse collections of semi-arboreal and arboreal mammals, reptiles, birds, and insects. The highest, emergent layer is home to smaller numbers of very large trees and specialised primates, birds, or mammals (Whitmore, 1998).

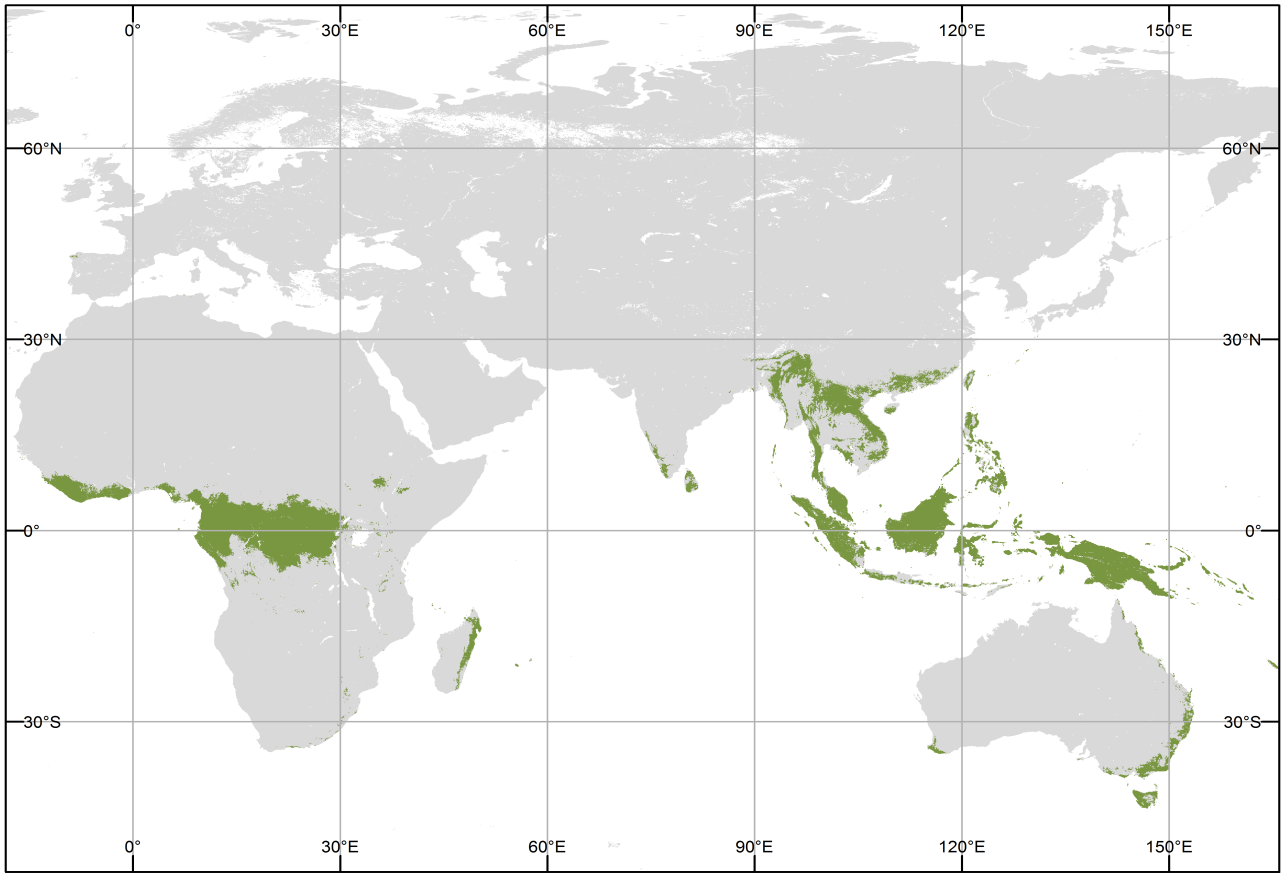


Figure 3.1. The current distribution of tropical forests in the Old World as determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the U.S. Geological Survey Earth Resources Observation System (EROS) Data Center (EDC).

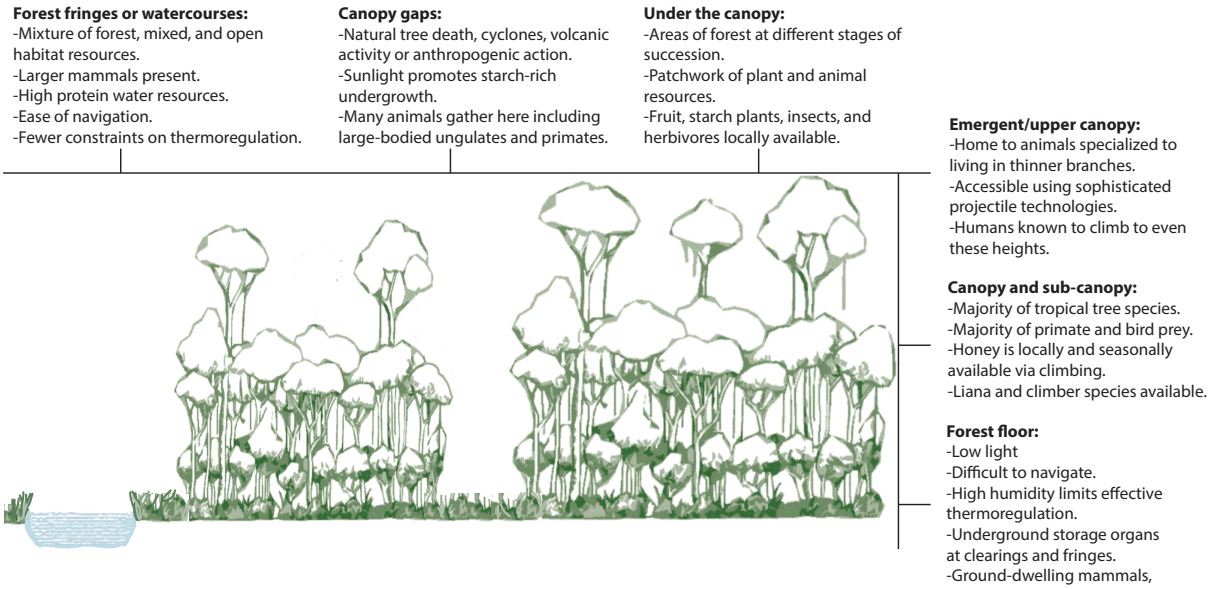


Figure 3.2. The distribution of plant and animal resources, and conditions, relevant to human subsistence in a rainforest ecosystem.

Nevertheless, rainforests are not static, monolithic communities even in their 'natural' ecological form. As a result of vegetation lifecycles, gaps constantly occur in the canopy, making this stratification a simplification, and ensuring that various patches exist at all stages of the growth cycle (Colinvaux and Bush, 1991). These gaps are rapidly colonised by seedlings and, as noted above, often facilitate increased densities of vegetation growth and competition (Whitmore, 1977; Denslow, 1987). The nature and frequency of gap formation varies over space and time, and are influenced by anthropogenic and climatic factors including disease, fire, and extreme weather events (Ghazoul, 2015). For example, Southeast Asia and Papua New Guinea are prone to cyclones, earthquakes, and volcanic eruptions, all of which can clear vast swathes of forest (Johns, 1986; Sémah and Sémah, 2012). The temporal and spatial expressions of these dynamic forces will impact the tropical rainforest environment met by human populations in different regions and rainforest locales.

Climatic factors, geology, and topography ensure that the composition of the 'finished' stratified rainforest also varies considerably within the coarse category of 'tropical rainforest', leading to its division by ecologists and botanists into a series of vegetation 'formations' (Whitmore, 1998) (Figure 3.3, Table 3.1). Rainforest formations are defined by forest structure (i.e. canopy coverage, tree height, the presence of tree crowns or layers, and the presence of climbers) and physiognomy (whether trees are buttressed (i.e. extensive horizontal root span – Tang *et al.* 2010), crown shape, the nature of leaves, to what extent the forest is evergreen or deciduous, and where flowers and fruits form on trees). These formations can, in turn, be grouped according to the main physical characteristics of their habitat (Holdridge, 1967; Holdridge *et al.,* 1971; Webb and Tracey, 1981; Brünig, 1983; Whitmore 1998) (Table 3.1). The frequency of these formations differs across those regions of the world where Late Pleistocene human rainforest interaction has been suggested (Chapter 2 – Section 2.1).

Tropical lowland evergreen rainforest

This dense, lofty (≥45m) evergreen forest type is the most species-rich of all plant communities and the pinnacle of rainforest complexity. It has three tree layers: a top layer of individual giant emergents over a main layer *c.* 24-26 m, and smaller shade-dwelling trees below that. Ground vegetation is sparse and consists mainly of small trees with patchy occurrences of herbs and shrubs. Buttresses are common, with big woody climbers. Some deciduous or semi-deciduous trees are present but do not widely affect the evergreen canopy. This is the main lowland formation of Southeast Asia and Melanesia. It also occupies western Amazonia and the Pacific coast of South America. In Africa it is restricted to the coast of West Africa. All regions with this formation have no regular annual dry season.

Tropical lowland evergreen rainforest



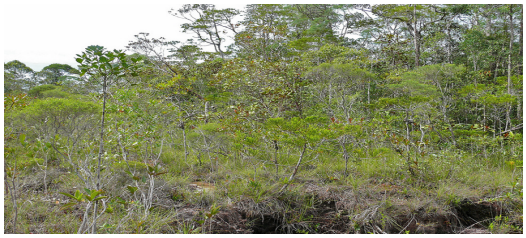
Tropical semi-evergreen rainforest



Montane rainforest



Heath forest



Peat swamp forest



Freshwater swamp forest



Figure 3.3. Rainforest formations discussed in the text (see also Whitmore, 1998): Tropical lowland evergreen forest (Brazilian Amazon, Source: Harris, 2001), Tropical semi-evergreen forest (Brazil, Source: Oliveira-Filho, 2014), Montane rainforest (Ecuadorean Andes, Source: Read, 2016), Heath forest (Malaysia, Source: Dupont, 2007), Peat swamp forest (Borneo, Source: Department of Forest Sciences, University of Helsinki, 2008), Freshwater swamp forest (Amazon, Source: Mlinaric, 2008).

Tropical semi-evergreen rainforest

This is closed, tall forest that includes both evergreen and, in the top of the canopy, deciduous trees. The number of species is high, but less so than in evergreen rainforest. Buttresses are frequent, occurring in evergreen and deciduous species. Its stature is less than evergreen rainforest, with local canopy stratification and emergents occurring as scattered individuals or groups. Large woody climbers and bamboos are abundant with many epiphytes present, including ferns and orchids. This formation occurs where there is a strong, regular annual period of moisture stress. It occupies most of the African rainforest block and occurs as a narrow fringe around the main Southeast Asian rainforest zone. Tropical semi-evergreen rainforest also forms the majority of the South Asian rainforest and most of the Australian tropical rainforest.

Montane rainforests

In contrast to the previous formations, which are dominated by trees with multi-veined mesophyll leaves and have uneven canopy surfaces, montane rainforests have lower, more even, single-vein microphyll canopies dominated by slender trees with dense subcrowns (Whitmore, 1989). Upper montane rainforest is often only 10 m tall or less, with trees heavily covered in bryophytes and ferns. On small mountains, upper montane rainforest directly borders lowland rainforest. However, on larger mountains, lower montane rainforest occurs as an intermediate formation. On higher peaks, upper montane rainforest is itself replaced by shorter, small-leaved formations called subalpine forests that are frequently suppressed by fire (Whitmore, 1998). Extensive montane forests exist in the Andes, Southeast Asia, and Melanesia (Van Steenis, 1972;

Denham and Haberle, 2008; Haberle *et al.,* 2012). They are less extensive in Africa, but do occur in Cameroon and at the eastern fringe of the Congo Basin.

Heath forest

This formation has a low, but orderly, canopy formed of small, young, thin trees (Whitmore, 1989; Brünig, 1996). The canopy is closed and dense with no trace of layering. Like montane forests, this formation has a predominance of microphyll trees, while long slender climbers and epiphytes dominate non-tree vegetation. Occurring on podsolised, acidic soils, heath forest is extensive in South America, including the Orinoco Basin, Brazil, and Guyana. There are also extensive heath forests in Southeast Asia, including Sarawak and Brunei in Borneo. More minor heath forests occur in Gabon, Cameroon, and Ivory Coast in Africa. The extremely acidic soil of these formations is toxic to the roots of many plants, including crops.

Peat swamp forest

This formation is defined more by its special habitat than by structure and physiognomy. Parts of Southeast Asia and Melanesia physiographically favour the formation of peat. Since sea-level rose at the end of the LGM, rivers have deposited silt on flood plains and as levees behind which swamps have developed, becoming less saline as their soil level was raised by continuous silt deposition (Whitmore, 1998). Lack of detrital decay leads to the formation of peat swamps that are home to varied forest types, ranging from open, stunted forest at the centre to 50 m tall forests on the outer edges. High acidity, peat-depth, and viscosity are problematic for many ground-

dwelling plants and crops. Peat swamp forests also occur in the Amazon Basin, as well as in Uganda and Congo-Kinshasa.

Freshwater swamp forests

Like peat swamp forests, these formations are defined primarily by habitat. This group includes a very diverse assemblage of forests flooded by river water that leads to soils richer in plant nutrients, and of a much higher pH, than those of peat swamp forests (Whitmore, 1998). Where flooding is periodic the periodic swamp forest group encapsulates additional variability. There may be a few centimetres of peat or organic-mineral soil. Where unstable banks of alluvium occur, extensive grasslands can develop during periods of low precipitation or tidal reach. Though little-studied, extensive and diverse permanent and periodic freshwater swamp forests occur in the Amazon, Melanesia, and the Congo Basin. The alluvial plains of Asia were once home to extensive swamp forests, but little now remains as a result of clearance for wetland rice cultivation (Whitmore, 1998).

Table 3.1. Tropical rainforest formations (after Whitmore, 1998 – Table 2.1). Those in bold are briefly summarised in the text.

Climate	**Soil water**		**Soils**	**Elevation**	**Forest formation**
Seasonally dry	Slight annual storage				**Semi-evergreen rainforest**
Everwet	Dryland		Zonal (mainly oxisols – acidic weathered, leaches and drained, and ultisols – weathered, acidic, clay, Ca and K deficient)	Lowlands	**Lowland evergreen rainforest**
				1200-1500 m	**Lower montane rainforest**
				1500-3000m	**Upper montane rainforest**
				3000m to tree line	Subalpine forest
			Podsolized sands	Mostly lowlands	**Heath forest**
			Limestone	Mostly lowlands	Forest over limestone
			Ultrabasic rocks	Mostly lowlands	Forest over ultrabasics
	Water table high (at least periodically)	Coastal salt-water			Beach vegetation Mangrove forest Brackish water forest
			Oligotrophic peats		**Peat swamp forest**
		Inland fresh-water	Eutrophic soils	Any where permanently wet	**Freshwater swamp forest**
				Any where periodically wet	**Freshwater periodic swamp forest**

3.2 – Rainforest palaeoenvironmental reconstruction across the Late Pleistocene and Holocene

Despite a recent surge in interest in the relationship between the world's rainforests and various climatic parameters (Baker *et al.,* 2004; D.A. Clark, 2004; Malhi and Wright, 2004), debate still surrounds the relative impacts of temperature change, atmospheric CO_2 concentration, precipitation change, and differences in seasonality on past rainforest structure and extent (Malhi and Wright, 2004; Mayle *et al.,* 2004; Feeley *et al.,* 2011). Where climate-rainforest relationships have been discussed, this has tended to be in the context of broad glacial-interglacial predictions. Tropical regions are characterised by distinctly low seasonality in temperature, with the annual variation in daily mean temperature as low as 1-4°C in lowland regions straddling the Equator (Osborne, 2000). In contrast to temperate regions, therefore, temperature has been a climatic parameter of limited importance in the tropics in the past. Estimates of temperature differences between glacial minima and maxima of 4-6°C have been recorded for equatorial Africa, Amazonia, and Melanesia (Bonnefille *et al.,* 1990; Stute *et al.,* 1995; Thompson *et al.,* 1995; Colinvaux and Oliveira, 2001; Hope, 2009). While such decreases in temperature in glacial periods would have had a significant impact on the world's tropical forests, reducing their area and diversity at the expense of expanding seasonal forests, compared to many of the world's environments, these changes are significant but not extreme (Mercader, 2002a; Boivin *et al.,* 2013).

The limited impact of temperature change on tropical environments in the past has meant that attention has focused on other parameters, such as atmospheric CO_2 concentration and precipitation, in analysing changes in tropical forest extent and structure across glacial periods. Interglacial levels of CO_2 were up to 50% higher than during glacial periods (Cowling, 1999; Monnin *et al.,* 2001). Dynamic vegetation

models, ecophysiological experiments, and stable carbon isotope records have all shown that CO_2-depleted atmospheres during glacial periods would have significantly reduced the water-use efficiency of C_3 plants (Polley *et al.,* 1993; Street-Perrot *et al.,* 1997; Cowling *et al.,* 2001). In some places, including montane areas of Africa, CO_2 reduction has, in itself, been argued to lead to complete forest replacement (Jolly and Haxeltine, 1997). Ehleringer *et al.* (1997) suggest that lower concentrations of atmospheric CO_2 during the LGM led to a more extensive distribution of C_4-grassland-ecosystems than occurs today. Beyond complete replacement, forest plants have also been argued to adapt their physiology to changing CO_2 conditions by producing smaller leaf size during CO_2-starved glacial conditions. As a result, rainforest structures during glacial periods likely changed in many regions, with reduced-sized leaves in the canopy leading to more open forest structures and increased frequencies of herbaceous taxa on the forest floor (Mayle *et al.,* 2004).

The influence of precipitation changes on rainforests during glacial episodes is a particular source of contention, as the relevant palaeoenvironmental proxies are less predictable and more regionally and temporally variable than records of temperature and CO_2 concentration (Hooghiemstra and Van der Hammen, 1998; Mayle *et al.,* 2004). The hypothesis that Pleistocene droughts fragmented tropical rainforests into isolated 'refugia' draws on biogeographical patterns of endemic distribution in the Amazon and Congo Basins (Haffer, 1969; Hamilton, 1972). In this 'refuge hypothesis' scenario, increased aridity during glacial periods is argued to have caused the dramatic removal of rainforest except for a few patches, where high species diversity, recognised in modern studies of floral and faunal endemism (Haffer, 1969), was fostered and preserved until later rainforest expansion. Others have argued, by contrast, that the wet tropics remained relatively hydrologically hospitable to rainforests during glacial

periods, with relatively minor reductions of precipitation and forest extent (between 20 to 40% - Maley and Brenac, 1998; Thomas, 2000).

In Africa it has been postulated that cooler temperatures moderated the evapo-transpiration cycle, reducing the frequency of convective rain that governs Central Africa's precipitation dynamics (Grainger, 1996b). Nevertheless, synthesis of stable isotope analysis of lacustrine organic matter (Talbot and Johannessen, 1992), geomorphological analysis of alluvial sequences (Thomas, 2000), records of lake levels, pollen data and other geochemical proxies (Farrera *et al.,* 1999) indicate that, while a smaller water budget during the LGM as a result of lower precipitation may have triggered forest fragmentation, it only resulted in partial savannah encroachment. Evidence from the Neotropics has demonstrated considerable variation in regional precipitation *within* Amazonia during the LGM, with the southern Amazonian lowlands being cooler and drier, and the northern basin cooler and wetter, than today (Thompson *et al.,* 1998; Baker *et al.,* 2001; Bush *et al.,* 2002; Mayle *et al.,* 2004; Colinvaux, 2014). Such findings warn against any global, or even regional, assumptions regarding precipitation change and its impact on tropical rainforests.

As the above might suggest, it is difficult to disentangle the relative impacts of precipitation, CO_2, temperature, and seasonality on past rainforest environments. Pollen analyses struggle to determine the relative impacts of temperature and precipitation, while global changes in CO_2 are difficult to correlate chronologically with regional floristic changes. It is particularly challenging to document temperature or precipitation seasonality, the greatest influence on rainforest persistence (Section 3.1), which relies on models built from modern datasets (Malhi and Wright, 2004; Mayle *et al.,* 2004; Gond *et al.,* 2013) or the future potential of high-resolution speleothem analysis in

tropical regions (Bertaux *et al.,* 2002; Tagami, 2013). Nevertheless, multidisciplinary compilation of many local and regional datasets can provide more detailed insights. Bush *et al.* (2002) have used palaeolimnological data from a cluster of lakes in northern Amazonia to infer that high water availability existed in the region during the LGM. On this basis, Mayle *et al.* (2004) argued that water stress during the LGM, manifested in a mixture of montane and lowland rainforest taxa, and more open forest structures, was primarily the result of lower CO_2 concentrations and temperature decrease rather than decreased precipitation (Cowling *et al.,* 201). By contrast, forest decline and an increase in fire frequency in the Early to Middle Holocene were caused by decreases in precipitation (Mayle *et al.,* 2004).

These studies demonstrate that researchers must understand all of the different potential climatic drivers in order to model past fluctuations in rainforest extent and structure. Moreover, regionally- and temporally-specific approaches to rainforest reconstruction are essential. Simplistic ecological overlaps of species endemism with areas of glacial remnant rainforest are proving dangerous as phylogenetic estimates suggest that high levels of genetic divergence precede the Pleistocene, and likely extend back to the pre- or early Quaternary and the Late Cenozoic period (da Silva and Patton, 1993; Bermingham and Dick, 2014; Patton and da Silva, 2014). On a more refined level, in equatorial Africa it has been shown that while palaeoenvironmental sequences from forest borders or altitudinal and vegetation transitions may show significant changes in forest extent during glacial periods, and even within the Holocene (Van Noten, 1977), lowland palynological records demonstrate forest persistence over the last 30,000 years (Maley and Brenac, 1998; Colinvaux, 2014). Similarly, marine cores indicative of savannah encroachment cannot be correlated directly with lowland rainforest ecologies (Mercader *et al.,* 2000). While ‘off-site’ palynological and phytolith sequences are often

the only ones to survive in the vicinity of tropical rainforests, one must carefully assess to what extent the 'catchment' of these records is relevant to human behaviour.

While we lack a detailed knowledge of the impacts of atmospheric, marine, and terrestrial climatic systems on past tropical rainforest systems, these will also most certainly have had temporally- and spatially-specific results. For example, the El Niño-Southern Oscillation (ENSO) is the dominant mode of variability in tropical precipitation on interannual timescales today (Dai and Wigley, 2000), altering cloud cover, rainfall, and temperature in ways that directly limit plant function, and the resources available for reproduction, in tropical rainforests in Amazonia, Africa, and Asia (Laurance *et al.,* 2001; Wright, 2014) (Figure. 3.4). However, Malhi and Wright (2004) modelled regionally specific impacts of temperature, precipitation, oscillations of the ENSO and seasonality on the world's rainforests since the 1970s. They demonstrate that while ENSO is known to impact temperature variations and precipitation fluctuations in the tropics of the Americas and Southeast Asia, it is in the rainforests of Africa and India where clear increases in dry-season intensity are documented. Furthermore, only African rainforests appear to demonstrate a significant overall 'drying' trend (Malhi and Wright, 2004).

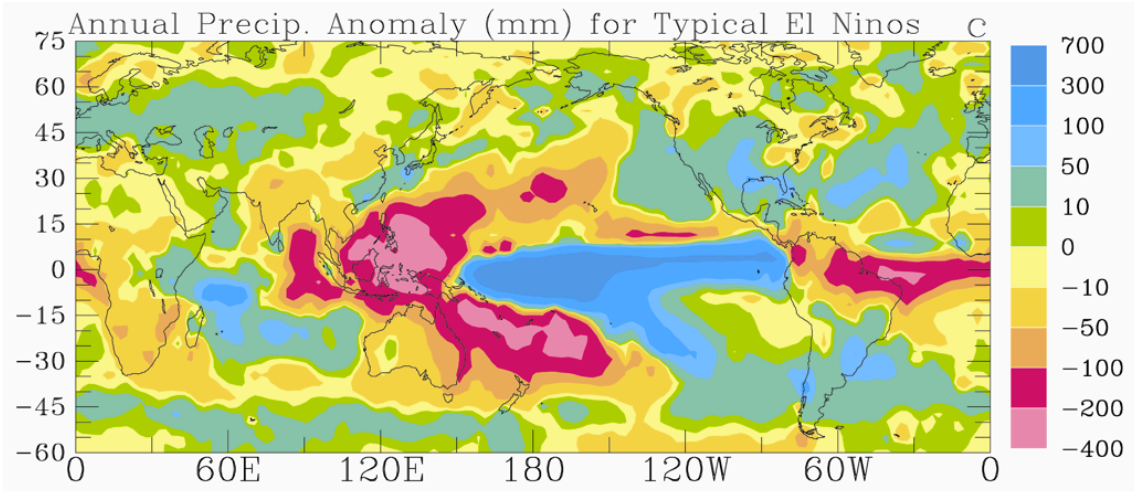


Figure 3.4. Annual precipitation anomalies associated with ENSO (pink = drought, blue= flooding). From Dai and Wigley (2000: 1284 – Figure 1c).

Despite these caveats, global, and region-specific, data suggest that there are some observable trends in rainforest structure and extent across the Late Pleistocene and Early Holocene. Pollen and phytolith records indicate that many tropical lowlands, or intermediate highlands, in the Americas, Africa, Southeast Asia, Melanesia, and South Asia, maintained at least some rainforest coverage through the LGM *c.* 25,000-18,000 years ago, though these forests were structurally and floristically different to their modern counterparts (Amazon: Colinvaux *et al.,* 1996; Mayle *et al.,* 2004; Colinvaux, 2014; Africa: Talbot and Johansen, 1992; Jahns *et al.,* 1998; Dupont *et al.,* 2000; Mercader *et al.,* 2000; Southeast Asia: Newsome and Flenley, 1988; Haberle *et al.,* 2012; Sémah and Sémah, 2012; South Asia: Farooqui *et al.,* 2010; Melanesia: Powell, 1982; Denham *et al.,* 2003; Denham, 2004; Denham and Haberle, 2008; Haberle *et al.,* 2012). There was an overall drop of temperature of approximately 5°C across tropical regions during glacial periods (Mercader 2002b). Atmospheric CO_2 concentration was lower during the LGM (*c.* 180-200 ppmV compared to 350 ppmV today – Ehleringer *et al.,* 1997), potentially causing significant changes in forest structure and distribution,

especially at higher altitudes (Jolly and Haxeltine, 1997). Rainfall may have also significantly decreased during the LGM, especially in colder, high-altitudinal areas in Africa, South Asia, Southeast Asia, the Americas and Melanesia, with coincident forest fragmentation (Newsome and Flenley, 1988; Gathorne-Hardy *et al.,* 2002; Prematilake and Gunatilaka, 2013).

While tropical rainforest expansion, back to, and beyond, the levels of the previous interglacial occurred with increasing temperatures, CO_2 concentrations, and precipitation across the Terminal Pleistocene and into the Holocene in a general sense, the situation is more complex on a regional basis. Firstly, many temporal fluctuations in forest types and forest species are recognised in the Amazon Basin, the Andes, Africa, and Southeast Asia *within* this period, with phases of aridity and temperature operating at a finer resolution than interglacial-glacial dynamics (e.g. Early to Middle Holocene arid phases and claims of the 'Younger Dryas' in Amazonia (Mayle *et al.,* 2004) and Africa (Bayon *et al.,* 2012)). Furthermore, in Australasia and Southeast Asia, this period also witnessed a significant rise of sea levels (from their minimum of *c.* -116m at the LGM) that had regionally-varied impacts on forest extent and structure (Kienast *et al.,* 2001; Lambeck *et al.,* 2002; Bird *et al.,* 2005; Wurster *et al.,* 2010).

Finally, significant human impacts on tropical forest structure and extent through forest burning and clearing have been documented in New Guinea *c.* 30,000 years ago (Haberle *et al.,* 2012), as well as being tentatively postulated in the vicinity of the Niah Caves, Sarawak, Borneo (Hunt *et al.,* 2007, 2012) and, more controversially, the sclerophyll forests of Australia (Kershaw *et al.,* 2002, Haberle *et al.,* 2010) as far back as *c.* 50,000 years ago. Human burning will have different impacts on forests with different capacities to burn, with a greater influence likely on subalpine or semi-

deciduous forests than on ever-wet evergreen lowland rainforest. Therefore, while there are certainly trends in palaeoclimate-rainforest dynamics across the Late Pleistocene-Holocene, independent, well-dated regional and local palaeoenvironmental records are essential if the spatial and temporal variance of past human rainforest ecologies across this period is to be reconstructed in any meaningful way.

3.3 – Global (and Sri Lankan) rainforest diversity and its impact on early human occupation and adaptation

Rainforest prehistory or prehistories?

This ecological and palaeoenvironmental discussion demonstrates that archaeologists analysing early human rainforest contact around the world need to search for appropriate palaeoenvironmental sequences in order to reconstruct, in detail, the regional and local rainforest environments available to humans during the Late Pleistocene (Figure 3.5). For example, the montane and evergreen-deciduous forests of the New Guinea highlands are prone to burning, and large openings frequently form as a result of cyclones (Whitmore, 1998). This may explain the early evidence for human burning in this region that would have stimulated the availability of a diversity of tropical floral resources and their consumers (Groube, 1989; Denham and Barton, 2006) (Chapter 2 – Section 2.1), but made the tracking of fauna through resurgent undergrowth difficult. This, and the susceptibility of these montane and subalpine rainforests to changes in temperature across the Late Pleistocene-Holocene transition, likely encouraged the highly mobile, multi-ecotonal lifeways documented for these populations, which may have involved the exploitation of grassland megafauna (Fairbairn *et al.,* 2006; Summerhayes *et al.,* 2010).

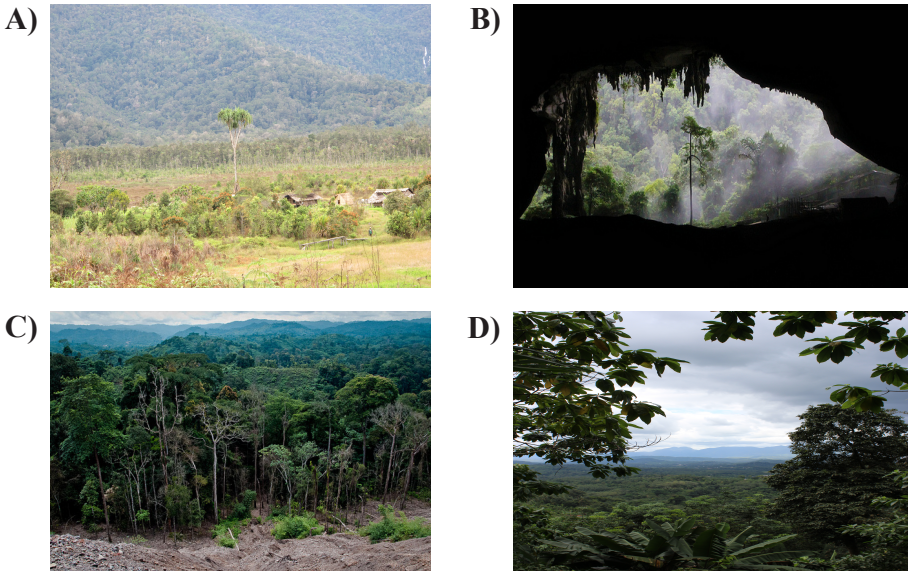


Figure 3.5. Photographs of rainforest from A) 2,000m in the Ivane Valley, Melanesia (courtesy of Glenn Summerhayes), B) View from the Niah Caves, Sarawak, Borneo (courtesy of Graeme Barker), C) the Congo-Kinshasa (Source: Wilson Center Staff, 2012), D) lowland rainforest of the Sri Lankan Wet Zone (photograph: Patrick Roberts).

Similarly, in Southeast Asia, the frequency of the formation of peat-swamp forests in this region, and the accompanying soil acidity, may be the reason behind a focus on wild boar and semi-arboreal mammal hunting at the Niah Caves, Sarawak. Poor soils would have resulted in limited floor-level plant resources, though some techniques were apparently developed to process hardy, toxic plant foods (Barker *et al.,* 2007; Rabett, 2012). Based on modern data, of all the regions where early human rainforest contact has been documented, Africa appears to be the most susceptible to rainforest reduction as a result of climatic impacts, likely leading to the relatively low floral diversity in African rainforests today (Maley, 1996; Malhi and Wright, 2004; Malhi *et al.,* 2013). During the last glacial period, the Central African rainforest contracted, resulting in an advance of seasonal, semi-deciduous forests and savannah grasslands at its fringes. This may go some way to explaining why the main distribution of Lupemban sites skirts the

border of the Central African rainforest as it sits today, though the dating of this industry remains highly problematic and site 'distribution' could be more a product of research focus and ease of access (Taylor, 2011; Cornelissen, 2013) (Figure 3.6). In sum, not every early human 'rainforest' is as similar as the category itself might belie.

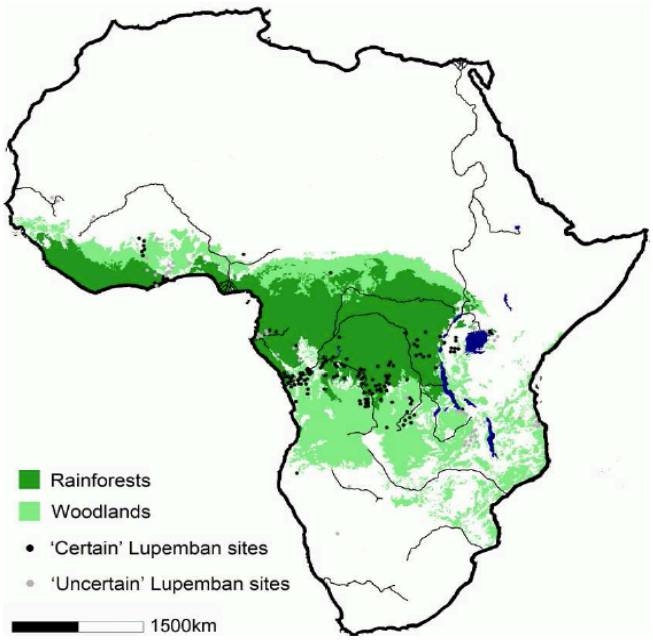


Figure 3.6. The distribution of certain and uncertain Lupemban sites after J.D. Clark (1967), shown with the main river basins of Africa and the contemporary extent of rainforest ecosystems as presented by Mayaux et al. (2004) for the year 2000. From Taylor (2011: 9 – Figure 6).

Sri Lanka's palaeoforests

As shown in Chapter 2, Sri Lanka sits on the same continental shelf as India and would have effectively been an extension of the Indian subcontinent during the Late Pleistocene (Rohling *et al.,* 1998). As a result, biogeographers have tended to emphasise continuity between the rainforests of Sri Lanka and the South Asian mainland, with Sri Lanka sharing many species with its neighbouring landmass (Wallace, 1876; Smith, 1943; Inger *et al.,* 1984; Myers *et al.,* 2000). Expectations of biotic affinity have not

always been met, however. Against the notion that there were frequent migrations across the Palk Strait land bridge during periods of low sea level, molecular phylogenies for several invertebrate and vertebrate faunal species reveal an unexpectedly large number of endemics (Meegaskumura *et al.,* 2002; Schulte *et al.,* 2002; Austin *et al.,* 2004; Bossuyt *et al.,* 2004; Pyron *et al.,* 2013), identifying the Western Ghats and Sri Lanka's Wet Zone as distinct units (Bossuyt *et al.,* 2004; Gunawardene *et al.,* 2007). Dry lowland species appear to have been more successful dispersers (Bossuyt *et al.,* 2004; Gunawardene *et al.,* 2007), suggesting, contrary to some models (Erdelen and Preu, 1990), that rainforest did not extend onto the land bridge during periods of low sea level. Studies of rainforest flora back this up, with distinct floristic compositions evident in high elevation forests in the Ghats and southern Sri Lanka, and half of the Sri Lankan forest species being endemic (Pemadasa and Amarasinghe 1982; Bonnefille *et al.,* 1999).

Palaeoenvironmental proxy evidence from Bay of Bengal and Arabian Sea marine cores indicate significant fluctuations in the intensity and position of the palaeo-monsoon throughout the Late Pleistocene (Schulz *et al.,* 1998; Prabhu *et al.,* 2004; Caley *et al.,* 2011; Rashid *et al.,* 2011; Deplazes *et al.,* 2014) that would have had significant impacts on regional vegetation distributions. Indeed, as seen in Chapter 2 (Section 2.2), this seasonal monsoonal precipitation, as well as the sharp climatic and vegetation gradients of Sri Lanka, make its rainforests particularly vulnerable to climatic influence. Although hard palaeovegetation evidence in Sri Lanka is limited, the correlation between available pollen datasets and global climatic proxies has been used to reconstruct vegetation patterns during the Holocene and Late Pleistocene.

Adams and Faure (1997) used a pan-Asian dataset to suggest that at 18 ka the Sri

Lankan peninsula and southern India would have been covered by tropical forest. However, given the coarse dataset used and evidence for tropical forest retreat during this period elsewhere, this model seems unlikely. By contrast the more refined models of Ray and Adams (2001) and Boivin *et al.* (2013), based on modern vegetation, palaeobotanical, and palaeoclimatic evidence, suggest that during the relatively arid period of Marine Isotope Stage (MIS) 4 a tropical savannah/woodland-grass mosaic existed throughout much of southern India, with greatly reduced tropical forests focused in the western part of the peninsula that probably also persisted in south-western Sri Lanka. The same situation likely existed for the arid periods of late MIS 3 and 2. Therefore, while tropical forest may have continued in the southern Wet Zone of Sri Lanka throughout MIS 4 to 2, including the LGM, it is possible that a more fragmented, mosaic landscape, existed across much of the Sri Lankan Wet and Intermediate Zones at this time, even during wetter phases such as MIS 5 (Boivin *et al.,* 2013) (Section 2.2).

Local sources of palaeoenvironmental information are essential if human-relevant environments are to be determined. Unfortunately such records are currently exceedingly limited in Sri Lanka. The pollen record from the Horton Plains highlands 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 occurred between 16,000 and 8,700 cal. years BP prior to a slow trend towards semi-arid conditions into the Middle Holocene. Yet, while this demonstrates Sri Lankan montane rainforest to be susceptible to climatic change, the central highlands are some distance, both spatially and topographically, from Late Pleistocene and Holocene Microlithic tradition sites in Sri Lanka. Moreover, while micromorphological analysis from the site of Kitulgala Beli-lena demonstrates broadly

corresponding trends of precipitation intensity (Kourampas *et al.,* 2009), it is questionable as to what extent this impacted vegetation in the mixed evergreen-deciduous lowland rainforest.

Although heavily curtailed by the urban and industrial expansion of Colombo today, the higher rainfall of the Wet Zone of Sri Lanka has made it home to the island's tropical rainforest flora of closed-canopy, wet, deciduous, and tropical evergreen, mixed dipterocarp forest ('Tropical lowland evergreen rainforest', 'Tropical semi-evergreen rainforest') (Ashton and Gunatilleke, 1987; Gunatilleke *et al.,* 2005), adjacent to more open, 'Intermediate' mixed evergreen and deciduous rainforests (Erdelen, 1988) (Chapter 2 – Section 2.2). The rainforests of Sri Lanka's Wet Zone have high floral diversity and yield a wide variety of fruits and starchy tubers. These primarily include yam species (*Dioscorea spp.*), palm fruits (*Caryota urens*), breadfruit (*Artocarpus nobilis*), wild banana (*Musa paradisica*), and *Canarium* sp. nuts (Ashton and Gunatilleke, 1987), some of which have been demonstrated to be present at Microlithic sites back to *c.* 36-29,000 years ago (Perera, 2010; Perera *et al.,* 2011) (Chapter 2 – Section 2.2). While large ungulates occur in much smaller groups than in the Dry Zone of Sri Lanka (S.U. Deraniyagala, 1992), the three main monkey taxa, the purple-faced leaf monkey, grey crested langur, and toque macaque, across the Wet and Intermediate Zones would have provided important semi-arboreal and arboreal protein packages. Wild boar, fish, reptiles, molluscs, and small arboreal fauna (including flying squirrels, giant squirrels, and civets) are also available in these forests (Phillips, 1980; Bambaradeniya, 2006), and are demonstrated at Microlithic tradition sites (Perera *et al.,* 2011).

It has often been argued that humans prefer rainforest fringe habitats or instigate

burning regimes to aid movement and encourage floristic and faunal diversity (e.g. Kershaw *et al.,* 2002). Indeed, the sharp climatic and vegetation ecotonal boundaries of Sri Lanka's rainforest (Chapter 2 – Section 2.2) may seem ideal from the perspective of mobile, broad-spectrum foragers. However, although vegetation reconstruction is limited to the island's 'montane forest', the rainforests of Sri Lanka have shown no evidence for prehistoric burning, even at altitudes where it would have been easier, until the Middle Holocene (Premathilake and Risberg, 2003). Indeed, although a semi-deciduous, evergreen mixture, with a theoretical dry-season, in practice Sri Lanka's lowland Wet Zone rainforest is unlikely to have presented an easy target for mass burning given high levels of water availability all year round. While burning may have been more feasible during the cooler, drier LGM or in the more open, drier Intermediate rainforests, no evidence has yet been found. Climatic opening of the rainforest, and increased access to more open Intermediate forests or the large ungulate populations of the Dry Zone, with lower temperature, CO_2 concentrations, and perhaps rainfall, at the LGM may, on the other hand, have been beneficial to human lifeways.

The exploitation of forest fringes and openings would have provided reliable access to an abundance of starchy plants, fruits, and nuts, and likely also increased faunal diversity. Indeed the three Sri Lankan Wet Zone cave and rockshelter sites show continuous occupation across this period (Perera *et al.,* 2011). That said, although dense, tropical semi-evergreen rainforests may yield a reduced concentration of key floral resources, they present fewer obstructions to human movement on the ground, especially in the context of monkey and wild boar hunting (Fortier, 2009). As a result, canopy opening, declines in forest extent, and associated increase in re-growth and forest-floor vegetation, may have posed problems rather than bounties to Sri Lankan hunter-gatherers focused on the hunting of a reliable source of game. Therefore, while

the ecotonal vegetation and climatic situation of Sri Lanka's rainforests may seem to be a perfect set-up for mobile, multi-niche foragers, such as those in Late Pleistocene New Guinea (Fairbairn *et al.,* 2006; Summerhayes *et al.,* 2010), the apparently high reliance on Wet Zone rainforest tree flora, and semi-arboreal and arboreal mammal exploitation, as well as tree nut species, at the Sri Lankan Microlithic tradition sites (Chapter 2 – Section 2.2) may have been better adapted to subsistence within closed forest formations.

3.4 – Ethnographic evidence for the nature of rainforest hunting and gathering: a review

Faunal (primate) resources

The fact that many rainforest plants cover their leaves and fruits with toxic substances (McKey, 1979), and the rapid decomposition of leaf-litter and fallen fruits (Anderson and Swift, 1983), has been argued to lead to a relative paucity of faunal opportunities, and therefore of protein, for human rainforest foragers in tropical rainforests (Odum and Pigeon, 1970; Medway, 1972; Kikkawa and Dwyer, 1992). On the other hand, many animals play an important role in rainforest ecosystems in the form of forest disturbance, pollination, seed predation, seed dispersal, folivory, frugivory, and as top predators (Terborgh, 1988, 1992; Cuarón, 2000). Species densities can vary significantly from place to place in relation to soil fertility, forest structure, and inter-specific competition (Emmons, 1984; Robinson and Redford, 1986). However, while the carrying capacity of tropical forests for hunter-gatherers can be low (<1 person km^2; Robinson and Bennett, 2000), the ethnographic literature lists a diversity of hunting techniques and strategies practised by human rainforest hunters to capture various faunal prey. In particular, although the importance of primates to Sri Lankan Microlithic

tradition foragers appears unparalleled ethnographically, primates do form important components of rainforest forager subsistence in many regions today.

The use of primate populations for food amongst indigenous societies varies considerably worldwide, fluctuating with taboos against eating 'human-like' animals, their relative abundance, ease of capture, access to hunting technology, and the availability of other sources of protein (Sabater Pi and Groves, 1972; Mittermeier, 1977, 1987; Fa *et al.,* 2005; Refisch and Koné, 2005; Fa and Brown, 2009; Remis and Robinson, 2012). In tropical rainforests, primates are frequently among the larger and more conspicuous sources of protein (Mittermeier, 1987). Their social behaviours while feeding and their diurnal strategies make them particularly susceptible to being spotted and captured by hunters (Cowlishaw and Dunbar, 2000). Primates form an important element in the diet of most Indigenous Amazonian groups (Vickers, 1988), making up to 35% of animals taken by gross weight amongst the Waorani of Ecuador (Yost and Kelly, 1983.). Large-bodied, arboreal primates, such as the woolly monkey (*Lagothrix lagotricha*) and howler monkey (*Alouatta seniculus*), tend to be those selected by hunters (Mittermeier, 1987). Similarly, in Africa large-bodied species such as guenons (e.g. *Cercopithecus diana*), mangabeys (*Lophocebus* sp. and *Cerocebus* sp.), colobus monkeys (*Colobus* sp.) and mandrills (*Mandrillus* sp.) are preferred (Mittermeier, 1987; Remis and Robinson, 2012), while in Asia macaques (*Macaca* sp.), leaf monkeys (*Trachypithecus* sp.) and gibbons (*Hylobates* sp.) form the prime targets (Mittermeier, 1987; Kuchikura, 1988).

Of the various techniques utilised, it is perhaps the blowpipe, or the poison-tipped arrow, that Hollywood has ensured are most linked to rainforest hunting in the public domain. Frequently made from a kind of bamboo, blowpipes can range up to 2 m in

length and are used to deliver small, thin darts, frequently tipped with poison, into rainforest prey. Kuchikura (1988), studying blowpipe use among the Semaq Beri in Peninsular Malaysia, argued that this technique provides an extremely reliable source of protein with blowpipe hunting accounting for 41.5% of animal foods consumed. The Semaq Beri tend to focus their blowpipe hunts on the arboreal dusky leaf monkey (*Trachypithecus obscurus*) and banded leaf monkey (*Trachypithecus melalophos*), gibbons, and arboreal squirrels, firing upon them during known periods of group feeding activity. Other records from Southeast Asia have noted the use of blowpipes and poisoned darts to also target pigs and deer (Bellwood, 1999; Endicott, 1999). Furthermore, the Waorani of Ecuador, with larger, higher velocity blowpipes, shoot at large, ground-dwelling birds, such as the currasows and tinamous, as well as peccaries and deer (Yost and Kelly, 1983). That said, research in both regions has maintained that projectile shot accuracy and strike-distances are optimised in the shooting of arboreal, rather than ground-dwelling, fauna (Yost and Kelly, 1983; Kuchikura, 1988).

The same is true of the bow and arrow which, although now generally replaced by firearms where local access permits (Corlett, 2007), are generally used in tropical rainforest hunting contexts in the shooting of large-bodied, arboreal prey such as primates, though they are also used by Southeast Asian groups that focus their hunting on wild pigs and Amazonian groups hunting peccaries and tapir (Dwyer, 1983; Peres and Dolman, 2000). In Africa, 65% of the mammalian kills of Mbuti pygmy bow hunters in Congo-Kinshasa are the medium-large sized canopy-dwelling colobus monkeys (Harako, 1982). Rainforest hunters often use their knowledge of primate feeding behaviours to lie in wait near social feeding spots. Hunters have also been known to fake primate predator calls, encouraging monkey vocalisation and mob behaviour, and making them an easier shot (Bshary, 2001). In many regions of the

African rainforest zone, it is large, arboreal primates that are most depleted by bow and arrow and shotgun hunting (Peres and Dolman, 2000; Refisch and Koné, 2005; N'Goran *et al.,* 2011), while small-medium semi-arboreal primates, with greater flexibility in diet, are found to be more resilient to this form of hunting (Peres and Dolman, 2000). However, others have argued that primates that travel and forage on the ground also make vulnerable targets for hunters (Bodmer *et al.,* 1997; Fa *et al.,* 2005).

In this context, another useful hunting technique employed by rainforest hunter-gatherers is trapping. Noss (1998) has argued that cable snare hunting is becoming the most widespread hunting method in Central African forests today as a result of the low cost of wire and ability to leave traps while engaging in other activities. Accompanying snare hunters from the village of Bayanga into the Dzanga-Sangha Special Reserve in the Central African Republic, Noss identified two types of snare. Foot snares captured a huge variety of mammals, as well as several birds and reptiles, while neck snares were mainly successful in the capture of large ground-dwelling birds, giant rats, and porcupines. Noss (1998) notes that all mammals identified were captured in snares, including semi-arboreal primates (where traps were set both on the floor and in low tree platforms), although the majority of captures were composed of three duiker species (*Cephalophus callipygus*, *C. dorsallis*, and *C. monticola*) and the brush-tailed porcupine (*Atherurus africanus*). The latter demonstrates a further use of traps and snares, the capture of nocturnal prey that is more difficult to stalk. Wire snares and deadfall traps have also been documented in Southeast Asia where they have been used to catch deer, pigs, and primates (Bennett and Robinson, 2000), as well as a wide range of other species (Rao *et al.,* 2005). Noss (1998) and Corlett (2007) argue that this technique has become more common with the rise of commercial hunting, where indiscriminate capture is less of a concern.

Another interesting rainforest hunting technique comes in the form of communal net hunting practised by the Aka pygmy foragers of the Central African Republic (Noss, 1997). Although the Aka employ spears, snares, crossbows, and guns, communal net hunting is most important in terms of yields and participation rates. Hunters form a circle or semicircle with the nets, hanging the nets on small trees or vines and pegging the bottom to the ground. Some, armed with spears, search the interior, beating leaves and shouting to drive out animals. Others drive the fleeing animals towards the nets, seizing them and killing them with spears, machetes or logs. The whole process then moves to another spot some 200 m away (Noss and Hewlett, 2001). The main prey taken is the blue duiker (*Philantomba monticola*) (75%), brush-tailed porcupine, the bay duiker (*Cephalophus dorsalis*), and Peter's duiker (*Cephalophus callipygus*) (Noss, 1997). By contrast, Fortier (2009) has described net hunting, combined with axes, in the reliable mass-procurement of semi-arboreal macaque and langur monkey species (up to 80% of their animal haul) by the Raute in the monsoonal forests of western Nepal. Interestingly, men and women of many ages, including those carrying infants, participate in communal net hunts and the resulting catch is shared across kinship ties and large portions of the community (Noss, 1997).

Significant amounts of protein and other essential nutrients are also available from smaller vertebrate and invertebrate sources in rainforest environments. Many communities are known to prize the high-sugar content of honey of various rainforest bee species (Dentan, 1991). Furthermore, numerous studies indicate that while firearms, bow and arrow, trapping, or net hunting may provide the primary source of faunal protein, opportunistic hand or machete/axe hunting of lizards, snakes, frogs, tortoises, terrapins, and various other small vertebrates is also frequently practised by rainforest foragers across the world (Bennett, 1992; Luiselli, 2003). The use of insects, high in

protein, essential minerals and vitamins, for food is also widespread (Posey, 1978; Dufour, 1987; Bennett, 1992; DeFoliart, 1999), including evidence for the consumption of ants, larvae of *Coleoptera* and *Lepidoptera*, palm grubs, caterpillars, and termites across the African, Melanesian, Southeast Asian, and South American rainforest regions (DeFoliart, 1999). Finally, fishing, through fish poisons, temporary damming, or harpooning, can form a major part of rainforest forager diets, and in many Amazonian communities is the predominnt source of protein (Bennett, 1992). Indeed, Tukanoan Indians have even protected flood forests, an important feeding ground for fish, to ensure high yields (Chernela, 1985).

Hunting pressure has different impacts on different species and rainforest ecosystems (Kumara and Singh, 2004). Large mammals, including primates, generally fare badly, with their smaller overall population sizes, and long gestation periods and birth intervals (Cardillo *et al.,* 2005), although primates are able to adapt their behaviour to counteract human hunting strategies (Bshary, 2001; Gurven *et al.,* 2006). Snare trapping indiscriminately kills all mammals large enough to trip the mechanism, while blowpipe and bow and arrow hunting, given the investment of time in equipment construction and use, tends to be more focused (Kuchikura, 1988; Noss, 1998). Primate species often live sympatrically within a rainforest ecosystem and when the numbers of one species are reduced others increase with the removal of competition (Peres and Dolman, 2000). A number of primate taxa, as opposed to frugivorous rodents and other terrestrial mammals, have also been shown to compensate for depletion in one group (Bodmer *et al.,* 1997; Refisch and Koné, 2005). Therefore, although modern market hunting and indiscriminate shooting and snaring may be leading to 'empty forests' (Harrison, 2011), and the removal of often key species in seed dispersal and floristic diversity (Stoner *et al.,* 2007; Wang *et al.,* 2007), systematic and strategic hunting for subsistence, that

follows fluctuations in prey availability and ecological characteristics, can be a highly sustainable source of protein in tropical rainforests (Van Vliet *et al.,* 2009).

Plant resources

Ethnographic exploitation of botanical resources has been at the heart of the anthropological debate regarding the viability of rainforests for long-term human occupation without access to agricultural crops (Headland and Reid, 1989) (Chapter 2 – Section 2.4). It has been argued that in tropical rainforests most of the energy stored in plants is in trunks or leaves too high in the canopy to be accessible to human gathering, even if edible (McElroy and Townsend, 1985; Bailey *et al.,* 1991). Furthermore, the depressed seasonality of tropical rainforests makes storage of energy and moisture in tubers less adaptive for plants than in zones with marked winters or dry seasons. Where such resources are present, they have been argued to be highly scattered (Kikkawa and Dwyer, 1992) and to not provide enough reliable starch to support foragers without agricultural connections (Hart and Hart, 1986; Bailey *et al.,* 1989). Nonetheless, as we have seen, seasonality can differ between rainforest formations, with some having short dry seasons or longer, less pronounced dry seasons (Whitmore, 1998). Furthermore, to focus on 'yams' and starch as the only sources of carbohydrate or botanical benefit to hunter-gatherer subsistence is to greatly understate the diversity of rainforest micro-habitats and resources available (Dentan, 1991). In the Amazon, the Chácobo of Bolivia employ 82% of the rainforest plants available, while the Quijos Quichua of Ecuador use more than 90% of identified tree species (Bennett, 1992).

Bahuchet *et al.* (1991) have performed a direct assessment of the ecological and nutritional availability of wild yams in the western Congo Basin, alongside linguistic

analysis, to suggest that yams *could* support independent rainforest foraging. Yasuoka (2009) has shown that annually reproducing wild yam species (*Dioscorea praehensilis* and *D. semperflorens*) favour habitats of canopy gaps, where sufficient light is present, and only cluster in specific places. Furthermore, the vegetative reproductive system of the yams means that they do not propagate extensively in the wild. On the other hand, the transplantation of yams by foraging groups such as the Baka can greatly increase their concentration and yield (Yasuoka, 2009). Dentan (1991) has argued that the Semang of West Malaysia may have been able to survive on wild yams as a subsistence staple, while other Southeast Asian foragers combined yams with a diversity of other floral resources. Rainforest fruits represent one alternative source of carbohydrate and sugar. For example, in Malaysia, cycad seed flour can provide a useful stored carbohydrate (Thieret, 1958), while the grains of Job's tears (*Coix lachrymae jobi*) are about 60% soluble carbohydrates, mostly starch (Burkhill, 1966). Malaysian ethnographic groups have been shown to tend wild trees, deliberately defecate seeds near campsites, and organise fruit tree collection in order to ensure stable availability (Ellen, 1988). The lack of seasonality cited as causing reduction in underground storage organ availability is, by contrast, likely to make rainforest fruits a reliable year-round source of carbohydrate.

Other plant resources exploited across the rainforests of Southeast Asia and Melanesia include fruit pandanus (*Pandanus conoideus*) and breadfruit (*Artocarpus incisa*). In the Amazon, most of the important foodstuffs and cash crops exploited today are South American natives, including manioc (*Manihot esculenta*), papaya (*Carica papaya*), sweet potato (*Ipomoea batatas*), pineapple (*Ananas comosus*), cacao (*Theobroma cacao*), yam (*Dioscorea sp.*), Brazil nuts (*Bertholletia excels*), and peach palm (*Bactris gasipaes*), that are freely available to rainforest foragers (Dufour, 1990; Bennett, 1992).

In addition, the biggest starch storage organs in the plant kingdom are not underground but in the trunks of the hapaxanthic palms, especially the genus *Corypha*, that grow in clumps across Southeast Asian, Melanesian, and Sri Lankan rainforests (Corner, 1966). The starch from these trees is available throughout the year and, once extracted and dried, is light and easy to carry (Strickland, 1986). In the case of the Penan of Malaysia it has been argued that a combination of wild yams and sago palm (*Eugeisonna utilis*) can comfortably provide enough starch to maintain independent rainforest foraging in rainforest interiors (Hong, 1987; Brosius, 1990, 1991; Dentan, 1991). The Penan cut a small number of mature trunks from a single clump of roots, never felling the entire root-stock and allowing for sustainable regeneration (Brosius, 1986).

Humans can also change rainforest ecosystems to their own advantage to preserve or stimulate fields of different floral resources across different seasons and across local rainforest environments (Kennedy, 2012). Hill and Baird (2003) use a combination of ecological, linguistic, and oral history datasets to demonstrate that the Kuku-Yalanji of Australia will burn rainforest vegetation to preserve different 'types' of rainforest. On the one hand, the most important wet season staple, *Beilschmiedia bancroftii* yams, are preserved by the protective burning of rainforest margins in order to ensure that no high-temperature fires developed. By contrast, in the dry season, fires are lit to improve access to *Cycas media* growing in open forest areas. This also enhances the seed productivity of this crop, an essential source of carbohydrate during the dry season. Diversity in these open forest areas is maintained by fire strategies that prevent these habitats reverting to rainforest (Hill *et al.,* 2001). Ichikawa (1999) has argued that most of the food plants important to the Mbuti pygmies (Aka and Baka groups) of northeastern Congo and southeast Cameroon are light-demanding trees, including the nut-bearing *Antrocaryon nannanii* and *Ricinodendron heudelotii*, and are often

exploited around previous clearings. The fruit-bearing vines of *Landolphia* spp. are also said to grow best in disturbed areas (Ichikawa, 1999).

Rainforest plants are not only useful from an explicitly nutritional perspective. The Shuar of the Amazon prepare *ayampakus*, transportable packages of meat and vegetables, that are then cooked on the fire, with large, broad monocot leaves. The leaves not only act as the 'cooking pot' but also flavour the food (Bennett, 1992). Ninety species provide the Shuar with wood and non-wood fuels, though not all are effective as fuel, while 198 species of plants are used to treat skin and gastrointestinal ailments (Bennett, 1992). The Shuar also make lances and blowguns from palm stem, and dart poisons are made from species of Loganiaceae and Menispermaceae. Cedar trees are often used for the construction of canoes in the Amazon Basin (Vickers, 1988). In Malaysia, the Penan and Semang have been show to make string and rope from fibrous leaf sheathes or climbers, respectively, while the fronds of many palms are known to be used as thatch and roofing for temporary shelters (Whitmore, 1973; Dentan, 1991). In many societies, rainforest fruits, tubers, and roots are used as bait for animals, while the clearings used to stimulate their growth can also attract terrestrial mammals (Dufour, 1990). For example, the Kayapo of Brazil purposefully spread their garden clearings to attract animals over a large area (Posey, 1984), with tapir and peccary being particularly attracted to the resulting concentrations of fallen fruits.

The Sri Lankan Veddas

The closest ethnographic comparison available for this study are the Vedda hunter-gatherers of Sri Lanka (Parker, 1909; Seligmann and Seligmann, 1911). Unlike the earliest Microlithic tradition groups, the 'Forest' Vedda occupy the open monsoonal

jungles of the Sri Lankan Dry Zone. Nevertheless, an abundance of 19th and 20th century observations of these communities mean they can still provide insight into procurement strategies relevant to the flora and fauna of Sri Lanka's tropical forests. While honey, yams, and wild fruits were staples (Spittel, 1924, 1961) (in the Wet Zone rainforests, *Canarium* sp., palm toddy and breadfruit provided further reliable sources of carbohydrate and sugar), it has been argued that meat was the more important source of nutrition (Sarasin and Sarasin, 1893). Fish was a less favoured item of the diet, though fishing pools provided a coveted source of food in which fish were harpooned and shot with arrows (Seligmann and Seligmann, 1911). A wide spectrum of fauna was (and still is) exploited by the Veddas, including bee grubs, terrapins, tortoise, pangolin (*Manis crassicaudata*), bandicoot rats (*Bandicota bengalensis*), porcupine (*Hystrix indica*), giant squirrel (*Ratufa macroura*), hare (*Lepus nigricollis*), jungle fowl (*Gallus lafayetti*), mongoose (*Herpestes* sp.), and freshwater eels and fish. Although the relative importance varied regionally, the Veddas focused their subsistence on large-bodied monitor lizards (*Varanus bengalensis*), macaques (*Macaca sinica*), langurs (*Semnopithecus priam thersites*), pigs (*Sus* sp.), mouse-deer (*Moschiola meminna*), barking deer (*Muntiacus muntjak*), spotted deer (*Axis axis*) and sambhur (*Rusa unicolor*) (Bailey, 1863; Sarasin and Sarasin, 1908; Seligmann and Seligmann, 1911).

The basic method of procuring this larger game was with bow and arrow, made entirely from available tree parts (Parker, 1909; Seligmann and Seligmann, 1911; Lewis, 1915). The arrow-shafts were also made from local wood, fletched with bird feathers, and tipped with iron (or occasionally bivalve shells) available through trade (Spittel, 1961). Interestingly, despite its ready availability, the Veddas did not use *Antiaris toxicania* (a favoured projectile poison in Southeast Asia) to tip their arrows, a pattern also seen in aboriginal Indian communities in the Western Ghats. The Veddas are noted as being

'unreliable' shots, requiring remarkable stalking abilities to get close enough to kill their prey (Seligmann and Seligmann, 1911). They focused their hunting around water resources where deer congregated, or frequently used dogs to track animals along known game trails. Monkeys were frequently driven and ambushed or driven and isolated on trees to be climbed after, shot at, or set upon by dogs (Spittel, 1961). Terrestrial birds were also shot at with smaller wood-tipped arrows, while land-monitor lizards were driven out of their burrows. Dead-fall traps and snares were set for smaller game including mouse deer, hare, mongoose, and pangolins. Elephants and large cattle were also occasionally hunted (Sarasin and Sarasin, 1893). Clearly then, although not occupying the rainforest *per se*, the Veddas provide evidence for a variety of strategies and techniques to procure floral and faunal resources in the tropical forests of Sri Lanka, many of which can also be found in the Wet Zone rainforests and, indeed, within the Microlithic tradition sequences (Chapter 2 – Section 2.2).

'Green deserts' or a patchwork of plenty?

From the above, and from the dynamism and variety involved in local and regional rainforest formations (Section 3.1), it should be clear that the plant and animal resources available to rainforest hunter-gatherers vary not only regionally but also locally. Therefore while Bailey *et al.* (1991) might envisage a 'green desert', perhaps from the perspective of the uniform, evenly spaced resources relied upon by agricultural societies (Hemming, 2009), indigenous peoples see an abundance of opportunities. In the context of plant resources, canopy gaps or forest fringes may provide access to more regular supplies of yams, fruits and nuts, climbers, and herbs, especially where successional regrowth encourages increased floral diversity. Indeed, as we have seen, humans often intentionally burn or open rainforest clearings in order to stimulate the growth of certain

resources (Hill and Baird, 2003). Furthermore, many Amazonian groups settle near the river where vegetation growth is more open and where fishing can provide a large and regular supply of protein (Dufour, 1990), sufficient indeed to support large, sedentary, and complex communities (Heckenberger *et al.,* 2008). However, humans will also act to preserve and utilise forest interiors, where fruits, palms, and some yam species provide plentiful carbohydrate resources under conditions of low light (Dentan, 1991). Different rainforest micro-habitats will be exploited by different, or the same, groups depending on availability, technology, and cultural preference.

In the case of the Sri Lankan Vedda, and indeed other hunter-gatherer populations, reliable protein packages can be obtained from tropical forests through the systematic hunting of semi-arboreal and arboreal mammals, including a particular focus on primate species. Peterson (1981, 1982) has argued that the successional regrowth and concentration of fruits and starchy plants at forest fringes, edges, or clearings support a higher density of game. Indeed, in the case of terrestrial frugivores such as pigs, mouse deer, and duikers this may be the case, often acting as bait and a suitable spot for hunters to 'await' their prey (Wadley *et al.,* 1997; Smith, 2005). Such hunting could be combined with the maintenance of clearings for floristic exploitation or fishing in rivers that provide drinking water for other animals (Smith, 2005). The setting of traps along visible tracks may also facilitate access to nocturnal, lone-ranging, skittish prey, including terrestrial and semi-terrestrial primates (Noss, 1998). On the other hand, large-bodied, arboreal primates, one of the most visible and significant sources of protein in many tropical rainforests, stay away from clearings, even where natural, confining themselves to canopies and the consumption of leaves or unripe fruits (Wadley *et al.,* 1997). In sum, while rainforests may not provide uniform planes of static resources, and floristic and faunal availability will differ across space and time,

those with knowledge can practise highly sustainable exploitation of floral and faunal resources across the patchwork.

3.5 – Rainforest prehistories and the search for new methods

This chapter highlights the fact that scholars should no longer be satisfied with the statement that prehistoric humans occupied or exploited 'rainforest'. Rather, increasing global and methodological scope in the investigation of these dynamic habitats should seek to provide more detail regarding the diversity of 'rainforest' environments occupied by Late Pleistocene and Holocene *Homo sapiens*. The dynamic variation within the category of 'rainforest' means that humans in different regions and time periods faced different species distributions, different patterns of resources, different climatic challenges, and different possibilities for rainforest manipulation. A 'rainforest prehistory' of our species was evoked almost 15 years ago (Mercader 2002a, 2002b). Now established, it is time to investigate and document the breadth and diversity of *prehistories* in what remain some of the most evocative ecologies in human environmental discourse today (Malhi *et al.,* 2013; Moritz *et al.,* 2014).

Reviewing the ethnographic literature, particularly for the region of interest, can provide useful analogies for the technological and strategic approaches available to prehistoric foragers in the procurement of rainforest floral and faunal resources. In the context of the Microlithic tradition of Sri Lanka, it appears that specialised primate hunting may have provided reliable access to some of the larger packages of protein and fat available to rainforest foragers. The accompanying collection of freshwater molluscs, a variety of arboreal and terrestrial small mammals, and use of the starch-rich *Canarium* sp. nut implies the utilisation of both tailored and diverse subsistence strategies (Chapter 2 –

Section 2.2). However, while the methods discussed in Chapter 2 (Section 2.3) can track the use of these resources into the past, it is only the stable isotope analysis of human and faunal tooth enamel that can provide direct insights into the extent of Sri Lankan human rainforest resource reliance across space and time, as well as indirect information regarding temporal and spatial variance in Sri Lankan rainforest structure and extent and the particular ecological niche occupied by Sri Lankan human foragers within these environments.

Chapter 4 – Reconstructing early human rainforest adaptations: stable carbon and oxygen isotope analysis of human and faunal tooth enamel

In this chapter I focus on stable carbon and oxygen isotope systematics in a tropical context, tracking their variability across different plant types, and ecological conditions, and into the tooth enamel of their consumers, with particular focus on the 'canopy effect'. This chapter uses these principles to highlight the potential of stable carbon and oxygen isotope analysis of human tooth enamel as a means of exploring rainforest reliance during the Late Pleistocene and Holocene. The necessary preservation considerations and protocols required when working on material excavated from tropical settings are discussed. I also interrogate the level of ecological detail that can be gained from the stable carbon and oxygen analysis of non-human primate tissues, including the role of modern botanical and faunal reference datasets in this context. The chapter finishes by outlining my approach for developing a human stable isotope ecology for the Sri Lankan Microlithic tradition.

4.1 – Stable carbon and oxygen isotopes in tropical environments

"The distinct advantage of a stable isotope natural abundance approach for dietary studies is that it reflects the foods *actually eaten* by an individual, or a group of individuals, rather than a palimpsest of waste of uncertain duration that typically preserves only a tiny fraction of the organic material and overlooks those organic remains with low survival rates…" (Lee-Thorp, 2008: 925).

In Chapters 2 and 3 I argued that existing methods used in the reconstruction of early human rainforest subsistence have been unable to discern relative dietary reliance on rainforest resources, as well as the ecological niche(s) occupied by early members of our species in these habitats. Working on the principle 'you are what you eat', stable isotope analysis of human and faunal tissues has been shown to provide a direct, long-term perspective of dietary intake of an individual that, as seen in Chapter 2 (Section 2.3), is not available from other bioarchaeological techniques (Vogel and van der Merwe, 1977; van der Merwe and Vogel, 1978; Lee-Thorp, 2008). Having been applied in archaeology for more than thirty years, stable isotope analysis has proven itself to have broad temporal, geographical, and theoretical scope, including the reliable reconstruction of hominin and faunal diets back to more than 9 million years ago (e.g. Lee-Thorp, 1989; Lee-Thorp *et al.,* 1989a; Bocherens *et al.,* 1991; Quade *et al.,* 1995; Richards *et al.,* 2000; Nelson, 2007; Lee-Thorp, 2008; Levin *et al.,* 2008; White *et al.,* 2009; Uno *et al.,* 2011). Furthermore, systematic reconstruction of prehistoric and modern 'stable isotope ecology' has demonstrated the potential of this method to detect subtle distinctions in human and faunal niche position, dietary habits, and dietary variability (Szostek, 2009; Sandberg *et al.,* 2012; Schoeninger, 2014; Crowley *et al.,* 2015). Yet, despite this versatility, stable isotope analysis has yet to be applied to the question of early human rainforest reliance and niche position, and has also remained relatively under-utilised in the tropics more generally beyond Africa (Krigbaum, 2001).

Stable isotope basics

Stable isotopes of an element differ slightly in their nuclear mass as a result of differences in the number of neutrons. The absolute stable isotope abundance of a sample is difficult to determine (Hayes, 1983). Consequently, isotope ratios are

expressed as the relative abundance of the heavy (minor) to light (major) isotope using the delta notation in per mil (McKinney *et al.,* 1950).

1) $\delta^{a}X\ (‰) = (R_{sample}/R_{standard}-1)*1000,$

where *R* is the ratio of the heavy (a) to light (b) isotope of X.

The mass difference in isotopes of the same element, caused by differences in the number of neutrons, result in small but significant variation in thermodynamic and kinetic properties (Sharp, 2006). Kinetic effects in fast, incomplete or unidirectional reactions involve lighter isotopes being more 'mobile' and reacting faster than heavier ones. In enzyme-driven biochemical reactions, the enzyme discriminates against the heavier isotope in the system. In equilibrium reactions, isotope effects generally relate to the effects of atomic mass on bond energy. Heavier isotopes form stronger bonds and will therefore be concentrated in phases with higher bond energy (Hoefs, 1997; Sharp, 2006). These fundamental fractionation phenomena cause subtle, but measurable, differences in isotope abundance in biogenic materials that can be related to biological processes such as photosynthesis and food metabolism, and environmental factors such as temperature (Koch, 1998; Sharp, 2006).

Stable carbon isotopes in a tropical context

All terrestrial plants are depleted in ^{13}C relative to atmospheric CO_2 (*c.* -6.5‰ prior to the Industrial Era), but the extent of this varies depending on which of the three main photosynthetic pathways is utilised: C_3, C_4 or CAM (Crassulacean Acid Metabolism) (Craig, 1953; Smith and Epstein, 1971). In land plants, the two dominant photosynthetic pathways, C_3 and C_4 (so-called because of the number of carbon atoms fixed in the first

product), differ in their net discrimination against ^{13}C during fixation of CO_2 (Smith and Epstein, 1971; Farquhar *et al.,* 1989). Most terrestrial plants, including trees, herbs, shrubs, and shade-loving, temperate, or high altitude grasses follow the C_3 photosynthetic pathway (Calvin and Benson, 1948). C_3 plants discriminate against ^{13}C by a small amount (*c.* 4‰) during diffusion and dissolution of CO_2 into their chloroplasts. However, during carboxylation, the enzyme ribulose bisphosphate carboxylase/oxygenase (RuBisCO) strongly discriminates against ^{13}C, leading to an overall average discrimination of -19‰ relative to atmospheric $\delta^{13}C$. In C_4 or Hatch-Slack photosynthesis, followed by most arid-adapted grasses and some sedges, CO_2 is fixed by phosphoenolpyruvate carboxylase (PEP) before it enters the RuBisCO cycle (Hatch *et al.,* 1967). This configuration enables increased efficiency in CO_2 assimilation but also means that the strong discrimination of RuBisCO against ^{13}C is barely expressed in C_4 plants. C_4 $\delta^{13}C$ values are consequently closer to atmospheric CO_2 compared to C_3 plants (Ehleringer and Osmond, 1991). C_3 $\delta^{13}C$ values vary from about -24 to -36‰ (global mean -26.5‰), while C_4 values range from approximately -9 to -17‰ (global mean -12‰ (Smith and Epstein, 1971)). C_3 and C_4 plants therefore have distinct and non-overlapping $\delta^{13}C$ values (Tieszen, 1991) (Figure 4.1).

This picture is made more complex by a smaller group of succulent CAM plants (Rundel *et al.,* 1999) and freshwater and aquatic systems (Fry and Sherr, 1984). CAM plants may either fix atmospheric carbon in the manner of C_3 plants (using RuBisCO) or through a modified, diurnal C_4 sequence in which phosphoenolpyruvate is carboxylated, then reduced, at night to form malate (O'Leary, 1981). During the day malate is then decarboxylated, with the resulting CO_2 fixed by RuBisCO. This variation leads to $\delta^{13}C$ values that are either within the range of C_3 or C_4 plants, or intermediate between the

two (O'Leary, 1981). However, CAM succulents and epiphytes are often adapted to xeric conditions, causing them to be rare in the tropics (Krigbaum, 2001). Where they are present in tropical forest habitats (Whitmore, 1998), they are unlikely to contribute significantly to human subsistence.

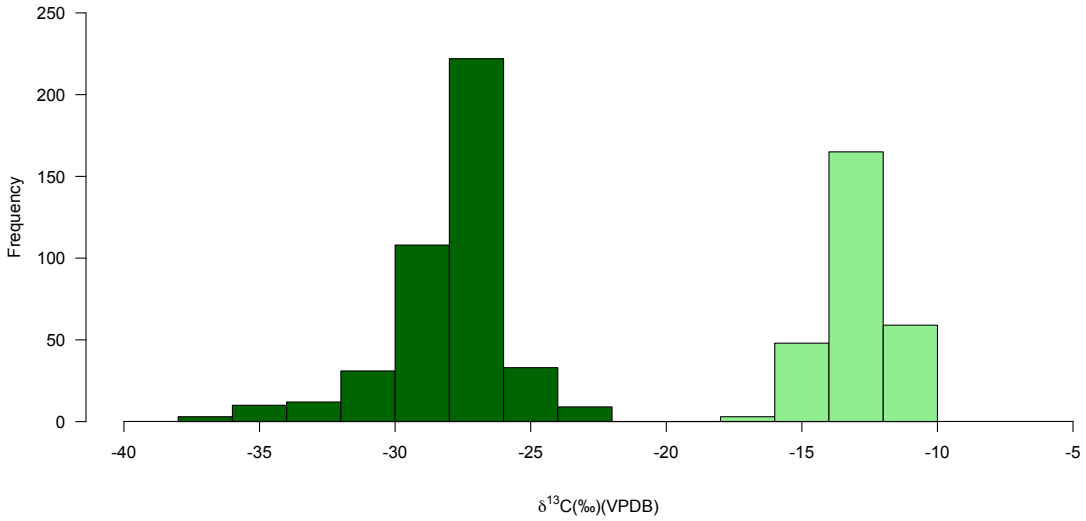


Figure 4.1. Histogram of $\delta^{13}C$ values of East and Central African plants collected between 1997 and 2006 (data from Cerling et al., *2010).*

Freshwater aquatic plants tend to follow a C_3-like pathway (Fry and Sherr, 1984; Peterson and Fry, 1987). Nonetheless, carbon in dissolved CO_2 can come from a number of sources, including carbonate detritus, mineral springs, atmospheric CO_2, and recycled organic matter, leading to widely varying $\delta^{13}C$ values (Fry and Sherr, 1984; Peterson and Fry, 1987). Marine plants and phytoplankton also follow the C_3-pathway. However, their source carbon comes from dissolved bicarbonate CO_2, offset from atmospheric CO_2 by +7‰ (Fry and Sherr, 1984; Peterson and Fry, 1987). This offset is reflected in marine plants and, while the terrestrial C_3 plant average is -26.5‰, marine phytoplankton has values averaging between -19 and -21‰ (Fry and Sherr, 1984;

Ambrose, 1993). Mangroves are a potentially important human resource in the tropics. Mangrove plants, and dependent estuarine/coastal foodstuffs, have been shown to have 'terrestrial' $\delta^{13}C$ rather than offshore marine signatures (Rodelli *et al.,* 1984).

C_3 and C_4 photosynthetic pathways, and their distinct $\delta^{13}C$ values, are adaptive responses to prevailing environmental conditions (Ehleringer *et al.,* 1997) namely light intensity, temperature, amount of precipitation, and recycling of CO_2. C_4 taxa have higher optimum leaf temperatures for photosynthesis (25-45°C) than C_3 plants (10-25°C) due to the fact they require more energy for the two-stage CO_2 fixation process (Ehleringer *et al.,* 1997). To minimise the resulting increased potential for water evaporation, C_4 plants can fix CO_2 at a faster rate and at lower pCO_2 levels than C_3 plants. Consequently, they can achieve the same rate of photosynthesis but with less water loss (Sage, 2004). This adaptation makes C_4 plants more efficient than C_3 plants at capturing carbon during photosynthesis under conditions of low CO_2 concentration, aridity, high light intensity and higher temperatures (Ehleringer *et al.,* 1997). As a result, in the tropics, C_3 plant taxa are distributed primarily within forest, woodland, or high altitude environments while C_4 grasses and sedges are restricted to more open, high solar insolation grassland biomes (Cerling and Harris, 1999). The wide $\delta^{13}C$ range within the C_3 photosynthetic plant group (Figure 4.1) is also controlled largely by environmental factors, including altitude, irradiance, temperature, humidity, and CO_2 concentration, that influence the rate of CO_2 fixation relative to water loss (Smith *et al.,* 1976; Farquhar *et al.,* 1982, 1989; Ehleringer *et al.,* 1986; Tieszen, 1991). In a tropical forest context, the primary environmental consideration in this regard is the so-called 'canopy-effect'.

C_3 vegetation growing in forests under dense canopy cover is significantly depleted in ^{13}C compared to secondary forest, woodland vegetation, and open areas (Smith *et al.,* 1976; Vogel, 1978; Medina and Minchin, 1980; Farquhar *et al.,* 1989; van der Merwe and Medina, 1989, 1991). A vertical gradient of $\delta^{13}C$ is also observed in leaf matter sampled along a transect from the canopy to the forest floor, where plant $\delta^{13}C$ has been shown to reach as low as -32 to -36‰ (van der Merwe and Medina, 1989; Farquhar *et al.,* 1989). These 'canopy effect' phenomena have been linked to the capture of soil-respired CO_2 (Medina and Minchin, 1980) and low light irradiance (Farquhar *et al.,* 1989) under the canopy. In a study of CO_2 $\delta^{13}C$ across a vertical transect in the Amazon rainforest Jackson *et al.* (1993) found atmospheric CO_2 at the top of the canopy to have average $\delta^{13}C$ values of -7.8‰ whereas soil-respired CO_2 was considerably depleted in ^{13}C ($\delta^{13}C$= *c.* -25 to -28‰). Mixtures of different proportions of soil respired CO_2 and atmospheric CO_2 are fixed into plant tissues along both horizontal and vertical gradients from 'closed' to 'open' conditions (Figure 4.2). Simultaneously, differential light irradiance at different points in the canopy, or at different levels of forest 'closure', affect intercellular CO_2 levels, with lower $\delta^{13}C$ occurring under more shaded conditions (Graham *et al.,* 2014). This 'canopy effect' has been demonstrated in temperate (Pearcy and Pfitsch, 1991; Hanba *et al.,* 1997; Bonafini *et al.,* 2013), subtropical (Ehleringer *et al.,* 1986), and tropical forest formations (Medina and Minchin, 1980; van der Merwe and Medina, 1989, 1991; Medina *et al.,* 1991; Buchmann *et al.,* 1997; Martinelli *et al.,* 1998; Cerling *et al.,* 2004; Ometto *et al.,* 2006; Graham *et al.,* 2014 Oelze *et al.,* 2014), the world over.

One further potential source of $\delta^{13}C$ variation in tropical forest environments is $\delta^{13}C$ differences between parts of a given plant. Non-photosynthetic (heterotrophic) tissues,

including fruits, seeds, stems, and wood, have been found to typically contain more ^{13}C and thus have higher $\delta^{13}C$ values (*c.* 1-2 ‰) than leaves (Medina *et al.,* 1991; Martinelli *et al.,* 1998; Codron *et al.,* 2005a, 2005b; Cernusak *et al.,* 2009; Blumenthal *et al.,* 2012, 2015). Differences of a similar magnitude and direction between leaves and fruits have been reported for a range of crops and legume species under controlled growing conditions (Yoneyama *et al.,* 1998, 2000; Cernusak *et al.,* 2002) and have also been documented in a number of tropical forest ecologies (Cerling *et al.,* 2004; Oelze *et al.,* 2011). Plant part distinctions are apparently maintained across species and across periods of environmental change (Pascual *et al.,* 2013). Cernusak *et al.* (2002) suggest that, given that the $\delta^{13}C$ of *Lupinus angustifolius* seeds matches that of phloem sap carbon, it is possible that lower $\delta^{13}C$ values in leaves might be the result of the foliar canopy being laid down earlier in the growing season when plants were subject to lower water stress (Pate and Arthur, 1998). However, it could also be the case that appreciable fractionation events during translocation to fruits, and eventual conversion of sugars to dry matter, drive the differences between the storage (fruits) and growth (leaves) parts of the same plants. Variation can also exist among leaves of the same plant in some tree species, with young leaves being ^{13}C-enriched relative to mature leaves (Cernusak *et al.,* 2009).

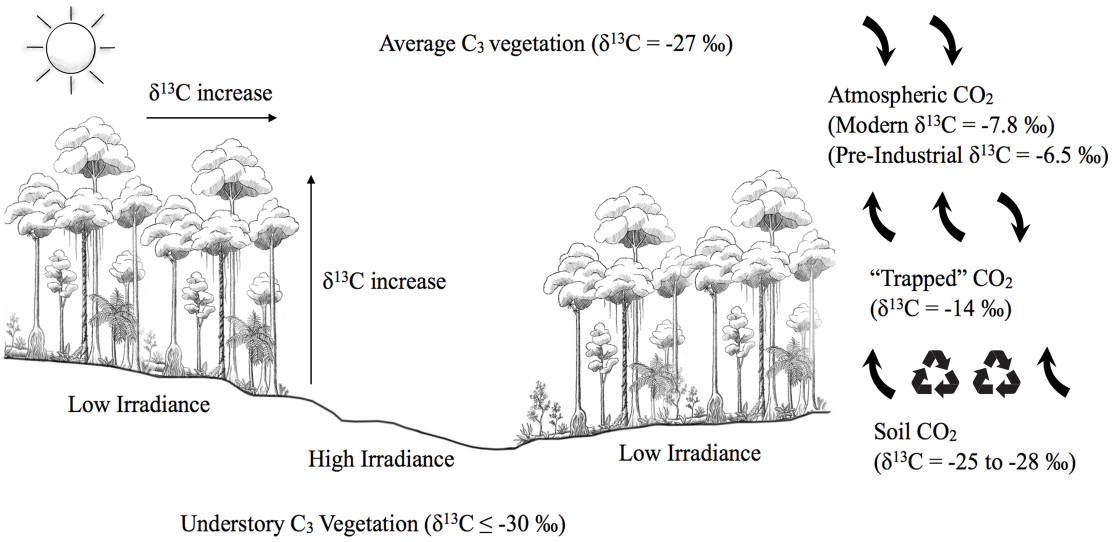


Figure 4.2. Diagram representing C_3 plant $\delta^{13}C$ variation in a tropical forest context. Low irradiance and recycled CO_2 result in lower $\delta^{13}C$ values in air, soil, and vegetation growing under a closed canopy relative to more open areas. In closed areas, understory vegetation is significantly depleted in ^{13}C, and vegetation has more negative $\delta^{13}C$ values, compared to that growing higher in the canopy. Adapted from Jackson et al. (1993), Quade et al. (1995), and Krigbaum (2003).

Stable oxygen isotopes in a tropical context

$\delta^{18}O$ from terrestrial records in the tropics and subtropics largely reflects hydrological conditions through isotope effects on precipitation and other sources of moisture (Dansgaard, 1964; Gat, 1996). Temperature-dependent processes of evaporation from the oceans and the continental advection of moisture masses structure global $\delta^{18}O$ patterns in precipitation (Dansgaard, 1964; Gat, 1996). Precipitation $\delta^{18}O$ is negatively influenced by temperature (moisture mass altitude and latitude), a Rayleigh distillation effect that is correlated with distance from the oceanic source ('continental effect'), and an 'amount effect' related to heavy rain (Dansgaard 1964; Rozanski *et al.*, 1993). Evaporation exerts a positive effect, so that continental water bodies and soils in regions with a water deficit are ^{18}O-enriched. In the tropics, where the $\delta^{18}O$ of precipitation is

primarily dictated by the amount effect (Gonfiatini *et al.,* 2001), precipitation $\delta^{18}O$ is lower in months with more rainfall and during intense storm events.

The source water for plants is generally soil moisture, so part of the signal in the oxygen isotopes of plants will come from the isotopic composition of precipitation. Nevertheless, there are several potential fractionation effects before water isotopes become fixed in plant organic material. The first occurs within the soil, where evaporation can alter the original isotopic ratio. There are also seasonal variations in the $\delta^{18}O$ of precipitation, and in the depth from which roots access water (Dawson and Pate, 1996). When plant roots take-up water there is no fractionation (Wershaw *et al.,* 1966). The critical site of fractionation is in the leaf, where evaporation (transpiration) leads to a loss of the lighter isotopes of H_2O and, as a consequence, enrichment in ^{18}O (Gonfiantini *et al.,* 1965). Craig and Gordon (1965) presented a model of evaporative enrichment of a free water surface that has commonly been applied to leaf water. The level of ^{18}O-enrichment of leaf water above source water at the sites of evaporation ($\Delta^{18}O_e$) is given by:

2) $\Delta^{18}O_e = \varepsilon^* + \varepsilon_k + (\Delta^{18}O_v - \varepsilon_k)e_a/e_i$,

where ε^* is the proportional depression of water vapour pressure by heavier $H_2{}^{18}O$, ε_k the fractionation as water diffuses through the stomata and leaf boundary layer, $\Delta^{18}O_v$ s the oxygen isotope composition of water vapour in the atmosphere relative to source water, and e_a and e_i are the ambient and intercellular vapour pressures (Craig and Gordon, 1965; Barbour *et al.,* 2002). ε^* varies slightly with temperature, but leaf enrichment depends mainly on the difference between the isotopic compositions of the source water and the ambient moisture vapour, and on the ratio of vapour pressure

inside to that outside of the leaf (Barbour, 2007). As a result, $\delta^{18}O$ measurements of leaf water are inversely related to relative humidity, with decreasing humidity resulting in higher $\delta^{18}O$ values (Flanagan *et al.,* 1991; Yakir *et al.,* 1994; Sheshshayee *et al.,* 2005). The degree of ^{18}O-enrichment over source water can vary with photosynthetic pathway, being significantly more ^{18}O-enriched in C_4 grasses relative to C_3 grasses (Helliker and Ehleringer, 2000, 2002).

Organic molecules reflect the water from which they are formed due to isotopic exchange between carbonyl oxygen and water (Sternberg *et al.,* 1986). However, the relationship between different tissues and leaf water is variable (Barbour, 2007). For example, sucrose has been shown to consistently and directly reflect leaf water enrichment, with an additional increase of 27‰ (Barbour *et al.,* 2005). By contrast, cellulose is not in full isotopic equilibrium with leaf water, making the relative exchange difficult to predict and likely to vary with rates of cellulose synthesis and sucrose import (Hill *et al.,* 1995; Barbour and Farquhar, 2000; Helliker and Ehleringer, 2002), although it has also been argued to conserve the $\delta^{18}O$ of metabolic water with a fairly constant effect (Yakir, 1992). These fractionation effects between different tissues can cause $\delta^{18}O$ variation (Farquhar *et al.,* 2007). Nevertheless, bulk $\delta^{18}O$ measurements of leaf organic matter should primarily reflect the significant increase in $\delta^{18}O$ of leaf water, relative to $\delta^{18}O$ source water, during transpiration.

In tropical forest contexts, although high relative humidity throughout the year results in reduced evapotranspiration and linked-$\delta^{18}O$ variation, relative to arid regions, the relationship between leaf organic matter $\delta^{18}O$ and evaporative potential can still be used to provide some insight into ecological variation. Plant matter growing in shaded, humid conditions will be more depleted in ^{18}O, and have lower $\delta^{18}O$, than those

growing in more open, arid areas with high irradiance (Sternberg *et al.,* 1989). As a result, the $\delta^{18}O$ of plant tissues, like $\delta^{13}C$, can in principle be used to infer canopy density in a rainforest environment. A vertical stratification of $\delta^{18}O$ has also been observed in tropical forests as a result of gradients in stomatal conductance (Sternberg *et al.,* 1989). Increased humidity on the forest floor results in low leaf $\delta^{18}O$ values, with enrichment of ^{18}O occurring observed along a vertical gradient with decreased humidity (Sternberg *et al.,* 1989; Buchmann *et al.,* 1997).

The impact of evapotranspiration on leaf $\delta^{18}O$ can also result in plant part $\delta^{18}O$ differences in tropical forest ecosystems. The active role of leaves in photosynthesis and their high surface areas and lower volume when compared to fruits, leads to greater ^{18}O-enrichment (and consequently increased $\delta^{18}O$) in leaf cellulose relative to cellulose from its roots and fruits (Epstein *et al.,* 1977; Sternberg *et al.,* 1984, 1986, 1989; Yakir, 1992). While high humidity in tropical forests might mute this effect, leaf organic matter can be expected to demonstrate higher $\delta^{18}O$ relative to fruits and woody plant parts at the same height or position. There has, however, been limited direct testing of $\delta^{18}O$ plant part distinctions using modern vegetation and variation could be linked to different tissue compositions in different plant parts. Cernusak *et al.* (2002) argued that higher observed $\delta^{18}O$ (by up to 3‰) in fruit, phloem sap, and xylem sap dry matter relative to the bulk structural dry matter of leaves is a result of fruit and sap sugars forming in close isotopic equilibrium with the leaf water during the day and leaf organic matter forming from diurnally averaged, lower, $\delta^{18}O$.

From plants to diets: stable carbon and oxygen isotopes in tropical tooth enamel

Modern studies have demonstrated that $\delta^{13}C$ measurements of faunal tooth enamel are reliable recorders of animal diet and behaviour (Lee-Thorp and van der Merwe, 1987; Cerling and Harris, 1999). In herbivores they have been shown to record the proportion of C_3 closed canopy, C_3, and C_4 resources in faunal diets, and can provide an environmental indicator of the presence and prominence of these biomes (Cerling and Harris, 1999; Levin *et al.,* 2008; Cerling *et al.,* 2015). There is a $\delta^{13}C$ enrichment factor between plant resources and herbivore tooth enamel, estimated to range between 9‰ (DeNiro and Epstein, 1978) and 12-14‰ (Lee-Thorp and van der Merwe, 1987; Lee-Thorp *et al.,* 1989b; Cerling *et al.,* 1997; Cerling and Harris, 1999) for different mammals. Passey *et al.* (2005a) have shown that the relationship of body water $\delta^{13}C$ to enamel carbonate $\delta^{13}C$ is constant, and that differences in this value between species are related to digestive physiology (Cerling and Harris, 1999). For the purposes of this thesis I use an enrichment $\delta^{13}C$ value of -13‰ between vegetation and tooth enamel as the midpoint between estimates of *c.* 12‰ (Lee-Thorp and van der Merwe, 1987) and *c.* 14 (Cerling and Harris 1999) for mammals, though much more work is needed to refine our understanding of this process in primates.

With this enrichment in mind, tooth enamel $\delta^{13}C$ lower than -14‰ likely documents the impact of a closed 'canopy effect' on faunal diets, while average herbivore values for C_3 and C_4 reliance are *c.* -12‰ and *c.* 0‰, respectively (Lee-Thorp *et al.,* 1989a, 1989b; Cerling *et al.,* 2004; Levin *et al.,* 2008) (Figure 4.3). It is important to note, however, that environmental factors, including temperature, precipitation, and atmospheric CO_2 concentration (Section 4.2), mean that C_3 and C_4 plant distributions and $\delta^{13}C$ end-points

will be context specific. As seen in Chapter 3 (Section 3.2), Ehleringer *et al.* (1997) have noted that lower $ppCO_2$ (*c.* 180-200 ppmV) during glacial periods, when compared to today (*c.* 350 ppmV), would have favoured C_4 taxa at the expense of C_3 grasses and tree taxa in many regions of the globe. While this will still produce a strong environmental signal in faunal $\delta^{13}C$, it can be difficult to disentangle the relative effects of atmospheric CO_2, temperature, and precipitation on these changes. Changes in CO_2 concentration will also potentially have an impact on the $\delta^{13}C$ of atmospheric CO_2, and therefore any vegetation. However, although modern atmospheric CO_2 $\delta^{13}C$ (-8‰) is around 1.5‰ lower relative to pre-1850 atmospheric CO_2 (Francey *et al.,* 1999), changes observed further back in time, in the Pleistocene, Pliocene, and Miocene, and during glacial periods specifically, appear to be much more subtle (Zachos *et al.,* 2001; Levin *et al.,* 2008; Lourantou *et al.,* 2010a, 2010b). Finally, faunal taxa have different feeding behaviours and will therefore document different aspects of the environment in their tooth enamel $\delta^{13}C$ (Figure 4.3). As a result, a multi-species stable isotope ecology is necessary to build up a reliable picture of the available vegetation and ecological contexts in a given region.

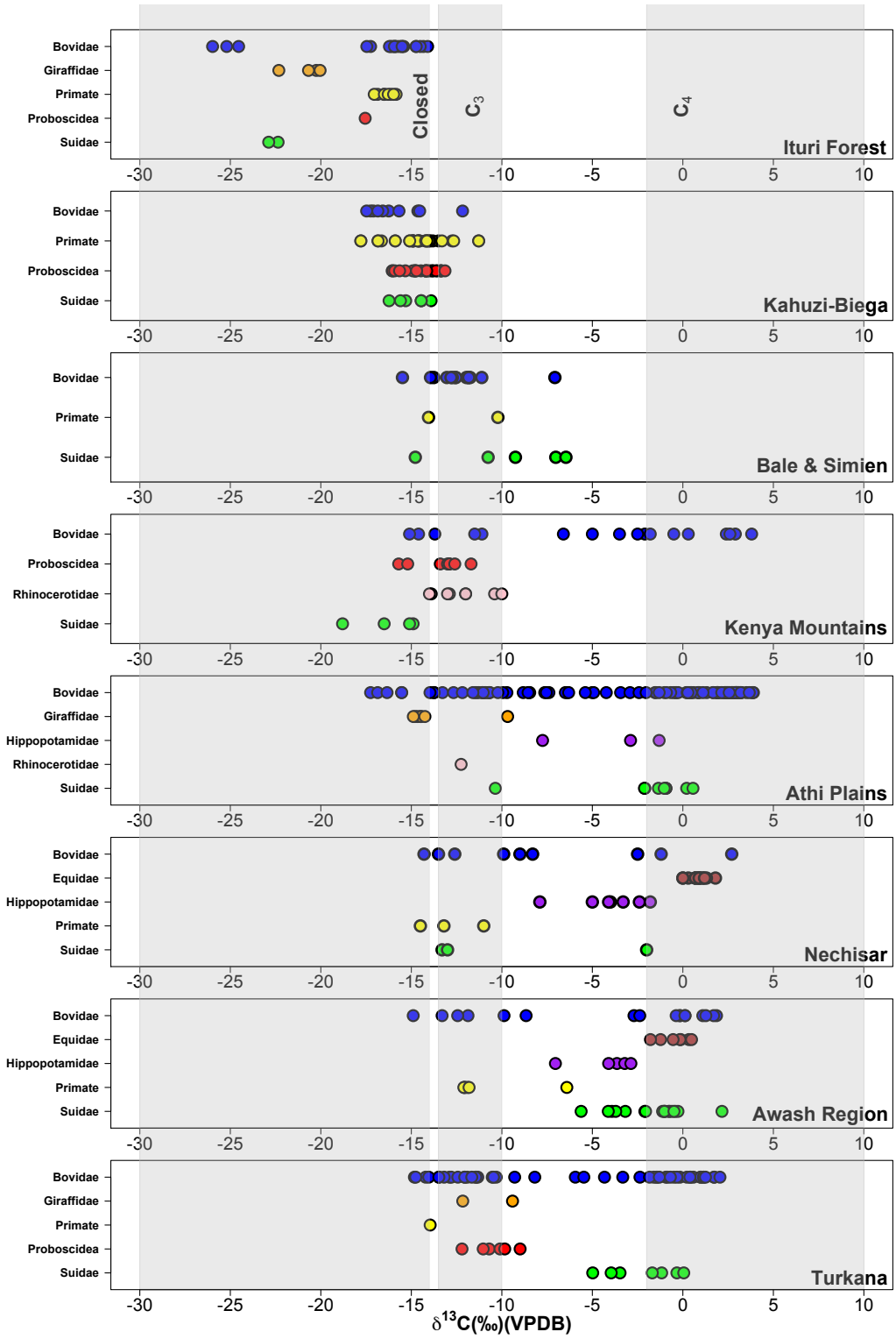


Figure 4.3. Plot of faunal tooth enamel $\delta^{13}C$ from extant herbivores in East Africa plotted by location: Ituri Forest, Congo-Kishasa (Cerling et al., *2004), Kenya Mountains and Athi Plains (Cerling* et al., *1999; Harris and Cerling, 2002; Cerling* et al., *2003a, 2003b), Kahuzi-Biega, Bale and Simien, Nechisar, Awash, and Turkana (Levin* et al., *2008). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, and C_4 diets are shown based on Lee-Thorp* et al. *(1989a), Cerling* et al. *(2004) and Levin* et al. *(2008).*

The $\delta^{18}O$ value of body water, and tooth enamel, is determined largely by the oxygen isotopic composition of ingested water, including plant water, plant tissue, drinking water, and inspired air (Luz *et al.,* 1984; Luz and Kolodny, 1985; Koch, 2007). Tooth enamel $\delta^{18}O$ has been used as a proxy for relative humidity (Longinelli, 1984; Quade *et al.,* 1995; Cerling *et al.,* 1997; Fricke *et al.,* 1998). However, physiological, including body size, and behavioural variables have been shown to influence how faunal enamel $\delta^{18}O$ responds to changes in evaporative potential (Kohn *et al.,* 1996). Herbivores that obtain most of their water from plant sources (non-obligate drinkers) have tooth enamel $\delta^{18}O$ that reflects relative environmental humidity (the main source of fractionation in plant leaf water $\delta^{18}O$) (Ayliffe *et al.,* 1992; Levin *et al.,* 2006). Levin *et al.* (2006) have argued that enamel $\delta^{18}O$ in 'evaporation sensitive' taxa, such as giraffids, oryx (*Oryx beisa*), dikdik (*Madoqua kirkii*), Grant's gazelle (*Gazella granti*), and buffalo (*Syncerus caffer*), tracks local aridity, while obligate-drinker species, such as hippopotamus (*Hippopotamus amphibius*), elephants (*Loxodonta africana*), and warthogs (*Phacochoerus africanus*), are relatively insensitive to these changes and more consistently reflect the $\delta^{18}O$ of meteoric water. Despite these distinctions, given constant rainfall $\delta^{18}O$, obligate drinkers obtaining their water from open, highly evaporated water sources (i.e. lakes) can be expected to show higher $\delta^{18}O$ than those drinking from meteoric (i.e. springs) or flowing (i.e. rivers, streams) water sources. Similarly, non-obligate drinkers feeding on plants living in open, evaporative regions will have higher $\delta^{18}O$ values than those feeding on plants in shaded, forest areas (Quade *et al.,* 1995).

The above principles mean that the $\delta^{13}C$ and $\delta^{18}O$ values of faunal tooth enamel can be used to discern the extent of forest coverage and shade experienced by animal

populations. Subtle differences in $\delta^{13}C$ and $\delta^{18}O$ have also been used to investigate subtle differences in animal feeding and drinking behaviours *within* tropical forest ecologies. For example, Cerling *et al.* (2004) demonstrated that $\delta^{13}C$ values for plants from the canopy top, from gaps in the canopy, and from the sub-canopy averaged -29.0±1.7‰, -30.4±0.9‰, and -34.0±1.5‰, respectively. Forest mammal enamel $\delta^{13}C$ tracked these differences with subcanopy browsers (such as okapi and dwarf antelope) having lower $\delta^{13}C$ values than subcanopy frugivores, animals that derive their food from the canopy top, and from folivores and omnivores living in gap or clearing areas (Figure 4.4). Cerling *et al.* (2004) argue that there is also a distinction in tooth enamel $\delta^{18}O$ between the obligate drinkers (lower $\delta^{18}O$) and non-obligate drinkers (namely the folivorous colobines - *Colobus angolensis*, *Colobus badius*) (higher $\delta^{18}O$). However, as will be seen in Section 4.3, equifinality complicates interpretation and faunal, and particularly non-human primate, tooth enamel $\delta^{13}C$ and $\delta^{18}O$ is also influenced by feeding height within the canopy and relative reliance on folivory versus frugivory in tropical forest contexts. One final possible source of isotopic ecological distinction could be the lower $\delta^{18}O$ measurements for tropical forest foliage, and nocturnal consumers, at night, as a result of cooler nocturnal temperatures and the incorporation of oxygen from atmospheric CO_2, water vapour and dewfall (Ometto *et al.,* 2005; Carter and Bradbury, 2015).

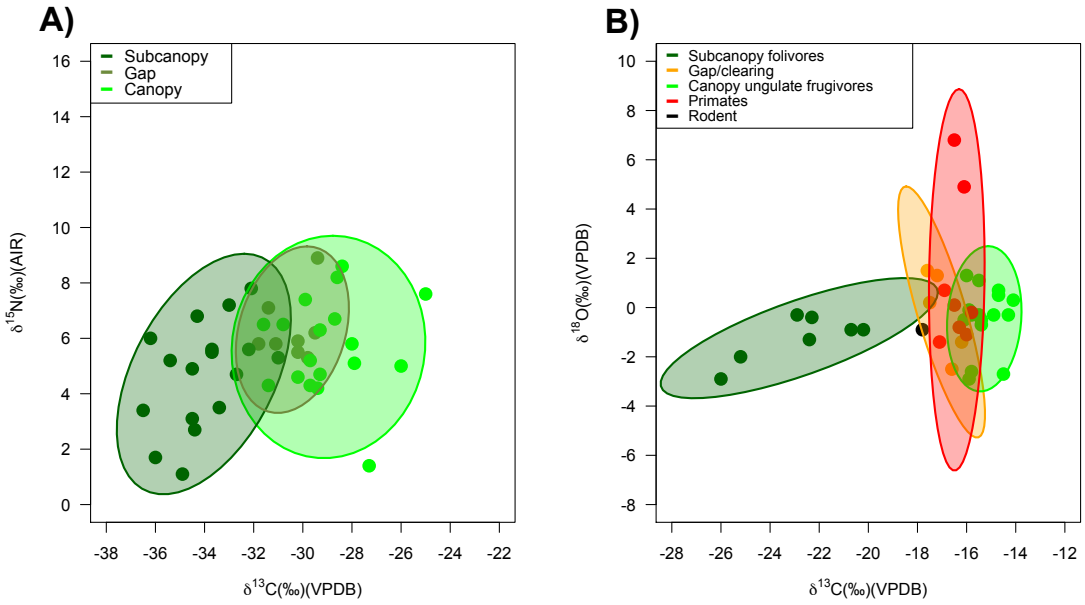


Figure 4.4. A) $\delta^{13}C$ and $\delta^{15}N$ of modern plants from the Ituri Forest, Congo-Kinshasa showing the vertical and horizontal $\delta^{13}C$ 'canopy effect' (data from Cerling et al., *2004). B) $\delta^{13}C$ and $\delta^{18}O$ of modern animals from the Ituri Forest and corresponding niche distinctions. The two primates with highest $\delta^{18}O$ are the colobines discussed in the text (data from Cerling* et al., *2004).*

4.2 – Stable isotope analysis of hominin and human tooth enamel in a tropical context

A variety of biological tissues have been used to trace hominin, human, and faunal diets, with hair, faeces, bone collagen, bone apatite, tooth dentine, and tooth enamel being employed in modern contexts, and skeletal elements forming the basis of prehistoric dietary investigation. Bone collagen and bone apatite provide the longest, averaged 'adult' signature of an individual diet due to the continuous nature of bone (Tieszen *et al.,* 1983; Hedges *et al.,* 2007). However, bone collagen degrades quickly in tropical zones that are hot and humid (Ambrose, 1990; Krigbaum, 2001, 2003) and bone mineral is susceptible to chemical alteration due to leaching and high water flow (Schoeninger *et al.,* 1989; Lee-Thorp and Sponheimer, 2003). By contrast, tooth enamel is primarily made up of an apatite crystal lattice (LeGeros, 1991) that is resistant to post-mortem diagenetic substitution and degradation (Lee-Thorp, 1989, 2002, 2008;

Wang and Cerling, 1994; Sponheimer and Lee-Thorp, 2006; Balter and Zazzo, 2014), while it also reflects the 'bulk diet' of an individual during the period of enamel formation (Ambrose and Norr, 1993; Lee-Thorp *et al.,* 1989b).

This has made tooth enamel the material of choice in archaeological and palaeontological stable isotope studies spanning to 9 million years ago and beyond (Lee-Thorp *et al.,* 1989a; Nelson, 2005; Ségalen *et al.,* 2007; Uno *et al.,* 2011), and across temperate, arctic, sub-tropical, and tropical environments (Krigbaum, 2001, 2003, 2005; Nelson, 2007; Lee-Thorp, 2008; White *et al.,* 2009; Ecker *et al.,* 2013). Tooth enamel $\delta^{13}C$ and $\delta^{18}O$ does represent a much shorter period of time than bone collagen that will differ depending on the tooth sampled. For humans, first molar enamel mineralises between birth and 3 years of age, premolars mineralise between 2 and 6 years of age, and third molars mineralise during adolescence, between 7 and 13 years (Massler *et al.,* 1941; Moorrees *et al.,* 1963; Hillson, 1996). In the case of the first molar enamel it forms, at least partly, prior to weaning and therefore in principle $\delta^{18}O$ measurements from this tooth may reflect milk rather than water or other food sources (Wright and Schwarcz, 1998).

Given that tooth enamel forms incrementally over its period of formation, to compare individual specimens, bulk samples can be taken along the growth axis. That said, this characteristic of tooth enamel also means that it can be sampled sequentially in order to investigate changes in diet, and therefore environment (Balasse, 2002; Nelson, 2005). When enamel initially forms it has only 20-30% of its mature mineral content. Mineralisation then continues in a complicated spatial and temporal pattern, resulting in considerable temporal mixing and influence from body stores (Balasse, 2002; Passey and Cerling, 2006). As a result, it is very difficult to pinpoint the exact point in dietary

change even when the growth and maturation parameters of a species' enamel are well known (Passey *et al.,* 2005b). However, although potentially dampened and temporally offset, chronologically ordered dietary change within a given tooth is observable (Balasse, 2002; Sponheimer *et al.,* 2006b), providing information regarding seasonal and inter-annual dietary variation for a given individual.

African hominins: out of the woods and onto the plains?

Robust datasets of $\delta^{13}C$ and $\delta^{18}O$ values for hominin, and associated faunal, tooth enamel now exist and have been used to track the changing diets and environments of our early ancestors in Africa. Particular focus has been on the relevance of C_3 closed-canopy, C_3, and C_4 resources to hominin subsistence, given that the development of 'human' traits of bipedalism, tool use, and subsistence strategies in the hominin clade have been linked to the expansion of open, savannah ecosystems (Potts, 1998; Lee-Thorp *et al.*, 2000, 2010; Sponheimer *et al.,* 2009; Domínguez-Rodrigo, 2014). It has been argued that the earliest known hominins, including *Orrorin tugenensis* (*c.* 6 Ma), *Ardipithecus kadabba* (*c.* 5.5 Ma), and *Ardipithecus ramidus* (*c.* 4.4 Ma), were forest-adapted, on the basis of associated faunal assemblages and limb adaptations (WoldeGabriel *et al.,* 1994, 2001; Pickford *et al.,* 2004). By contrast, Australopithecines and the genus *Homo* post *c.* 3 Ma have been linked to more specialised bipedal movement, the procurement of medium to large mammalian resources, and the manufacture of the earliest stone tool technologies at a time of expanding savannah ecosystems (Lee-Thorp *et al.,* 1994; Sponheimer and Lee-Thorp, 1999; Cerling *et al.,* 2010; Lee-Thorp *et al.,* 2010).

Direct testing of this theory using stable carbon and oxygen isotope analysis of hominin tooth enamel, however, has proved this picture to be too simplistic from a dietary perspective. Figure 4.5 suggests a very coarse trend for the increased consumption of more C_4-derived resources over time, from *A. ramidus*, *Australopithecus anamensis*, and *Au. afarensis* (though see *Australopithecus sediba*) to *Au. africanus*, *H. habilis*, and *P. robustus* (Lee-Thorp *et al.,* 2010; Sponheimer *et al.,* 2013). However, work on *A. ramidus*, indicates that it, and its associated fauna, is best associated with mixed C_3/C_4 vegetation rather than dense forest (White *et al.,* 2009) (Figure 4.6). Research at a number of *A. ramidus* bearing localities, as well as on *Australopithecus sediba*, has demonstrated variable ecological preferences, including evidence for dietary consumption of C_3 vegetation unaffected by the 'canopy effect' back to 3.8 Ma (Levin *et al.,* 2008, 2015). As a result, *A. ramidus* cannot be associated solely with forest habitats. Furthermore, *H. habilis*, *P. robustus* and *Au. africanus* display highly variable reliance on C_4 resources (van der Merwe *et al.,* 2008). The most obvious overall pattern for the hominin clade is arguably substantial intra-species variability. It could therefore be the maintenance of dietary flexibility (at least from *c.* 3 Ma) that characterises the evolution of our early hominin ancestors (Lee-Thorp *et al.,* 2010; Sponheimer *et al.,* 2013) rather than any fundamental environmental or ecological shifts.

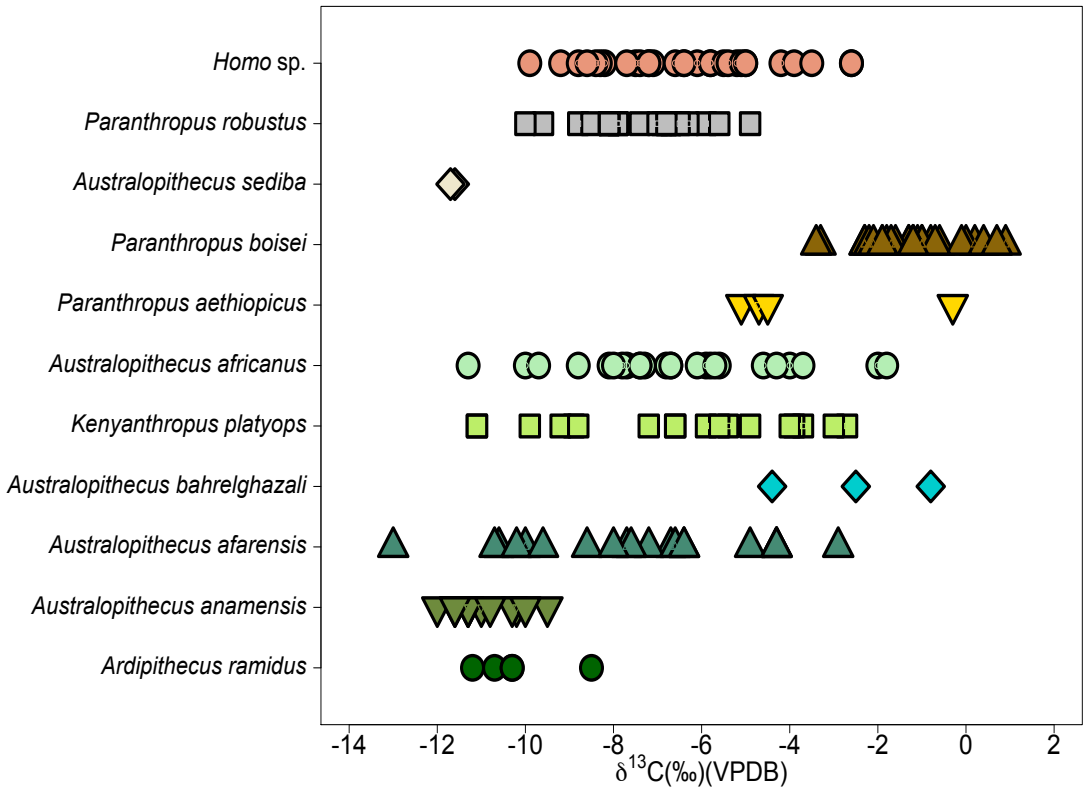


Figure 4.5. $\delta^{13}C$ of hominin tooth enamel from southern, eastern, and central Africa plotted by genus/species (as per. Levin et al., *2015). Hominin taxa are arranged from oldest (bottom) to youngest (top) (as per. Levin* et al., *2015). Data from Lee-Thorp* et al. *(1994), Sponheimer and Lee-Thorp (1999), Lee-Thorp* et al. *(2000), van der Merwe* et al. *(2003), Sponheimer* et al. *(2005, 2006b), van der Merwe* et al. *(2008), White* et al. *(2009), Cerling* et al. *(2011), Henry* et al. *(2012), Lee-Thorp* et al. *(2012), Cerling* et al. *(2013), Sponheimer* et al. *(2013), Wynn* et al. *(2013), Levin* et al. *(2015).*

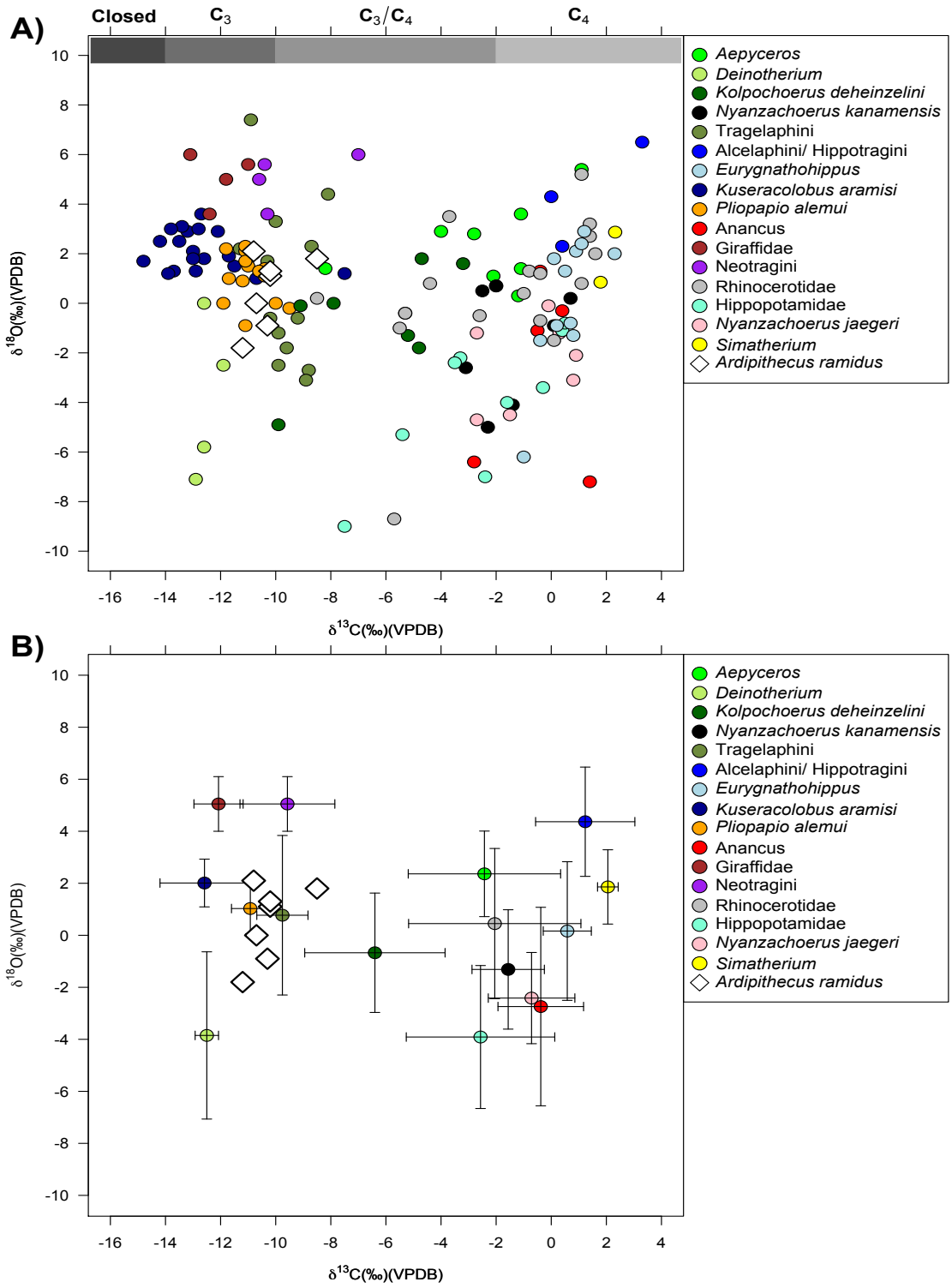


Figure 4.6. $\delta^{13}C$ and $\delta^{18}O$ values for tooth enamel from Ardipithecus ramidus *and associated fauna from the Lower Aramis Member of the Sagantole Formation in the Middle Awash Valley, Ethiopia: A) Individual $\delta^{13}C$ and $\delta^{18}O$ values plotted by taxon, B) bivariate means ±1 standard deviation. Data from White* et al. *(2009). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, C_3/C_4 mixed, and C_4 diets are shown based on Lee-Thorp* et al. *(1989a), Cerling* et al. *(2004) and Levin* et al. *(2008).*

The variation and flexibility seen within hominin species in Figure 4.5 has also been demonstrated on an intra-individual basis in the form of the sequential stable isotopic analysis of individual hominin teeth. Sponheimer *et al.* (2006b) used laser-ablation analysis of $\delta^{13}C$ on four *P. robustus* tooth crowns to demonstrate differences of up to 5‰ within a given tooth. These data suggest a considerable shift from a diet dominated by C_3 to a diet dominated by C_4 resources in certain individuals on both intra- and inter-annual scales. Lee-Thorp *et al.* (2010) performed similar analyses on three *Au. africanus* molar crowns from Sterkfontein Member 4. Variability in the reconstructed proportions of C_3 and C_4 resources between and within individuals was on a similar scale to that of *P. robustus*. One individual indicated a more or less uniform C_3 preference, while another showed variance of *c.* 6‰ through time. Although the precise timescales of this variation are hard to pinpoint given maturation complexities, the differences again demonstrate that C_4 resources formed an important, but highly variable, component of their diets. This appears to extend at least as far back as *Au. africanus*, and likely as far back as *Au. afarensis* (*c.* 2.9 to 3.9 Ma) (Figure 4.5), a species initially associated with a regular preference for forest and woodland feeding and mobility (Zonneveled *et al.,* 1994; Green and Alemseged, 2012).

It has been argued that early hominin origins, and indeed the origins of bipedalism, are to be sought with arboreality and forest settings rather than savannahs (White *et al.,* 2009; Thorpe *et al.,* 2014). However, it is also clear that while $\delta^{13}C$ and $\delta^{18}O$ measurements of *A. ramidus* and *Au. anamensis* show little or no evidence for the input of C_4 resources, they are also indicative of open woodland, or woodland/grassland mixtures, rather than closed-canopy forest. We have to go a long way back into the Miocene to identify an isotopic composition that unambiguously reflects the canopy

effect and tropical forest reliance in our early ancestors. The Miocene hominoid *Sivapithecus*, from the Siwalik sediments of Pakistan has some of the lowest $\delta^{13}C$ values of all fauna found in the S-level (dated to 9.3-9.2 Ma) (between -13‰ to -14‰), indicative of closed-canopy forest dwelling, and some of the highest $\delta^{18}O$ (-2.6‰), with Nelson (2003, 2007) suggesting that it obtained most of its water from upper canopy vegetation (Figure 4.7). The early Pleistocene ape, *Gigantopithecus blacki*, has still lower $\delta^{13}C$ (*c.* -12 to -16.5‰), overlapping that measured from Pliocene and Pleistocene orang-utans from southern China and Thailand (Figure 4.8) (Bocherens *et al.,* 2015). The $\delta^{13}C$ values of these species are similar to those of modern chimpanzees from Uganda and the Congo-Kinshasa, implying that they occupied closed humid tropical/subtropical, canopied forest (Nelson, 2014). Therefore, while $\delta^{13}C$ and $\delta^{18}O$ measurements of tooth enamel have provided direct insight into the roles of forests in the ecologies and diets of our hominoid and hominin ancestors, no hominin species has yet demonstrated a reliance on, or even preference for, closed-canopy tropical forest resources.

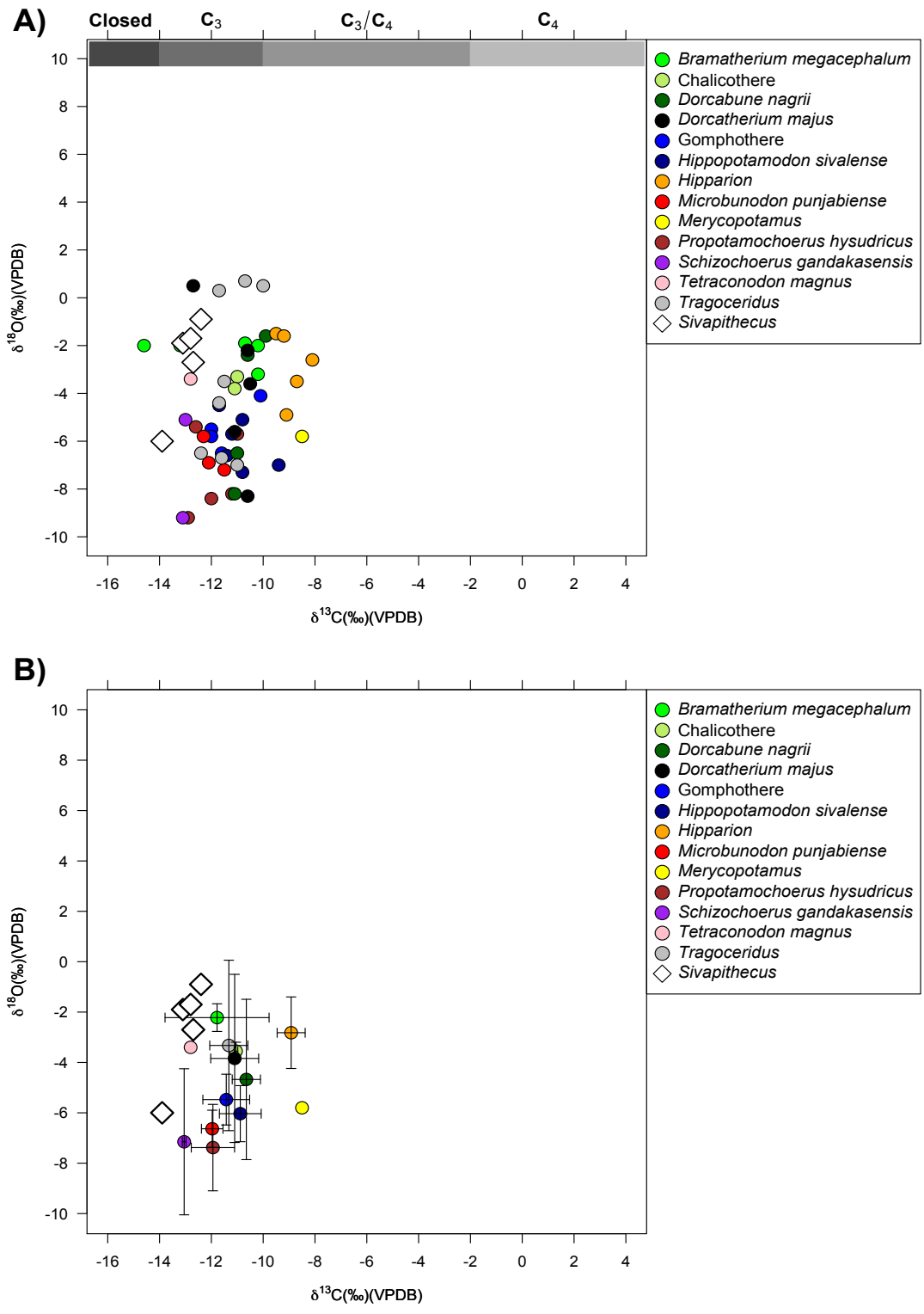


Figure 4.7. $\delta^{13}C$ and $\delta^{18}O$ values for tooth enamel from the hominoid Sivapithecus *and associated fauna within the S-Level (9.3-9.3 million years ago) of the Miocene Siwalik Group of Pakistan. A) Individual $\delta^{13}C$ and $\delta^{18}O$ values plotted by taxon, B) bivariate means ±1 standard deviation Data from Nelson (2007). $\delta^{13}C$ range estimates of enamel representative of closed canopy, C_3, C_3/C_4 mixed, and C_4 diets are shown based on Lee-Thorp* et al. *(1989a), Cerling* et al. *(2004) and Levin* et al. *(2008).*

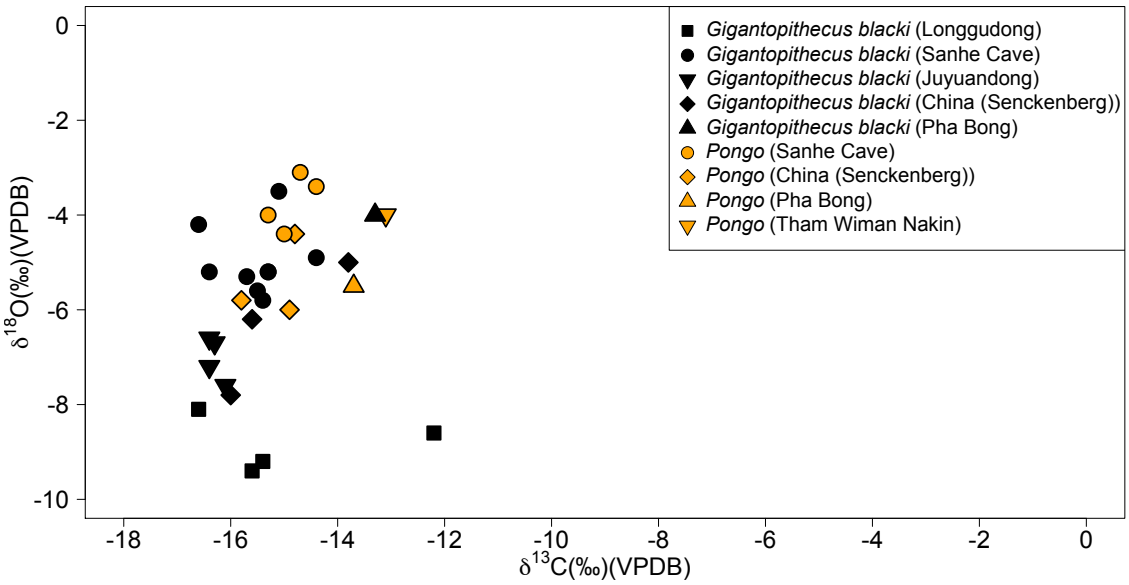


*Figure 4.8. $\delta^{13}C$ and $\delta^{18}O$ values of tooth enamel for orang-utans (*Pongo*) and the giant ape* Gigantopithecus blacki *from the Plio-Pleistocene of Southern China and the Pleistocene of Thailand. Adapted from Bocherens* et al. *(2015) that incorporates data from Pushkina* et al. *(2010), Nelson (2014), Qu* et al. *(2014) and Bocherens* et al. *(2015).*

A test of early human rainforest reliance?

Despite a long history of high-profile applications to the ecological preferences of numerous hominin species, including a test of their relative preference for forested environments, stable carbon and oxygen isotope analysis of tooth enamel has yet to be systematically applied to the potential rainforest adaptations of our own species, *Homo sapiens*. One notable exception is the work of John Krigbaum on Pre-Neolithic and Neolithic human skeletons in Southeast Asia (Krigbaum, 2001, 2003, 2005). Krigbaum applied stable carbon and oxygen isotope analysis to human tooth enamel to three penecontemporaneous sites in Sarawak, East Malayasia (the Niah Caves, Lubang Angin, Gua Cha, and Gua Sireh), that are today all situated in C_3-dominant lowland, primary rainforest, with a view to reconstructing the extent to which human groups relied on cultigens versus foraged rainforest resources through time. Krigbaum (2003, 2005) interpreted significant differences in $\delta^{13}C$ between sites and across time periods

as reflecting variations in foraging pattern, namely closed forest resource gathering versus open forest horticulture. Lower values in the Pre-Neolithic specimens from Gua Cha and the Niah Caves implied dependence on closed rainforest resources while higher values in Neolithic individuals from the Niah Caves, Gua Cha, and Gua Sireh suggested more open forest horticulture, subsistence, habitat modification, and potentially food production (Figure 4.9). Interestingly, Neolithic/Early Metal individuals from Lubang Angin demonstrate continued dependence on rainforest resources following the introduction of agriculture in the region.

Although this study lacked firmly associated faunal specimens with which to form a detailed stable isotope ecology, and the dating of human fossils remained coarse (either pre-Neolithic, Neolithic or Neolithic/Metal Age), the results suggest that $\delta^{13}C$ analysis of human tooth enamel has great potential for the direct investigation of human rainforest resource reliance. Furthermore, while comparison across such temporal depth can be problematic, especially without contextual faunal information, the $\delta^{13}C$ of Pre-Neolithic human individuals measured by Krigbaum are substantially more negative than those measured for *A. ramidus*, *Au. afarensis*, *Au. anamensis* and even *Sivapithecus*, reaching as low as -15.5‰ (Figure 4.9). There is therefore the tantalising hint that our species may be the only hominin to demonstrate reliance on closed-canopy forest and rainforest resources. In spite of this, systematic stable carbon and oxygen isotope analysis of human foragers, and a variety of spatially and temporally associated fauna, from rainforest environments have yet to be undertaken. This is particularly surprising in the context of Late Pleistocene human rainforest adaptations, where the existing partial, indirect, and often coarse palaeosubsistence datasets provide

unsatisfactory insight into the longevity and nature of human rainforest resource reliance (Chapters 2 and 3).

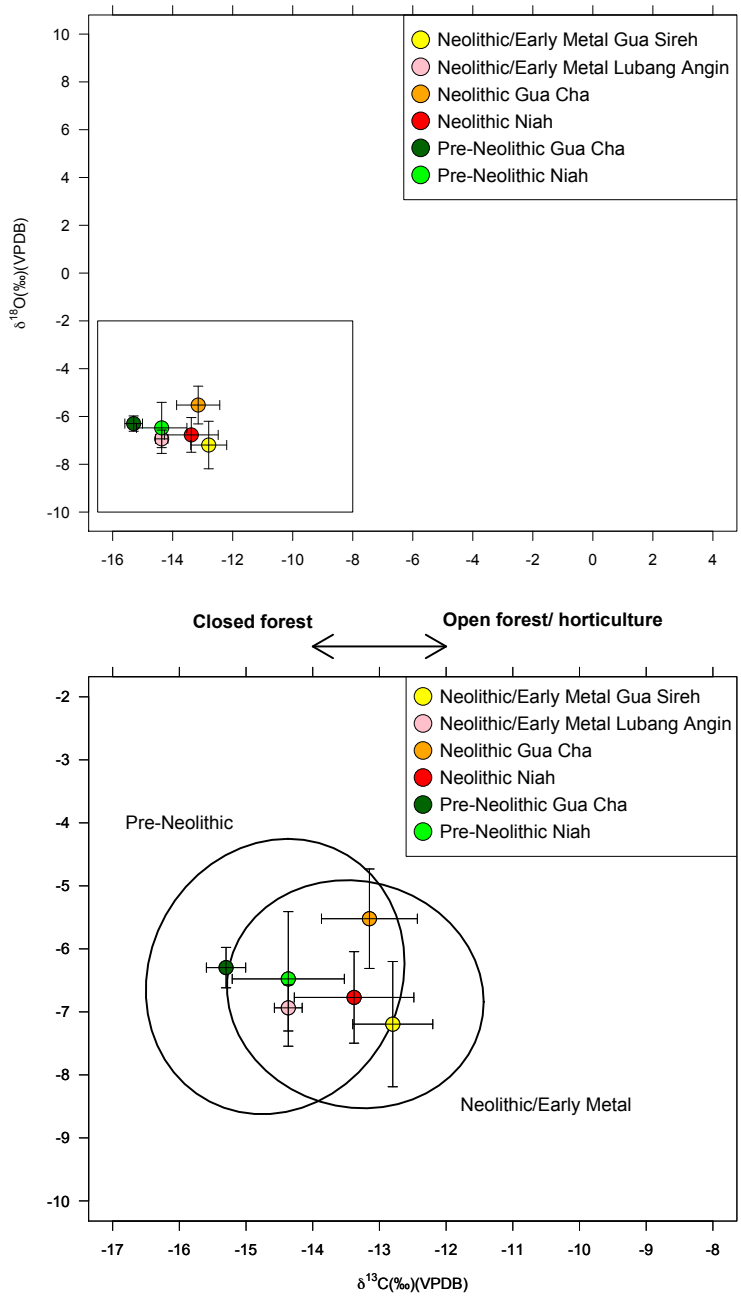


Figure 4.9. $\delta^{13}C$ and $\delta^{18}O$ values of tooth enamel from Pre-Neolithic and Neolithic human skeletons from Gua Sireh, Lubang Angin, Gua Cha, and the Niah Caves, Sarawak. Data from Krigbaum (2001, 2003, 2005).

Enamel preservation in a tropical rainforest environment

As discussed above, the high density and crystallinity of enamel apatite makes it extremely resistant to post-mortem change (LeGeros, 1967, 1991; Sponheimer and Lee-Thorp, 2006; Lee-Thorp, 2008; Balter and Zazzo, 2014). That said, while reliable dietary signals and environmental distinctions have been demonstrated across millions of years (Lee-Thorp *et al.,* 1989a) protocols to check the structural preservation of tooth enamel specimens, and the potential impacts this might have on the reliability of measured isotopic values, remain necessary. This is particularly the case in harsh taphonomic environments such as the hydrologically active, ion rich soils of tropical rainforests. The primary source of concern in this regard is the origin of tooth enamel carbonate, from which stable carbon and oxygen isotope ratios are obtained. Post-mortem recrystallisation and crystal growth (Ostwald ripening) can introduce foreign carbonate ions into apatite crystal structures through adsorption onto crystal surfaces (Zazzo *et al.,* 2004; Sponheimer and Lee-Thorp, 2006; Jacques *et al.,* 2008), replacement of hydroxyl ions at external 'A'-sites, and more fundamental structural replacement of phosphate ions at 'B'-sites (Lee-Thorp, 2008). It is not inevitable that the original isotope composition is altered during this process, with rearrangement and incorporation often being internally constituted. Adsorbed secondary minerals, such as calcite, have also been shown to be effectively removed by acid treatment (Lee-Thorp, 1989). By contrast, external, secondary carbonates forming *within* the crystal lattice are more problematic. Comparison of fauna with known dietary habits (e.g. C_3 or C_4 preferences) will provide some indication of the reliability of $\delta^{13}C$ measurements (Lee-Thorp *et al.,* 1989a), though the reliability of $\delta^{18}O$ values is more difficult to detect in this way (Sponheimer, 1999; Lee-Thorp, 2008).

A more thorough assessment of enamel structure and composition is the application of Fourier Transform Infra-red (FTIR) spectroscopy to enamel samples. This method irradiates a sample with an infrared beam. Some radiation is absorbed at discrete vibrational frequencies related to the functional groups present (e.g. CO_3^{2-}, PO_4^{3-}). The intensity of absorbance is proportional to the concentration of the absorbing molecule, and yields information on both the molecular species present and their concentrations in a sample. As a result, the overall infrared spectra of phosphate minerals with different structures, such as enamel, dentine, and bone apatite, are distinct, while biological apatites are also very different from carbonate minerals like calcite. This makes FTIR a useful way to detect diagenetic carbonate minerals (Michel *et al.,* 1996; Stuart-Williams *et al.,* 1996; Sponheimer, 1999; Lee-Thorp and Sponheimer, 2003). Michel *et al.* (1995) observed alteration in fossil enamel by using a combination of absorption bands that allowed examination of changes in both A (band 1545cm^{-1}) and B (1415cm^{-1}) carbonate sites. Indices reflecting the amount of type B carbonate to phosphate (BPI), type A carbonate to phosphate (API), the relative amount of B to A-site carbonate (BAI) and 'crystallinity' (PCI) were used by Sponheimer (1999) to compare a suite of modern and fossil samples. While no evidence for the introduction of calcite or substantial changes in the crystal structure as a result of exogeneous carbonate was found in fossil samples dated to 2 million years ago, some subtle changes during fossilisation were identified.

Another potential diagenetic problem in a rainforest environment is the penetration of metallic ions, such as iron or manganese, into the crystal lattice from highly mobile, ion-rich rainforest soil waters. Depending on the compounds they form, the presence of these minerals within the enamel structure has the potential to alter the original isotopic signal. This is more likely for $\delta^{18}O$, through the formation of compounds such as FeO_2,

and it has never been demonstrated to affect $\delta^{13}C$ values. The elemental analyser of a Scanning Electron Microcope (SEM) can be used to detect metallic ions in tooth enamel (Frahm, 2014). While it cannot indicate the exact compound present, it can give some indication of external introductions into fossil enamel and their relative concentrations. In the context of U-series dating, the influx of heavy elements, such as uranium and strontium, appears to affect the outer surface of the enamel least (Eggins *et al.,* 2003; Grün *et al.,* 2008; Benson *et al.,* 2013). If this is the case then a) sampling the outer surface of the enamel should provide the most reliable $\delta^{13}C$ and $\delta^{18}O$ signatures and b) SEM analysis of a tooth section should be able to track the relative concentrations of external ions across the dentine-enamel structure.

4.3 – Stable isotope analysis of tropical primate niches and the importance of a modern reference

Non-human primates are frequently used as referential models for the earliest ecological adaptations of our species (Wrangham, 1987; Whiten *et al.,* 2005; Whiten and Van Schaik, 2007). This is also the case in stable isotope studies where the reconstruction of non-human primate niches has been explored as a way to better understand adaptations amongst our hominin ancestors (Sponheimer *et al.,* 2006a; Oelze *et al.,* 2011; Macho and Lee-Thorp, 2014). Most existing stable isotope work on modern tropical forest primates has focused on the $\delta^{13}C$ and $\delta^{15}N$ measurement of their organic tissues as proxies for the relative importance different plant parts or food sources in their diets, or their usage of different canopy 'depths'. Thus far, fewer studies have utilised the $\delta^{13}C$ and $\delta^{18}O$ measurements of inorganic non-human primate tissues.

Schoeninger *et al.* (1997) found that hair $\delta^{13}C$ from four New World monkeys (*Alouatta palliata* – the mantled howler, *Ateles geoffroyi* – the spider monkey, *Cebus capucinus* –

the capuchin, and *Brachyteles arachnoides* – the woolly-spider monkey) was bimodally distributed and reflected the level of leaf cover independently of any species' diet. The two monkey populations living in an evergreen forest were similar to each other and different from the two monkey species occupying dry, deciduous forests (Schoeninger *et al.,* 1997) (Figure 4.10). Similarly, Loudon *et al.* (2007) found small but significant differences in $\delta^{13}C$ (and $\delta^{15}N$) of sympatric ring-tailed lemurs (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve, Madagascar, that reflected the degree to which different lemur groups utilised forested versus open habitat (Figure 4.11).

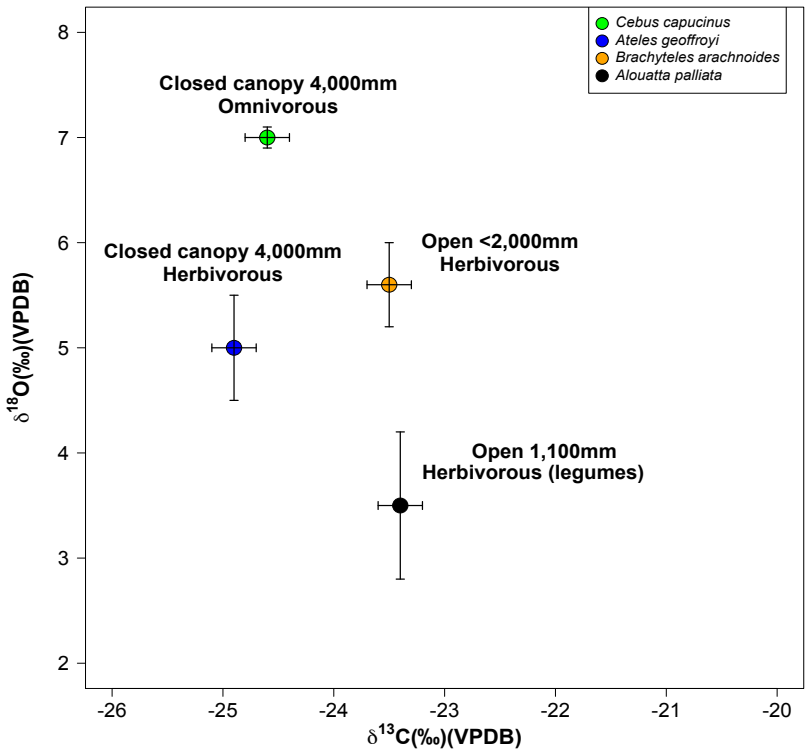


Figure 4.10. Bivariate mean $\delta^{13}C$ and $\delta^{15}N$ measurements from the hair of four monkey species from Central and South America ± 1 standard deviation. Data from Schoeninger et al. *(1997).*

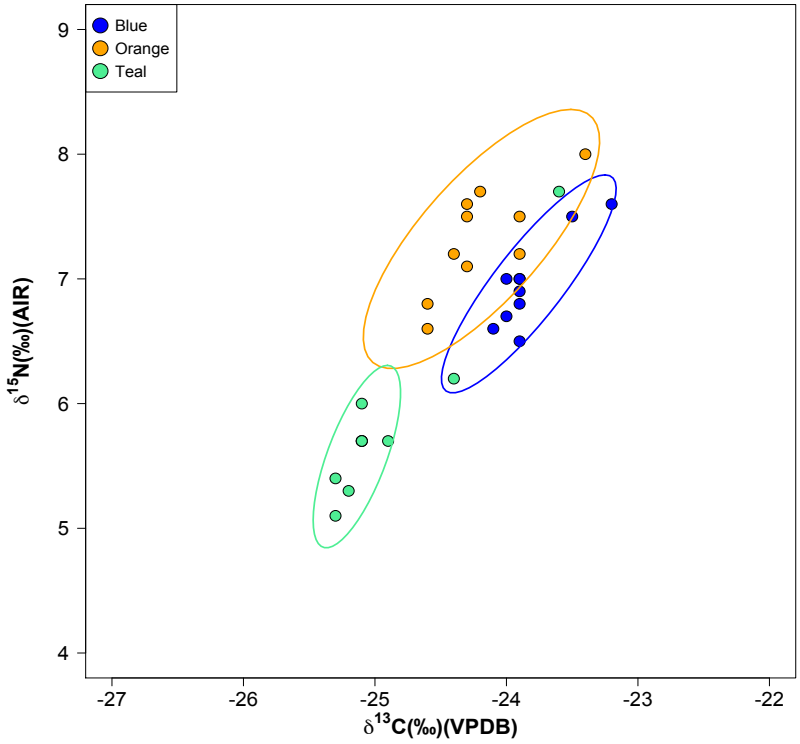


Figure 4.11. $\delta^{13}C$ and $\delta^{15}N$ measurements of lemur hair from Madagascar plotted by 'group'. Data from Loudon et al. *(2007).*

Non-human primate $\delta^{13}C$ and $\delta^{18}O$ measurements have also been argued to provide more refined insight into primate niches and environments, although long-term studies of modern primate tissues and their ecologies have revealed complexities in their interpretation. For example, nuanced $\delta^{13}C$ distinctions have been noted between gorilla and chimpanzee populations living in West Africa. Oelze *et al.* (2014) interpreted this as a difference in feeding strategy, with chimpanzees feeding on ^{13}C-enriched fruits higher in the canopy and folivorous gorillas feeding on the ground (Figure 4.12). By contrast, Macho and Lee-Thorp (2014) argued that this distinction operated on a horizontal environmental level, with differences of 1-2‰ between sympatric gorillas and chimpanzees in Cameroon reflecting exploitation of different zones of forest density. Furthermore, it is possible that Oelze *et al.* (2014) underestimate the degree of

$\delta^{13}C$ variation of the same plant part (e.g. leaves, fruits, roots) *between* plant species (Codron *et al.,* 2013, Blumenthal *et al.,* 2015).

Krigbaum *et al.* (2013) suggest that the bone apatite $\delta^{18}O$ of seven non-human primate species from the Taï Forest, Ivory Coast, is correlated with mean observed feeding height (Figure 4.13). However, this conclusion is based on very few outliers and it appears unlikely that the 'height' data they report for primate feeding can be accepted with such absolute certainty (Figure 4.13). $\delta^{18}O$ differences between non-human primates in this study could reflect varying relative reliance on folivory versus frugivory rather than being explicable purely by feeding height. Carter and Bradbury (2015) have argued that *both* feeding height high in the canopy and the proportion of leaves in the diet of colobines influences higher $\delta^{18}O$ in primate species. Expected $\delta^{18}O$ differentiation between folivory versus frugivory will also potentially be more obvious higher in the canopy where evapotranspiration will have a greater effect on leaf tissue $\delta^{18}O$ (Crowley *et al.,* 2015). Isotopic differences between obligate and non-obligate drinking non-human primate taxa will further confound dietary interpretations of $\delta^{18}O$ (Levin *et al.,* 2006).

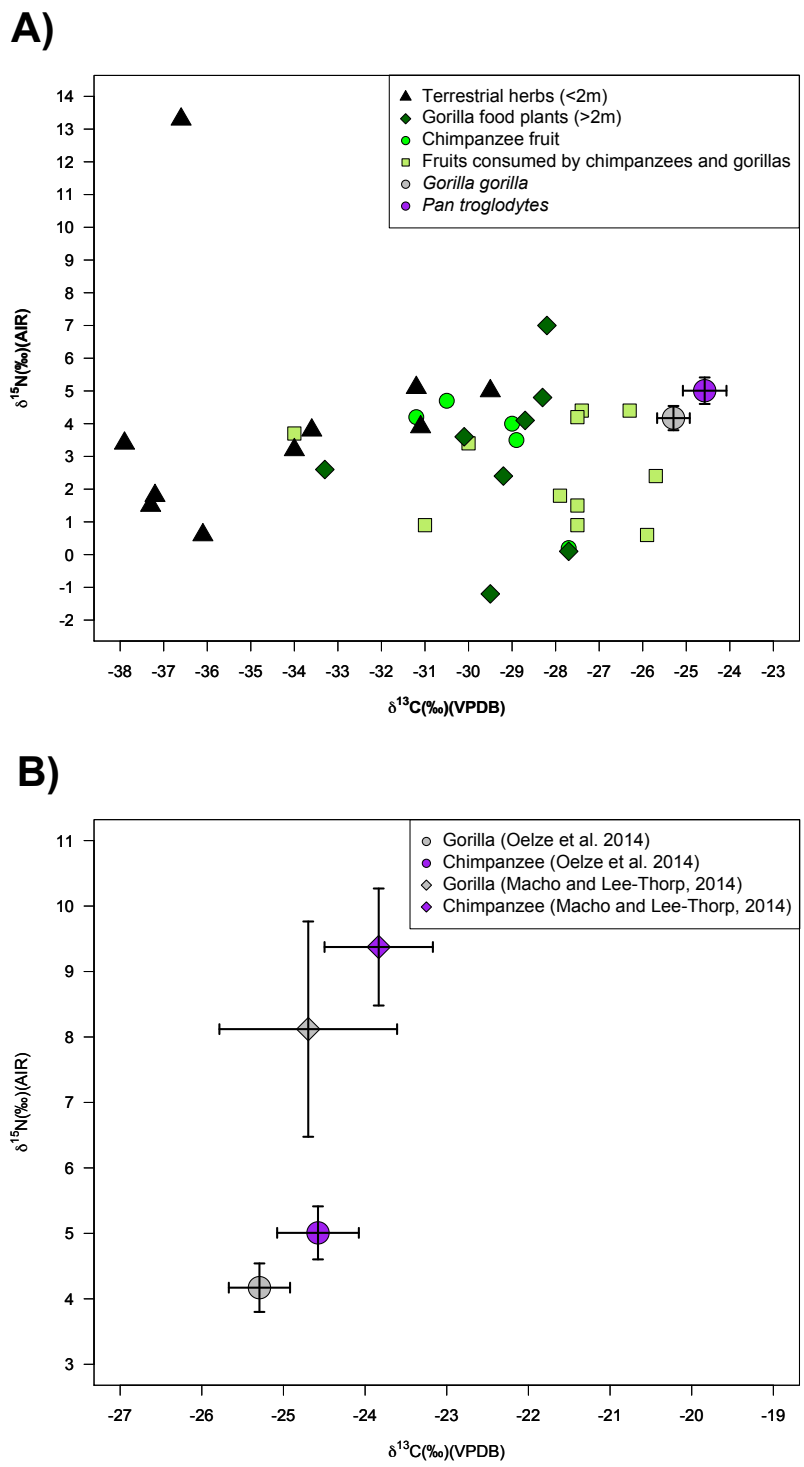


Figure 4.12. $\delta^{13}C$ and $\delta^{15}N$ measurements of A) food plants of chimpanzees and gorillas plotted with bivariate mean ± standard deviation of chimpanzee and gorilla hair from Loango National Park, Gabon. Data from Oelze et al. *(2014) and B) bivariate mean ± standard deviation of modern chimpanzee and gorilla hair from Loango National Park, Gabon measured by Oelze* et al. *(2014) and historic chimpanzee and gorilla hair from central Cameroon measured by Macho and Lee-Thorp (2014).*

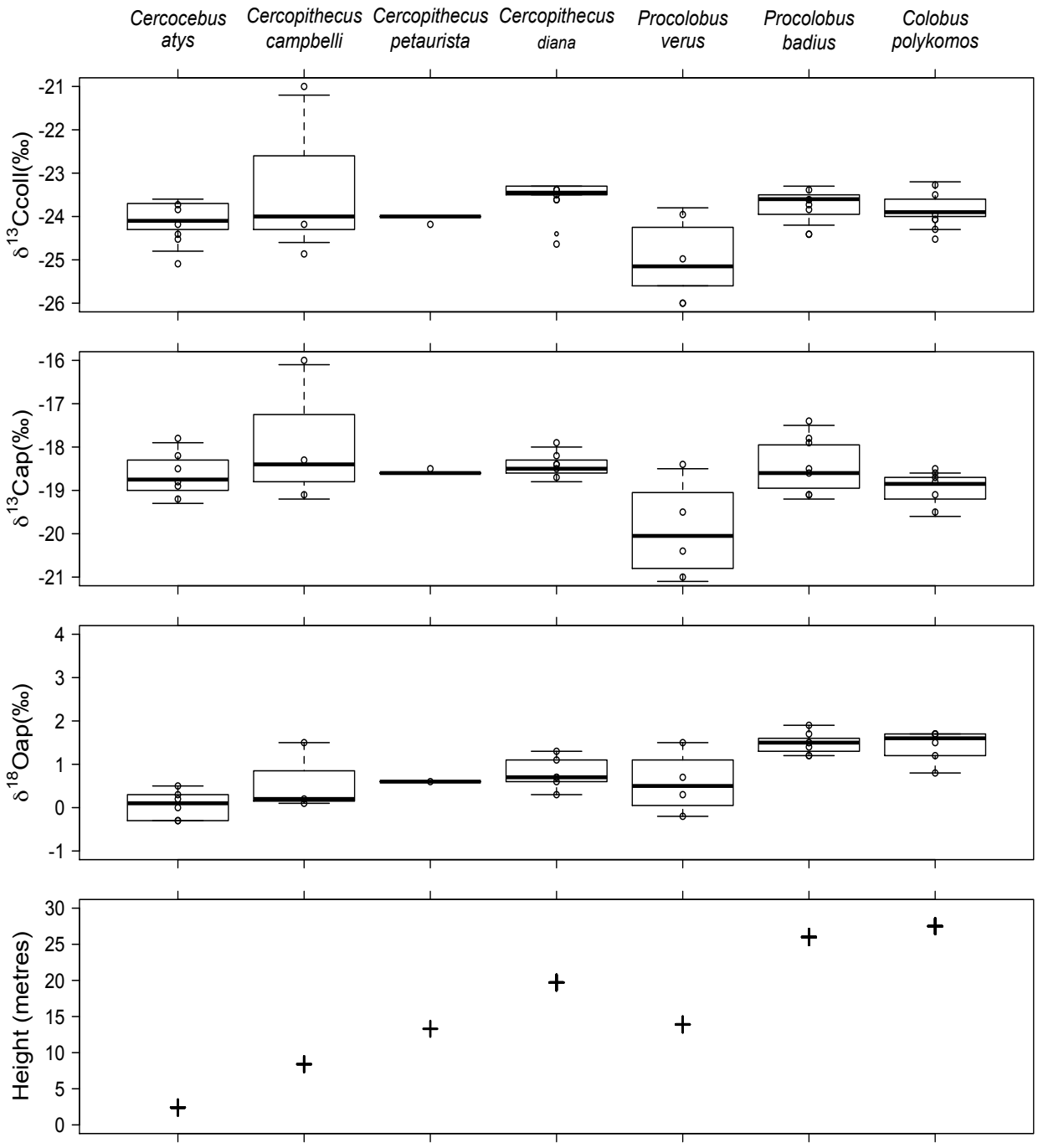


Figure 4.13. Average δ^{13}Ccoll (collagen), δ^{13}Cap (apatite) and δ^{18}Oap for modern primate species living in the Taï Forest, Ivory Coast alongside observed average feeding heights. Data from (Krigbaum et al. *2013).*

As a result, while $\delta^{13}C$ and $\delta^{18}O$ analysis of non-human primate tissues has been argued to provide highly detailed tropical forest niche information among primate groups, equifinality of interpretation is a key problem in many studies. To address this, expensive, long-term research programmes that observe isotopic variation between and within primate species, and within their environment have to be undertaken. Although modern observational data, isotopic measurements of food sources and preferences, and isotopic measurements of modern individuals are not *directly* relevant to prehistoric timescales over which primate behaviour, diet, and even metabolism might have changed, they are the closest we can get to understanding the greatest source of isotopic variation in the diets of the primates of interest. Yet, very few isotopic datasets for primate botanical foodstuffs, and their taxonomic and economic affiliations, are currently available even from modern primate studies (though see Cerling *et al.,* 2004; Oelze *et al.,* 2011, 2014). In particular, no study has so far been designed to discern the extent of $\delta^{13}C$ *and* $\delta^{18}O$ variation between patches of forest with low and high irradiance, different plant parts (i.e. leaves and fruits), vegetation growing at different heights in the canopy, and the inherent variation between leaves (or fruits) of different plant species within a tropical forest ecology (though see Codron *et al.* (2005, 2013) and Blumenthal *et al.* (2015) for $\delta^{13}C$ and $\delta^{15}N$ studies).

4.4 – Stable isotope analysis and the Sri Lankan Microlithic tradition

Sri Lankan human forager rainforest resource reliance

Unlike many of the regions in which Late Pleistocene rainforest exploitation has been postulated (Chapter 2 – Sections 2.1 and 2.2), Sri Lanka has a bountiful record of prehistoric human remains, stretching from the Late Pleistocene, through the Terminal

Pleistocene, and into the Holocene (S.U. Deraniyagala, 1992; Kennedy, 2000; Perera, 2010; Roberts *et al.,* 2015a). On the basis of the stable isotopic principles above, as well as Sri Lanka's ecological context (Chapter 2 – Section 2.2), $\delta^{13}C$ and $\delta^{18}O$ measurements of Microlithic tradition human tooth enamel should primarily reflect an individual's relative dietary reliance on resources ranging from closed canopy C_3 rainforest, 'Intermediate' C_3 rainforest/ C_3 forest and open mosaics, open C_3 vegetation, to open C_4 grassland during the 'sub-adult' period of formation. The movement of C_4 crops such as millet into Sri Lanka does not occur until the Late Holocene (S.U. Deraniyagala, 1992, 2007). In order to ensure that meaningful conclusions can be made in this regard, especially given the potential for past spatial and temporal variability in atmospheric CO_2 concentration and precipitation dynamics (and therefore environmental isotopic baseline values (Cerling and Harris, 1999)), the construction of a detailed temporal and spatial stable isotope ecology of the Sri Lankan Microlithic tradition is essential. Fortunately, unlike Krigbaum's study in Southeast Asia, the Microlithic tradition human fossils of Sri Lanka are directly associated with numerous faunal remains of diverse tropical mammalian taxa whose analysis facilitates isotopic reconstruction of the variety of rainforest ecological niches available to Sri Lankan human foragers at different points in time (Chapter 5 – Section 5.2).

Three sites, Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa, have Terminal Pleistocene/Holocene deposits (*c.* 12,000-3,000 cal. years BP) that are located across the spectrum (Wet Zone rainforest, Intermediate Zone rainforest, and Dry Zone floodplain/grassland, respectively) of the island's modern climate and vegetation zones (Chapter 1 – Figure 1.1, Chapter 2 – Section 2.2). As a result, these sites will enable the evaluation of the potential for these vegetation boundaries to have existed in the past, as well as the ecological setting of humans excavated from various layers throughout these

sequences. Using this Terminal Pleistocene/Holocene dataset as a tentative baseline, human specimens, in association with fauna across archaeological contexts dated from *c.* 36,000-29,000 to *c.* 12,000 cal. years BP, from the site of Batadomba-lena present the possibility of testing the extent and nature of early human rainforest foraging back to the earliest phase of Late Pleistocene rainforest occupation in Sri Lanka. As shown in the case of hominin studies above, additional resolution of the intra- and inter- annual importance of resource-types (in this case rainforest resources) can be obtained by taking a series of $\delta^{13}C$ and $\delta^{18}O$ measurements down the growth axis of human tooth enamel (Chapter 5 – Section 5.2) (John Krigbaum pers. comm.). This represents the first *direct* test of Late Pleistocene human rainforest reliance anywhere in the world.

A palaeoenvironmental record

The well-stratified faunal sequences, spanning the Late Pleistocene, Terminal Pleistocene, and Holocene (Chapter 5 – Section 5.1), also mean that mammalian tooth enamel $\delta^{13}C$ and $\delta^{18}O$ can provide a dated, palaeoenvironmental sequence for tropical Sri Lanka across globally interesting climatic periods. As shown in Chapter 3 (Section 3.2), changes in rainforest extent and character have been documented for Africa, Southeast Asia, Melanesia, South America, and South Asia (Colinvaux *et al.,* 1996; Mercader *et al.,* 2000; Denham *et al.,* 2003; Mayle *et al.,* 2004; Farooqui *et al.,* 2010; Haberle *et al.,* 2012) across the LGM. Persistently cool and dry climatic conditions throughout the LGM have been described for the Asian monsoon region, attributable to a strengthened winter monsoon (van Campo *et al.,* 1982; von Rad *et al.,* 1999; Cosford *et al.,* 2010; Fleitmann *et al.,* 2011, Chabangborn *et al.* 2013), although discrepancies suggest that LGM climate in the Asian monsoon region was highly regionally variable, and that in many areas short wet intervals punctuated generally cool and dry climatic

conditions (Rashid *et al.,* 2007). As discussed above, atmospheric CO_2 concentrations during glacial periods may also have played a significant role in the distribution of C_3/C_4 plants, forests and grasslands.

$\delta^{13}C$ and $\delta^{18}O$ measurements of faunal tooth enamel from a range of faunal taxa from dated contexts can provide on-site records of the wider regional environment available to human foragers in Sri Lanka. Taking various faunal niches into account, changes in overall enamel $\delta^{13}C$ through time will primarily reflect the degree of forest canopy closure or proportion of C_3/C_4 taxa in the vicinity of a given site. Differences in faunal enamel $\delta^{18}O$ through time and between sites may also indicate different canopy coverage. This will be complicated by different body sizes and drinking strategies (obligate versus non-obligate drinkers) in the fauna sampled, although very few very large animals are included in the dataset presented here (Chapter 5 – Section 5.2). In addition, any changes in $\delta^{18}O$ of source water and precipitation through time will also influence faunal enamel $\delta^{18}O$. Tropical forest plant tissues have been shown to document temporal changes in precipitation amount *and* source on different temporal and spatial scales around the world (Evans and Schrag, 2004; Ballantayne *et al.,* 2011; Managave *et al.,* 2011).

In Sri Lanka, the major influence in this regard is the relative amount and spatial extent of rainfall brought by the southwestern monsoon winds from the Indian Ocean between May and October, and the northeastern monsoon winds from the Bay of Bengal between December and March (Chapter 2 – Section 2.2), both of which are directly determined by the Asian monsoon climatic system (Wang *et al.,* 2005). Statistical relationships have been observed in the tropics between $\delta^{18}O$ and rainfall amount

(Dansgaard, 1964; Rozanski *et al.,* 1993; Risi *et al.,* 2008; Breitenbach *et al.,* 2010). However, research in and around the Indian subcontinent, and more preliminary work in Sri Lanka (Jayasena *et al.,* 2008), also identify moisture source, and transport dynamics, as the primary drivers of rainfall, and therefore groundwater, $\delta^{18}O$ in South Asia (Aggarwal *et al.,* 2004; Breitenbach *et al.,* 2010). Long-term amount weighted annual means of precipitation $\delta^{18}O$ are higher on the western coast of India (-1.5‰), as a result of minimal transport and rainout over land. In eastern and northeastern India (-3.7‰), Sri Lanka (-3.4‰), and Myanmar (Burma) (-4.3‰), lower $\delta^{18}O$ indicates mixing of residual, ^{18}O-depleted moisture transported east (during Sri Lanka's southwestern monsoon) and oceanic moisture from the Bay of Bengal (Sri Lanka's northeastern monsoon).

Nonetheless, Aggarwal *et al.* (2004) argue that precipitation transport systems and their spatial distinctions remained largely intact at the LGM on the basis of $\delta^{18}O$ measurements of groundwater from aquifiers from Bangladesh, Thailand, and Vietnam (although issues with the dating of these samples are considerable and involve multiple corrections). They suggest that the only real shift is an increase of oceanic $\delta^{18}O$ values (by a maximum of 1.2‰) caused by the ice-volume effect of the glacial (Schrag *et al.,* 1997). Furthermore, Chabangborn and colleagues (2013) suggest little to no change in precipitation in southern India and Sri Lanka during the LGM. As a result, it is unlikely that the precipitation source for the Sri Lankan Wet Zone changed significantly during the LGM. If a change did occur, namely an increased influence of the northeastern monsoon winds in Sri Lanka, it is likely to be subtle given the relatively minor spatial $\delta^{18}O$ variation between the west coast of India and the Bay of Bengal today (Aggarwal *et al.,* 2004). Overall then, significant shifts in faunal enamel $\delta^{18}O$ will more likely

reflect precipitation amount or proximate environmental changes, such as forest extent or animal food/ water choices, rather than broader climatic system changes.

Ecological details and the importance of monkeys

The variety of predicted drinking behaviours and feeding patterns demonstrated in the taxa available from the Late Pleistocene, Terminal Pleistocene, and Holocene Microlithic tradition archaeological sequences (Chapter 5 – Section 5.2) also offers the opportunity to indirectly reconstruct the position of human foragers within a rainforest ecosystem. Taxa ranging from subcanopy browsers (mouse deer – *Moschiola meminna*, wild boar – *Sus indica*) to nocturnal feeders (porcupines – *Hystrix indica*) and animals with preferences for forest clearings (muntjak – *Muntiacus muntjak*), as well as taxa such as elephants and hares associated with feeding and drinking in more open forests and grasslands, at the Intermediate Zone site of Balangoda Kuragala, allow a variety of Sri Lankan forest niches to be probed and compared isotopically. In particular, the presence of at least two of the three Sri Lankan monkey species (toque macaque – *Macaca sinica*, grey crested langur – *Semnopithecus priam thersites*, and purple-faced leaf monkey – *Trachypithecus vetulus*) at each site allows comprehensive comparison between non-human primate niches and human adaptive strategies in these biomes (Figures 4.14-4.16). The high importance of these monkeys in hunted mammalian assemblages at the sites studied also means that niche details available from enamel $\delta^{13}C$ and $\delta^{18}O$ measurements can provide additional insight into human hunting strategies and flexibility.



Figure 4.14. Macaca sinica – *Toque macaque (photograph: Patrick Roberts).*

Macaca sinica – Toque macaque

Three subspecies: common toque macaque (*Macaca sinica sinica*); pale-fronted toque macaque (*Macaca sinica* aurifrons) and hill zone toque macaque (*Macaca sinica opisthomelas*) (Phillips, 1980; Nahallage *et al.,* 2008).

Range: *Macaca sinica* is found in all three of Sri Lanka's major climatic zones wherever there is an adequate year-round source of drinking water, from sea level to about 2,100 m.

Body mass: *c.* 2-6 kg (Kanelos, 2009).

Feeding habits: *Macaca sinica* feeds chiefly on fruit (*c.* 70-80%) (Hill, 1942; Hladik and Hladik, 1972; Dittus, 1974, 1975; Fooden, 1979), but will also consume flowers, buds, leaves, and resin (12-14%), fungi (1-4%), and invertebrates and small vertebrates (Fooden, 1979; Dittus, 1984; Cheverud *et al.,* 1992). It will utilise shrubs and herbs when staple fruits are scarce (Dittus, 1984).

Drinking habits: *Macaca sinica* is an obligate drinker requiring access to regular surface water. It will make daily trips to waterholes, wells, and irrigation canals during the dry season of the Dry Zone (Fooden, 1979; Dittus, 1984).

Other: Generally characterised as semi-terrestrial, *Macaca sinica* can spend up to 75% of its overall time, and 66% of its foraging time, in trees (Fooden, 1979). It lives in troops of *c.* 25 individuals (Dittus, 1975; Fooden, 1979).



Figure 4.15. Semnopithecus priam thersites – Grey crested langur (photograph: Patrick Roberts).

Semnopithecus priam thersites – Grey crested langur

Range: This monkey is primarily found throughout the well-wooded areas of the Dry Zone from south of Jaffna in the north to the shores of the extreme southern coast, though it can also be found in the Intermediate rainforests of the island (Phillips, 1980; Nekaris and Jayawardene, 2009; Nahallage *et al.,* 2008).

Body mass: *c.* 10-20 kg (Semke, 2011).

Feeding habits: *Semnopithecus priam thersites* is a colobine with the digestive capability to ingest large quantities of foliage. Leaves account for *c.* 50% of its diet, with a particular focus on young leaves. Despite this, it prefers to ingest large amounts of fruits, flowers, and immature leaves even when immature leaves are available (Vandercone *et al.,* 2012).

Drinking habits: Although *Semnopithecus priam thersites* can obtain water from the large amounts of leaves ingested, it will also occasionally drink at shallow ponds in the ground, particularly during the dry season (Vandercone *et al.,* 2012).

Other: *Semnopithecus priam thersites* is semi-terrestrial, although its ability to digest leaf tissues means it can be more regularly found in the canopy than *Macaca sinica*.



Figure 4.16. Trachypithecus vetulus – *Purple-faced leaf monkey (photograph: Patrick Roberts).*

Trachypithecus vetulus – Purple-faced leaf monkey

Four subspecies: southern purple-faced langur (*Trachypithecus vetulus vetulus*); highland purple-faced langur (*Trachypithecues vetulus monticola*); northern purple-faced langur (*Trachypithecues vetulus philbricki*); and western purple-faced langur (*Trachypithecus vetulus nestor*) (Phillips, 1980; Nahallage *et al.,* 2008).

Range: *Trachypithecus vetulus* is mostly found within the canopied Wet Zone and Intermediate Zone rainforests of Sri Lanka, with the exception of the northern purple-faced langur that can be found in undisturbed forests of the northern and central Dry Zone (Vandercone *et al.,* 2012).

Body mass: *c.* 5-10 kg (Phillips, 1980).

Feeding habits: *Trachypithecus vetulus* is a highly folivorous colobine with a specialised diet of mature leaves high in forest canopies (Hladik, 1977). However, recent work suggests that at certain times of the year large portions of their diet can consist of seasonal plant parts, including fruit and flowers (Dela, 2007, 2012).

Drinking habits: *Trachypithecus vetulus* is a non-obligate drinker, obtaining all of its water from the plants it consumes (Dela, 2007; Vandercone *et al.,* 2012).

Other: The shyest of the Sri Lankan primates, it rarely ventures down from the higher reaches of the forest canopy.

The ecological differences between these primates, as well as the isotopic principles outlined in Sections 4.1 and 4.3, should mean that these taxa are distinguishable based on $\delta^{13}C$ and $\delta^{18}O$ measurements of their tooth enamel. At the Polonnaruwa Nature Sanctuary and Archaeological Reserve in northern Sri Lanka, where all three species exist sympatrically, long-term observational data demonstrates that *Trachypithecus vetulus* is a specialised folivore, obtaining 70% of its food from the mature leaves of three species. *Semnopithecus priam thersites*, by contrast, obtains *c.* 70% of its food from ten tree species, including 48% leaves, 7% flowers, and 45% fruits by wet weight (Hladik and Hladik, 1972; Hladik, 1977) (Chapter 5 – Section 5.4). The generalist macaques 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, 1974). However, although ecologically significant, even a diet of 100% fruit versus 100% leaves would likely only differ by a maximum of 2‰ in both $\delta^{13}C$ and $\delta^{18}O$.

Greater distinctions in enamel $\delta^{13}C$ and $\delta^{18}O$ may be caused by the different drinking strategies and feeding heights of the three taxa. In particular we might expect *Trachypithecus vetulus,* a non-obligate drinker feeding higher in the canopy, to have higher $\delta^{18}O$ values than the semi-terrestrial non-obligate drinker *Semnopithecus priam thersites* and the semi-terrestrial obligate drinker *Macaca sinica* (Figure 4.17). However, as noted in Section 4.3, it is also possible that the consumption of different plant species and horizontal differentiation in the depth of canopy in which these species feed could also influence primate tissue $\delta^{13}C$ and $\delta^{18}O$. In order to address the likely relative impact these, potentially equifinal, factors on primate enamel $\delta^{13}C$ and $\delta^{18}O$, this study will build up a comprehensive isotopic dataset of the $\delta^{13}C$, $\delta^{18}O$ and

$\delta^{15}N$ measurements of plants known to be consumed by the different primate species at the Polonnaruwa Nature Sanctuary and Archaeological Reserve, including the height, plant part, species, and level of irradiance relevant to each sampling locale. Alongside a small sample of modern tooth enamel $\delta^{13}C$ and $\delta^{18}O$, collected during the 1980s, this modern vegetation baseline will help to discern which factors play the most important role in isotopic dietary distinctions of these primates in a modern context (Chapter 5 – Section 5.4). Any distinctions, if observed in the past, should provide some basis for inferring the human hunting strategies undertaken during the Sri Lankan Microlithic tradition in order to achieve high yields of these different monkey taxa.

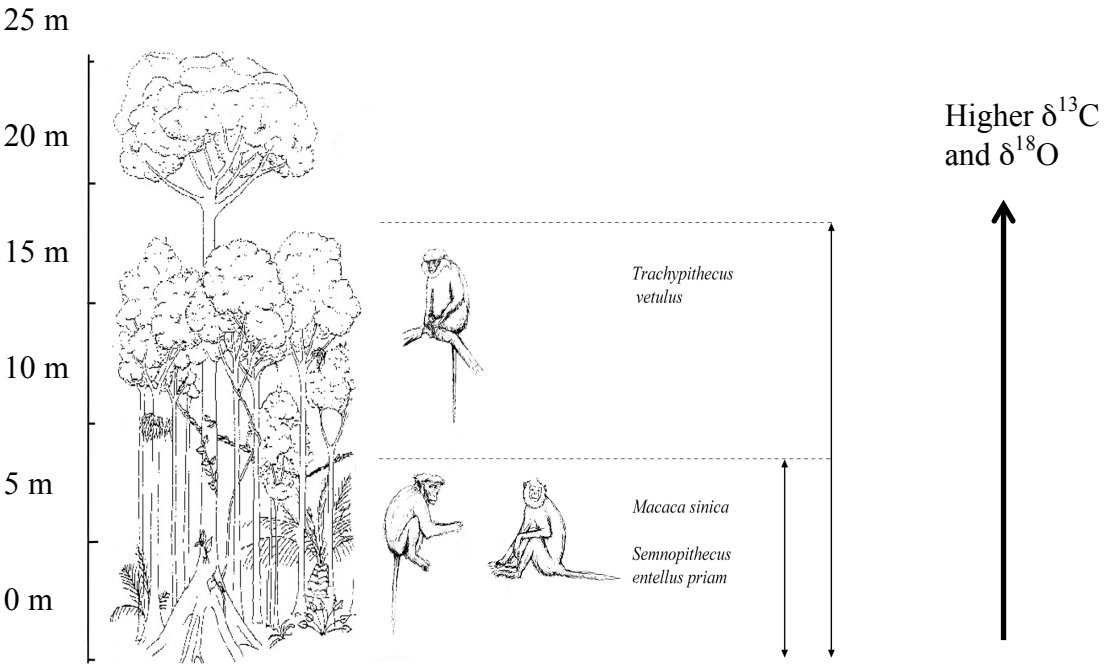


Figure 4.17. Expected feeding positions of Macaca sinica*,* Semnopithecus entellus priam*, and* Trachypithecus vetulus *in the canopy and the expected corresponding effects on enamel $\delta^{13}C$ and $\delta^{18}O$ values.*

Chapter 5 – Sites, samples, and methods

This chapter provides an overview of the sites, samples, and methods used in this study. It begins with a discussion of the archaeological records, chronologies, and tooth enamel samples of the prehistoric sequences of Fa Hien-lena, Balangoda Kuragala, Bellan-bandi Palassa, and Batadomba-lena. It then discusses existing issues in fossil enamel pretreatment and diagenesis, before outlining the preferred methods used in this thesis. This is followed by a description of the modern isotopic sampling and analysis of plants and primates from the Polonnaruwa Nature Sanctuary and Archaeological Reserve. The chapter finishes with a detailed description of the stable isotope and statistical analytical methods applied here to archaeological and modern samples.

5.1 – Archaeological sites analysed in this thesis

All of the prehistoric sites sampled, with the exception of Bellan-bandi Palassa, are cave and rockshelter sequences, meaning that the levels of archaeological and organic preservation are exceedingly high for a rainforest environment (S.U. Deraniyagala, 1992; Perera *et al.,* 2011; Roberts *et al.,* 2015a, 2015b). Bellan-bandi Palassa is an open air site located in the less humid Dry Zone of Sri Lanka and has yielded an abundance of stone artefacts, bone technologies, and faunal remains (S.U. Deraniyagala, 1992; Perera, 2010). Good preservation of charcoal at all sites has meant that robust radiocarbon chronologies exist for the stable isotope datasets produced here. I have calibrated the available radiocarbon dates from the four sequences sampled against the IntCal13 calibration curve (Reimer *et al.,* 2013) using the OxCal (v 4.2) (Bronk Ramsey, 1995, 2009) software.

For Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala I have produced new Bayesian models for the available radiocarbon dates. This was not attempted for Bellan-bandi Palassa which only has radiocarbon dates available from Context 10. In the models, each site was treated as a 'sequence' of contiguous 'phases' or layers on the basis of archaeological stratigraphic information. These phases were separated using 'boundaries' that represent transitions between the phases. The models assume that the dates within each phase are more or less contemporary and that each consecutive phase is younger than the preceding one. Given the fact that all existing radiocarbon measurements from these sites come from charcoal samples, the most recent Charcoal Outlier Model (Dee and Bronk Ramsey, 2014) was applied to account for the possibility of inbuilt age problems. The results for each model are shown in Figures 5.3, 5.6 and 5.11 and Tables 5.1, 5.2, 5.3 and 5.4.

Fa Hien-lena

Fa Hien-lena (80°12'E, 6°38'N) is one of the largest known cave sites in Sri Lanka, and is located in the Wet Zone rainforest (Chapter 1 – Figure 1.1), near Bulathsinhala in the Kalutara District. The cave is east-facing, cut into gneiss rock, with a mouth of *c.* 30 m and has an average height of 20 m above the ground surface. The site was first examined by Siran Deraniyagala in 1968 and excavated over several seasons between 1986 and 1988 by the then Assistant Commissioner of the Archaeological Department, W.H. Wijeyapala. Full excavation results from the 1980s are described by Wijeyapala (1997) in his thesis. Two shelters of the cave complex, termed A and B, were probed with a view to developing an understanding of the cultural sequence. Although the prehistoric deposits of Shelter A were found to have been disturbed by Buddhist

construction activities, Shelter B preserved a long stratigraphic record of Late Pleistocene/Holocene human occupation (Wijeyapala, 1997) (Figure 5.1).

The 1980s excavations of Shelter B defined five main layers dated to between *c.* 38,000 and 5,400 cal. BP. Fa Hien-lena Shelter B is frequently cited as yielding the oldest *Homo sapiens* fossils in Sri Lanka, alongside a limited occurrence of geometric micoliths, shell beads, and bone tools (Kennedy *et al.,* 1987; Wijeyapala, 1997; Kennedy, 2000; Perera *et al.,* 2011). The initial array of radiocarbon dates produced by Wijeyapala (1997) was used to suggest an onset date of *c.* 38,000 cal. years BP for human fossil presence, and microlith, shell bead, and bone tool production in Wijeyapala's Layer 5 of the site (Perera *et al.,* 2011). However, recent reassessment and Bayesian modelling of these dates indicates that Layer 5 most likely spans the period 38,500-35,000 cal. years BP (Roberts *et al.,* 2015a). Layer 4 covers the period 36,000 to 26,000 cal. years BP, prior to a large gap until *c.* 8,000 cal. years BP.

Despite the potential significance of early dates at Fa Hien-lena, Wijeyapala (1997) undertook limited recording or analysis of the stone artefacts, bone toolkits, and faunal remains found during the 1980s excavations, and the human remains from these excavations do not include teeth. In 2011 and 2012 the Department of Archaeology, Government of Sri Lanka, decided to re-excavate the sequence, undertaking more systematic stratigraphic analysis and recording, and re-dating the sequence using AMS methods (rather than bulk charcoal radiocarbon dates from earlier excavations) (Oshan Wedage pers. comm.). Particular focus was placed on the apparently missing Terminal Pleistocene deposits (Figure 5.2). Uncertainty regarding the exact relationship between Layers 237, 139 and 141 and Layer 174 and 247, mean that for the Bayesian model produced for the Terminal Pleistocene/Holocene sequence here, the radiocarbon

determinations produced during the 2011/2012 excavations were divided into three broad 'phases' (Table 5.1) (Figures 5.2 and 5.3).

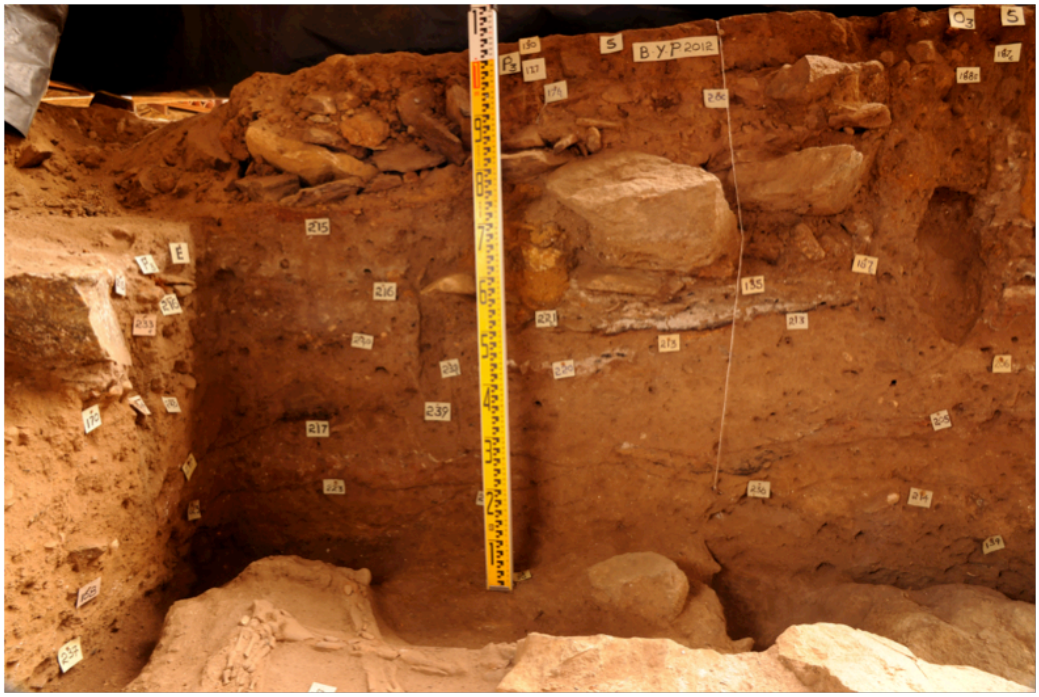


Figure 5.1. South-facing view of the 2011-2012 excavation section at Fa Hien-lena Shelter B (photograph: Oshan Wedage).

The first phase includes Layers 247 and 174 and, according to the model, likely lasted between 12,497 and 12,126 cal. years BP (Table 5.1). A near-complete human skeleton was uncovered from Layer 248, a feature described as being within 247 (Figure 5.2). Sample OxA-26614 FH5 was taken from near the sciatic notch of the skeleton's pelvis while OxA-26615 FH6 comes from below the burial. Given that both of these dates produce a modelled age of *c.* 12,000 cal. years BP, Layers 247 and 248 are best treated as contemporaneous. The second phase of this sequence comprises Layers 139, 141, and 237, and dates to approximately the same period as Layers 247 and 174 (though potentially slightly younger), lasting somewhere between 12,335 and 11,992 cal. years BP (Table 5.1). There then appears to be a fairly substantial chronological gap until the

third and final phase, which is made up of just Layer 136, that likely spanned the period 7,925 to 7,667 cal. years BP (Table 5.1) (Figure 5.3).

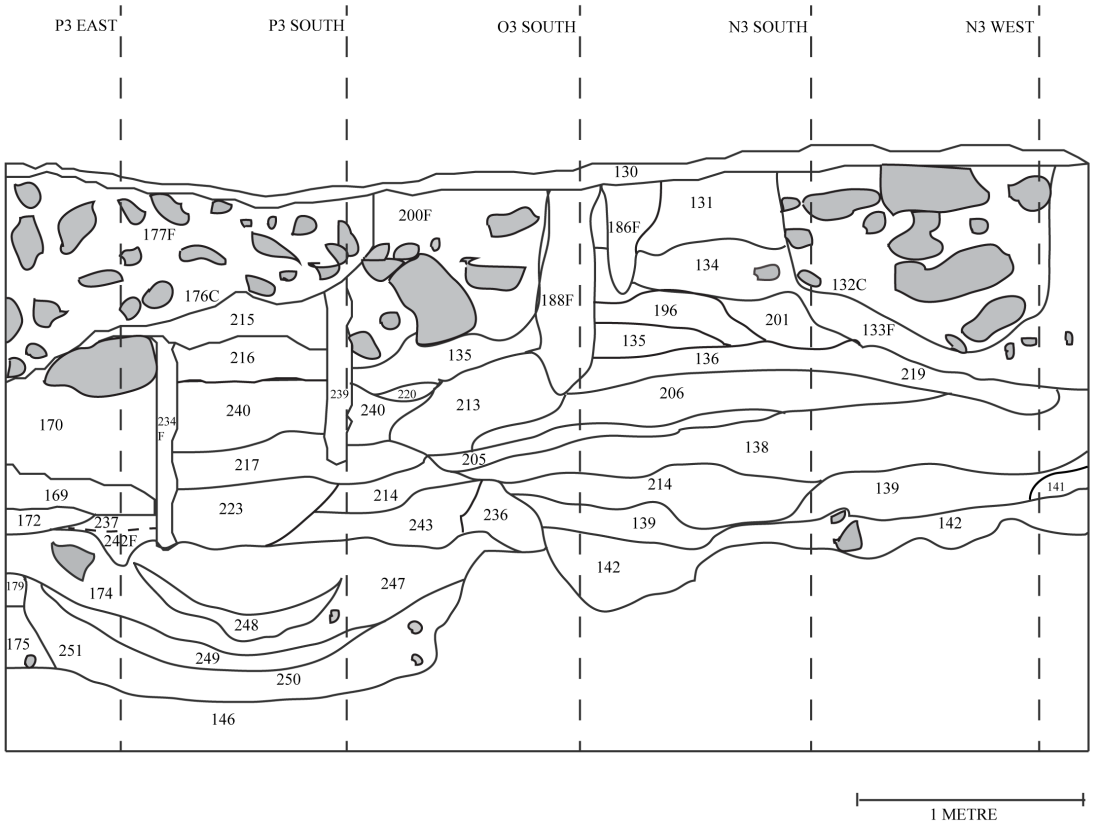


Figure 5.2. Stratigraphic diagram of 2011-2012 excavations at Fa Hien-lena (adapted from Roberts et al.*, 2015b) (Oshan Wedage, pers. comm.).*

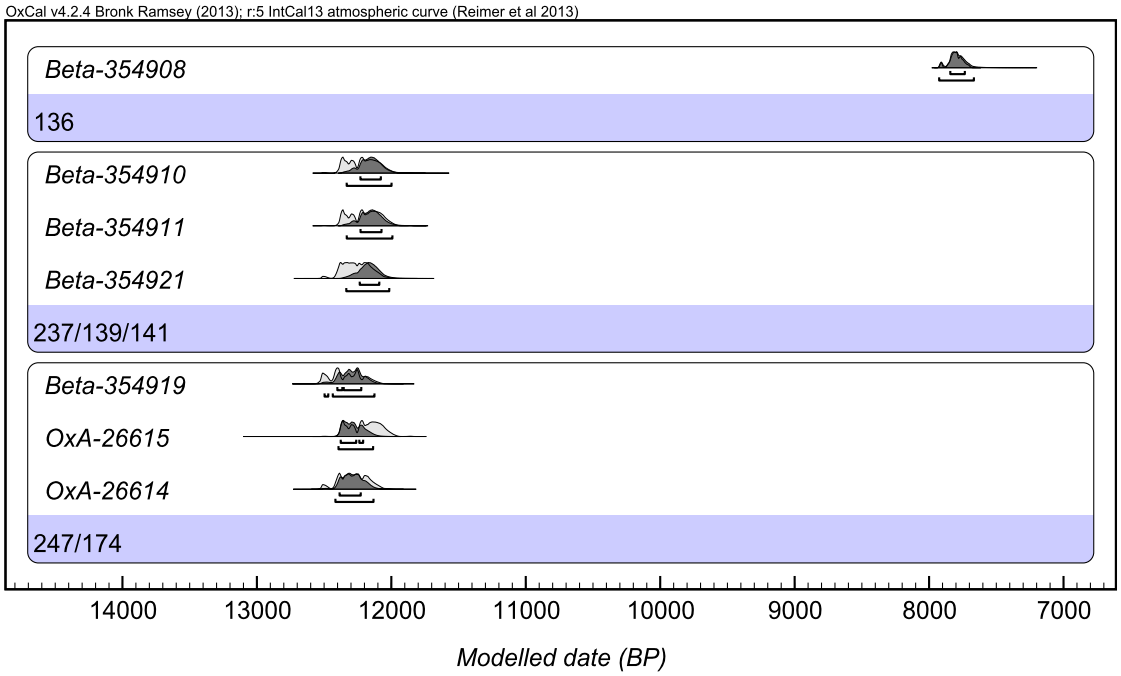


Figure 5.3. The Bayesian date model for the site of Fa Hien-lena treats Layers 247 and 174 as 'Phase 1', Layers 237, 141, and 139 and 'Phase 2' and Layer 136 as 'Phase 3'. These phases are, in turn, treated as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer et al., *2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014).*

It is possible that future radiocarbon dating of this sequence can resolve the site chronology further between *c.* 12,000 and 8,000 cal. years BP (Figures 5.2 and 5.3). Overall, however, the 2011/2012 excavations have produced a well-stratified, well-dated sequence of Terminal Pleistocene/Holocene human occupation, including abundant faunal remains and stone artefacts, though no bone tools were recovered. While there remains the exciting possibility for stable isotope analysis of Fa Hien-lena's earlier material excavated during the 1980s and 2011/2012, sampling for this thesis was focused on the well-characterised Terminal Pleistocene/Holocene faunal collection from the 2011/2012 excavations (Figures 5.1-5.3), in association with the recently exhumed human skeleton from Layer 248 dated to *c.* 12,000 cal. years BP, as an ecological baseline for the Sri Lankan Wet Zone, and its human inhabitants, at this time.

Table 5.1. Dates available from the 2011-2012 excavation at Fa Hien-lena associated with the faunal samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Fa Hien-lena treats Layers 247 and 174 as 'Phase 1', Layers 237, 141, and 139 and 'Phase 2' and Layer 136 as 'Phase 3'. These phases are, in turn, treated as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer et al., *2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014).*

Layer	**Lab code**	**Material**	**^{14}C**	**Unmodelled**			**Modelled**		
				From	To	%	From	To	%
136	Beta-354908	Charcoal	6970 ± 30	7923	7705	95.4	7925	7667	95.4
139	Beta-354910	Charcoal	10350 ± 40	12392	12025	95.4	12332	11999	95.4
141	Beta-354911	Charcoal	10340 ± 40	12389	12007	95.4	12332	11992	95.4
237	Beta-354921	Charcoal	10390 ± 40	12419	12062	95.4	12335	12016	95.4
174	Beta-354919	Charcoal	10440 ± 40	12530	12121	95.4	12497	12126	95.4
247	OxA-26615	Charcoal	10410 ± 40	12389	12007	95.4	12393	12136	95.4
247	OxA-26614	Charcoal	10340 ± 40	12518	12086	95.4	12416	12133	95.4

Balangoda Kuragala

Balangoda Kuragala (80°52'E, 6°37'N) is a rockshelter site located in the Ratnapura District in the Intermediate Zone of Sri Lanka. Sitting directly on the border of the transect between the Wet Zone rainforest, Intermediate rainforest, and open Dry Zone semi-evergreen forest and grassland plains (Chapter 1 – Figure 1.1), this archaeological site is of particular interest to analyses of the relationship between palaeoenvironmental and archaeological change in Sri Lanka. Today, the site is surrounded by more open, Intermediate Zone rainforest, with the Dry Zone grassland plains of the Walawe Valley clearly visible below the Kalkota escarpment from which the rockshelter is formed (Figure 5.4). Preliminary investigation of the site in 2013 indicated that, although recent construction had disturbed the upper layers of the prehistoric deposit, substantial, well-preserved deposits existed behind the drip-line of the rockshelter.



Figure 5.4. Photograph taken from the site of Balangoda Kuragala in the Intermediate Zone of Sri Lanka, showing the steep gradient in elevation and vegetation from mountainous rainforest and intermediate hilly rainforest in Sri Lanka's Wet and Intermediate Zones to open grassland in the Dry Zone (photograph: Patrick Roberts).

Later in 2013, a team from the Department of Archaeology, Government of Sri Lanka, led by Nimal Perera, began detailed excavation of Balangoda Kuragala. Geometric microliths, shell beads and a long sequence of human and faunal remains were uncovered at the site. The model produced here, based on radiocarbon determinations collected from this excavation, suggests that the sequence spans from 15,210 to 14,127 cal. years BP in Layer 35 to 2,957 to 2,393 cal. years BP in Layer 17 and, therefore, the Terminal Pleistocene/Holocene boundary (Table 5.2) (Figures 5.5 and 5.6) (Nimal Perera, pers. comm.; Roberts *et al.,* 2015b). In sum, Balangoda Kuragala presents a well-stratified record of Terminal Pleistocene/Holocene human hunter-gatherers from the modern Intermediate Zone of Sri Lanka that is broadly contemporaneous with the Fa Hien-lena Wet Zone record discussed above.

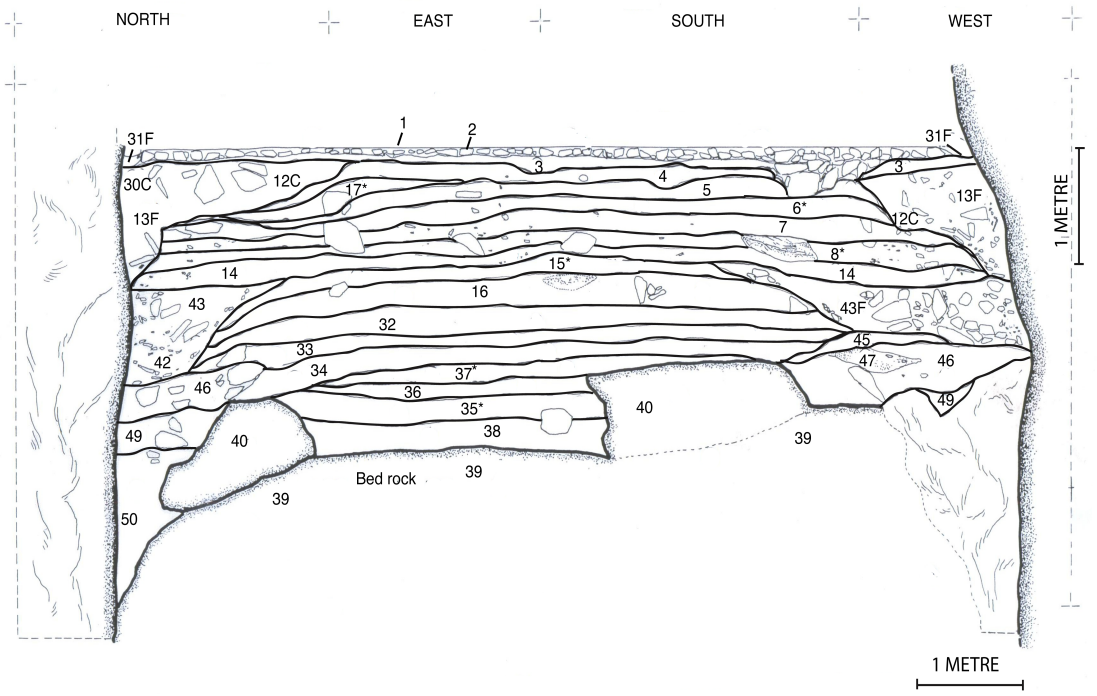


Figure 5.5. Stratigraphic diagram of 2013 excavations at Balangoda Kuragala (courtesy of Nimal Perera) (see also Roberts et al., *2015b).*

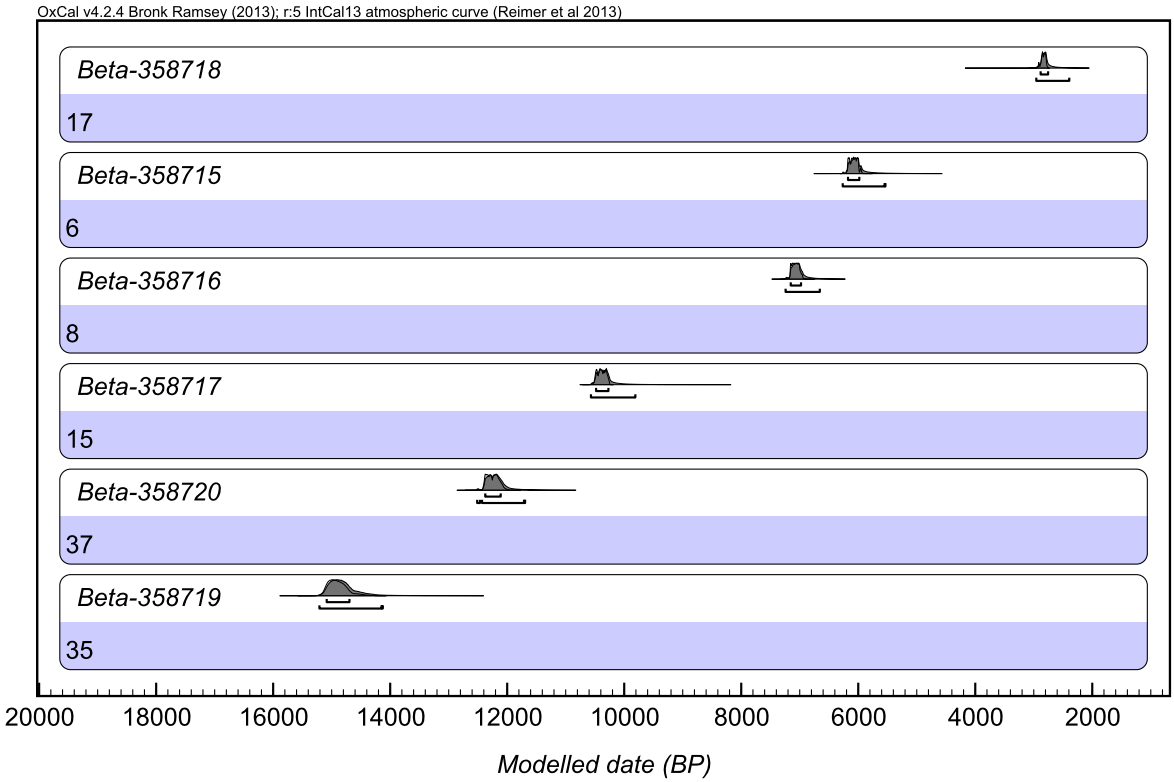


Figure 5.6. The Bayesian date model for the site of Balangoda Kuragala treats each Layer as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer et al., *2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014).*

Table 5.2. Dates available from the 2013 excavation at Balangoda Kuragala associated with the faunal samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Balangoda Kuragala treats each layer as contiguous, bounded units. The model was run using OxCal4.1 (Bronk Ramsey, 2009) and the calibration curve IntCal13 (Reimer et al., *2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014).*

Layer	**Lab code**	**Material**	**^{14}C**	**Unmodelled**			**Modelled**		
				From	To	%	From	To	%
17	Beta-358718	Charcoal	2750 ± 30	2925	2771	95.4	2957	2393	95.4
6	Beta-358715	Charcoal	5300 ± 40	6200	5945	95.4	6266	5536	95.4
8	Beta-358716	Charcoal	6170 ± 40	7170	6949	95.4	7242	6657	95.4
15	Beta-358717	Charcoal	9230 ± 40	10511	10261	95.4	10569	9810	95.4
37	Beta-358720	Charcoal	10380 ± 40	12411	12061	95.4	12513	11694	95.4
35	Beta-358719	Charcoal	12580 ± 60	15181	14533	95.4	15210	14127	95.4

Bellan-bandi Palassa

Bellan-bandi Palassa (80°49'E, 6°32'N) is located in the Ratnapura District, 2 km from the Uda Walawe River within the Uda Walawe National Park, just into Sri Lanka's Dry Zone, and has been key in exploring the earliest forays of the Sri Lankan Microlithic tradition beyond the Wet Zone of Sri Lanka (Chapter 1 – Figure 1.1). Lying 10 km from the Kalkota escarpment that acts as the divide between the Wet and Dry Zones in this region, the site sits in an open glade beside the seasonal Bellan-bandi stream. Bellan-bandi Palassa was first systematically investigated by P.E.P. Deraniyagala between 1956 and 1961, who uncovered numerous burials within the basal cultural deposit and recovered a large assemblage of human remains (P.E.P. Deraniyagala, 1958, 1963; Kennedy, 2000). P.E.P. Deraniyagala described the basal layer (what he termed D1) as containing human bones, stone artefacts, including microliths, and pottery. Despite these finds, P.E.P. Deraniyagala's excavation report was limited and fragmentary (Perera, 2010). Excavation by S.U. Deraniyagala found a series of microlithic stone tools, faunal remains, and pottery between the mixed deposits of Contexts 2-6 (S.U. Deraniyagala and Kennedy, 1972) (Figure 5.7). However, during this research a large, intact occupation deposit (Context 10 – Figure 5.7), containing numerous burials, was also found (S.U. Deraniyagala and Kennedy, 1972). Associated with this deposit were high densities of stone artefacts, including microliths, and faunal remains (Perera, 2010).

A thermo-luminescence date of 6,500 ± 700 BP obtained on fired rock crystal in direct association with one of the burials provided the initial chronology for Context 10 (Wintle and Oakley, 1972; S.U. Deraniyagala, 1992). In 2005, excavations initiated by Nimal Perera sought to gain a more complete picture of the stratigraphy, chronology,

and material culture of the site. Part of this included the re-dating of Context 10 using the AMS radiocarbon methodology, which placed the context at 12,000-11,000 cal. years BP (Perera, 2010). Calibration of the two available radiocarbon dates from Context 10 here using OxCal4.2 (Bronk Ramsey, 1995, 2009) and the calibration curve IntCal13 (Reimer *et al.,* 2013), with the latest Charcoal Outlier Model included (Dee and Bronk Ramsey, 2014), provides a date range of 12,217 to 11,309 cal. years BP for Context 10 (Table 5.3) (Figure 5.8). Given known problems with calculating dose rates and assessing the relationship between sediments and archaeological contexts in a mobile fluvial setting (Berger, 1990; Richter, 2007), the radiocarbon estimations have been preferred in this study (see also Perera, 2010; Perera *et al.,* 2011). This chronology places a geometric microlith industry, that demonstrates strong similarity to those from the Wet Zone rockshelters, in the Dry Zone of Sri Lanka at *c.* 12,000-11,000 cal. years BP. Importantly, fossil faunal remains from this layer provide a Terminal Pleistocene stable isotope reference for the Sri Lankan Dry Zone. Unfortunately, given political issues concerning the rich assemblage of human remains from Context 10 (currently housed at the National Museum of Colombo) no human samples from Bellan-bandi Palassa could be analysed in this thesis.

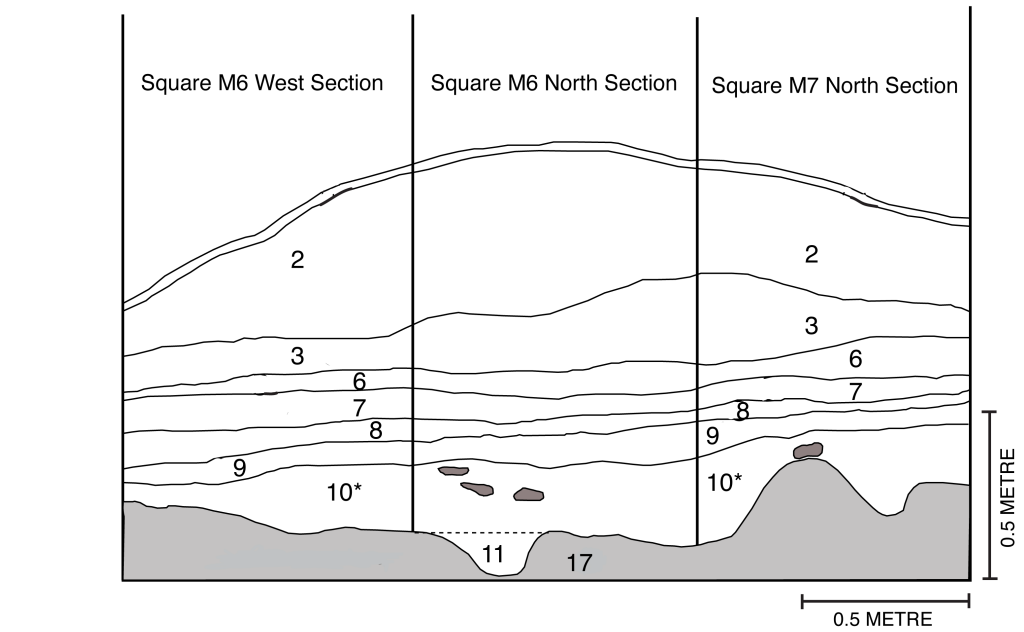


Figure 5.7. Stratigraphic diagram of 2005 excavations at Bellan-bandi Palassa, See also Perera (2010).

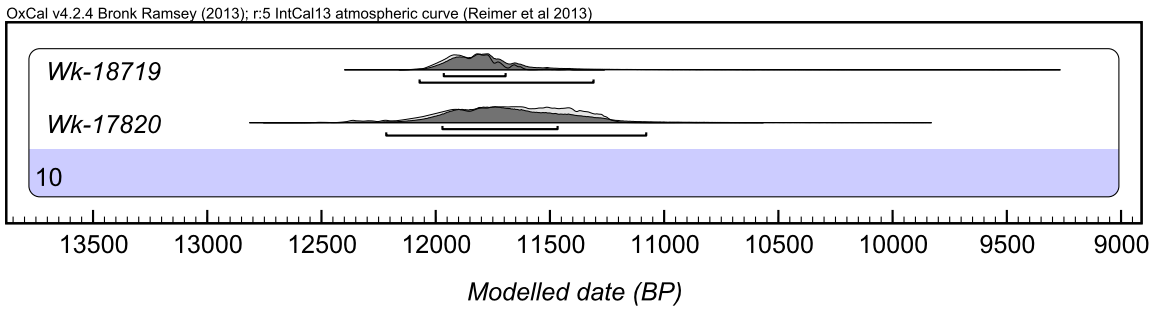


Figure 5.8. Available radiocarbon determinations from 2005 excavations at Bellan-bandi Palassa (Perera, 2010 calibrated using the OxCal 4.2 software and the IntCal13 calibration curve (Reimer et al., 2013) with the latest Charcoal Outlier Model applied (Dee and Bronk Ramsey, 2014). Both dates were modelled as part of a single contiguous phase.

Table 5.3. Dates available from 2005 excavations at Bellan-bandi Palassa (Perera, 2010) associated with the faunal samples analysed in this study. All radiocarbon determinations have been calibrated using the OxCal 4.2 software and the IntCal13 calibration curve (Reimer et al., 2013) with the latest Charcoal Outlier Model applied (Dee and Bronk Ramsey, 2014). Both dates were modelled as part of a single contiguous phase.

Context	**Lab code**	**Material**	**^{14}C**	**Unmodelled**			**Modelled**		
				From	To	%	From	To	%
10	Wk-17820	Charcoal	10086 ± 142	12364	11227	95.4	12217	11079	95.4
10	Wk-18719	Charcoal	10163 ± 45	12041	11624	95.4	12071	11309	95.4

Batadomba-lena

Batadomba-lena is a cave on the banks of a stream in the Wet Zone rainforest of Sri Pada, Ratnapura District, *c.* 80 km east of Colombo (6°46'N, 80°12'E) (Figure 5.9). This northeast-facing cave has an area of *c.* 10 x 15 metres, making it slightly larger than Fa Hien-lena Shelter B. As with Fa Hien-lena, the cave is formed of the gneiss bedrock of the Precambrian Highland Complex that constitutes the mountainous centre of Sri Lanka (Cooray, 1994). Batadomba-lena is currently surrounded by dense, lowland evergreen forest, relatively untouched by agricultural modification or industrial clearance (Perera, 1975) (Chapter 1 – Figure 1.1), and represents one of Sri Lanka's most intensively researched prehistoric sites. Detailed excavation of the site began in 1979 under the direction of S. U. Deraniyagala (1992) and produced a detailed stratigraphic understanding of the site that indicated the presence of human fossils, geometric microliths, single and double bone points, charcoal hearths, faunal remains, and molluscs from the earliest horizon upwards.



Figure 5.9. View into Batadomba-lena rockshelter. The sides of the 2005 excavation trench (Figure 5.8) have been supported by bricks (centre-left of shot) (photograph: Patrick Roberts).

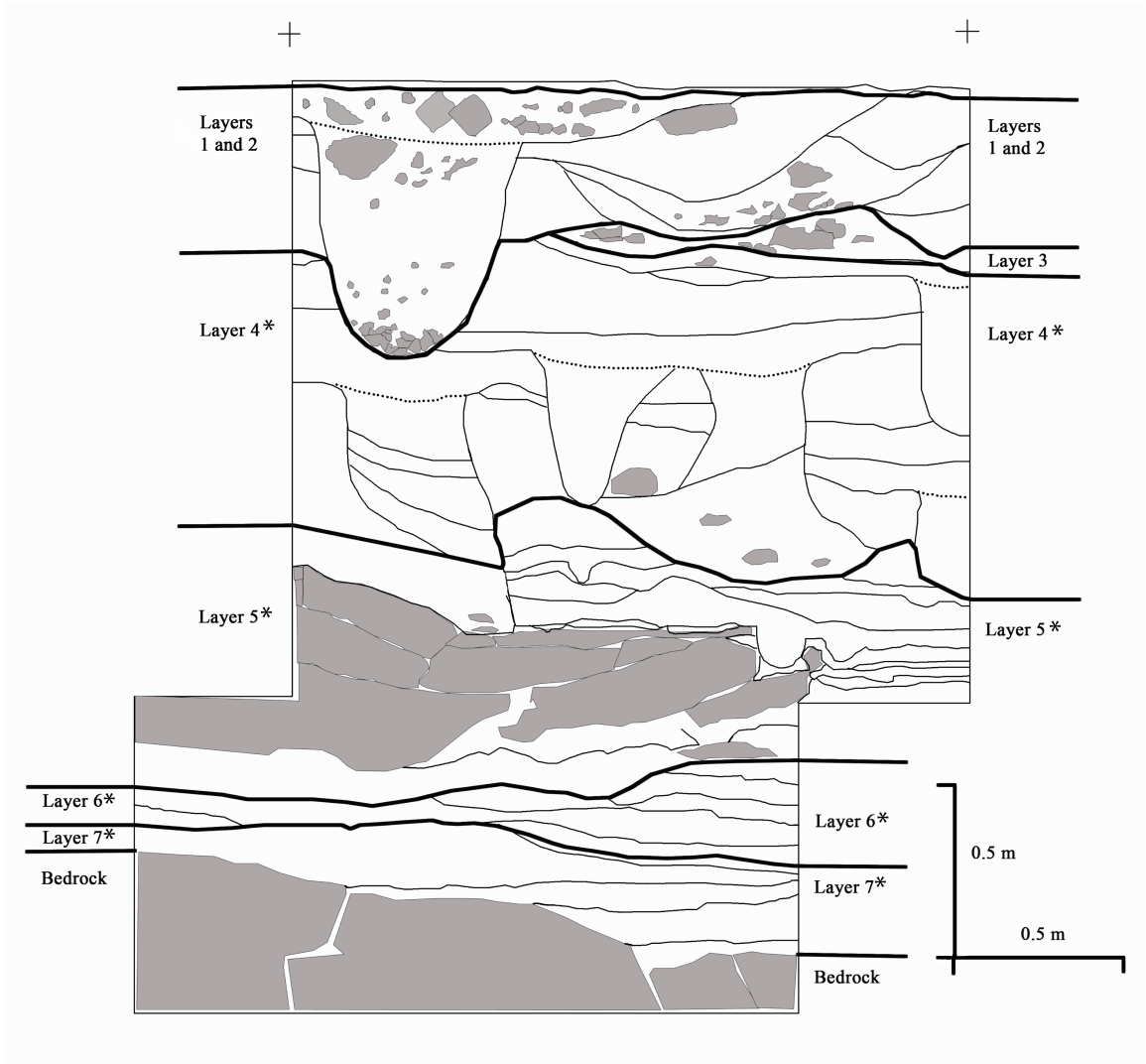


*Figure 5.10. Stratigraphic diagram of 2005 excavations at Batadomba-lena. See also Perera et al. (2011). * denote layers with radiocarbon dates (Table 5.4, Figure 5.9).*

Deraniyagala obtained 10 bulk charcoal radiocarbon dates, which indicated a period of occupation from *c.* 28,500 cal. BP to *c.* 12,000 cal. years BP (S.U. Deraniyagala, 1992). At the time, this made the Sri Lankan microlith technologies the earliest beyond Africa (Perera, 2010). In 2005, these dates were re-calibrated and two new bulk and four new AMS radiocarbon dates were added to the series as part of a re-excavation of the site (Perera, 2010; Perera, *et al.,* 2011). This led to a stratigraphic sequence of Layers 7c to 1 (Figure 5.10), dated from 36,000 cal. BP to 12,000 cal. BP (Perera, 2010; Perera *et al.,* 2011, in press). 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 earliest layer, Layer 7c, along with the earliest human fossils, bone tools, and microliths at the site, was *c.* 36,000 cal. years BP. However, given the large range of the bulk radiocarbon date (common among many of the Late Pleistocene Sri Lankan dates), such a method seems inappropriate (Roberts *et al.,* 2015a).

Here I update an existing Bayesian model of the radiocarbon dates from Batadomba-lena (Roberts *et al.,* 2015a), by applying the latest charcoal outlier model (Dee and Bronk Ramsey, 2014) (Figure 5.11). The new model indicates that the start of Layer 7c most likely spans 35,862 to 28,769 cal. years BP (Figure 5.11; Table 5.4), though it could stretch as early as 38,000 cal. years BP (Table 5.4), thus overlapping with Fa Hien-lena Layer 5 (Figure 5.11; Table 5.4; Roberts *et al.,* 2015a). Layers 6b, which contain a wealth of human fossil material, and Layer 6a, span 19,497-17,238 cal. years BP and 17,809-15,883 cal. years BP, respectively, and demonstrate occupation of the site around the time of the LGM (Perera *et al.,* 2011; Roberts *et al.,* 2015a) (Figure 5.11; Table 5.4). Layers 5, 4b, and 4a indicate that the sequence then extends down to *c.* 12,000 cal. years BP. Future AMS radiocarbon dating using the more rigorous Acid Base Oxidation Scintillation (ABOX-Sc) pre-treatment, which removes contamination by younger carbon at Late Pleistocene archaeological sites (Bird *et al.,* 1999; Higham *et al.,* 2009), could see the chronology for Batadomba-lena extended significantly back in time. Overall, however, Batadomba-lena apparently represents a relatively continuous period of occupation, microlithic manufacture (Lewis *et al.,* 2014), and bone point use (Perera *et al.,* in press) from *c.* 36-29,000 to *c.* 12,000 cal. years BP.

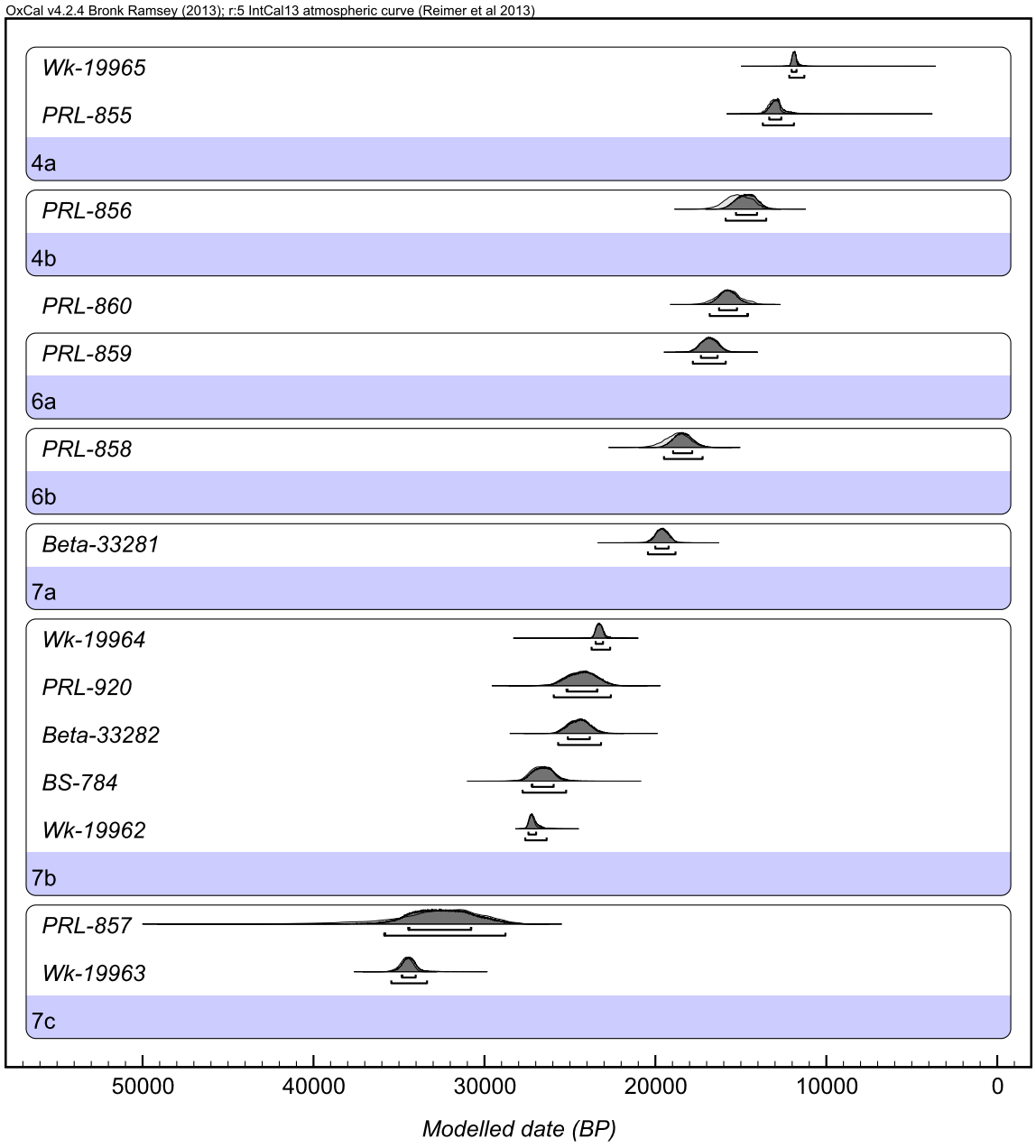


Figure 5.11. The Bayesian date model for the site of Batadomba-lena based on available dates from S.U. Deraniyagala (1992) and Perera et al. (2011) that treats each archaeologically-identified layer (e.g. 7c, 7b, 7a) as contiguous, bounded units (Roberts et al., *2015a) (see also Table 5.4). Models were run using OxCal4.2 and the calibration curve IntCal13 (Reimer et al. 2013). The latest Charcoal Outlier Model was also applied (Dee and Bronk Ramsey, 2014).*

Most of the human teeth sampled for this thesis come from the 1980s excavations of Layer 6b, which appears to represent a LGM/post-LGM occupation phase. Three were labelled 6b/7a, which places them somewhere between *c.* 20,435-17,238 cal. years BP (Figure 5.11; Table 5.4). Given evidence elsewhere in the world for significant changes in rainforest structure and extent during the LGM (Chapter 3 – Section 3.2), this rich assemblage of human teeth provides a large sample size with which to investigate human responses to any climate-linked ecological changes at this time. Previously recorded human teeth excavated from Layer 7c during the 1980s (S.U. Deraniyagala, 1992; Kennedy, 2000) could not be found for analysis. However, upon inspection of 1980s faunal remains from Layer 7c, a further human tooth was identified and photographed (Figure 5.12). There is no reason to doubt the stratigraphic integrity at the site, which has little evidence for taphonomic re-working (Perera *et al.,* 2011; Lewis *et al.,* 2014). As such, this sample represents the oldest existing, accessible human fossil in Sri Lanka, and indeed South Asia (*c.* 36-29,000 cal. years BP). Few fauna from the earliest layers were recovered from the 2005 excavations. Therefore, while samples from Layers 6, 5 and 4 were taken from the more recent assemblage, those from Layers 7c, 7b, 7a, and 6 come from the 1980s assemblage in order to ensure even coverage throughout the sequence. Comparison of the resulting stable isotope ecology with the ecological baselines constructed for the Wet Zone, Intermediate Zone, and Dry Zone during the Terminal Pleistocene/Holocene at the other three sites provides a better diachronic sample and the potential to identify changes in forest extent and structure in the Sri Lankan Wet Zone during the LGM and beyond.



Fig. 5.12. Human incisor from Batadomba-lena 7c examined in this study (photograph: Ian Cartwright).

Table 5.4. Dates available from 1980s and 2005 excavations at Batadomba-lena (S.U. Deraniyagala, 1992; Perera, 2010; Perera et al., *2011) associated with the faunal and human samples analysed in this study. Unmodelled and modelled calibrated determinations are shown. The Bayesian date model for the site of Batadomba-lena treats each layer as contiguous, bounded units. The model was run using OxCal4.2 and the calibration curve IntCal13 (Reimer* et al., *2013), and include the latest Charcoal Outlier Model (Dee and Bronk Ramsey, 2014).*

Layer	**Lab code**	**Material**	**^{14}C**	**Unmodelled**			**Modelled**		
				From	To	%	From	To	%
Context 18 (Layer 4a)	Wk-19965	Charcoal	10193 ± 57	12113	11626	95.4	12167	11286	95.4
Layer 4a	PRL-855	Charcoal	11200 ± 330	13776	12426	95.4	13715	11894	95.4
Layer 4b	PRL-856	Charcoal	12770 ± 470	16574	13749	95.4	15891	13517	95.4
Layer 5	PRL-860	Charcoal	13130 ± 440	17046	14215	95.4	16822	14594	95.4
Layer 6a	PRL-859	Charcoal	13880 ± 270	17848	15844	95.4	17809	15883	95.4
Layer 6b	PRL-858	Charcoal	15390 ± 610	20239	17298	95.4	19497	17238	95.4
Layer 7a	Beta-33281	Charcoal	16220 ± 300	20310	18889	95.4	20435	18822	95.4
Context 134 (Layer 7b)	Wk-19964	Charcoal	19350 ± 121	23635	22959	95.4	23734	22647	95.4
Layer 7b	PRL-920	Charcoal	20150 ± 740	25961	22661	95.4	25945	22603	95.4
Layer 7b	Beta-33282	Charcoal	20320 ± 500	25709	23394	95.4	25688	23179	95.4
Layer 7b	BS-784	Charcoal	22360 ± 650	27851	25491	95.4	27768	25221	95.4
Context 104 (layer 7b)	Wk-19962	Charcoal	22903 ± 172	27574	26788	95.4	27611	26362	95.4
Layer 7c	PRL-857	Charcoal	27700 ± 2090	38873	28075	95.4	35862	28769	95.4
Context 71 (Layer 7c)	Wk-19963	Charcoal	30603 ± 400	35364	33894	95.4	35448	33358	95.4

5.2 –Faunal and human archaeological samples

Archaeological faunal samples

All archaeological faunal enamel samples used in this study are shown in Catalogue Table A1. Jude Perera had previously identified all teeth sampled to genus and species level using modern reference collections at the Department of Archaeology, Government of Sri Lanka and the Postgraduate Institute for Archaeology, Colombo (Perera, 2010; Perera *et al.,* 2011). For each stratigraphic layer, an average sample size of *c.* 15 teeth had been identified to this level, though much smaller sample sizes exist for those layers with few faunal remains. Most intensive identification, and therefore sampling, was undertaken on layers with direct dates or human remains. Given the focus of this study, and indeed Sri Lankan Microlithic tradition hunters, on primate taxa, three to five samples from each primate species present were identified for each layer where possible. Where available, the same tooth was sought to ensure different individuals were being sampled. Third molars were generally favoured as representative of the late juvenile/adult period of primate diet, on the basis of histological studies of *Macaca nemestrina* (Sirianni and Swindler, 1985), baboons, chimpanzees and gorillas (Dirks, 1997), while first molars were avoided due to potential issues of the weaning signal (Chapter 4 – Section 4.2). In all cases a single 'bulk' sample was taken by drilling along the full length of the buccal surface of each sample, using gentle abrasion with a diamond-tipped drill, in order to maximise the period of formation represented.

At Balangoda Kuragala some larger cervid (*Cervus unicolor*), elephant (*Elephas* sp.), and pig (*Sus scrofa*) teeth were subjected to additional intra-tooth sampling whereby sequential samples were obtained along the buccal surface, from the tooth-enamel

junction to the top of the crown. Each sample was a 1-2 mm-wide groove perpendicular to the tooth growth axis, through the thickness of the enamel layer, taken using the same diamond tipped drill bits as above. The distance of each sample from the enamel/root junction from the furthest sample margin was recorded (Balasse *et al.,* 2012; Zazzo *et al.,* 2012). For this initial sequential 'pilot' in Sri Lanka the number of samples, and therefore the resolution, obtained is relatively coarse compared to existing, intra-tooth studies (Balasse, 2002; Zazzo *et al.,* 2010; Balasse *et al.,* 2012). This methodology should, nevertheless, provide some understanding of whether there is variation in the diet and drinking behaviours of these animals during enamel formation. Intra-tooth analysis focused on premolars and second and third molars for cervid and elephant specimens as representative of the longest period of formation. However, canines and incisors were sampled for pig specimens following recent recommendations that these teeth demonstrate the longest period of growth in pigs (Frémondeau *et al.,* 2012). All teeth were photographed, with images available from the author on request, and were then returned to the Department of Archaeology, Government of Sri Lanka.

While the ecological settings of Sri Lanka's three monkey species were discussed in detail in Chapter 4 (Section 4.4), it is now worth briefly addressing the feeding and drinking behaviours of the other faunal taxa peculiar to Sri Lanka identified in Catalogue Table A1. This has yet to be discussed, in detail, in the context of the Sri Lankan Microlithic, yet is crucial to the examination of the stable isotope ecology associated with prehistoric hunter-gatherers in this region of the world. The following summary has been adapted from W.W.A. Phillips' (1980) seminal '*Manual of the Mammals of Sri Lanka*' and Yapa and Ratnavira's (2013) '*The Mammals of Sri Lanka*'.



Fig. 5.13. Axis axis (ceylonensis) – *Ceylon spotted deer (Source: Aravinda, 2014).*

Axis axis (ceylonensis) – Ceylon spotted deer

Range: *Axis axis* lives mainly in the remote lowland jungles and forests of the Intermediate and Dry Zone.

Body mass: *c.* 25-75 kg (Lundrigan and Gardner, 2000).

Feeding habits: This species eats grasses and herbs in open glades and grassy areas in forests. However, it will also browse the leaves of various bushes, saplings and scrub in jungles, as well as flowers and fallen forest fruits. It feeds at dawn and in the early evening.

Drinking habits: *Axis axis* drinks at waterholes, river-beds, and from pools around midday.

Other: This skittish species feeds at dawn and early evening, and rests in shade during the day.



Fig. 5.14. Cervus unicolor (unicolor) - *Ceylon sambhur (Source: Drriss and Marrionn, 2013).*

Cervus unicolor (*unicolor*) – Ceylon sambhur

Range: *Cervus unicolor* is found throughout Sri Lanka though prefers dense forest habitats.

Body mass: *c.* 100-350 kg though it can reach *c.* 550 kg.

Feeding habits: This species consumes grasses as well as the leaves and shoots of many shrubs and trees. It also eats fallen forest fruits, fresh young grasses that emerge after local burning, and riverine vegetation. *Cervus unicolor* feeds primarily at night, though it will also feed in early morning and late evening in secluded regions.

Drinking habits: *Cervus unicolor* drinks at night from small open water sources.

Other: This species is the largest of Sri Lanka's deer and, while generally solitary, is regularly the target of human hunting near watercourses and forest paths.



Fig. 5.15. Elephas maximus maximus – *Sri Lankan elephant (photograph: Patrick Roberts).*

Elephas sp. – Asiatic elephant (*Elephas maximus maximus* - Sri Lankan subspecies) –

Range: This elephant was once plentiful throughout forests and jungles of Sri Lanka in all climate zones. It is now restricted to northern, eastern and south-eastern districts of the Dry Zone, although it also remains present in the Sinharajah Forest of the Wet Zone and the Adam's Peak Wilderness further east.

Body mass: *c.* 2,000-5,500 kg.

Feeding habits: The Sri Lankan elephant eats various species of succulent grasses, supplemented by creepers, bamboo, shoots, leaves, fruits, and the bark and sappy stems of a number of trees. It is primarily a grazer, but a mixed diet appears essential to its survival in modern Sri Lanka. *Elephas maximus maximus* feeds during both the day and night.

Drinking habits: Herds of this elephant head for open water sources, mainly lakes, to drink just before sunrise and in early evening (Blanford, 1891).

Other: Sri Lankan elephants, particularly male bulls, are aggressive when met by humans in the wild and are responsible for a number of deaths in Sri Lanka each year.



Fig. 5.16. Herpestes *sp. – Mongoose (Source: Issadeen, 2012).*

Herpestes sp. – (There are four species of mongoose in Sri Lanka: (*Herpestes edwardsii lanka*, *Herpestes fuscus*, *Herpeststst smithii zeylanicus,* and *Herpestes vitticollis*)) –

Range: The various mongoose species and subspecies are found throughout the climatic and vegetation zones of Sri Lanka.

Body mass: *c.* 1-2 kg (Graham, 2004).

Feeding habits: All Sri Lankan mongoose species eat small mammals, birds (and their eggs), lizards, smallish snakes, grubs, insects and, to a lesser extent, fruits, berries and roots of certain sorts are all eaten. Sri Lankan mongooses will hunt and forage throughout the day.

Drinking habits: Mongooses are obligate drinkers and remain close to rivers.

Other: While a good climber, *Herpestes* sp. is rarely seen in trees except when chased and is generally found amongst undergrowth and root holes.



Fig. 5.17. Hystrix indica – *Indian crested porcupine (Source: Souza, 2011).*

Hystrix indica – Indian crested porcupine

Range: *Hystrix indica* is common in the tropical shrublands and forests of the Sri Lankan Wet Zone and Intermediate Zone, though it prefers locales with rocky hillsides.

Body mass: *c.* 10-20 kg (Schlimme, 2000).

Feeding habits: It consumes a variety of plant material including roots, bulbs, grains, and tubers, along with insects and small vertebrates. It has also been known to chew on bones to acquire minerals such as calcium. *Hystrix indica* is nocturnal and will forage mainly in close proximity to their burrows where they sleep during the day.

Drinking habits: The species drinks from open water sources at night.

Other: The Indian crested porcupine spends most of its time underground and forms substantial fat reserves. When threatened the porcupine will erect its quills to appear larger.



Fig. 5.18. Lepus nigricollis (singhala) – *Ceylon black-naped hare (Source: Wijeratne, 2013).*

Lepus nigricollis (singhala) – Ceylon black-naped hare

Range: *Lepus nigricollis (singhala)* is plentiful throughout Sri Lanka though it avoids dense forest.

Body mass: *c.* 1-7 kg (Lundrigan and Foote, 2003).

Feeding habits: *Lepus nigricollis (singhala)* mainly eats grasses and the leaves and young shoots of tender plants.

Drinking habits: This species is an obligate drinker.

Other: Unlike many other hares around the world, *Lepus nigricollis (singhala)* is more of a 'jungle' species in that it appears to prefer the undergrowth and scrub on the verges of woods and forests rather than more open grasslands.



Fig. 5.19. Muntiacus muntjak (malabaricus) – *South Indian muntjac or Barking deer (Source: Sani, 2010).*

Muntiacus muntjak (*malabaricus*) – South Indian muntjac or barking deer

Range: *Muntiacus muntjak* (*malabaricus*) is found throughout Sri Lanka, though it is more locally abundant in the lowland hills and forests of the Intermediate and Dry Zones.

Body mass: *c.* 15-35 kg (Jackson, 2002).

Feeding habits: This species of deer eats succulent grasses with the addition of a few leaves and young shoots browsed from various shrubs and seedlings.

Drinking habits: *Muntiacus muntjak* (*malabaricus*) is an obligate drinker and remains near open water sources.

Other: Generally, the barking deer grazes and browses alone or in pairs on the outskirts of jungle, along forest paths and clearings, and rarely wanders very far from cover. Following intensive human encounters, it is now essentially nocturnal except in the most remote of areas.



Fig. 5.20. Paradoxurus *sp. – Palm cat or Palm civet (Source: Dupont, 2003).*

Paradoxurus sp. – Palm cat or palm civet

Range: Palm cats are plentiful across Sri Lanka, but are locally distributed to wherever there are rocky outcrops and/or trees.

Body mass: *c.* 2-5 kg (Schweighoefer, 1999).

Feeding habits: *Paradoxurus* sp. has a diet partly of small mammals, birds, frogs, and insects, but mainly of fruits and berries of various kinds. It is often seen climbing palm (*Caryota urens*) trees at night in Sri Lanka to devour the sugar-rich seeds (Phillips, 1980) and is almost entirely nocturnal.

Drinking habits: *Paradoxurus* sp. drinks from open water sources at night.

Other: The palm cat is frequently found amongst the dense foliage of tree-tops. Nevertheless, Sri Lankans report that it is relatively easy to track and bait.



Fig. 5.21. Petaurista philippensis – Indian giant flying squirrel (Source: Francey, 2015).

Petaurista philippensis – Indian giant flying squirrel

Range: This giant flying squirrel is locally distributed throughout the Wet Zone Hills of the central mountain ranges, between *c.* 500-1,000 m a.s.l..

Body mass: *c.* 0.1-2 kg (Ringgenberg, 2013).

Feeding habits: *Petaurista philippensis* eats wild fruits, berries, nuts, young shoots, leaves, flowers, and immature bark form the main dietary items, though it will also opportunistically forage for insects and larvae. This animal is essentially arboreal and nocturnal.

Drinking habits: *Petaurista philippensis* drinks from open water sources at night.

Other: This species spends the daytime in the hollow of a tree before heading for tall, spreading trees to feed at dusk.

Petinomys fuscocapillus (*layardi*) –Ceylon Small Flying Squirrel

This small flying squirrel is one of the rarest of the indigenous mammals of Sri Lanka. Like *Petraurista philippensis*, its range is limited to the Hills of the Wet Zone rainforest at medium altitudes. Its diet and drinking habits are much the same as the previous species and it is even less conspicuous.



Fig. 5.22. Pteropus giganteus (giganteus) – *Common flying fox (Source: Mennerich, 2013)*.

Pteropus giganteus (giganteus) – Common flying fox

Range: This flying fox is plentiful over most of the cultivated and jungle areas of Sri Lanka, with the exception of the Highlands.

Body mass: *c.* 0.6-1.6 kg (Silbernagel, 2005).

Feeding habits: *Pteropus giganteus (giganteus)* feeds mainly upon the pulp and juices of the flowers and fruits of many species of trees including coconut palms, guavas (*Psdium guajava*), plantain or banana (*Musa paradisiaca*), pawpaws (*Carica papaya*), jackfruit (*Artocarpus integra*), and mango (*Mangifera indica*). This species hides in tall trees with dense foliage for most of the day prior to feeding at night.

Drinking habits: *Pteropus giganteus (giganteus)* drinks after sunset mainly around rivers.

Other: This flying fox is regularly found in dense groups and will often fly considerable distances to its nightly feeding areas. It is also reportedly easy to tame.



Fig. 5.23. Ratufa macroura – *Giant squirrel (Source: Garvie, 2009).*

Ratufa macroura – Giant squirrel

Range: *Ratufa macroura* has an island-wide distribution in Sri Lanka. Three distinct subspecies exist, however: *Ratufa macroura macroura* (forests and woodlands of the Wet, Intermediate and Dry Zones); *Ratufa macroura melanochra* (wet and evergreen forests of the Wet Zone); and *Ratufa macroura dandolena* (lowland jungles of the Dry Zone). *Ratufa macroura melanochra* (the black and yellow giant squirrel) is particularly prevalent around the Wet Zone and Intermediate Zone sites of the Sri Lankan Microlithic tradition.

Body mass: *c.* 1.5-3 kg (Kane, 1999).

Feeding habits: All of the Sri Lankan subspecies eat leaves, bark, young twigs, and shoots of the trees in which they live, together with wild fruits, berries and nuts. *Ratufa macroura* will also forage for insects and grubs, as well as the occasional bird's egg. It is essentially diurnal and arboreal, and lives exclusively in the trees in the forests and woods within their range.

Drinking habits: All of the Sri Lankan subspecies drink during early mornings and evenings.

Other: While shy, giant squirrels have a loud cry when mobile during the mornings and evenings. Local villagers consider giant squirrels to be excellent food and will hunt them when the opportunity arises.



Fig. 5.24. Sus scrofa – *Wild boar (Source: Garvie, 2009).*

Sus scrofa – Wild boar

Range: Today, there is one subspecies of wild boar, common to India and Sri Lanka (*Sus scrofa cristatus* – the Indian wild boar), that can be found across Sri Lanka's climate and vegetation zones.

Body mass: *c.* 100-150 kg.

Feeding habits: In forests *Sus scrofa cristatus* consumes fallen fruits and nuts, as well as spending much time uncovering roots and tubers, especially those growing in swamps and in semi-dried up lake beds. *Sus scrofa* is omnivorous and has been seen feeding on carcasses, snakes, the eggs and young of ground-nesting birds, grubs, and insects. It feeds both by day and night.

Drinking habits: *Sus scrofa* drinks day and night at waterholes, swamps, pools in semi-dry river beds, rivers, and pools.

Other: *Sus scrofa cristatus* will make loud, discernible noises while feeding, however, it will scatter quickly when it spots predators, including humans.



Fig. 5.25. Tragulus meminna (Moschiola meminna) – *The Indian spotted chevrotain or mouse-deer (Source: Dupont, 1994).*

Tragulus meminna (*Moschiola meminna*) –Indian spotted chevrotain or mouse-deer

Range: *Tragulus meminna* is relatively plentiful throughout the forests and jungles of the lowlands and lower Hills of Sri Lanka's Wet and Dry Zones

Body mass: *c.* 3 kg (Zhao, 2015).

Feeding habits: This species feeds mainly upon grasses, herbaceous plants, and the leaves of low-growing bushes and seedlings, though will also favour fallen forest fruits and berries. *Tragulus meminna* is a shy, retiring, and mainly nocturnal animal that is rarely sighted.

Drinking habits: *Tragulus meminna* drinks during the night at open water sources.

Other: This ruminant is very small in stature, standing about 25 cm in height at the shoulder. It has been described as a moderately good climber of trees, taking refuge there when hunted by dogs. Human hunters generally avoid *Tragulus meminna* in Sri Lanka today.



Fig. 5.26. Viverricula indica – *Sri Lankan small civet cat (Source: Abad, 2013).*

Viverricula indica (mayori) – Sri Lankan small civet cat (subspecies).

Range: *Viverricula indica (mayori)* is commonly spotted in scrub, jungles, forests, and fern brakes throughout Sri Lanka in the Wet and Dry Zones.

Body mass: *c.* 2-4 kg (Shirley, 2009).

Feeding habits: *Viverricula indica (mayori)* lives mainly upon birds, small mammals (such as rodents, including squirrels), insects, grubs, frogs, and also on fruits and roots. It is more carnivorous than the palm-cats (*Paradoxurus* sp.). *Viverricula indica (mayori)* is primarily nocturnal in its feeding habits, though it has also been seen hunting during the day in dense forest.

Drinking habits: *Viverricula indica (mayori)* drinks from open water sources, mainly at night.

Other: Though *Viverricula indica (mayori)* can climb well, it very rarely does so, and is very rarely found in trees unless chased.

Archaeological human samples

All archaeological human enamel samples used in this study are shown in Catalogue Table A2. Jude Perera, Department of Archaeology, Government of Sri Lanka, and Jay Stock, Department of Biological Anthropology, University of Cambridge, confirmed all identifications (Perera, 2010; Perera *et al.,* 2011; Roberts *et al.,* 2015b). All available human teeth from the Terminal Pleistocene/Holocene layers at Balangoda Kuragala and Fa Hien-lena, and from Layer 6b(/7a) and 7c at Batadomba-lena were sampled. A number of different teeth have been sampled, each with its own period of formation (Hillson, 1996) (Catalogue Table A2). While it has been argued that teeth forming from birth will display an isotopic 'weaning effect' (Wright and Schwarcz, 1998) (Chapter 4), this has not been adequately demonstrated for $\delta^{18}O$, and for $\delta^{13}C$ will depend on the type of weaning foods introduced. Regardless of this, given the magnitude of difference expected in $\delta^{13}C$ between C_3 versus C_4 biomes and closed versus open environments, this will not effect the overall interpretation of forest reliance. As with the fauna, a single 'bulk' sample was taken for this study by drilling along the full length of the buccal surface of each sample.

Balangoda Kuragala provided a particularly rich sequence of human teeth ranging from specimens dating to *c.* 15-12,000 cal. years BP to the Iron Age *c.* 3,000 cal. years BP, while Batadomba-lena Layer 6b(/7a) yielded a large assemblage of human teeth dated to around the LGM. Single teeth from Layer 7c at Batadomba-lena (dated to *c.* 36-29,000 cal. years BP) and *c.* 12,000 cal. years BP at Fa Hien-lena are not desirable as sample sizes. However, the temporal importance of the former and the presence of the latter in the Wet Zone contemporaneous with some of the earlier Balangoda Kuragala specimens make them essential points of comparison. Some particularly large first,

second and third molar and incisor teeth from Fa Hien-lena, Balangoda Kuragala, and Batadomba-lena Layer 6b were chosen for intra-tooth analysis (Catalogue Table A2). As with the fauna, 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 of hominin teeth (Sponheimer *et al.,* 2006b; Lee-Thorp *et al.,* 2010), this methodology should provide preliminary insight into potential dietary and drinking variability throughout the period of formation (though intra- versus inter-annual variability will not be resolvable). All teeth were photographed, with images available from the author on request, and were then returned to the Department of Archaeology, Government of Sri Lanka.

5.3 – Enamel pre-treatment and diagenesis

Tooth enamel sample pre-treatment

Despite the high degree of fossil and organic preservation at the archaeological sites sampled, potential diagenetic changes in hydrologically mobile and acidic tropical environments must be considered prior to any isotopic analysis (Chapter 4 – Section 4.2). Commonly employed treatment methods generally include both an oxidising step to remove organics and a low pH step to remove non-lattice bound, secondary carbonates. However, both reaction times and the chemicals employed by researchers vary considerably, with limited consideration as to what this variability may do to stable carbon and oxygen isotope values of the sample (Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). Typically, fossil enamel studies rely on 1-3% bleach

(NaClO) or 30% hydrogen peroxide (H_2O_2) to remove organics and 0.1 or 1M acetic acid (sometimes buffered with calcium acetate) to remove exogenous carbonates. Nevertheless, there has been a growing desire to investigate how these frequently used reagents may alter *in vivo* isotope ratios (e.g. Sponheimer, 1999; Yoder and Barelink, 2010; Crowley and Wheatley, 2014; Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). While experiments investigating these effects have tended to focus on bone (Koch *et al.,* 1997; Garvie-Lok *et al.,* 2004), there is a growing literature relating to the impacts of pretreatment on enamel structure and $\delta^{13}C$ and $\delta^{18}O$ measurements. These isotopic effects may result from incomplete reactions, adsorption of reaction-produced secondary material onto crystalline surfaces, or partial dissolution and recrystallisation (Lee-Thorp and van der Merwe, 1991; Sponheimer, 1999; Lee-Thorp, 2000; Zazzo *et al.,* 2006; Crowley and Wheatley, 2014).

Isotopic fractionation during pretreatment has been associated with partial dissolution and re-precipitation of carbonate. Secondary minerals, such as brushite, have been shown to form during long-term exposure to non-buffered acid, even in modern treated enamel (Lee-Thorp and van der Merwe, 1991; Sponheimer, 1999), leading to lower $\delta^{13}C$ values and higher $\delta^{18}O$ values than for untreated enamel (Lee-Thorp and van der Merwe, 1991; Crowley and Wheatley, 2014). This is one reason why, in general, more recent enamel pretreatment methods prefer the use of a weaker (0.1M), or buffered, form of acetic acid, for shorter periods of time, as a method for removing secondary carbonates (Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). Similarly, NaClO, or common bleach, has regularly been used to remove organic materials from enamel and bone carbonate. However, exposure to NaClO for 24 hours has been shown to elevate $\delta^{13}C$ and $\delta^{18}O$ values in modern enamel, potentially as a result of the

production of bicarbonate from atmospheric CO_2 or the oxidation of organic matter (Zazzo *et al.,* 2006; Crowley and Wheatley, 2014). That said, other oxidising reagents, such as H_2O_2, have been shown to be less effective than NaClO at removing organic matter from a sample (Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016).

In this study the decision was taken to undertake the same pretreatment protocol for all samples, both fossil and modern. As a result, I opted to use NaClO as an effective oxidiser of organic components, likely to be particularly prevalent in the modern samples. Recent experimental work has demonstrated that sequential treatment using this oxidiser followed by a low pH step does not have as substantial an impact on enamel $\delta^{13}C$ and $\delta^{18}O$ values (Sponheimer and Lee-Thorp, 1999; Crowley and Wheatley, 2014; Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). In this thesis, 2ml of 1.5% NaClO was added to every sample for 60 minutes. This was followed by three rinses in purified H_2O and centrifuging before 2 ml 0.1M acetic acid was added to each sample for 10 minutes, followed by another three rinses in purified H_2O. All sample sizes were kept the same (8 mg) to keep an even surface area/volume ratio for the reagents to act upon (Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016). This method is the same as that used for a large number of African hominin samples that are likely to be useful datasets for comparison with that produced here (Sponheimer *et al.,* 2005; Lee-Thorp *et al.,* 2012) (Chapter 4 – Section 4.2). I monitored the impacts of pretreatment on the FTIR spectra of ten modern and ten fossil faunal samples (Catalogue Table A3).

FTIR diagenetic screening

The three polyatomic ions of interest for the infrared study of enamel apatite are phosphates (PO_4^{3-}), carbonates (CO_3^{2-}), and hydroxyl groups (OH^-). The observed absorbance bands during the FTIR analysis of enamel can be ascribed to the internal vibrations of these molecular groups (Farmer, 1974; LeGeros, 1991). These inter-atomic vibrations correspond to the stretching or bending of chemical bonds (Fig. 5.27) (see Table 5.5 for the interpretation of major infrared signals of modern tooth enamel). In this thesis I use the empirical indices from Sponheimer (1999), Sponheimer and Lee-Thorp (1999), and Roche *et al.* (2010) to characterise the crystal-chemical properties of enamel bioapatite (Table 5.6). The index PCI, related to crystallinity, is defined from the phosphate deformation bands (Farmer, 1974). This index is sensitive to the broadening of the absorption bands that increases with the number of crystal-chemical defects. The crystallinity of apatite increases when its crystals become better organised, characterised by thin phosphate bands. Other indices based on the carbonate stretching bands (API and BPI) account for the structural CO_3 content in apatite and its distribution among the A- and B- sites (BAI) (Sponheimer, 1999, Lee-Thorp and Sponheimer, 2003). The amount of water-organic fraction in enamel is assessed on the basis of the water-amide (H_2O-NH_2) band at 1650 cm^{-1} (see WAMPI in Table 5.8) (Roche *et al.,* 2010). Calcite was monitored for in all samples by checking for a peak at 711 cm^{-1}, that appears in calcite but not modern enamel. While the size and shape of powder particles can contribute to the width of absorption bands in certain FTIR methodologies, this is not the case with the Attenuated Total Reflectance (ATR) method used here (Thompson *et al.,* 2009).

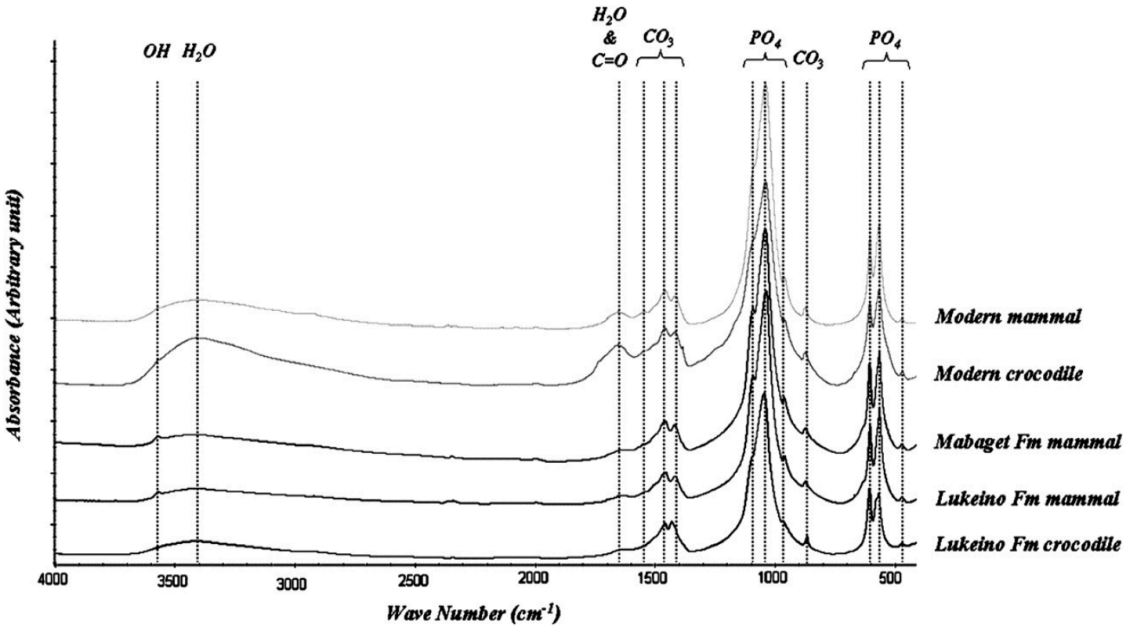


Figure 5.27. FTIR spectra of five fossilised faunal enamel sample analysed by Roche et al. *(2010). The chemical groups causing the absorption bands (as per Table 5.7) are indicated. From Roche* et al. *(2010: 1692 – Fig. 1).*

Table 5.5. Description of the FTIR spectrum of bioapatite (based on LeGeros, 1991; Michel et al., *1995; Sponheimer and Lee-Thorp, 1999; Trueman* et al., *2008; and Roche* et al., *2010) (adapted from Roche* et al. *2010).*

Approximate positions of apparent bands (cm^{-1})	**Approximate positions of decomposed bands (cm^{-1})**	**Chemical groups**	**Location of chemical groups**	**Chemical bonds and vibrational modes**
Dome between 2,400 and 3,800	3,570	Hydroxyl (OH)	A-site of apatite	O-H Stretching
	Between 3,300 and 3,430 (two bands at least)	Water (H_2O)	Adsorbed on apatite surface *and* A-site of apatite	O-H Stretching $\nu 1$ and $\nu 3$
1,650	Between 1,660 and 1,670	Amide (CO-NH)	Organic matrix	C=O Stretching $\nu 1$
	Between 1,620 and 1,640	Water (H_2O)	Adsorbed on apatite surface *and* A-site of apatite?	O-H Bending $\nu 2$
1,540	1,545	Carbonate (CO_3)	A-site of apatite	C-O Stretching $\nu 3$
1,450	1,500	Carbonate (CO_3)	Not determined	C-O Stretching $\nu 3$
	1,470	Carbonate (CO_3)	B-site of apatite *and* adsorbed on apatite surface?	C-O Stretching $\nu 3$
	1, 450	Carbonate (CO_3)	A-site of apatite *and* adsorbed on apatite surface?	C-O Stretching $\nu 3$
1,415	1,415	Carbonate (CO_3)	B-site of apatite	C-O Stretching $\nu 3$
1,090	1,090	Phosphate (PO_4)	B-site of apatite	P-O Stretching $\nu 3$
1,040	1,040	Phosphate (PO_4)	B-site of apatite	P-O Stretching $\nu 3$
960	960	Phosphate (PO_4)	B-site of apatite	P-O Stretching $\nu 3$
880	880	Carbonate (CO_3)	A-site of apatite	C-O Bending $\nu 2$
875	875	Carbonate	B-site of	C-O Bending

		(CO_3) Hydrogenophosphate?	apatite B-site of apatite	$\nu 2$ P-O Stretching $\nu 3$
	865	Carbonate (CO_3)	Not determined	C-O Bending $\nu 2$
605	630	Hydroxyl (OH)	A-site of apatite	O-H bending
	605	Phosphate (PO_4)	B-site of apatite	P-O Bending $\nu 4$
565	575	Phosphate (PO_4)	B-site of apatite	P-O Bending $\nu 4$
	565	Phosphate (PO_4)	B-site of apatite	P-O Bending $\nu 4$
470	470	Phosphate (PO_4)	B-site of apatite	P-O Bending $\nu 2$

Table 5.6. Description of the FTIR indices of enamel bioapatite. 'B' and 'V' denote the height of the bands and the valleys, respectively. Numbers in parentheses represent the approximate positions of the apparent bands (adapted from Roche et al. *2010).*

Indices	**Formulae**	**References**
PCI (Phosphate Crystallinity Index) other names: CI_{IR} (Crystallinity Index $_{InfraRed}$) IRSF (InfraRed Splitting Factor)	$\frac{B(605)+B(565)}{V(590)}$	Sponheimer and Lee-Thorp, 1999 Shemesh, 1990 Weiner and Bar-Yosef, 1990
BPI (B-carbonate on Phosphate Index)	$\frac{B(1415)}{B(605)}$	LeGeros, 1991
API (A-carbonate on Phosphate Index)	$\frac{B(1545)}{B(605)}$	Sponheimer and Lee-Thorp, 1999
BAI (relative amount of B- to A-site carbonate)	$\frac{B(1415)}{B1540}$	Sponheimer, 1999; Sponheimer and Lee-Thorp, 1999b
WAMPI (Water-Amide on Phosphate Index)	$\frac{B(1650)}{B(605)}$	Roche *et al.,* 2010

Fifteen fossil faunal samples each from Fa Hien-lena, Balangoda Kuragala, Bellan-bandi Palassa, 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 pretreatment in order to determine the potential for diagenetic structural and compositional modification of enamel during burial (Catalogue Table A4). The fossil spectra were compared to those of 11 'modern' primate and cervid samples, taken from a 1980s collection of Wolfgang Dittus and obtained during sampling trips between 2014-2015 (Catalogue Table A5), and 15 'modern' (late 19th and early 20th century) Sri Lankan human enamel samples from the Duckworth Collection, University of Cambridge, and the Department of Anatomy, University of Edinburgh (Catalogue Table A6). These groups act as a 'control' for non-buried, non-diagenetic specimens.

For all samples, powdered enamel was analysed between 400 and 4,000 cm-^{1} by FTIR-ATR (Agilent Technologies Cary 640 FTIR with GladiATR^{TM} from Pike Technologies). While the results are not directly comparable to those from the widely used 'transmission mode' KBr method and are less quantitative (Thompson *et al.,* 2009; Beasley *et al.,* 2014), the ATR mode allows fast and efficient screening of enamel samples. 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 *c.* 1035 cm-1 were taken into account. The reproducibilities of the indices BPI, API, BAI, and PCI are ±0.01, ±0.004, ±0.1 and ±0.1, respectively.

SEM diagenetic screening

Scanning Electron Microscopy (SEM) was applied to six fossil faunal samples in order to track the leaching of metallic ions across the dentine-enamel boundary at high spatial resolution (Catalogue Table A7). The samples chosen, unlike the majority of the assemblage, had a dark hue suggestive of manganese or iron inclusions. Samples were prepared using standard protocols at the Research Laboratory for Archaeology and the History of Art, University of Oxford. A total of 1 cm^3 was broken from each tooth to be analysed and an edge showing the dentine to enamel transition was ground flat by hand, using P120 silicon carbide abrasive grinding paper without a lubricant. The samples were then placed flat side down in 3 cm diameter plastic moulds. The moulds were filled to *c.* 2 cm in depth with Struers CaldoFix-2 heat curing epoxy with a vacuum pump used to increase penetration of the resin into the material. The moulds were then placed in the oven at 75°C for 2 hours and left to stand overnight. Following removal from the mould the samples were then ground and polished using decreasing grit-size silicon carbide abrasive papers: P180, P240, P320, and P600. Each sample was ground on each paper on a mechanical grinding wheel with running water for about 15 minutes at 100rpm with the quality of the surface checked repeatedly using a reflecting light microscope.

Samples were then polished using a diamond polishing system on a descending scale of abrasive size: 9 µm diamond paper, 3 µm diamond paper, 1 µm diamond paste in a short nap cloth, and 0.25 µm diamond paste in a short nap cloth, all using a water-based lubricant. Samples were polished on the 9 µm paper for 20 minutes at 100 rpm, on the 3 µm paper for 15 minutes at 100 rpm, on the 1 µm cloth for 5 minutes at 150 rpm, and on the 0.25 µm cloth for 5 minutes at 150 rpm. Samples were coated with a carbon coat,

mounted using conducting carbon putty in an aluminium sample-holder, and earthed with adhesive copper tape. They were then analysed in a Jeol JSM 5910 scanning electron microscope in backscatter electron mode with chemical analyses carried out using an Oxford Instruments INCA Energy 300 energy dispersive analysis (EDA) system. Samples were analysed at 20kV with a 'region' size of 300 x 300µm, and at a working distance of 9mm. Two 'regions' were analysed in the enamel and dentine of each sample, respectively, using Oxford Instruments' INCA software to obtain semi-quantitative chemical information on the presence and prevalence of different inclusions at a minimum detection limit of 0.1 weight percentage. X-ray spectra for the analyses were collected over an acquisition time of 50 seconds. The results of the chemical analyses were combined with high-resolution pictures to help track these changes across the tooth structure.

5.4 – Modern plant and primate study at the Polonnaruwa Nature Sanctuary

Stable isotope analysis of modern plants and primates in Sri Lanka was undertaken at the Polonnaruwa Nature Sanctuary and Archaeological Reserve in the north-western Dry Zone of Sri Lanka (07°56'N, 81°00'E) (Figure 5.28). This reserve is home to all three of Sri Lanka's main monkey species (Chapter 4 – Section 4.4) – the toque macaque (*Macaca sinica*), the gray langur (*Semnopithecus priam thersites*), and the purple-faced leaf monkey (*Trachypithecus vetulus*) (Hladik and Hladik, 1972). The reserve was primarily selected for analysis due to the wealth of information available regarding both the wet season and dry season diets of each primate species, including information on the proportion of fruits versus leaves in primate diets and the ecological feeding behaviours and social interactions of each species (Hladik and Hladik, 1972; Dittus, 1977a, 1977b, 1977c, 1985a, 1985b; Hladik, 1977, 1978) (Chapter 4 – Section

4.4). Although the reserve itself is located in the drier forest of Sri Lanka's Dry Zone, rather than the Wet Zone rainforests, this detail is crucial for pulling apart dietary and ecological impacts on stable carbon and oxygen isotope values of Sri Lankan primate enamel in a tropical forest setting.

As with the rest of the Dry Zone, most of the precipitation at Polonnaruwa is brought by convectional rains from October to November, prior to the onset of the Northwest Monsoon, which brings rainfall between December and February (Dittus, 1977a; 1985a). The dry season peaks between May and August (Chapter 2 – Section 2.2). Botanically, the Sanctuary is a peninsula of semi-evergreen forest bounded by water and cultivation, and continuous with extensive expanses of forest by only a narrow neck (Dittus, 1975, 1977a, 1985a). The Polonnaruwa forest can be classified, following Dittus (1977a, 1977b), into three main strata: an understory that consists of a non-woody herb and woody shrub layer up to 5 m in height, a subcanopy tree layer between 5m and 15 m, and a canopy land emergent layer between 15 and 30 m. Unlike the species-rich Wet Zone rainforest, the semi-evergreen subcanopies and canopies of the Dry Zone are dominated by a few species, including *Drypetes sepiara* (*Euphorbiaceae*) (*c.* 21% at Polonnaruwa), *Schleichera oleosa* and *Vitex pinnata* (Dittus, 1977a). Furthermore, Polonnaruwa's forest canopy becomes more open, and emergent defoliated, during the peak of the dry season, although most trees in the canopy layer retain their foliage all year round (Dittus, 1977a, 1985a). This feature, as well as measures of species diversity, has been argued to place the forest of the reserve as an intermediate type between tropical evergreen rainforest and seasonally defoliated forest (Walter, 1971; Dittus, 1977a, 1977b).

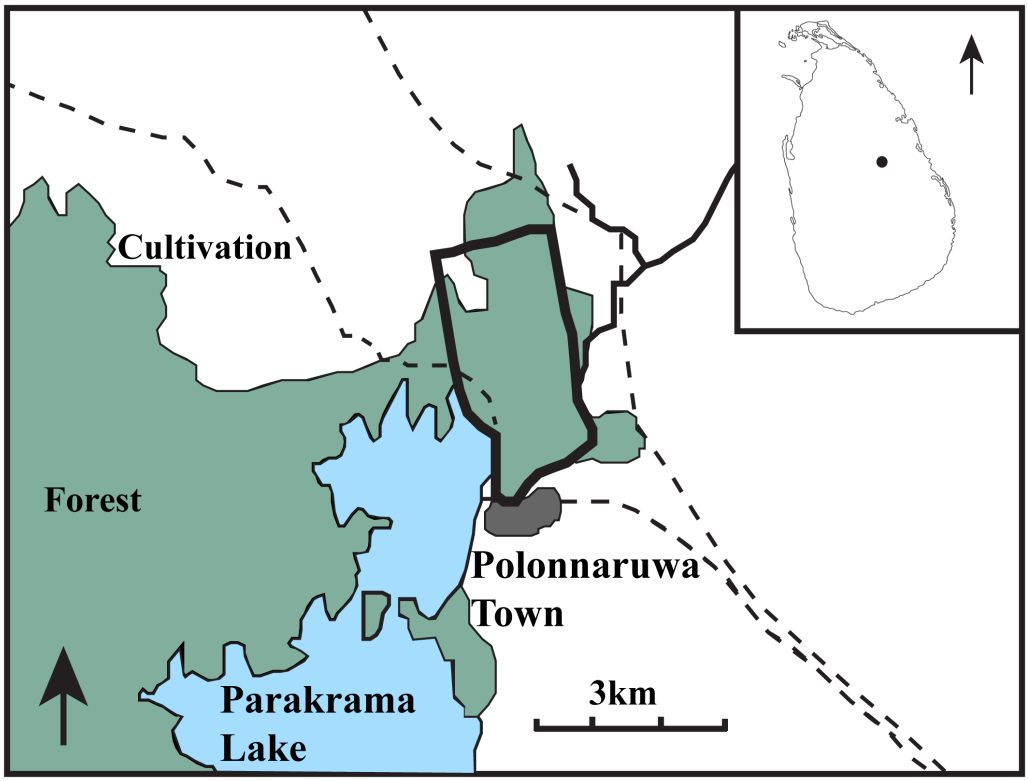


Figure 5.28. The Polonnaruwa Nature Sanctuary and Archaeological Reserve. The irrigation channel (solid) line delimits the southern portion of the study area. The main road and the railway lines are marked by dashed and dotted lines, respectively. Adapted from Dittus (1975).

Although slightly drier and more open, the forest of Polonnaruwa therefore shares similarities with the vegetation of the 'Intermediate' rainforest of Sri Lanka's Intermediate Zone (Erdelen, 1988). The fauna represented within the reserve is also characteristic of the Intermediate and Dry Zone forests of Sri Lanka. The ecological and social behaviours of all three of Sri Lanka's monkey species have been continuously studied at Polonnaruwa for over four decades (1968-2013) (Dittus, 2013). While numbers are becoming increasingly curtailed by the expansion of agriculture and the tourist industry, all three species remain relatively plentiful. For example, the toque macaque population was recorded at over 1,000 distributed between 33 social groups in 2013 (Dittus, 2013). Other mammals present included the spotted deer, the muntjac,

mouse-deer, golden jackal (*Canis aureus*), fishing cat (*Felis viverrina*), jungle cat (*Felis chaus*), mongooses, and many others. Larger mammals such as the elephant, leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), wild boar, and sambhur deer are absent, however. Domestic cattle and water buffalo (*Bubalus bubalis*) also graze in some open places within the study area. Various sources of accumulated water exist within the reserve, including water holes, a lake, irrigation channels that border part of the Reserve, ancient wells, and water accumulated in tree cavities. During the wet season macaques are able to gain enough water from their food, though during the dry season these obligate drinkers will trek, often over great distances, to the above-mentioned water sources depending on their social group and home range (Dittus, 1977b, 1977c). Continuous foliage throughout the year provides an important water source for the non-obligate drinking primate species, the grey crested langur and the purple-faced leaf monkey.

Primate dietary information

The wealth of ecological observations of primates at Polonnaurwa allows some picture of the diets of each species to be constructed. In the existing literature, the purple-faced leaf monkey is seen as reliant on the mature leaves of *Adina cordifolia*, *Schleichera oleosa*, *Drypetes sepiaria* and *Adina cordifolia* (Hladik, 1977) (*c.* 70%), though it will also eat leaves from *Walsura piscida* and *Garcinia spicata*, as well as, albeit less frequently, leaves and fruits from *Ficus* sp., *Syzigium cumini* and a series of other species (Hladik and Hladik, 1972). The grey crested langur, by contrast, has been shown to have a more varied diet, more evenly contributed to by *Adina cordifolia* (leaves), *Ficus benghalensis* (leaves and fruits), *Walsura piscidia* (leaves), *Drypetes sepiaria* (leaves and fruits), *Schleichera oleosa* (leaves and fruits), *Streblus asper* (leaves),

Cassia fistula (leaves and flowers), *Cassia roxburghii* (leaves, fruits and flowers), and *Mimosa pudica* (leaves and fruits), among others. Crucially, of these, the grey crested langur can consume *c.* 80-90% fruits or near 50% mature leaves while the purple-faced leaf monkey will usually eat *c.* 80% mature leaves (Hladik, 1977). Finally, the toque macaque at Polonnaruwa has been argued to generally consume around 77% fruits (including *Ficus benghalensis*, *Schleichera oleosa*, *Ficus amplissima*, and *Drypetes sepiaria*, *Ficus retusa*), 14% flowers from *Cassia fistula* and *Cassia roxburghii*, and a remainder of leaf shoots, shrub leaves, roots, tubers, invertebrates of various species (Hladik and Hladik, 1972; Dittus, 1974, 1977b, 1984, 1985a). While these data present some interesting distinctions, they are from at least three decades ago and do not provide taxonomic detail regarding known seasonal variation in the plant species and parts consumed (Hladik and Hladik, 1972; Hladik, 1977, 1978). As a result, for this study, observations of the three species of primate made by the team of researchers at the Polonnaruwa Nature Sanctuary and Archaeological Reserve were used to reconstruct their principal dietary components during the dry and wet season (Catalogue Tables A8 and A9, respectively).

Modern vegetation sampling

The full list of modern vegetation samples, including species information, growing conditions, and height in the canopy, can be found in Catalogue Tables A10 and A11. Two sampling seasons were undertaken, in August (2014) and February (2015), to capture the isotopic variation in primate plant foods towards the end of the dry season (Catalogue Table A10) and wet season (Catalogue Table A11), respectively. Funding and time limitations meant that it was not possible to sample *all* trees and plant parts known to be part of primate diets at Polonnaruwa, as these are often sporadically

available or variable between the primate social groups monitored. However, samples of all tree and plant species known to compose a *regular* part of the diet of each species of monkey during the period of sampling were taken. While this is not representative of the *whole* diet, the existing literature and ecological observations suggest that the resulting dataset is illustrative of the broader patterns of feeding behaviour in the three species.

Where available, at least three different trees/plants were sampled across different locations and environments to capture intra-species variation in $\delta^{13}C$ and $\delta^{18}O$ (Catalogue Tables A10 and A11). If important to primate diets, fruits, flowers, leaves, and leaf shoots were obtained from the same tree. Height in the canopy, according to the forest stratification described by Dittus (1977a) for the Reserve (i.e. low: 0-5 m, middle: 5-15 m, upper: 15-30 m), was recorded and, where possible, multiple samples of different plant parts were collected at different heights in the canopy within the same tree. The relative insolation of each sample when taken was also recorded qualitatively as: low (fully shaded), middle (part-shaded) or high (no shade). For each sample in Catalogue Tables A10 and A11, between eight and ten samples of each plant part, at each location within a plant/tree, have been combined in order to take into account natural $\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) variation. Plant parts were reached using a secure ladder system and a pair of leaf cutters. Samples were placed in brown, acid-free paper bags and dried thoroughly using an oven. They were then stored in larger bags with silica gel in order to avoid rotting.

Modern enamel samples

Wolfgang Dittus, head of the Polonnaruwa Primate Sanctuary and Polonnaruwa Primate Research, and an affiliate of the Smithsonian Institute of Primate Studies, also provided a collection of primate skulls, and two *Cervus* sp. mandibles, dated to the 1980s to this study (Catalogue Table A5). Although small, this sample set includes all of the different monkey species present at the Polonnaruwa Reserve. Furthermore, comparison of these teeth with the isotopic information gained from the 'known' plant diets of each species (above) may provide some understanding of the relative importance of plant species and part consumed to primate enamel $\delta^{13}C$ and $\delta^{18}O$ variation, as opposed to other environmental factors such as drinking behaviour, feeding height in the canopy, and preferences for shade or open habitats (Chapter 4 – Section 4.4). Third molars were selected from each primate skull.

Two additional modern samples of toque macaque and gray langur came from victims of traffic accidents in the Intermediate Zone courtesy of Nimal Perera. These were used as part of the 'Modern fauna' group in the pretreatment and diagenesis FTIR studies discussed above (Catalogue Table A3 and A4). These full mandibles also enabled $\delta^{13}C$ and $\delta^{18}O$ variation within the jaws of these primates to be tested (Catalogue Figures A1 and A2). $\delta^{13}C$ variation of around 2‰ (*Macaca sinica*) and 1‰ (*Semnopithecus priam thersites*) was found between teeth within the same jaw Catalogue Figures A1 and A2, respectively. This variation is primarily driven by lower $\delta^{13}C$ in the first molars in both cases, likely linked to the weaning effect (Wright and Schwarcz, 1998). This justifies the avoidance of sampling fossil primate first molars. No consistent effect was found for

$\delta^{18}O$ though variation was found to be between 1-2‰ for teeth within the same jaw (Catalogue Figures A1 and A2).

Finally, Oshan Wedage, Department of Archaeology, Government of Sri Lanka recovered one additional modern *Macaca sinica* mandible from the south coastal sands of Bundala, Sri Lanka, near archaeological Site 50 (Chapter 2 – Section 2.2). This and some of the other modern specimens provided comparative FTIR spectra for the pretreatment and diagenetic studies discussed above (Catalogue Table A4). Species identification of all of the modern faunal teeth was confirmed by Jude Perera using the same modern reference collections at the Department of Archaeology, Government of Sri Lanka, and the Postgraduate Institute for Archaeology, Colombo, that were used for the fossil fauna. Photographs were taken of each sample.

5.5 –Mass spectrometry and statistical analysis

Analysis of archaeological and modern enamel

All fossil and modern teeth or teeth fragments were cleaned using air-abrasion to remove any adhering external material. After drilling, the resulting enamel powder was then pre-treated using the consistent technique outlined above. The remaining residue was lysopholised in a freeze drier for a period of 2 hours. Samples were weighed out to approximately 0.200 mg using a Sartorius CP2 P microbalance. The resulting powder was transferred into glass vials with sealed lids. These vials were then placed in a heated tray maintained at 70°C. 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, using a two-point calibration, against the TS-Limestone international carbonate standard (NBS 19 ($\delta^{13}C$=2.0‰, SD not quoted; $\delta^{18}O$=-2.2‰ SD not quoted) – iaea.org), and calcium carbonate (MERCK ($\delta^{13}C$=-35.5‰; $\delta^{18}O$=-17.0‰)). The MERCK standard is a Suprapur $CaCO_3$ whose values were determined through repeated analysis, alongside certified international standards, at the University of Bradford (Andrew Gledhill, pers. comm.). Replicate analysis of in-house standards (OES) normalised to the International Standard NBS 19, suggests that machine measurement error is *c.* ± 0.1‰ for $\delta^{13}C$ and ± 0.2‰ for $\delta^{18}O$. All measurements are reported in 'permil' ‰ with respect to the standards of VPDB.

Analysis of modern vegetation

All dried vegetation samples were homogenised into dried bulk organic matter powder using a 6770 Freezer/Mill® (SPEX® SamplePrep) with liquid nitrogen immersion bath. The resulting powder was weighed out to 1 mg and *c.* 3 mg for carbon and nitrogen stable isotope analysis, respectively. Stable carbon and nitrogen isotopes were analysed by mass spectrometry using a Sercon Geo 2022 IRMS coupled to Sercon Europa EA-GSL running with continuous flow mode with helium carrier gas 80 mL/min at the Research Laboratory for Archaeology and the History of Art, University of Oxford. Carbon and nitrogen isotope values were compared, using a two-point calibration, against international sucrose (IAEA-CH-6 ($\delta^{13}C$=-10.4‰, SD=0.0) – iaea.org) and polyethylene (IAEA-CH-7 ($\delta^{13}C$=-32.2‰, SD=0.1) – iaea.org) standards for $\delta^{13}C$ measurements and nitrate (IAEA-N_2 ($\delta^{15}N$=20.3‰, SD=0.2) – iaea.org) and caffeine

(IAEA-600 ($\delta^{15}N$=1.0‰, SD=0.2) – iaea.org) standards for $\delta^{15}N$ measurements. Replicate analysis of an in-house alanine international standard ($\delta^{13}C$=-26.9‰, SD=0.1; $\delta^{15}N$=1.6‰, SD=0.2, Peter Ditchfield, pers. comm.) suggests that machine measurement error was *c.* ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$. All measurements are reported in δ 'permil' notation relative to the standards of VPDB and AIR, respectively.

Aliquots of powder from the same samples were also weighed out separately for the measurement of stable oxygen isotopes using a Sercon Geo 2022 IRMS coupled within a Sercon HTEA running at 1400°C over glassy carbon. In eco-physiological literature, plant $\delta^{18}O$ measurements usually come from extracted plant water or extracted cellulose, due to concerns regarding the complicated relationship between leaf water and organic molecules (Chapter 4 – Section 4.1) (Hill *et al.,* 1995; Barbour and Farquhar, 2000; Helliker and Ehleringer, 2002; Barbour, 2007). However, bulk organic matter $\delta^{18}O$ from leaves, fruits, and flowers was considered to be a more relevant measure of primate food $\delta^{18}O$ in this study, especially given different digestive physiologies and behaviours, and therefore different cellulose or water intake as a proportion of overall food and water $\delta^{18}O$, in the primate taxa studied. Significant evapotranspiration-linked distinctions relative to forest coverage, height in the canopy, and plant part noted should also outweigh variation in tissue $\delta^{18}O$ (Chapter 4 – Section 4.1). Oxygen isotope values were compared, using a two-point calibration, against the international standards EMA-P1 ($\delta^{18}O$=21.0‰, SD=0.7 – Elemental Microanalysis Ltd) and EMA-P2 ($\delta^{18}O$=26.9‰, SD-2.2 – Elemental Microanalysis Ltd). Replicate analysis of the EMA-P1 standard suggests that the machine precision was *c.* ± 0.2‰ for $\delta^{18}O$. The resulting measurements were reported in δ 'permil' notation relative to the standards of VSMOW.

Statistical analysis of archaeological samples

ANOVA tests followed by post-hoc Tukey HSD-corrected pair-wise comparisons were performed for each of the main FTIR indexes of enamel apatite (PCI, PO_4RF, BPI, API, and WAMPI – as per Roche *et al.,* 2010) 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. For those specimens used as part of the pretreatment study, paired T-tests for PCI, PO_4RF, BPI, API, and WAMPI were undertaken on samples prior to and after pre-treatment in order to monitor the impacts of the protocol.

ANOVA tests were also performed on faunal enamel $\delta^{13}C$ and $\delta^{18}O$ at each site to determine the influence of species and stratigraphic layer on isotopic variation. Where variance was found to be significant, this was combined with a post-hoc Tukey HSD-corrected pair-wise comparison to determine which taxa or stratigraphic layers were significantly different from each other in terms of $\delta^{13}C$ and $\delta^{18}O$. ANOVA tests and post-hoc Tukey HSD-corrected pair-wise comparisons were also repeated separately on $\delta^{13}C$ and $\delta^{18}O$ for each monkey species by layer, where sample sizes permitted, in order to study differences in primate responses to potential environmental changes through time.

The significance of $\delta^{13}C$ and $\delta^{18}O$ variation between Terminal Pleistocene and Holocene fauna by site (from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa, as well as the Late Pleistocene fauna of Batadomba-lena) was also determined using ANOVA comparative tests, followed by post-hoc Tukey HSD-corrected pair-wise comparison to determine which sites were significantly different from each other in

terms of $\delta^{13}C$ and $\delta^{18}O$ (Roberts *et al.,* 2015b). The relationship between faunal and human $\delta^{13}C$ and $\delta^{18}O$ at the sites of Balangoda Kuragala, Fa Hien-lena and Batadomba-lena was assessed using unpaired T-tests (as per Roberts *et al.,* 2015b).

All of the enamel $\delta^{13}C$ and $\delta^{18}O$ datasets being statistically analysed were tested for normality using the Shapiro-Wilk test and observation of their histogram distributions. Where datasets were found to be non-normal a Mann-Whitney U or Kruskal-Wallis test was applied in addition to the T-test or ANOVA comparative tests listed above. In all cases the Mann-Whitney U and Kruskal-Wallis tests support the patterns identified in the T-test and ANOVA results, respectively. I consequently only report the results of the T-test, ANOVA and, where relevant, post-hoc Tukey pair-wise HSD-corrected comparison tests in order to provide consistency across the datasets. These parametric tests are highly conservative and robust to violations of their assumptions.

Statistical analysis of modern plant samples

Principal Components Analysis was performed on modern vegetation sample $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$ values to determine whether $\delta^{13}C$, $\delta^{18}O$, or $\delta^{15}N$, or various combinations of these variables, best described variation in the data.

Linear models and corresponding ANOVA tests were developed to determine the significance of different categorical effects on plant $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$. The effects included were season of collection, species, plant part, insolation, and canopy height. Initially, the most complicated models were constructed, treating each effect separately and randomly, as well as having an interaction effect with all other effects. If a certain effect had no influence on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ it was removed (stepwise) from the

subsequent model until only significant effects remained. Post-hoc Tukey HSD pair-wise comparison tests were then performed on the effects included in the final ANOVA model in each case.

Finally, $\delta^{13}C$ and $\delta^{18}O$ measurements from plant species and parts listed as being important (i.e. numbered "1" and "1 and 2") to the diet of each monkey species in Catalogue Tables A8 and A9 were averaged for each plant species/part. ANOVA testing was performed to see if the modelled diets of each monkey species, based on Catalogue Tables A8 and A9, were significantly different in terms of $\delta^{13}C$ and $\delta^{18}O$.

As for the enamel samples, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ datasets for the modern plant data were all tested for normality using the Shapiro-Wilk test and observation of their histogram distributions. Where datasets were found to be non-normal a Kruskal-Wallis test was applied in addition to the ANOVA tests discussed above. In all cases the Kruskal-Wallis tests supported the patterns identified in the ANOVA results. I therefore only report the results of the ANOVA and, where relevant, post-hoc Tukey HSD-corrected pair-wise comparison, tests.

All statistical analyses were conducted using the free program R software.

Chapter 6 – Human stable isotope ecology during the Sri Lankan Microlithic tradition

This chapter presents the results of the FTIR, SEM, and stable carbon and oxygen isotope analyses of the human and faunal enamel samples studied. Results of the FTIR and SEM investigations of diagenesis and pretreatment are presented first. Stable carbon and oxygen isotope results from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa are then discussed sequentially, providing a stable isotope 'baseline' for the Sri Lankan Wet Zone, Intermediate Zone, and Dry Zone, respectively, for the Terminal Pleistocene/Holocene transition. Stable carbon and oxygen isotope results of humans and fauna from Batadomba-lena provide an earlier, Late Pleistocene record of human rainforest reliance during a time of potentially significant change in Sri Lanka's tropical forests before, during, and after the LGM (see Chapter 3 – Section 3.3).

6.1 – Results of FTIR and SEM studies

FTIR

Full results of the infrared indices (BPI, PCI, API, WAMPI and BAI) of samples subjected to FTIR analysis are shown in Catalogue Table B1. All of the fossil and modern enamel samples displayed classic enamel FTIR spectra (Figure 6.1), showing the absorbance bands associated with the structural oxyanions (PO_4^{3-}, CO_3^{2-}, OH^-) of apatite, molecular water (H_2O), and the amide function (C-N) of the organic matrix. No additional bands from secondary carbonate (e.g. calcite at 710cm^{-1} – Farmer, 1974) were observed in the spectra of the fossil samples. ANOVA testing indicated significant differences in BPI ($F(7,103)=6.36$, $p<0.05$) (Catalogue Tables B2 and B3), PCI ($F(7,103)=5.86$, $p<0.05$) (Catalogue Tables B4 and B5), API ($F(7,103)=50.02$, $p<0.05$)

(Catalogue Tables B6 and B7), WAMPI ($F(7,103)=19.34$, $p<0.05$) (Catalogue Tables B8 and B9), and BAI ($F(7,103)=8.77$, $p<0.05$) (Catalogue Tables B10-B11) between the sample groups. 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 ($p<0.05$) (Catalogue Table B3). The same is true of PCI, with the exception of the Bellan-bandi Palassa sample ($p<0.05$) (Catalogue Table B5). Fossil human enamel demonstrates increased PCI relative to the modern human group ($p<0.05$) (Catalogue Table B5), but no significant differences in terms of A-site carbonation ($p>0.05$) (Catalogue Table B7), B-site carbonation ($p>0.05$) (Catalogue Table B3), dehydration/organic decay (WAMPI) ($p>0.05$) (Catalogue Table B9), or B-site/A-site carbonation ratio (BAI) ($p>0.05$) relative to the same group (Catalogue Table B11).

Some significant crystal-chemical variations are present among the sample groups, however (Figure 6.2). Fossil mammalian enamel demonstrates A-site de-carbonation ($p<0.05$) (Catalogue Table B7), dehydration and organic decay (lower WAMPI) ($p<0.05$)) (Catalogue Table B9), and higher BAI (B-site to A-site ratio ($p<0.05$)) (Catalogue Table B11) relative to modern mammal samples. Lower API for fossil, relative to modern, fauna was also observed by Roche *et al.* (2010) and Sponheimer (1999). A loss of water organic content (as indicated by WAMPI) is expected over time-scales beyond the Holocene, particularly in tropical areas with limited organic preservation. As seen here, Roche *et al.* (2010) demonstrated that this parameter was correlated with API, arguably as a result of enamel bioapatite A-sites containing organic hydroxyl or water groups. Sponheimer (1999) noted an increase in the BAI of fossil fauna, relative to modern enamel, similar to that observed here. He suggests that either exogenous B-site carbonate incorporation, endogenous carbonate loss at the A-site, or

endogenous carbonate reorganisation could be responsible for this change (Sponheimer, 1999). 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.

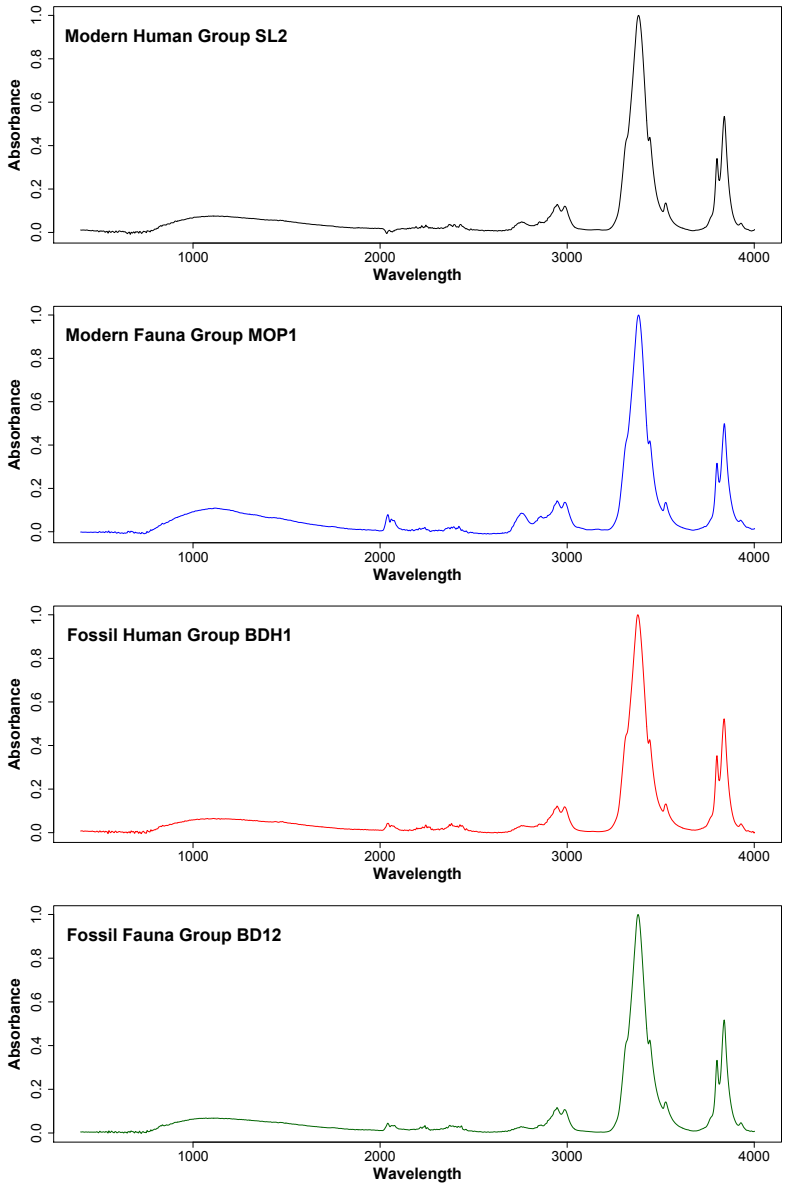


Figure 6.1. FTIR spectra for samples from the Modern Human Group (SL2), Modern Fauna Group (MOP1), Fossil Human Group (BDH1), and Fossil Fauna Group (BD12).

Comparison of the Late Pleistocene Batadomba-lena faunal groups with the Terminal Pleistocene-Holocene groups of Balangoda Kuragala, Fa Hien-lena, and Bellan-bandi Palassa fails to reveal a clear relationship between fossil sample age and API, BPI, WAMPI, PCI, or BAI (Catalogue Table B1) (Figure 6.2). This suggests that any crystallographic change occurs fairly early during fossilisation, consistent with existing research (Lee-Thorp, 1989; Sponheimer, 1999; Sponheimer and Lee-Thorp, 1999; Lee-Thorp, 2000). There is some apparent variation in the degree of change in carbonate environments between sites. For example, the Balangoda Kuragala, 1980s Batadomba-lena, and 2005 Batadomba-lena faunal groups demonstrate greater A-site decarbonation relative to the Fa Hien-lena and Bellan-bandi Palassa groups ($p<0.05$) (Catalogue Table B7). PCI (Catalogue Table B5) and BAI (Catalogue Table B11), by contrast, show little or no variation between fossil faunal groups, with the exception of PCI between the 1980s Batadomba-lena group and the Bellan-bandi Palassa and Fa Hien-lena groups ($p<0.05$) (Catalogue Table B5).

Assessment of the infrared indices of fossil human versus modern human groups in this study also suggests there may be some inter-species variation in enamel structure or response to burial environments. Unlike other mammalian fauna, fossil humans do not show a reduction in API ($p>0.05$) (Catalogue Table B7) and WAMPI ($p>0.05$) (Catalogue Table B9) relative to their modern counterparts, perhaps indicating less organic degradation. Fossil humans do show increased PCI ($p<0.05$) (Catalogue Table B5) relative to modern human samples (Figure 6.2). However, given that they still fall well within the range of the other fossil faunal PCI ranges (Catalogue Table B1), this may be a result of fossil human samples coming from a wide variety of temporal periods and geographical locations in Sri Lanka, compared to the modern group

collected during the late 19th and early 20th centuries, rather than any inherent structural change.

Overall, the fossil spectra are virtually indistinguishable from modern spectra to the naked eye (e.g. Figure 6.1). Calcitic intrusion can be excluded for all of the fossil faunal and human samples as no peak was present at 710cm^{-1} in any of the fossil spectra. As noted by Sponheimer (1999), 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). Subtle differences noted in faunal enamel apatite during fossilisation, as evidenced by increased BAI, decreased WAMPI, and decreased API, appear to be linked almost completely to the reduction in organic material within the apatite matrix through time, though some other form of A-site carbonate restructuring or loss cannot be ruled out. Similar changes have been noted elsewhere (Michel *et al.,* 1995; Sponheimer, 1999; Roche *et al.,* 2010) and are not considered to have major impacts on overall enamel apatite structure. Furthermore, although there appear to be some subtle differences in fossilisation processes between archaeological sites, a lack of any clear patterns in infrared indices within fossil groups by age suggests that any change occurs relatively rapidly upon burial and is generalisable across the time periods and sequences under study here. A similar situation exists for the fossil humans analysed in this study. Although they indicate slightly increased PCI relative to the modern human group, it is well within the range of other fossil faunal groups.

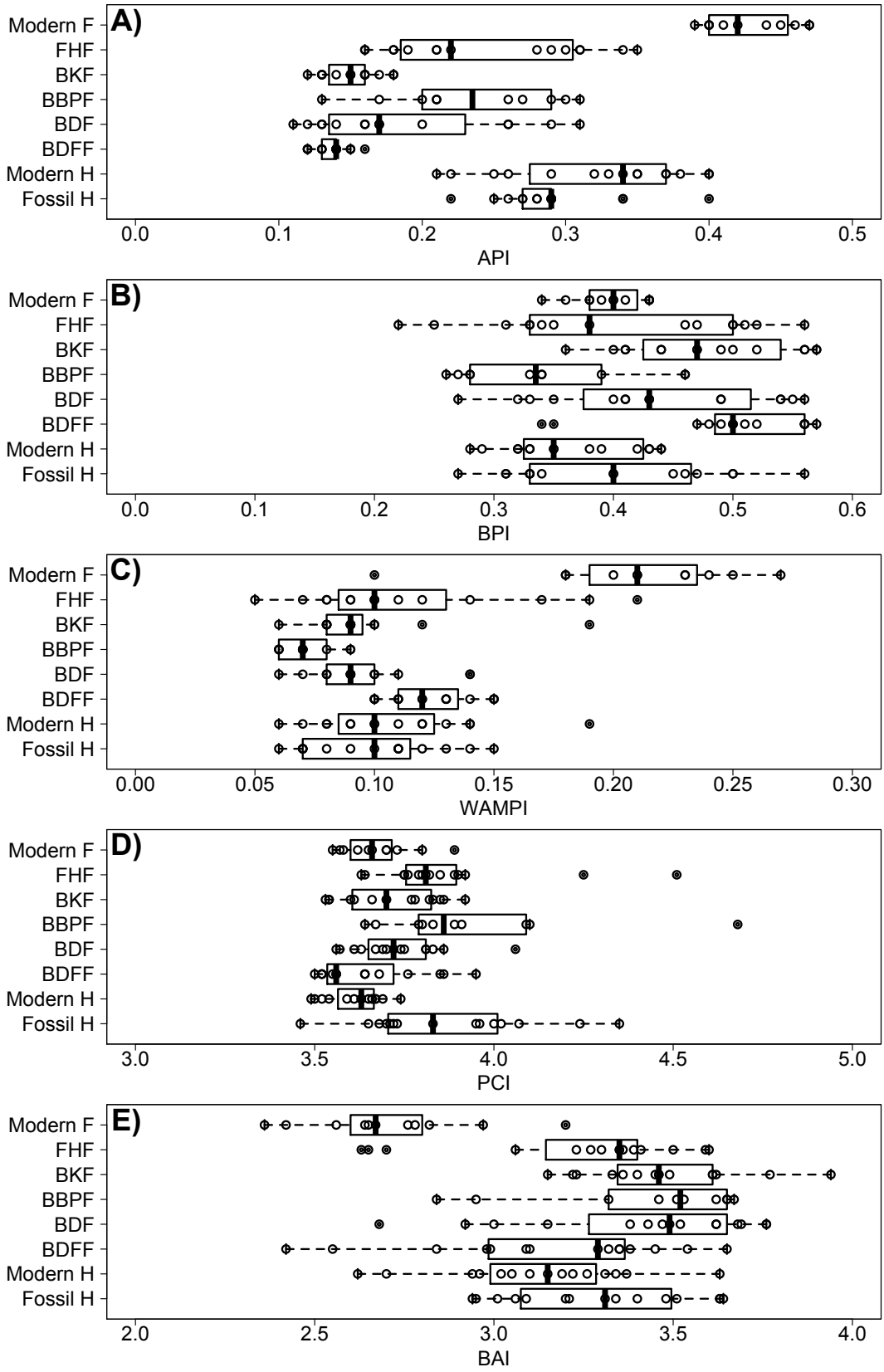


Figure 6.2. Box plots of the infrared indices (A=API, B=BPI, C=WAMPI, D=PCI, E=BAI) for the investigated groups (as per Roche et al., *2010).*

FTIR pretreatment study

Despite relatively similar FTIR spectra across the fossil and modern samples analysed, subtle, but significant, differences between fossil and modern faunal and human FTIR indices, between sites, between species, and within sites (Figure 6.2) suggest that different samples may have experienced fossilisation in slightly different ways. As suggested by Lee-Thorp and van der Merwe (1991) and Sponheimer (1999), *ipso facto* pretreatment is therefore necessary prior to isotopic analysis. This is particularly the case in the context of comparing modern and fossil samples, given the evidence for differences in organic degradation between the two groups discussed in Section 6.1. Figure 6.2 and Catalogue Table B12 indicates that the pretreatment protocol undertaken here effectively mimics the organic degradation seen in fossil samples for modern samples. Modern sample API ($t(2,9) = -8.21$, $p<0.05$) and WAMPI ($t(2,9) = -9.07$, $p<0.05$) decreases, and BAI increases ($t(2,9) = -8.19$, $p<0.05$), following pre-treatment. Smaller, but still significant shifts in modern sample PCI ($t(2,9) = 3.26$, $p<0.05$) following pretreatment could be associated with structural impacts linked to acid treatment (Sponheimer, 1999; Sponheimer and Lee-Thorp, 1999). However, no change was seen in BPI ($t(2,9) = -1.83$, $p>0.05$).

In contrast to the modern samples, fossil samples show no significant difference in API ($t(2,9) = 0.38$, $p>0.05$), WAMPI ($t(2,9) = 0.25$, $p>0.05$), and BAI ($t(2,9) = 1.21$, $p>0.05$) following pretreatment. This is unsurprising given that it was demonstrated above that organic degradation occurred in these samples during burial and further supports the statement that API, WAMPI, and BAI are primarily linked to this process within the assemblage under study here. As with the modern samples, pretreatment has also impacted PCI ($t(2,9) = 3.84$, $p<0.05$). It did not, however, have a significant impact on

fossil BPI ($t(2,9) = -1.83$, $p>0.05$). As can be seen in Figure 6.3 any impacts on modern and fossil PCI, caused by pretreatment, occur in the same direction (elevated following pretreatment). Overall, FTIR analyses indicate that the pretreatment protocol undertaken here effectively removes organic elements remaining in modern enamel samples (as per Snoeck and Pellegrini, 2015; Pellegrini and Snoeck, 2016), to leave their API, WAMPI and BAI indices comparable with fossil samples. Although the pretreatment protocol does appear to have some directional effect on modern and fossil enamel structure (PCI changes), this is consistent across the groups and suggests that, providing pretreatment is consistent, the resulting residue will be broadly comparable in terms of FTIR indices and $\delta^{13}C$ and $\delta^{18}O$ measurements.

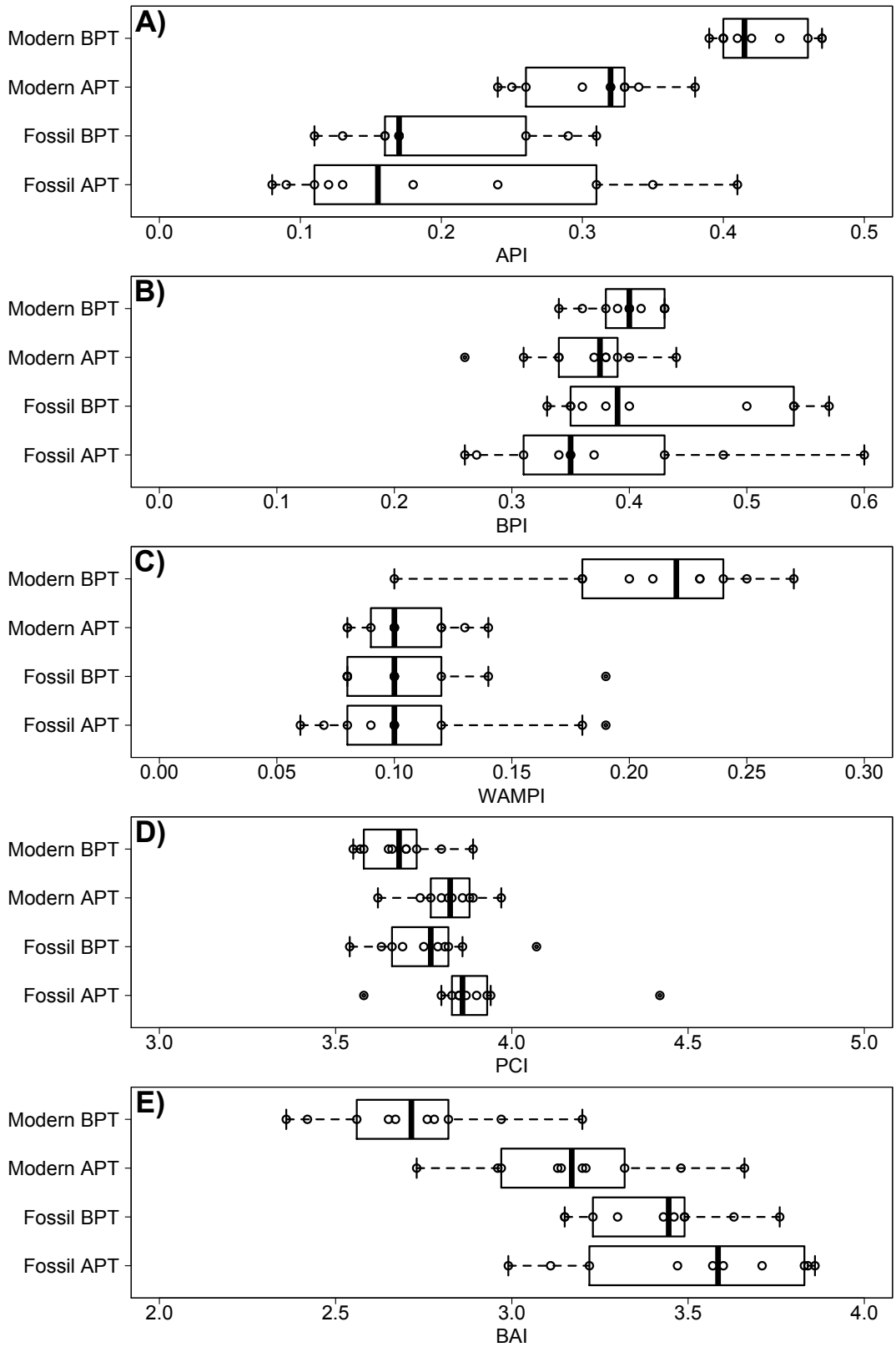


Figure 6.3. Box plots of the infrared indices (A=API, B=BPI, C=WAMPI, D=PCI, E=BAI) for groups studied in pretreatment screening (as per Roche et al., *2010).*

SEM study

The results of SEM energy dispersive analysis (EDA) indicate that the fossil tooth enamel sampled here is unlikely to be influenced by the inward leaching of metallic ions and the formation of metallic oxides (see Catalogue Figures B1-B30 for full results). For each sample, the enamel/dentine boundary is clearly demarcated in backscatter electron mode suggesting clearly different, but uniform, compositional and structural characteristics (Catalogue Figures B1, B6, B11, B16, B21, B26). In all cases, while small traces of metallic or mineral ions (including Mg, Mn, Fe, Al, and Zn) are occasionally found in the dentine, they are absent from the enamel. This result is consistent with previous studies that demonstrate that the influx or leaching of heavy elements, such as uranium and strontium, affects the outer surface of the enamel the least, leaching in through the dentine first and reaching the outer enamel surface last (Eggins *et al.,* 2003; Grün *et al.,* 2008; Benson *et al.,* 2013).

As a consequence, sampling the outer surface of the enamel for $\delta^{13}C$ and $\delta^{18}O$ measurements will provide results that are least influenced by metallic penetration, at the resolution of the EDA used here, even when a sample is visibly stained. This is encouraging for future isotopic analysis of enamel in a rainforest environment and suggests the viability of SEM-EDA analysis as a screening tool for suitable enamel samples. However, even had portions of Mn and Fe been found in the enamel it would not be possible to discern whether these are present in elemental or compound form using this analysis. Given that it is only by being part of the enamel structure, as carbonate or oxide compounds, that such ions could affect $\delta^{18}O$ measurements, while SEM-EDA can indicate which enamel samples have *not* experienced an influx of

metallic ions, SEM-EDA cannot differentiate between enamel samples with elemental metallic ions and those with metallic ions in the form of structural compounds.

6.2 – Human and faunal stable carbon and oxygen isotope measurements from the Wet, Intermediate, and Dry Zones of Sri Lanka across the Terminal Pleistocene/Holocene transition

Catalogue Tables B13 and B14 show the $\delta^{13}C$ and $\delta^{18}O$ measurements of each faunal and human sample, respectively, from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa. $\delta^{18}O$ measurements are all shown relative to the VPDB international standard following the conversion equation (Coplen *et al.,* 1983):

$$\delta^{18}O(VPDB) = 0.97001[\delta^{18}O(VSMOW)]-29.99$$

Standard deviations shown for each sample in Tables A25 and A26 are those resulting from the ten Gasbench measurements of a single sample. These values provide a measure of the consistency of the measurement in any single gas sample and the stability of the mass spectrometer. Low standard deviations throughout the analyses suggest that high precision was obtained during measurement.

$\delta^{13}C$ and $\delta^{18}O$ measurements on the two standards (NBS 19 and MERCK) used in two-point calibration of the tooth enamel samples obtained are shown in Catalogue Table B15 and B16, respectively. In both cases the measurements are within 0.1‰ of the certified values for these standards (NBS 19 – $\delta^{13}C$=1.9‰, SD=0.1; $\delta^{18}O$=-2.2, SD=0.2; n=44) (MERCK – $\delta^{13}C$=-35.4‰, SD=0.2; $\delta^{18}O$=-17.0, SD=0.2; n=44), with low standard deviations across the runs demonstrating consistency of measurement. Levels of isotopic variation within the tooth enamel samples themselves were analysed by taking five separate $\delta^{13}C$ and $\delta^{18}O$ measurements (and their standard deviations) from a

single bulk sample from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa (Tables 6.1-6.3). In all cases isotopic variation (standard deviation) within a sample is minimal (Fa Hien-lena: $\delta^{13}C$=0.1, $\delta^{18}O$=0.2, Balangoda Kuragala: $\delta^{13}C$=0.1, $\delta^{18}O$=0.1, Bellan-bandi Palassa: $\delta^{13}C$=0.1, $\delta^{18}O$=0.2).

Table 6.1. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample FH 54 from Fa-Hien lena.

Sample	**FH 54**	**FH 54A**	**FH 54B**	**FH 54C**	**FH 54D**	**Mean**	**Standard deviation**
$\delta^{13}C$ (‰) (VPDB)	-16.5	-16.3	-16.4	-16.5	-16.6	-16.5	0.1
$\delta^{18}O$ (‰) (VPDB)	-6.9	-6.7	-6.7	-7.0	-7.1	-6.9	0.2

Table 6.2. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample BK 129 from Balangoda Kuragala.

Sample	**BK 129**	**BK 129A**	**BK 129B**	**BK 129C**	**BK 129D**	**Mean**	**Standard deviation**
$\delta^{13}C$ (‰) (VPDB)	-12.4	-12.6	-12.7	-12.5	-12.4	-12.5	0.1
$\delta^{18}O$ (‰) (VPDB)	-5.1	-5.3	-5.2	-5.2	-5.0	-5.2	0.1

Table 6.3. $\delta^{13}C$ and $\delta^{18}O$ measurements of five subsamples subdivided from bulk sample BBP 5 from Bellan-bandi Palassa.

Sample	**BBP 5**	**BBP 5A**	**BBP 5B**	**BBP 5C**	**BBP 5D**	**Mean**	**Standard deviation**
$\delta^{13}C$ (‰) (VPDB)	-11.5	-11.5	-11.6	-11.4	-11.5	-11.5	0.1
$\delta^{18}O$ (‰) (VPDB)	-6.1	-6.4	-6.6	-6.3	-6.4	-6.4	0.2

Fa Hien-lena (Wet Zone)

$\delta^{13}C$ and $\delta^{18}O$ measurements of fauna and humans from Fa Hien-lena are shown in Catalogue Tables B13 and B14, and Figure 6.4.

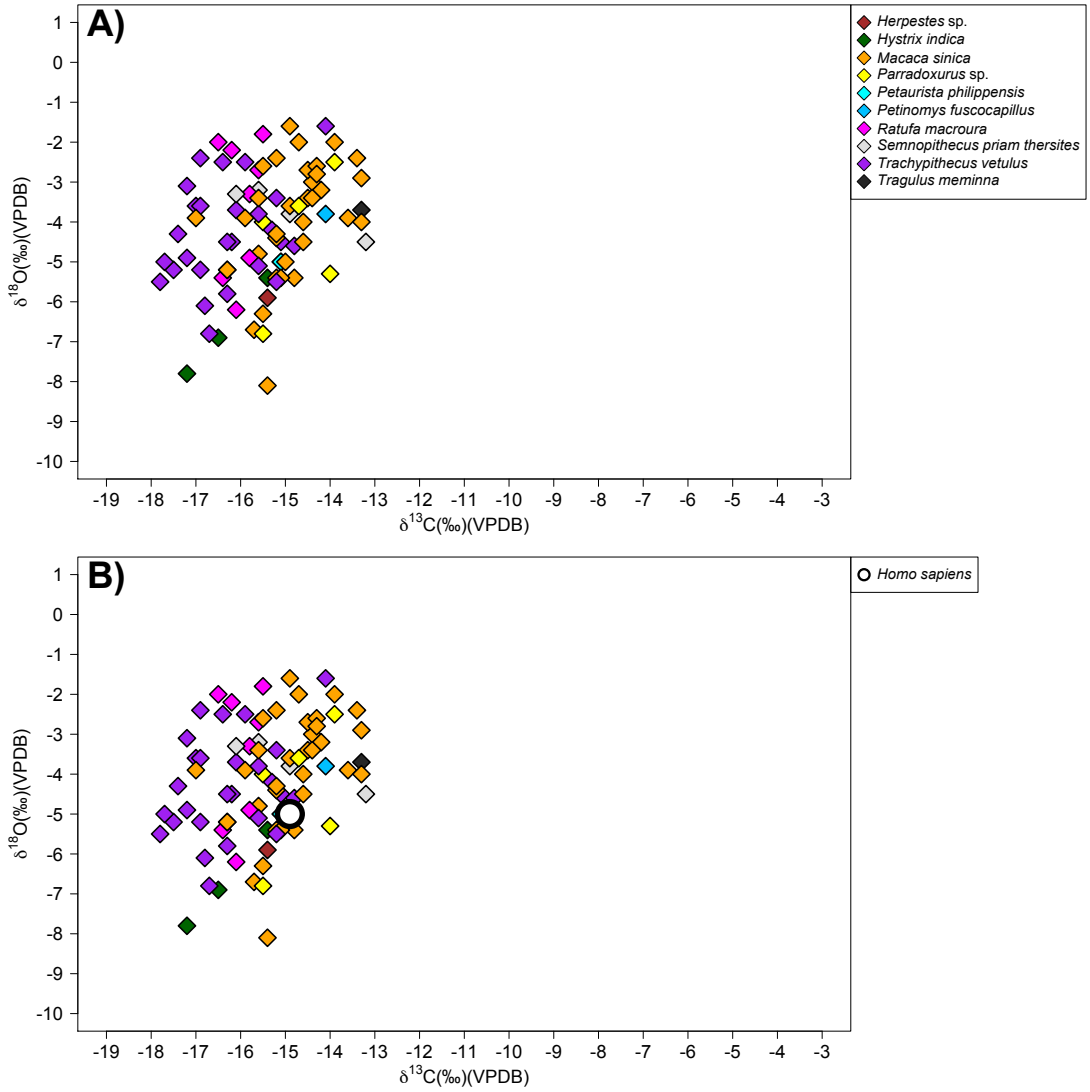


Figure 6.4. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna and B) fauna over-plotted by the human specimen from Layer 248 from Fa Hien-lena.

The fauna identified at Fa Hien-lena are all characteristic of the Wet Zone rainforest of Sri Lanka today (Catalogue Table A1). The $\delta^{13}C$ range of the measured samples (-17.8 to -13.2‰) supports this and, when compared to published modern faunal data and

taking into account the fossil fuel effect (Cerling *et al.,* 2004; Levin *et al.,* 2008) (Chapter 4 – Sections 4.1 and 4.2), is generally indicative of closed-canopy forest conditions with minor elements of more open forest. The mean $\delta^{13}C$ values of the *Trachypithecus vetulus* (-16.3 ± 0.9‰), *Hystrix indica* (-16.4 ± 0.7‰), and *Ratufa macroura* (-16.0 ±0.3‰) samples, corroborate their known preference for dense forest habitats (Chapter 5 – Section 5.2). Similarly, fauna with slightly higher mean $\delta^{13}C$ values, including *Macaca sinica* (-14.9 ± 0.8‰), *Paradoxurus* sp. (-14.7 ± 0.8‰), *Tragulus meminna*, and the two flying squirrel individuals, are known to seek out forest clearings and rocky outcrops where open water is available. The presence of *Semnopithecus priam thersites* at Fa Hien-lena, which is absent from Sri Lanka's rainforests today, also potentially implies the existence of patches of more open forest in this part of the Wet Zone in the past. ANOVA in $\delta^{13}C$ by layer and species, followed by post-hoc Tukey pair-wise comparison, suggests that species does impact $\delta^{13}C$, but only draws out *Trachypithecus vetulus* as being distinct from *Macaca sinica* and *Paradoxurus* sp. ($F(9,66)=6.191$, $p<0.05$) (Catalogue Tables B17 and B18).

There is a large spread of $\delta^{18}O$ across the fauna at the site (-8.1 to -1.6‰). In some cases this may be the result of varied drinking preferences and/or the impacts of evaporative stress. For example, *Hystrix indica* (-6.3 ± 1.2‰) has values towards the lower end of the range that is unsurprising given it drinks at night when conditions are least evaporative. However, other nocturnal feeders and drinkers, including *Paradoxurus* sp., *Petaurista philippensis*, and *Petinomys fuscocapillus*, occupy the middle of the range, perhaps indicating that lower $\delta^{18}O$ in *Hystrix indica* is related to dietary focus on underground plants, not subject to evaporative ^{18}O-enrichment, rather than nocturnal foraging *per se*. In general, while there is a large range in faunal $\delta^{18}O$ at

Fa Hien-lena, it is not explicable on the basis of species distinctions, as confirmed by an ANOVA test of variance and post-hoc Tukey pair-wise comparison ($F(9,66)=1.237$, $p>0.05$) (Catalogue Tables B19 and B20).

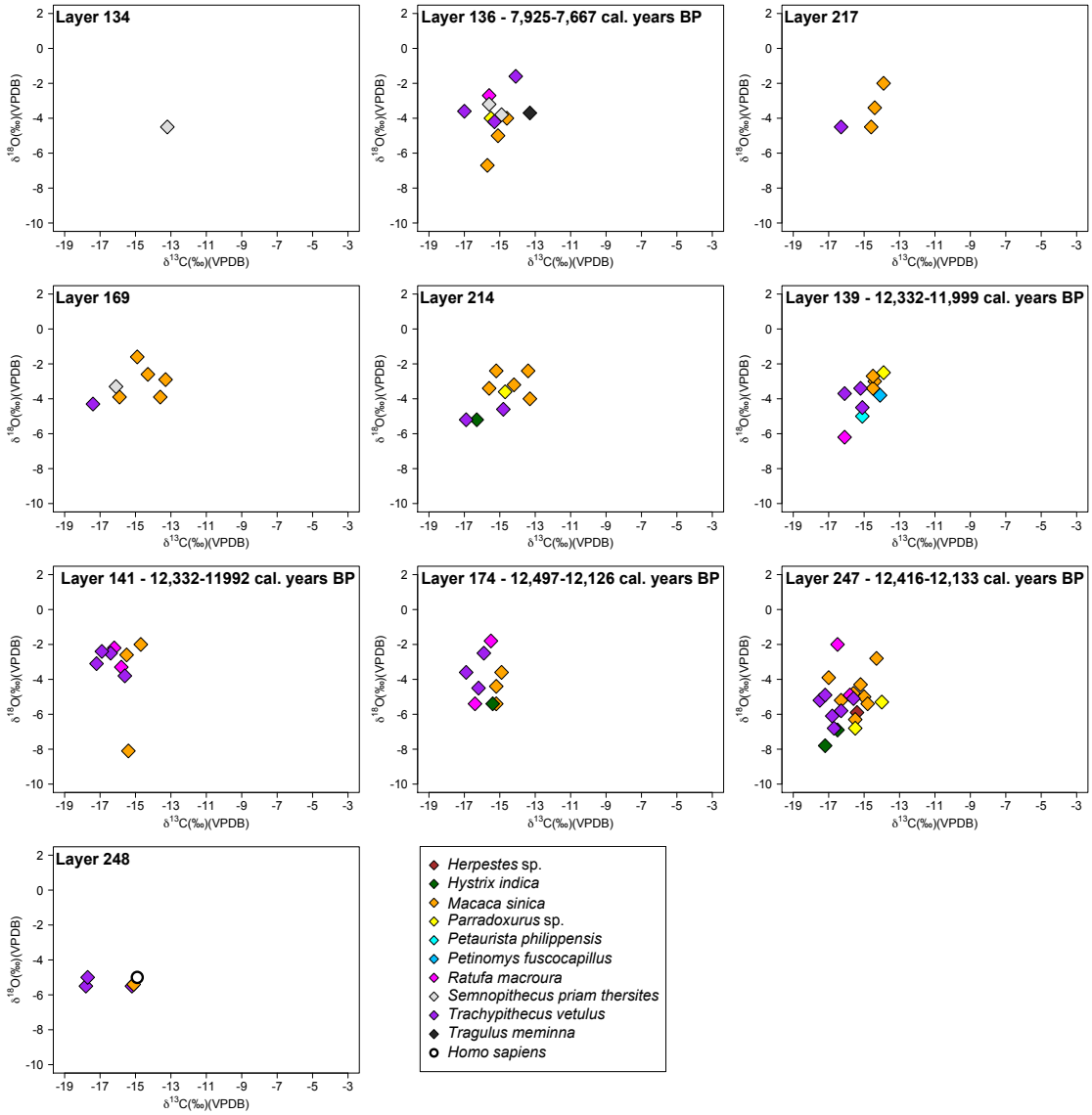


Figure 6.5. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Fa Hien-lena plotted by stratigraphic layer. Available radiocarbon dates from Table 5.1 are shown.

Faunal $\delta^{13}C$ and $\delta^{18}O$ at Fa Hien-lena can also be viewed on a layer by layer basis in order to examine to what extent wide ranges in faunal $\delta^{13}C$ and $\delta^{18}O$ at the site are a product of changing climatic and environmental conditions through time (Figure 6.2). Some ecological differences do become more apparent in this schematic. For example, *Petaurista philippensis* and *Petinomys fuscocapillus* fall towards the lowest end of the $\delta^{18}O$ range in the layer (Layer 139) in which they are found, in support of their known ecological preference for nocturnal drinking. Similarly, in each layer where they are present together, *Macaca sinica* almost always presents higher $\delta^{13}C$ than *Trachypithecus vetulus*, suggesting dietary or ecological distinctions (Chapter 4). That said, the period of time represented by the majority of the Fa Hien-lena layers (*c.* 12,497-11,999 cal. years BP) is minute by archaeological standards.

Where there is a distinct chronological shift, namely between Layers 134 and 136 in the Holocene and the other stratigraphic layers of the Terminal Pleistocene, there is no obvious change in $\delta^{13}C$ and $\delta^{18}O$ ranges (Figure 6.5; Figure 6.6). ANOVA testing indicates that there are greater $\delta^{13}C$ differences between layers than within them (Catalogue Tables B17 and B18), with a post-hoc Tukey pair-wise comparison suggesting that Layers 248 and 247 are distinct from Layer 139 and 134 ($F(9,66)=4.620$, $p<0.05$). Figure 6.6 suggests that there is some $\delta^{18}O$ variation between layers. An ANOVA test confirms this with post-hoc Tukey pair-wise comparison finding Layer 247 to be distinct from Layers 169 and 141 in terms of $\delta^{18}O$ ($F(9,66)=3.429$, $p<0.05$) (Catalogue Tables B19 and B20). Together, lower $\delta^{13}C$ and $\delta^{18}O$ at the start of the Fa Hien-lena sequence may be indicative of slightly more humid, and denser forest, conditions at this time.

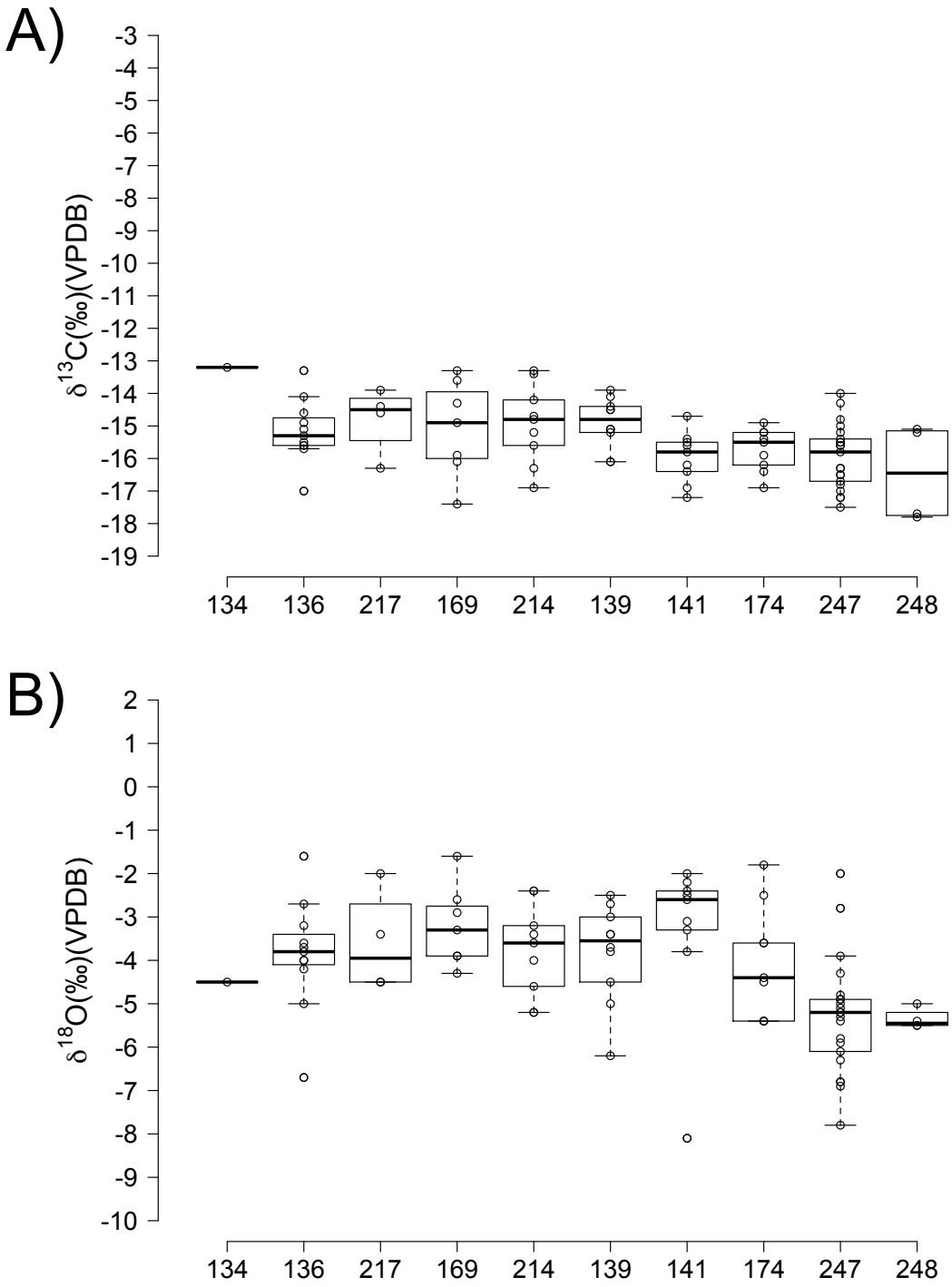


Figure 6.6. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Fa Hien-lena by stratigraphic layer.

Overall, stable carbon and oxygen isotope evidence from the Fa Hien-lena fauna suggests that humans inhabiting the cave were utilising closed canopy Wet Zone rainforest environments. This picture is supported by the one direct measurement of human enamel available at Fa Hien-lena from Layer 248 ($\delta^{13}C$ = -14.9‰, $\delta^{18}O$= -5.0‰) (Figure 6.4-6.5). $\delta^{13}C$ and $\delta^{18}O$ of this individual sits between the closed canopy dwellers and the slightly more open forest feeders and drinkers at the site. When compared to existing modern and fossil primate datasets (Nelson 2003, 2014; Cerling *et al.,* 2004; Bocherens *et al.,* 2015) (Chapter 4 – Section 4.1), accounting for the fossil fuel effect, the $\delta^{13}C$ values of this individual clearly indicate that closed canopy resources dominated this individual's diet. While any difference would be practically meaningless with a sample size of one, T-tests confirm that there is no significant difference between this human and the fauna of Fa Hien-lena in either $\delta^{13}C$ ($df=84$, $t=-0.499$, $p>0.05$) or $\delta^{18}O$ ($df=84$, $t=0.565$, $p>0.05$). Sequential analysis of this human tooth further indicates that the diet of this individual changed little throughout the period of enamel formation and certainly did not deviate from a reliance on forest resources (Figure 6.7) (Catalogue Table B21). $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna throughout the Fa Hien-lena sequence suggest that this forest environment was relatively stable for human foraging, even across the Terminal Pleistocene/Holocene transition that, elsewhere in the tropics, has often been associated with significant palaeoenvironmental change in forest extent and structure (White *et al.,* 2004; Mayle *et al.,* 2005; Bayon *et al.,* 2012).

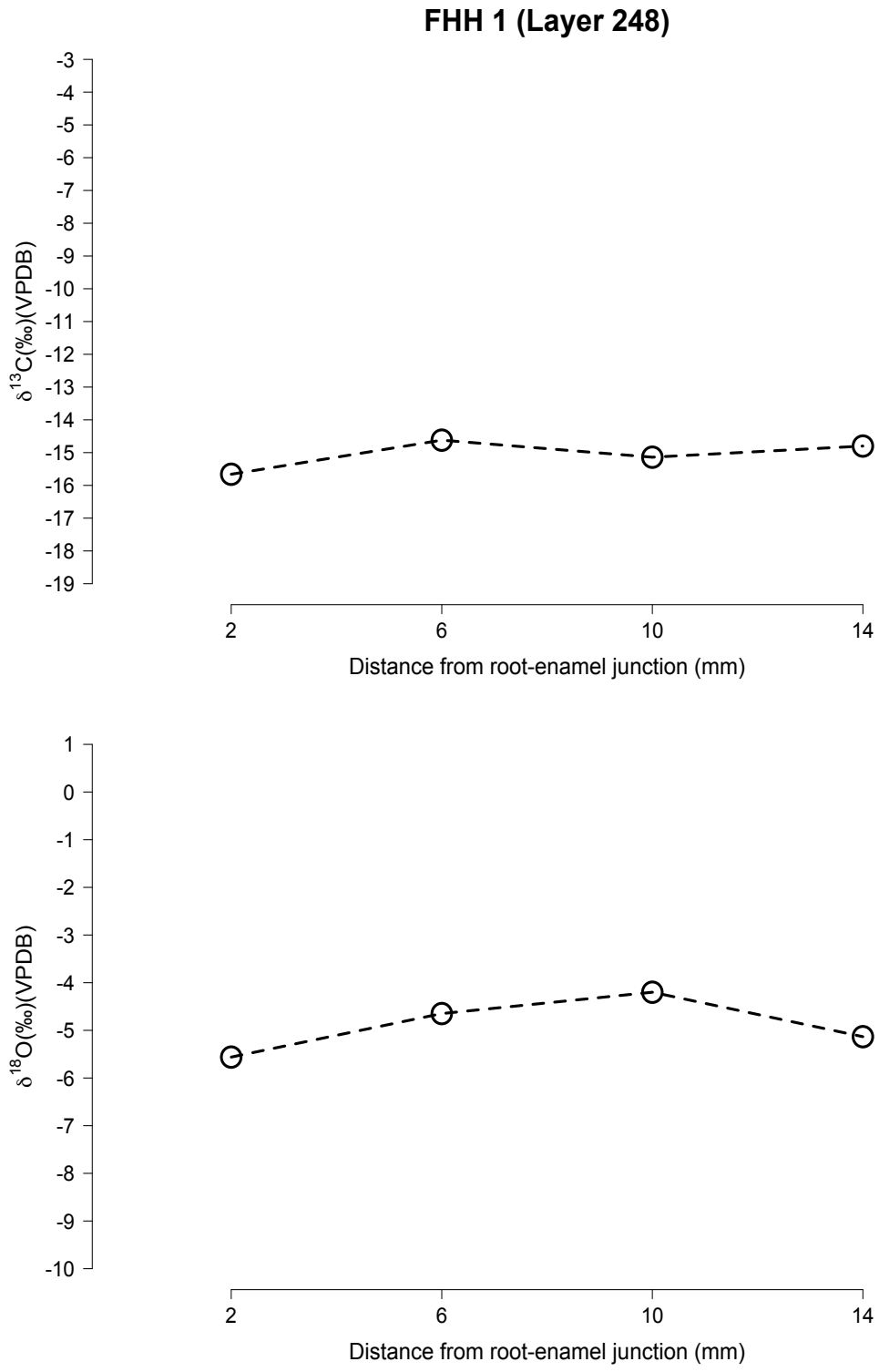


Figure 6.7. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human sample FHH 1 (Layer 248) from Fa Hien-lena.

Balangoda Kuragala (IZ)

$\delta^{13}C$ and $\delta^{18}O$ measurements of fauna and humans from Balangoda Kuragala are shown in Catalogue Tables B13 and B14, and Figure 6.8.

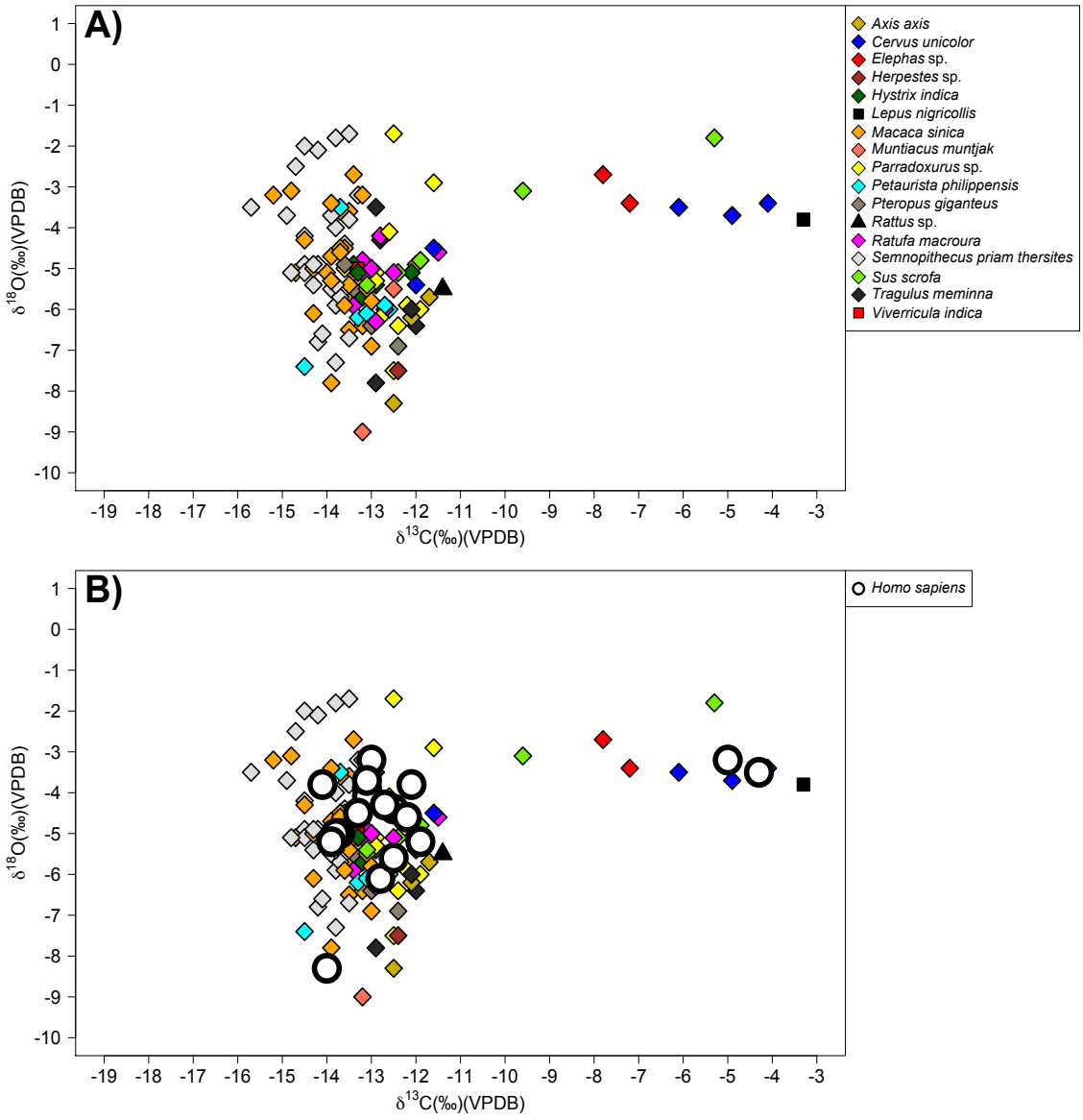


Figure 6.8. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna and B) fauna over-plotted by human samples from Balangoda Kuragala.

The fauna identified at Balangoda Kuragala is broadly characteristic of a range of habitats from closed forest to more open grassland and shrubland (Catalogue Table A1)

(Chapter 5 – Section 5.2). This habitat variability is supported by the $\delta^{13}C$ range of the measured faunal samples (-15.7 to -3.3‰) (Figure 6.8). Based on existing modern faunal datasets (Cerling and Harris, 1999; Cerling *et al.,* 2004; Sponeimer *et al.,* 2006a; Levin *et al.,* 2008), when correcting for the fossil fuel effect, the lowest end of the Balangoda Kuragala faunal range, with $\delta^{13}C$ values *c.* -15.7 to -13.0‰ and dominated by primate taxa, is indicative of the influence of the canopy effect and closed forest conditions. Fauna from around -12.0 to -11.0‰ either represent dietary reliance on more open forest conditions, akin to that of the modern Intermediate Zone rainforest today, or the use of a mosaic of closed and open C_3 environments. Values from -10.0 to -3.0‰ likely represent variable contributions of C_4 plants, from open tropical grasslands, to animal diets and the resources consumed by fauna at the highest end of the $\delta^{13}C$ range show no indication of the "canopy effect". The large spread of $\delta^{18}O$ at Balangoda Kuragala (-9.0 to -1.7‰) supports this dietary variability, with fauna consuming C_4 foodstuffs as parts of their diet having $\delta^{18}O$ towards the higher end of the site range, perhaps as a result of feeding and drinking in more open settings.

$\delta^{13}C$ values of *c.* -12.0 to -11.0‰ would not necessarily be out of place in a mixed forest/woodland/'savannah' C_3 environment in modern Africa based on modern faunal research (Sponheimer *et al.,* 2006a; Levin *et al.,* 2008). However, on the basis of the ecological preferences of the identified Balangoda Kuragala species with $\delta^{13}C$ values between -15.7 and -11.0‰ (Chapter 5 – Section 5.2) it is highly probable that here they are representative of the more open 'Intermediate' rainforest observed in Sri Lanka today. The taxa with values between -10.0 and -3.0‰, by contrast, solely include *Elephas* sp., *Cervus unicolor*, *Sus scrofa*, and *Lepus nigricollis* that are known to prefer grazing or feeding in more open settings, despite references to the Sri Lankan *Elephas*

sp. as a 'forest' elephant (Chapter 5 – Section 5.2). While *Cervus unicolor* and *Sus 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 in modern Sri Lanka. The statistical validity of this ecological distinction was 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 for both $\delta^{13}C$ and $\delta^{18}O$. This analysis correctly predicted group membership for all 120 individuals with 100% accuracy after Jackknifing (Catalogue Table B22). However, it should be borne in mind that such an analysis is biased by the categories placed into the model.

Sequential analysis was also performed on the two *Elephas* sp. samples analysed at Balangoda Kuragala (Figure 6.9), as well as two *Sus scrofa* samples (Figure 6.10) and three *Cervus unicolor* samples, all from the 'Open' group, to test whether there was any variation in diet or water source during enamel formation (Figure 6.11) (Catalogue Tables B23-B29). *Elephas* sp. cheek teeth (i.e. premolars and molars) consist of thick, enamel-covered plates that grow from the occlusal surface towards the cervical margin, making the base the youngest part. All length measurements in this study begin at the cervical margin (after Uno *et al.,* 2013). Due to the lengthy period of elephant enamel maturation the resulting sequences will demonstrate considerable averaging at each point (Kohn, 2004; Uno *et al.,* 2013). However, given that the aim here was to analyse *whether* there was significant variation within the period of formation rather than *when*, this is not of concern.

Elephas sp. sample BK 144 demonstrates relatively consistent $\delta^{13}C$ and $\delta^{18}O$ signals throughout the period of enamel formation. Sample BK 130, on the other hand, demonstrates considerable variation in both diet and water source (Figure 6.9). The *Sus scrofa* specimens have relatively stable $\delta^{13}C$ signatures (Figure 6.10). Simultaneous decline in $\delta^{13}C$ and $\delta^{18}O$ for sample BK 97 suggest that this individual may have included 'forest' components in its diet and is consistent with the assertion that evaporative ^{18}O-enrichment of open water sources is lower within the forest settings. Finally, two *Cervus unicolor* individuals demonstrate relatively variable $\delta^{13}C$ sequences, though they never move into the 'Intermediate' forest group (Figure 6.11). By contrast the 'Intermediate' forest *Cervus unicolor* demonstrates a more stable $\delta^{13}C$ signal. Overall, the sequential enamel data indicate dietary variation within the 'open' group, though at no stage do these values cross into what has been defined here as an 'Intermediate' rainforest range.

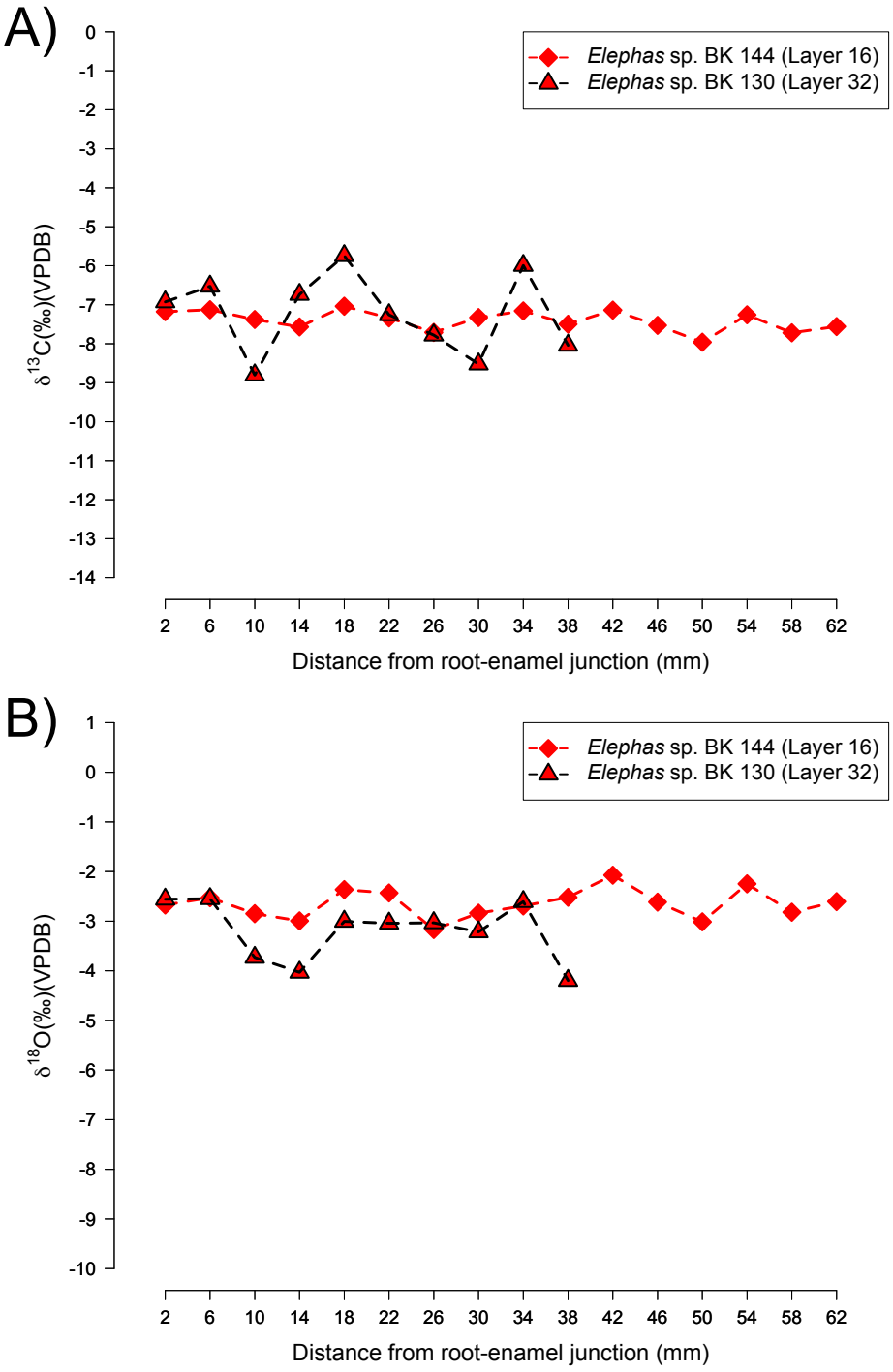


Figure 6.9. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of Elephas *sp. samples BK 144 (Layer 16) and BK 130 (Layer 32) from Balangoda Kuragala.*

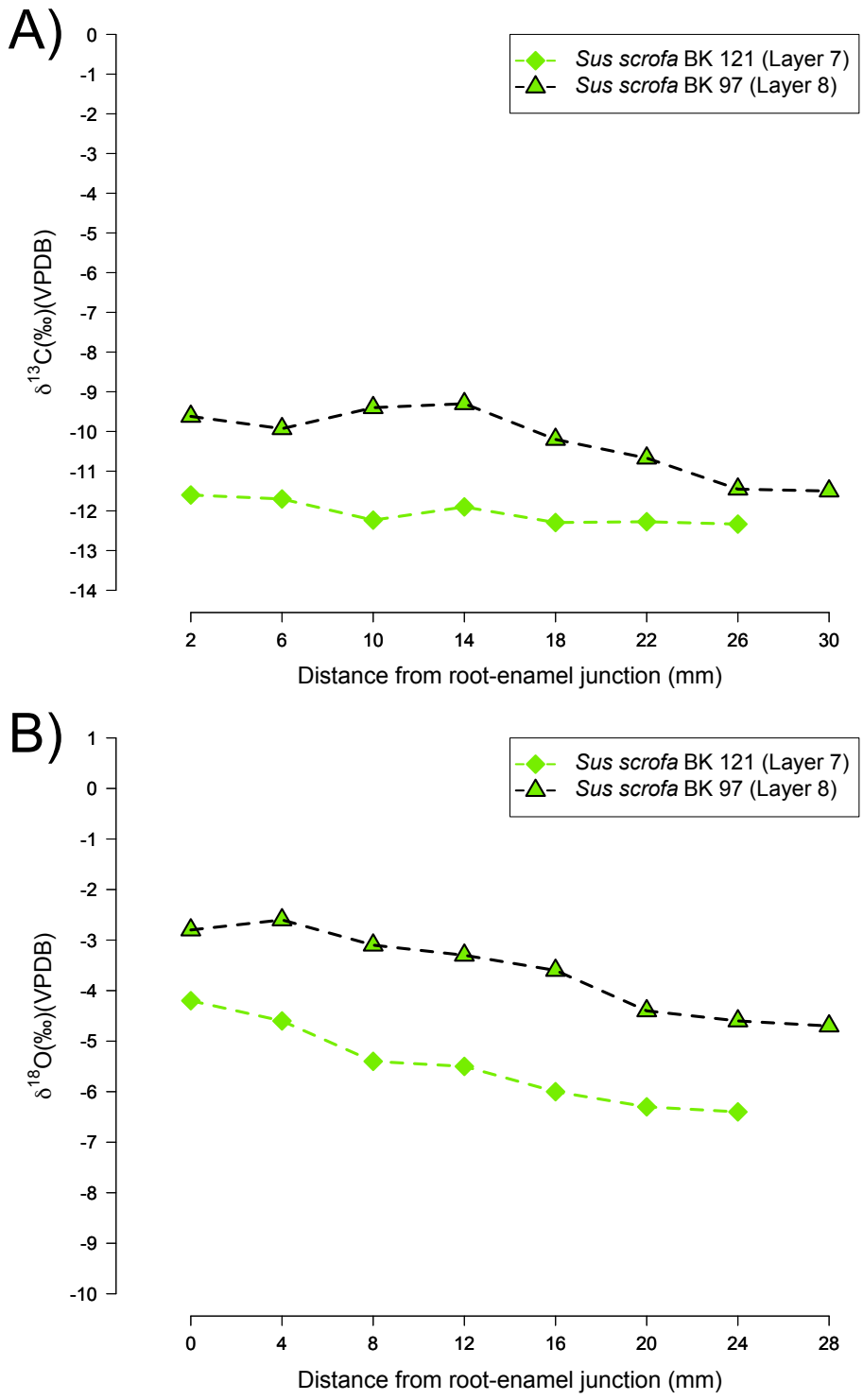


Figure 6.10. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of Sus scrofa *samples BK 121 (Layer 7) and BK 97 (Layer 8) from Balangoda Kuragala.*

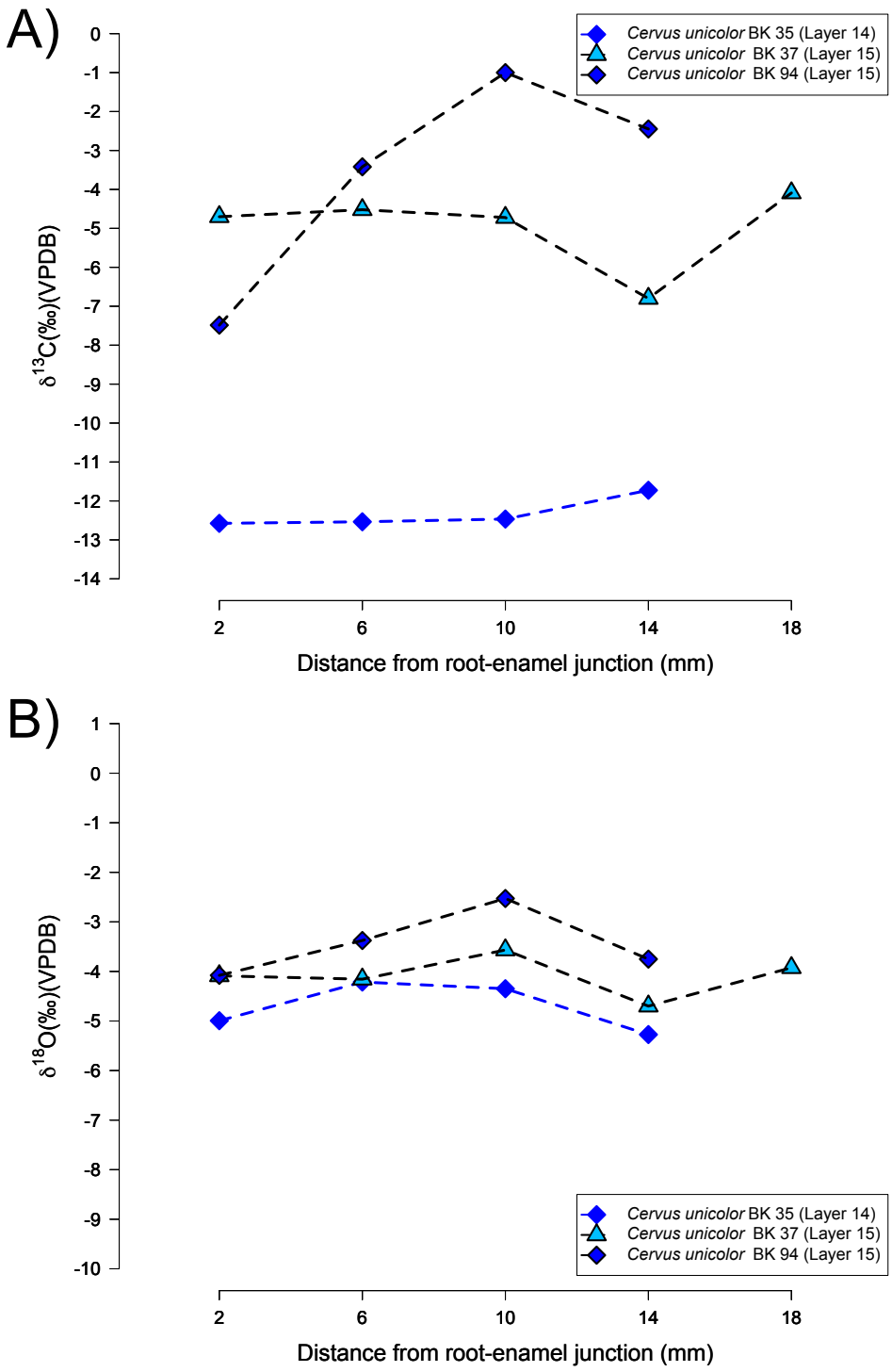


Figure 6.11. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of Cervus unicolor *samples BK 35 (Layer 14), BK 37 (Layer 15) and BK 94 (Layer 15) from Balangoda Kuragala.*

Habitat variability from closed forest, through intermediate forest or a forest/open C_3 mosaic, to open C_4 grassland appears to be the main driver of $\delta^{13}C$ variation at Balangoda Kuragala. An ANOVA test ($F(16,94)=16.272$, $p<0.05$) followed by post-hoc Tukey pair-wise comparison indicates that *Elephas* sp., *Lepus nigricollis*, *Cervus unicolor* and, to a lesser extent, *Sus scrofa*, are distinct from the 'forest' group taxa, despite the latter two species having individuals within that group (Catalogue Tables B30 and B31). High variability in vegetation, and animal behaviour, forest-open ecotones in subtropical/tropical Africa (Sponheimer *et al.,* 2006a; Levin *et al.,* 2008) appears to also operate here with *Elephas* sp. *Cervus unicolor* and *Sus scrofa*, that consume closed forest, open C_3, and C_4 resources, being distinct from *Lepus nigricollis* that confines itself to open, C_4 grassland environments (Chapter 5 – Section 5.2) ($F(16,94)=16.272$, $p<0.05$).

The test also indicates that *Semnopithecus priam thersites* is distinct from *Paradoxurus* sp. (Figure 6.8). This could either be a result of dietary differences, for example that the grey crested langur's gut is adapted to eat leaves and other plant parts that are often lower in $\delta^{13}C$, or that *Paradoxurus* sp. is favouring tree-top foliage that is has higher $\delta^{13}C$ (Chapter 5). $\delta^{18}O$ variation at Balangoda Kuragala also appears to be primarily explicable in terms of the distinction between 'forest' and 'open' grassland. An ANOVA test of the influence of species on $\delta^{18}O$ suggests that this parameter is significant ($F(16,94)=1.974$, $p<0.05$), however a post-hoc Tukey pair-wise comparison failed to produce an specific inter-taxon differences (Catalogue Tables B32 and B33). The much more refined chronology at Balangoda Kuragala, relative to that of Fa Hien-lena, however, enables thorough testing as to whether any species-level distinction is being masked by temporal changes in environment and representation (Figure 6.12).

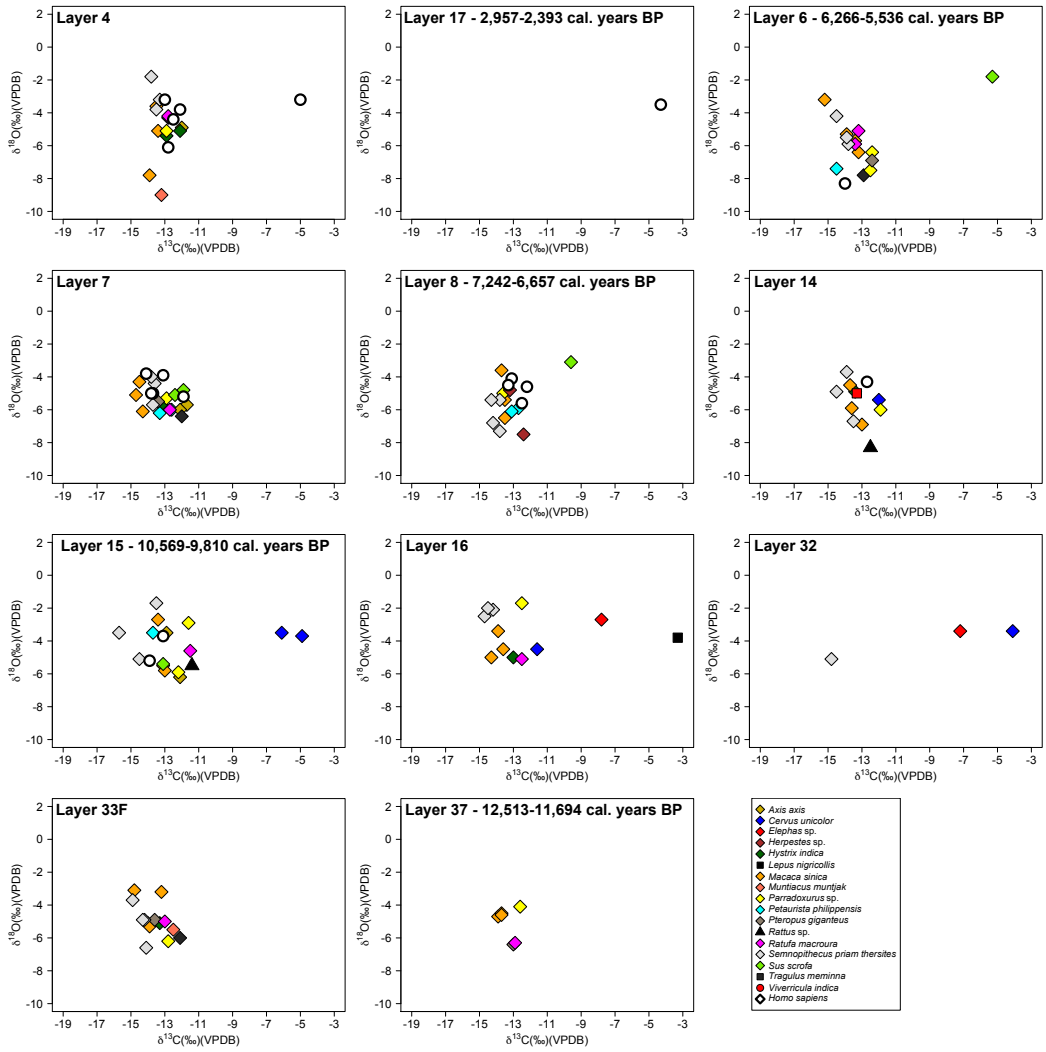


Figure 6.12. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Balangoda Kuragala plotted by stratigraphic layer. Available radiocarbon dates from Table 5.2 are shown.

As at Fa Hien-lena, plotting faunal $\delta^{13}C$ and $\delta^{18}O$ by layer improves the clarity of some ecological relationships. Individuals of the same taxa cluster much more closely by layer in Figure 6.12 than they do in Figure 6.8. For example, no *Sus scrofa* or *Cervus unicolor* individuals show both 'forest' and 'open' preferences within the same layer. *Macaca sinica*, *Semnopithecus priam thersites*, and *Ratufa macroura* also show a higher degree of clustering on a layer by layer basis. Beyond that, however, faunal $\delta^{13}C$ and $\delta^{18}O$ ranges in Figure 6.12 remain broadly comparable where similar sample sizes

are available. $\delta^{13}C$ stability is also indicated in Figure 6.13, with the exception of Layer 32. While an ANOVA test ($F(9,94)=7.582$, $p<0.05$) and post-hoc Tukey pair-wise comparison draws out Layer 32 as distinct in $\delta^{13}C$ compared to all layers, this is based on a very small sample size (Catalogue Tables B30 and B31). This could be indicative of more open conditions in the locale at this time. However, no other layers demonstrate significant differences from each other and the identified 'open' group does not appear limited to a particular period. Figure 6.13 also suggests there is $\delta^{18}O$ variation between layers at Balangoda Kuragala, with a trend towards higher values in Layers 32, 16, and 15, dated towards the end of the Terminal Pleistocene/Holocene transition. This is somewhat supported by an ANOVA test ($F(9,94)=4.121$, $p<0.05$) and post-hoc Tukey pair-wise comparison that suggests Layer 16 is distinct from Layers 14, 8, 7 and 6 (Catalogue Tables B32 and B33). In general, however, the Balangoda Kuragala sequence demonstrates relatively stable faunal $\delta^{13}C$ and $\delta^{18}O$ values, and the persistent presence of some 'open' faunal preferences, across its period of human occupation.

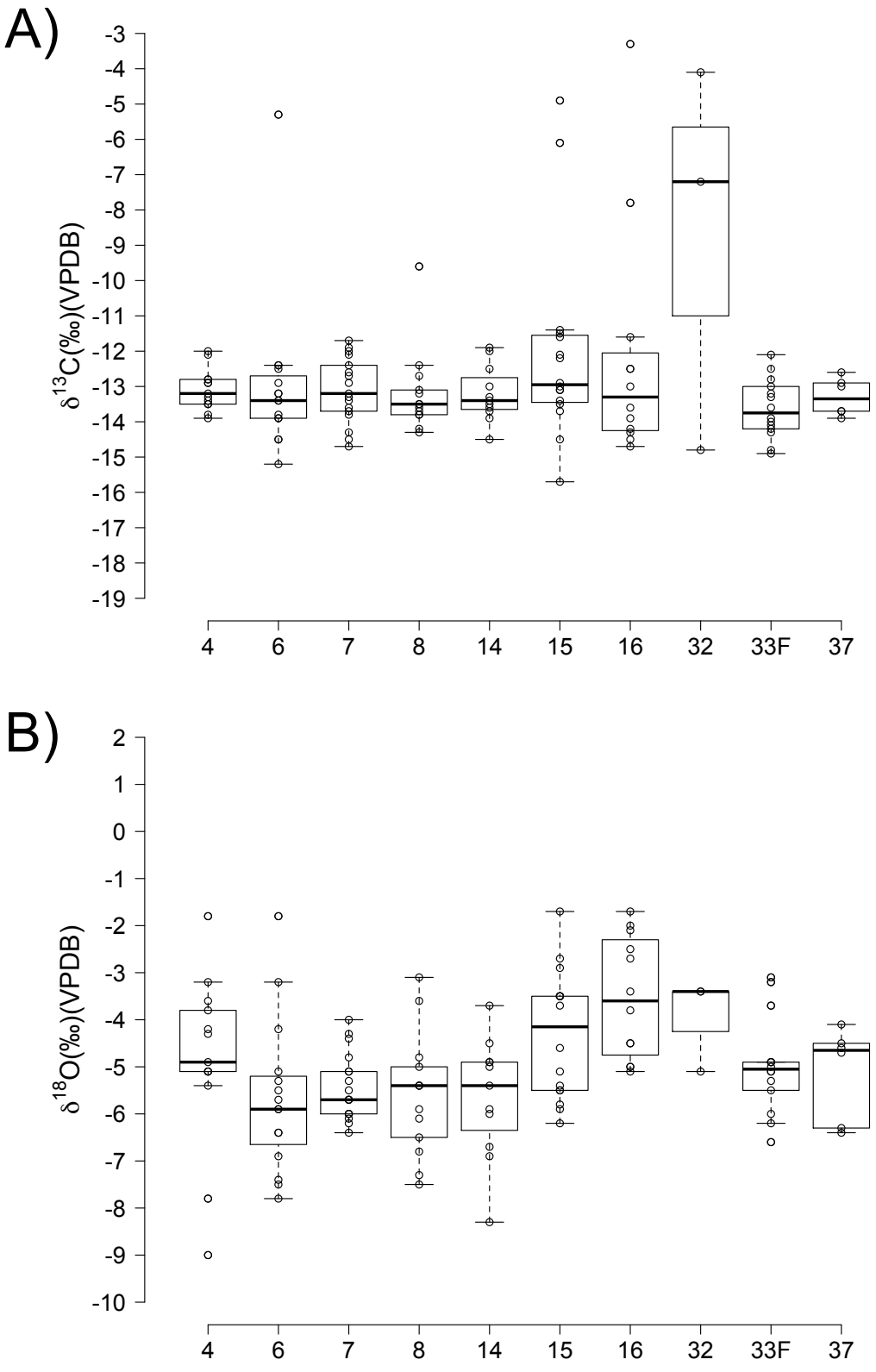


Figure 6.13. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Balangoda Kuragala by stratigraphic layer.

When compared to existing modern and fossil primate datasets (Lee-Thorp *et al.,* 1989a; Nelson, 2003, 2007, 2013; Sponheimer *et al.,* 2006a; Bocherens *et al.,* 2015), the $\delta^{13}C$ range of human tooth enamel at Balangoda Kuragala -14.1 to -4.3‰ is, as with the fauna, indicative of a dietary range from closed-canopy C_3 resources, through intermediate C_3 forest resources/forest-open C_3 mosaic, and open C_4 grassland resources. However, aside from two individuals (with values of -4.3‰ and -5.0‰) the remainder of the human $\delta^{13}C$ measurements fall between -14.1 to -11.9‰. These two individuals are dated to the Sri Lankan Iron Age *c.* 3,000 cal. years, these individuals likely represent the contribution of agriculture and forest clearance to the Wet Zone of Sri Lanka (S.U. Deraniyagala, 2007; Roberts *et al.,* 2015b). The remainder of the humans could indicate a reliance on resources from a mosaic of closed canopy, more open forest, and open grasslands. However, given that hominins (Chapter 4 – Section 4.2) tend to utilise C_4 grassland resources where they are available, their restriction here to the lower end of the C_3 scale, alongside the ecological preferences of fauna identified at the same site with a similar $\delta^{13}C$ range, suggests a reliance on slightly open forest environments, akin to those found in the Intermediate rainforests of Sri Lanka today.

With the two 'open' individuals removed from the dataset, a T-test demonstrates that all other human foragers at Balangoda Kuragala show no distinction in $\delta^{13}C$ ($df=135$, $t=0.433$, $p>0.05$) and $\delta^{18}O$ ($df=135$, $t=-0.666$, $p>0.05$) from the 'Intermediate' forest faunal group. Relative human reliance on these resources is also indicated by sequential human tooth analysis that demonstrates no perceptible shift in the contribution of 'Intermediate' forest resources to the human diet during the period of enamel formation (Figure 6.14) (Catalogue Tables B34 and B35). There is an apparent difference in $\delta^{18}O$ between individuals BKH 19 (Layer 6 – second molar) and 21 (Layer 7- third molar) in

Figure 6.14. This is likely linked to variation in rainfall amount or relative humidity during the formation of each tooth, although no overall difference in $\delta^{18}O$ between Layers 6 and 7 was noted for the faunal dataset ($F(9,16,94)=4.121$, $p<0.05$) (Catalogue Table B33). Alternatively, these individuals may have made use of different water sources within the Intermediate rainforest setting. Overall, while stable isotope measurements of their tooth enamel suggests humans at Balangoda Kuragala made sporadic use of resources from open habitats, they most likely demonstrate a reliance on 'Intermediate' rainforest resources throughout the period of occupation. Similar to Fa Hien-lena, the maintenance of this strategy through time was possibly aided by the relative lack of changes in the local forest environment across the Terminal Pleistocene/Holocene boundary.

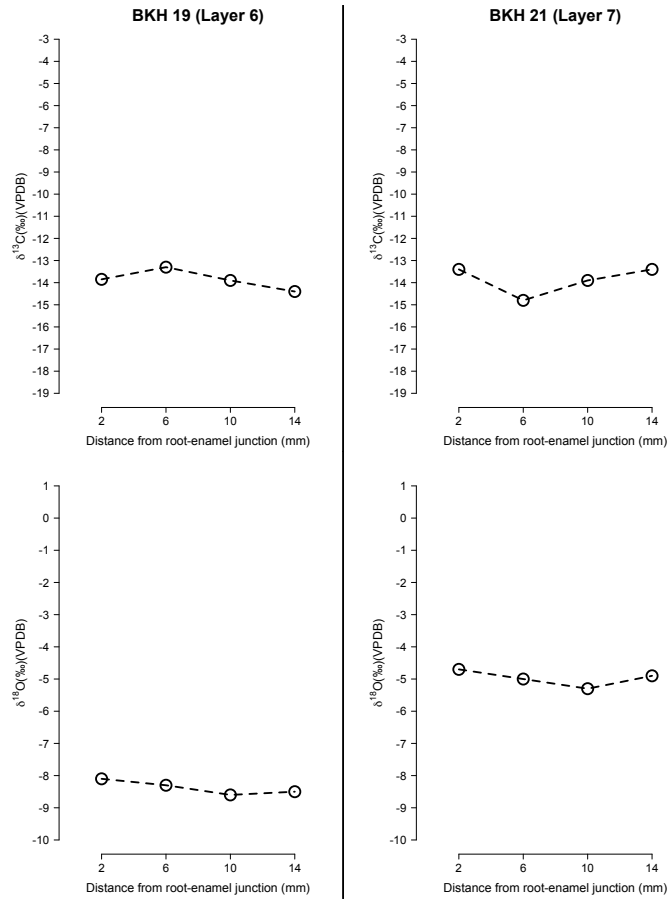


Figure 6.14. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BKH 19 (Layer 6) and BKH 21 (Layer 7) from Balangoda Kuragala.

Bellan-bandi Palassa (DZ)

$\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from Bellan-bandi Palassa are shown in Catalogue Table B13, and Figure 6.15.

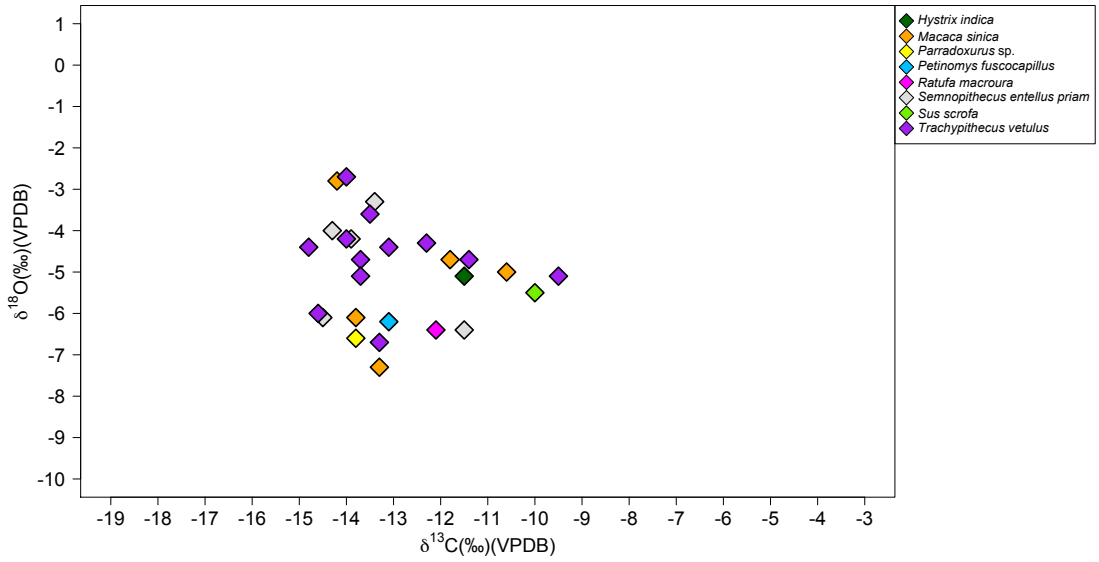


Figure 6.15. $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from Bellan-bandi Palassa.

The $\delta^{13}C$ range of the fauna analysed from Bellan-bandi Palassa (-14.8 to -9.5‰) is demonstrative of a mixture of diets reliant on closed canopy C_3 resources, more open C_3 forest, or a mosaic of C_3 forest and open C_3 resources. The fauna identified have modern preferences for Sri Lanka's 'Wet Zone' rainforest and more open 'Intermediate' rainforests, rather than the open jungles and grasslands of the Dry Zone (Catalogue Table A1) (Chapter 5 – Section 5.2). In contrast to the Balangoda Kuragala dataset, there is little evidence for the consumption of C_4 resources by any of the fauna, perhaps further suggesting a dominance of 'Intermediate' rainforest in the vicinity of the site *c.* 12-11,000 cal. years BP. If this was the case, then this vegetation type may have extended further into the Dry Zone at this time than it does today. The faunal $\delta^{18}O$ range (-7.3 to -2.7‰) is relatively small compared to the other sites, although this is likely a

result of the Bellan-bandi Palassa dataset including fewer samples and being representative of just one stratigraphic layer and period of time. ANOVA tests indicate that there is no distinction between species in either $\delta^{13}C$ ($F(7,19)=1.020$, $p>0.05$) or $\delta^{18}O$ ($F(7,19)=0.708$, $p>0.05$) (Catalogue Tables B36 and B37).

Of particular interest at Bellan-bandi Palassa is the presence of *Trachypithecus vetulus* in this more open 'Intermediate' rainforest group. Given the distinctive $\delta^{13}C$ values between the *Trachypithecus vetulus* at Bellan-bandi Palassa and at Fa Hien-lena it is possible that this species had already separated into the two subspecies that inhabit the Wet Zone and Dry Zone today by 12-11,000 cal. years BP (Chapter 4 – Section 4.4). The lack of isotopic differentiation between this primate and *Macaca sinica* and *Semnopithecus priam thersites* at Bellan-bandi Palassa, in contrast to primate niche distinctions seen at Fa Hien-lena, further suggests a different, more generalist dietary niche for *Trachypithecus vetulus* at this site (Chapter 7 – Section 7.1). Overall, faunal $\delta^{13}C$ and $\delta^{18}O$ values from Bellan-bandi Palassa suggest that while this site has been used as evidence for the first forays of human hunter-gatherers beyond the Wet Zone and Intermediate Zone rainforests of Sri Lanka (Perera, 2010; Roberts *et al.,* 2015a), the environment at this Dry Zone locality *c.* 12-11,000 cal. years BP was probably dominated by 'Intermediate' rainforest rather than grassland. As a result, the site likely represents a continuation of the forest preferences of the Sri Lankan Microlithic rather than any large-scale adaptive shift.

6.3 – Human rainforest resource reliance during the Terminal Pleistocene/Holocene transition

Faunal $\delta^{13}C$ and $\delta^{18}O$ measurements from the archaeological sequences of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa suggest that the modern day climatic division of Sri Lanka into a Wet Zone, Intermediate Zone, and Dry Zone, and their associated vegetation distributions of closed rainforest, more open intermediate rainforest, and open grassland conditions, may have persisted through the Terminal Pleistocene and Holocene (Figures 6.16 and 6.17). Animals known to occur in the Wet Zone rainforests of Sri Lanka from the deposits of Fa Hien-lena have $\delta^{13}C$ values from -17.8 to -13.2‰, whereas the mixture of forest-adapted and open-adapted fauna of Balangoda Kuragala and Bellan-bandi Palassa have $\delta^{13}C$ ranges of -15.7 to -3.3‰ and -14.8 to -9.5‰, respectively, indicative of more open, Intermediate rainforest and open grassland conditions. ANOVA testing followed by post-hoc Tukey pair-wise comparison indicate that $\delta^{13}C$ values from these sites do not form a single population ($F(2,229)=62.963$, $p<0.05$) (Catalogue Tables B38 and B39), with both Bellan-bandi Palassa and Balangoda Kuragala being statistically different from Fa Hien-lena. ANOVA testing followed by post-hoc Tukey pair-wise comparison demonstrates the same for $\delta^{18}O$ ($F(2,229)=8.933$, $p<0.05$) (Catalogue Tables B40 and B41), although it is difficult to find obvious directionality in this parameter in Figure 6.16. It is possible that some changes in rainforest extent and the exact positions of these boundaries may have occurred during this time. For example, Bellan-bandi Palassa appears to have been surrounded by Intermediate rainforest *c.* 12-11,000 cal. years BP, while $\delta^{13}C$ and $\delta^{18}O$ from some layers within the Balangoda Kuragala and Fa Hien-lena suggest that more subtle variations in humidity and forest openness may have occurred during the periods of occupation.

On the whole, however, temporal variation in faunal $\delta^{13}C$ and $\delta^{18}O$ across these sites during the Terminal Pleistocene and Holocene transition is negligible. Faunal isotopic differences between the sites and their inferred ecologies can be seen in Figures 6.16 and 6.17. For graphical display, 90% confidence ellipses were defined for $\delta^{13}C$ and $\delta^{18}O$ measurements of the large faunal samples from Fa Hien-lena and Balangoda Kuragala to produce hypothetical reference groups of closed 'Wet Zone' rainforest, 'Intermediate' rainforest, and 'Open' environments (Figure 6.17). This was done using the dataEllipse function in the free R software statistical package and superimposes normal-probability contours over the plotted data (as per Roberts *et al.,* 2015b). Following Catalogue Table A1, the different groups were classified on the basis of known ecological preferences of the mammals sampled and identified, and comparison of their isotopic values with modern faunal datasets in accordance with the 'canopy' effect and C_3/C_4 preferences documented for forest-dwelling and open-habitat fauna across the tropics (Lee-Thorp *et al.,* 1989a; Cerling *et al.,* 2004; Levin *et al.,* 2008) (Catalogue Table A1).

The 'Open' ellipse is formed using fauna at Balangoda Kuragala known to favour open grassland, some contribution of C_4 resources, and differentiated from the remainder of fauna at the site on the basis of comparison of their $\delta^{13}C$ values (*c.* -9.6 to -3.3‰) with the existing literature (Catalogue Table B22). While the sample size of this group is small, its individuals clearly stand apart ecologically, and in terms of their bulk and sequential $\delta^{13}C$ and $\delta^{18}O$ (Figure 6.17). The remainder of the fauna at Balangoda Kuragala has a $\delta^{13}C$ range of -15.7 to *c.* -11.0‰. While the higher end of this range could indicate a mosaic of C_3 forest/open C_3 savannah resource consumption (Sponheimer *et al.,* 2006a; Levin *et al.,* 2008), the ecological preferences of the fauna

that make up this group are for forest resources. As a result, and due to the lack of any indication of C_4 resource consumption, this group has been used here to draw an 'Intermediate' rainforest ellipse. Finally, the 'Wet Zone' rainforest ellipse was formed using faunal sample data from the site of Fa Hien-lena whose $\delta^{13}C$ values (-17.8 to -13.2‰) demonstrate the clear influence of the canopy effect across the Terminal Pleistocene/Holocene in the modern-day Wet Zone of Sri Lanka.

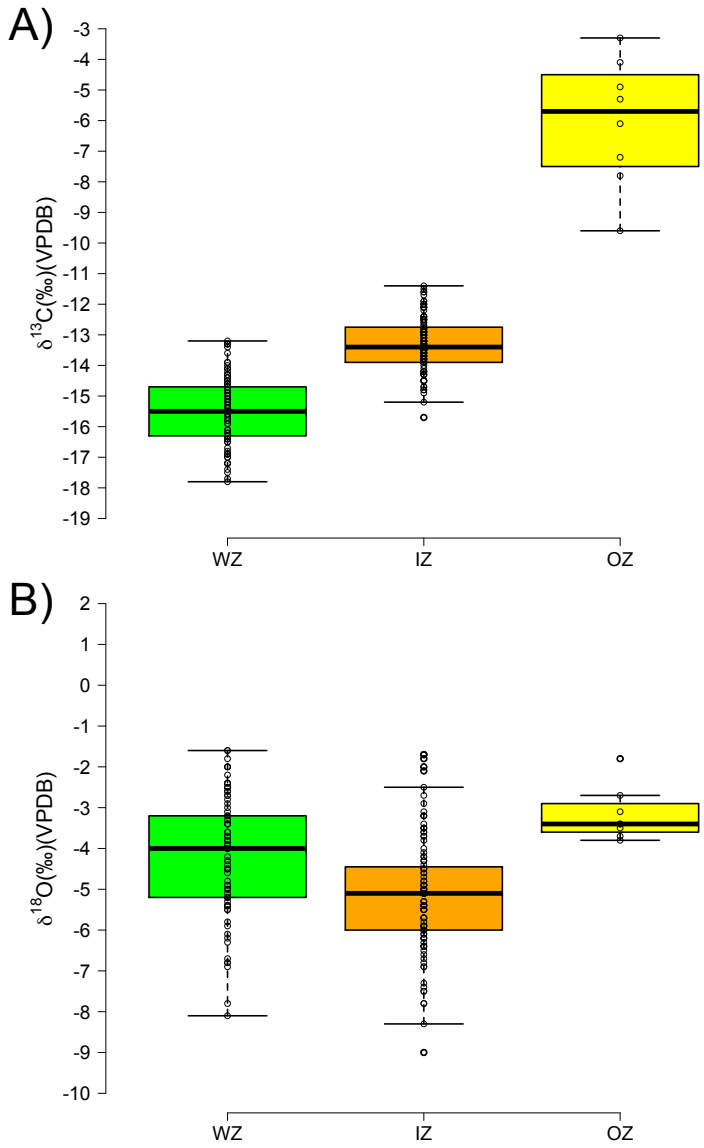


Figure 6.16. Boxplots of faunal A) $\delta^{13}C$ and B) $\delta^{18}O$ used to form the 'Wet Zone', 'Intermediate Zone', and 'Open' zone ellipses in Figure 6.17.

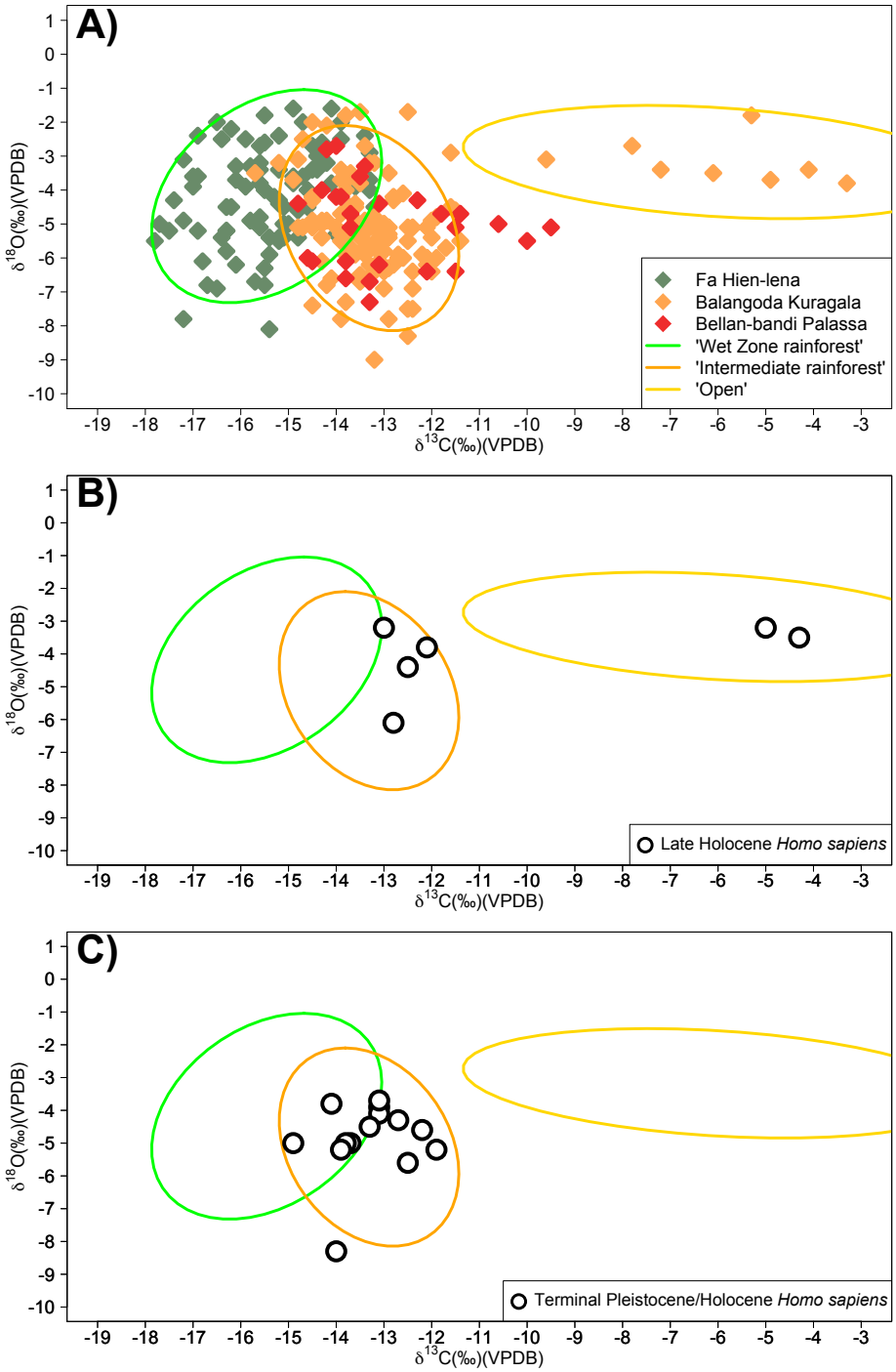


Figure 6.17. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa. The isotopic values from characteristic rainforest fauna from Fa Hien-lena and forest and open grassland fauna from Balangoda Kuragala have been used to construct 90% confidence ellipses [using the R software dataEllipse function] indicative of closed 'Wet Zone' rainforest, 'Intermediate' rainforest, and 'Open' conditions (Roberts et al., 2015b), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Late Holocene deposits at Balangoda Kuragala, C) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Terminal Pleistocene/Early Holocene deposits from Fa Hien-lena and Balangoda Kuragala.

Faunal $\delta^{13}C$ and $\delta^{18}O$ measurements provide a useful reference for the interpretation of the long-term ecological niches of Terminal Pleistocene/Holocene human foragers in Sri Lanka. $\delta^{13}C$ and $\delta^{18}O$ measurements from human tooth enamel from Fa Hien-lena and Balangoda Kuragala plot directly over the forest faunal isotopic niches at these sites. As indicated above, T-tests have shown the $\delta^{13}C$ and $\delta^{18}O$ of human and faunal enamel to be indistinguishable at both sites ($p>0.05$). On the basis of the faunal isotope data, the Fa Hien-lena human dated to *c.* 12,000 cal. years BP, occupied either closed 'Wet Zone' rainforest environments or more open 'Intermediate' rainforest. Sequential analysis shown in Figure 6.7 indicates that this niche persisted across the period of enamel formation. Balangoda Kuragala human specimens, dated to between *c.* 12,000 and 3,000 cal. years BP, demonstrate similar forest reliance though there is a distinct preference for more open forests, akin to Sri Lanka's modern 'Intermediate' rainforest.

The group of open grassland fauna at Balangoda Kuragala, although apparently present throughout the sequence of occupation (Figure 6.12), did not contribute significantly to Terminal Pleistocene/Early Holocene human subsistence at either site. This is also consistent with the sequential analysis of two human teeth from Balangoda Kuragala from this period that demonstrate little deviation in forest reliance during enamel formation (Figure 6.14). Two Balangoda Kuragala human individuals with $\delta^{13}C$ of -5.0 and -4.3‰, respectively, are from layers dated to *c.* 3,000 cal. years BP, a point by which forests are likely to have opened in the region as a result of agricultural clearance. However, as indicated above, and in Figure 6.17, a number of human foragers retained their forest reliance at this time suggesting that, as in other tropical forest regions (Krigbaum, 2003, 2005), agriculture did not arrive as a sudden, uniform wave to the rainforests of Sri Lanka.

6.4 – Human and faunal stable carbon and oxygen isotope measurements from Batadomba-lena: the early Microlithic tradition of the Wet Zone

$\delta^{13}C$ and $\delta^{18}O$ measurements of humans and fauna from Batadomba-lena are shown in Catalogue Tables B13 and B14, and Figure 6.18.

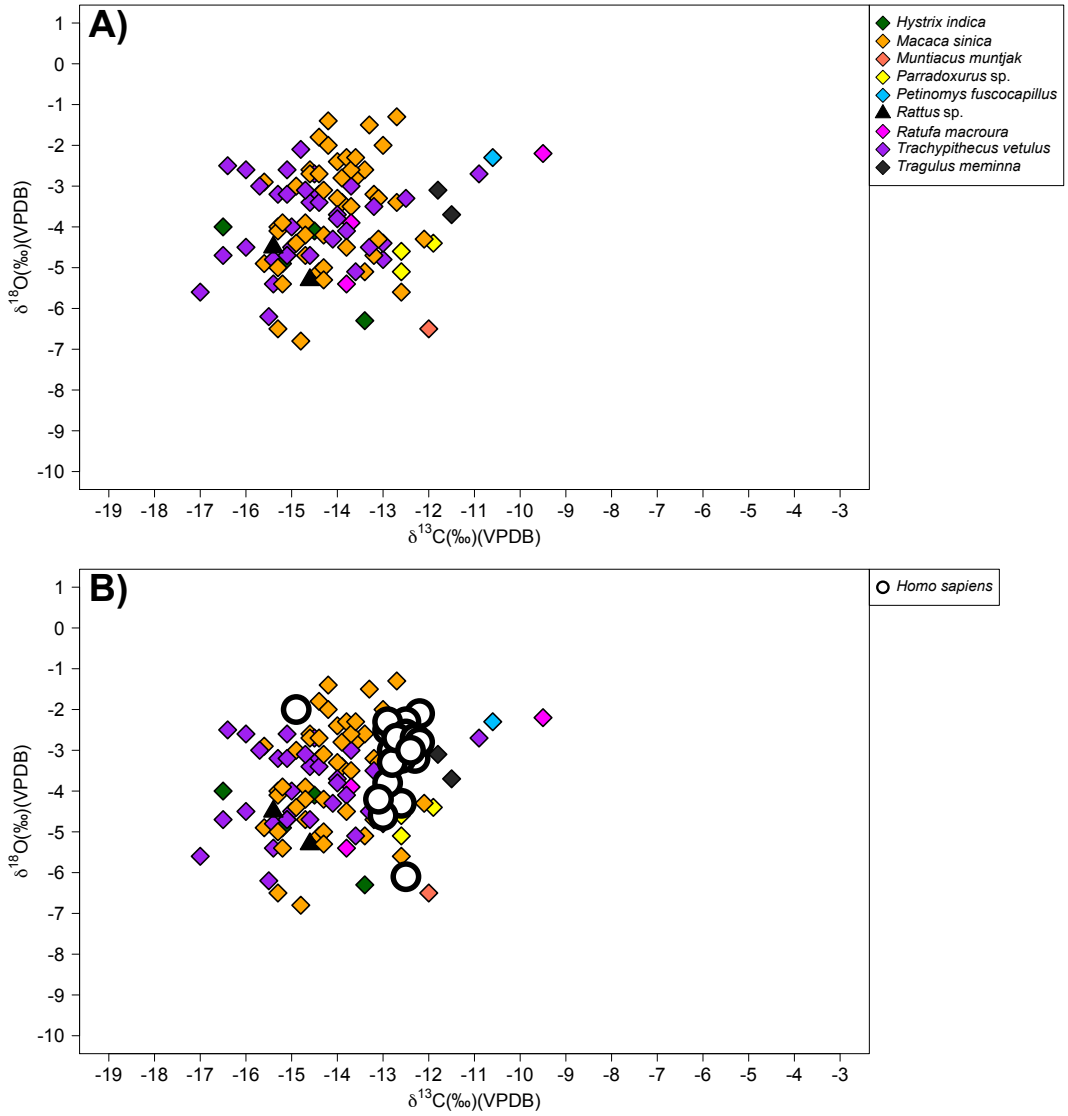


Figure 6.18. $\delta^{13}C$ and $\delta^{18}O$ measurements of A) fauna from Layers 4, 5, 6, 7a, 7b, and 7c and B) fauna over-plotted by the human specimens from Layers 6b, 6b/7a, and 7c from Batadomba-lena.

The fauna identified at Batadomba-lena, like that from Fa Hien-lena, is characteristic of the 'Wet Zone' rainforest of Sri Lanka (Catalogue Table A1) (Chapter 5 – Section 5.2). The $\delta^{13}C$ mean and range of the measured samples (-17.0 to -9.5‰: mean= -14.1‰) suggest that, while the faunal diets were dominated by closed-canopy forest, significant elements of more open C_3 forest conditions and clearings were also consumed. The mean $\delta^{13}C$ values of *Trachypithecus vetulus* (-14.6 ± 1.2‰) and *Hystrix indica* (-14.9± 1.3‰) represent closed forest niches, while *Paradoxurus* sp. (-12.4 ± 0.4‰), *Tragulus meminna* (-11.7‰ ± 0.2‰), and the *Petinomys fuscocapillus* (-10.6‰) and *Muntiacus muntjak* (-12.0‰) individuals, demonstrate reliance on the forest fringe and clearing habitats they are known to prefer today. Unlike at Fa Hien-lena, *Ratufa macroura* (mean -12.3 ± 2.5‰) appears to have also utilised these clearing habitats, while the generalist primate *Macaca sinica* (mean -14.1 ± 0.9‰) foraged in more closed forest than it appears to have at Fa Hien-lena or Balangoda Kuragala (Chapter 7 – Section 7.1).

ANOVA test of variance in $\delta^{13}C$ confirms that species does influence $\delta^{13}C$ significantly ($F(8,84)=5.160$, $p<0.05$). However, post-hoc Tukey pair-wise comparison fails to draw out any species as significantly different from each other (Catalogue Tables 42 and B43). *Rattus* sp., which is more likely indicative of local cave conditions rather than being the focus of human hunting, has a mean $\delta^{13}C$ of -15.0 ± 0.6‰ suggesting that the immediate vicinity of Batadomba-lena was surrounded by dense, canopied forest when it was present. The range of $\delta^{18}O$ at Batadomba-lena (-6.8 to -1.3‰) is much smaller than that of Fa Hien-lena and Balangoda Kuragala and ANOVA testing followed by post-hoc Tukey pair-wise comparison suggest that species differences do not impact $\delta^{18}O$ variation at the site ($F(8,84)=1.501$, $p>0.05$) (Catalogue Tables B44 and B45).

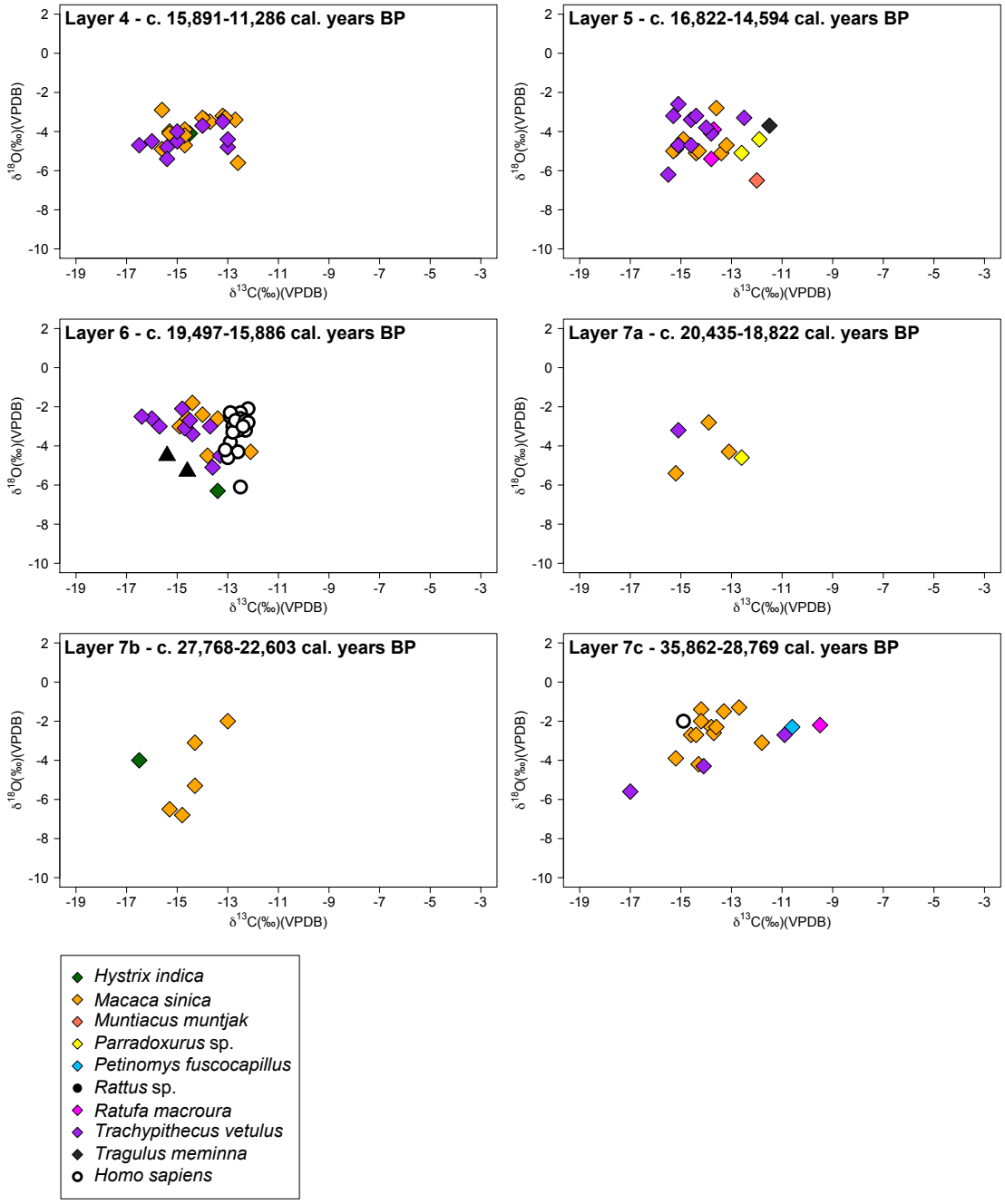


Figure 6.19. $\delta^{13}C$ and $\delta^{18}O$ measurements of human and fauna from Batadomba-lena plotted by stratigraphic layer. Available radiocarbon dates from Table 5.4 are shown. For the purposes of this plot the three human samples labelled 6b/7a have been shown in Layer 6.

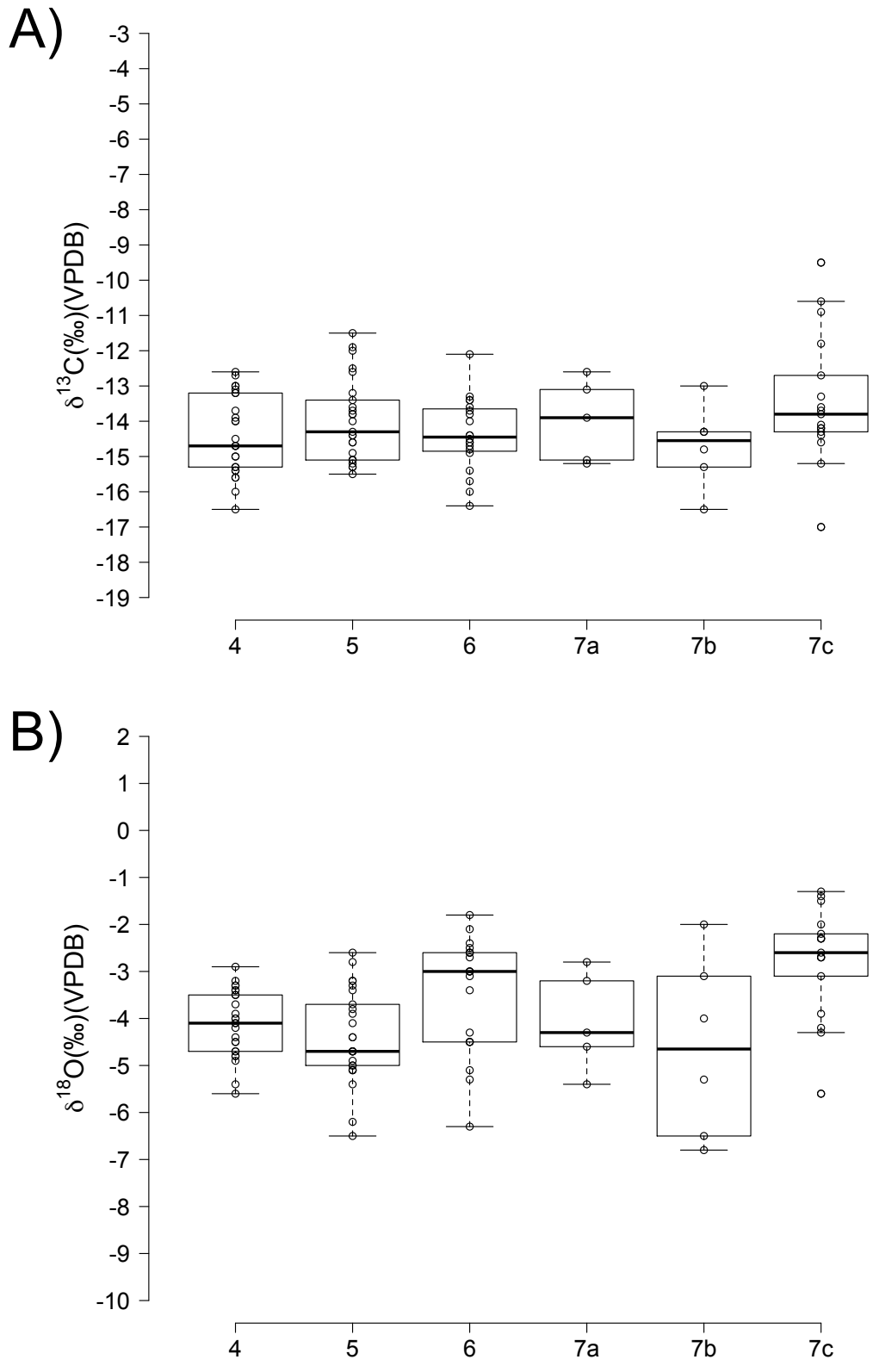


Figure 6.20. Boxplots of faunal $\delta^{13}C$ (A) and $\delta^{18}O$ (B) at Batadomba-lena by stratigraphic layer.

Plotting faunal $\delta^{13}C$ and $\delta^{18}O$ at Batadomba-lena by stratigraphic layer (Figures 6.19 and 6.20) indicates stable $\delta^{13}C$ and $\delta^{18}O$ values through the LGM period from *c.* 20,000-16,000 cal. years BP. Figures 6.19 and 6.20 show higher $\delta^{18}O$, and increased $\delta^{18}O$ variation, in Layers 7b and 7c, *c.* 36,000-23,000 cal. years BP, while Layer 7c also potentially demonstrates increased variation in $\delta^{13}C$ *c.* 36-29,000 cal. years BP. ANOVA testing indicates that stratigraphic layer plays a role in $\delta^{13}C$ variation at Batadomba-lena ($F(5,84)=2.456$, $p<0.05$). However, a post-hoc Tukey pair-wise comparison fails to draw out any layers as distinctively different from each other (Catalogue Table B42 and B43). By contrast, ANOVA test and post-hoc Tukey pair-wise comparisons in $\delta^{18}O$ demonstrate that Layer 7c is distinct from Layers 7b, 5 and 4, perhaps suggestive of the availability of more open, evaporative habitats at the time of earliest occupation ($F(5,84)=6.356$, $p<0.05$) (Catalogue Tables B44 and B45).

From this, and from Figures 6.19 and 6.20, it appears that closed canopy C_3 resources persisted in the vicinity of the Batadomba-lena during the LGM, albeit with potentially more open C_3 elements than apparently existed during the Terminal Pleistocene at Fa Hien-lena. Although based on a small sample size, this environmental spectrum appears to span back at Batadomba-lena, prior to the LGM, to *c.* 36,000-23,000 cal. years BP, with perhaps more environmental variability existing at this time (Figure 6.19). As with Fa Hien-lena and Balangoda Kuragala, faunal $\delta^{13}C$ and $\delta^{18}O$ measurements from the Batadomba-lena sequence indicate that while mainly 'rainforest' fauna were exploited, humans also likely exploited a variety of more open 'Intermediate' rainforest or mosaics of closed forest and open C_3 habitats, potentially including rainforest clearings, to meet their subsistence needs.

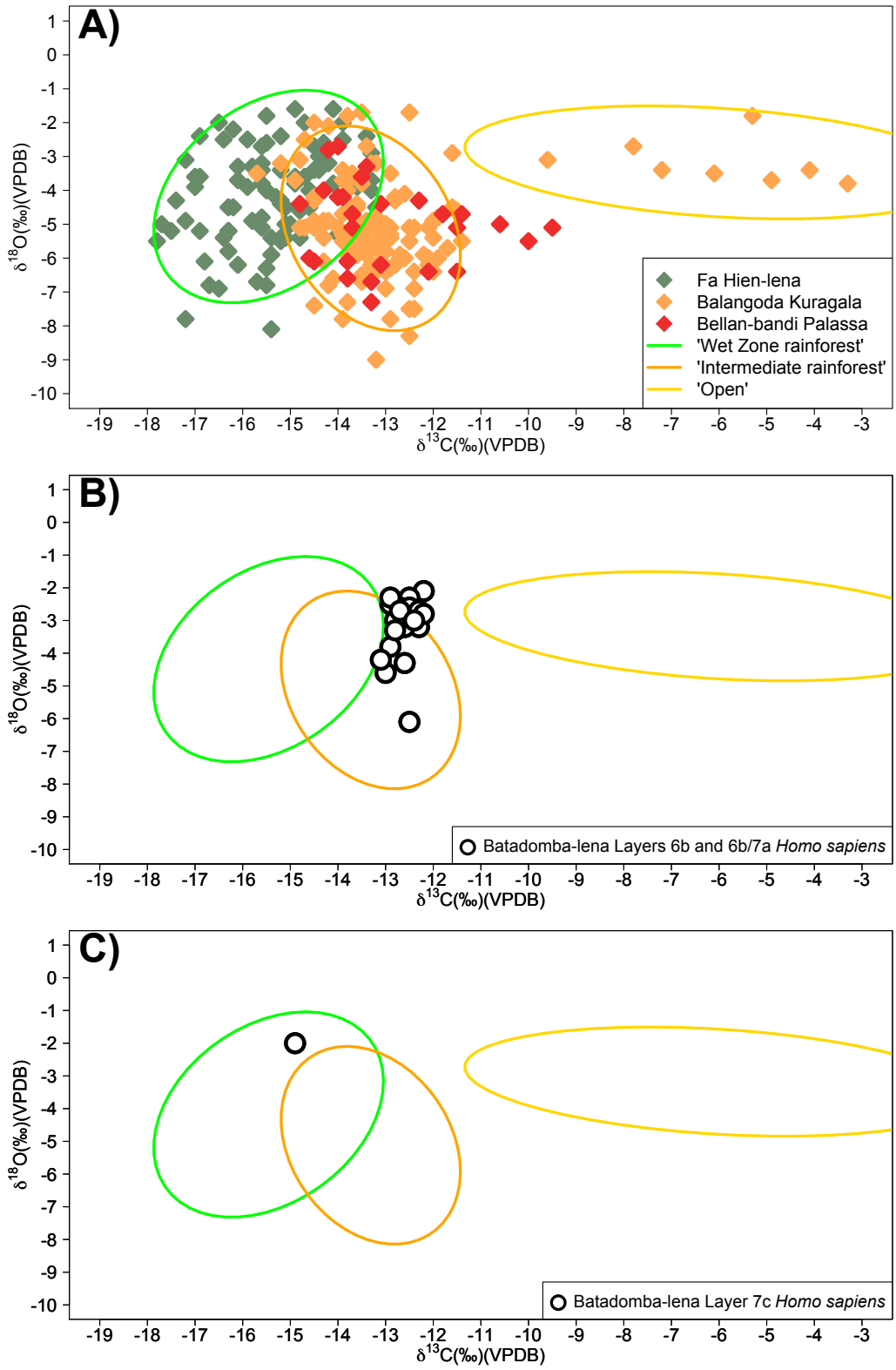


Figure 6.21. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa with 90% confidence ellipses representing Wet Zone rainforest, Intermediate rainforest, and Open conditions (see Figures 6.16 and 6.17), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Layer 6b and 6b/7a of Batadomba-lena, C) $\delta^{13}C$ and $\delta^{18}O$ values of the human specimen from Layer 7c of Batadomba-lena.

Direct $\delta^{13}C$ and $\delta^{18}O$ measurements from human tooth enamel at Batadomba-lena are consistent with this picture and plot within the 'Wet Zone' rainforest and 'Intermediate' rainforest Ellipses defined above, albeit with a clear preference for the latter (Figure 6.21). T-tests demonstrate that the Batadomba-lena *Homo sapiens* have higher $\delta^{13}C$ (mean= -12.7 ± 0.5‰) (df=119, t=-5.012, $p<0.05$) and $\delta^{18}O$ (mean= -3.1 ± 0.9 ‰) (df=119, t=-2.707, $p<0.05$) than fauna from the same site. It therefore appears that although more open forest conditions existed in the Wet Zone of Sri Lanka during the LGM, as indicated by the faunal data, *Homo sapiens* continued to rely upon rainforest resources, albeit within a more open canopy in this part of Sri Lanka (Figure 6.21). This reliance is further indicated by sequential human tooth analysis that demonstrates no perceptible shift in the contribution of forest resources to the human diet during the period of enamel formation for individuals from Layer 6b and 6b/7a (Figures 6.22 and 6.23) (Catalogue Tables B46-B50). The earliest human fossil in this study, from Layer 7c *c.* 36,000-29,000 cal. years BP has a $\delta^{13}C$ measurement (-14.9‰) that is indistinguishable from that of the Wet Zone Fa Hien-lena individual (-14.9‰), and is indicative of a reliance on closed-canopy forest resources. This suggests that the earliest human sample relied on closed rainforest resources even at a time when open patches of forest and clearings were available (Figure 6.19, Figure 6.21).

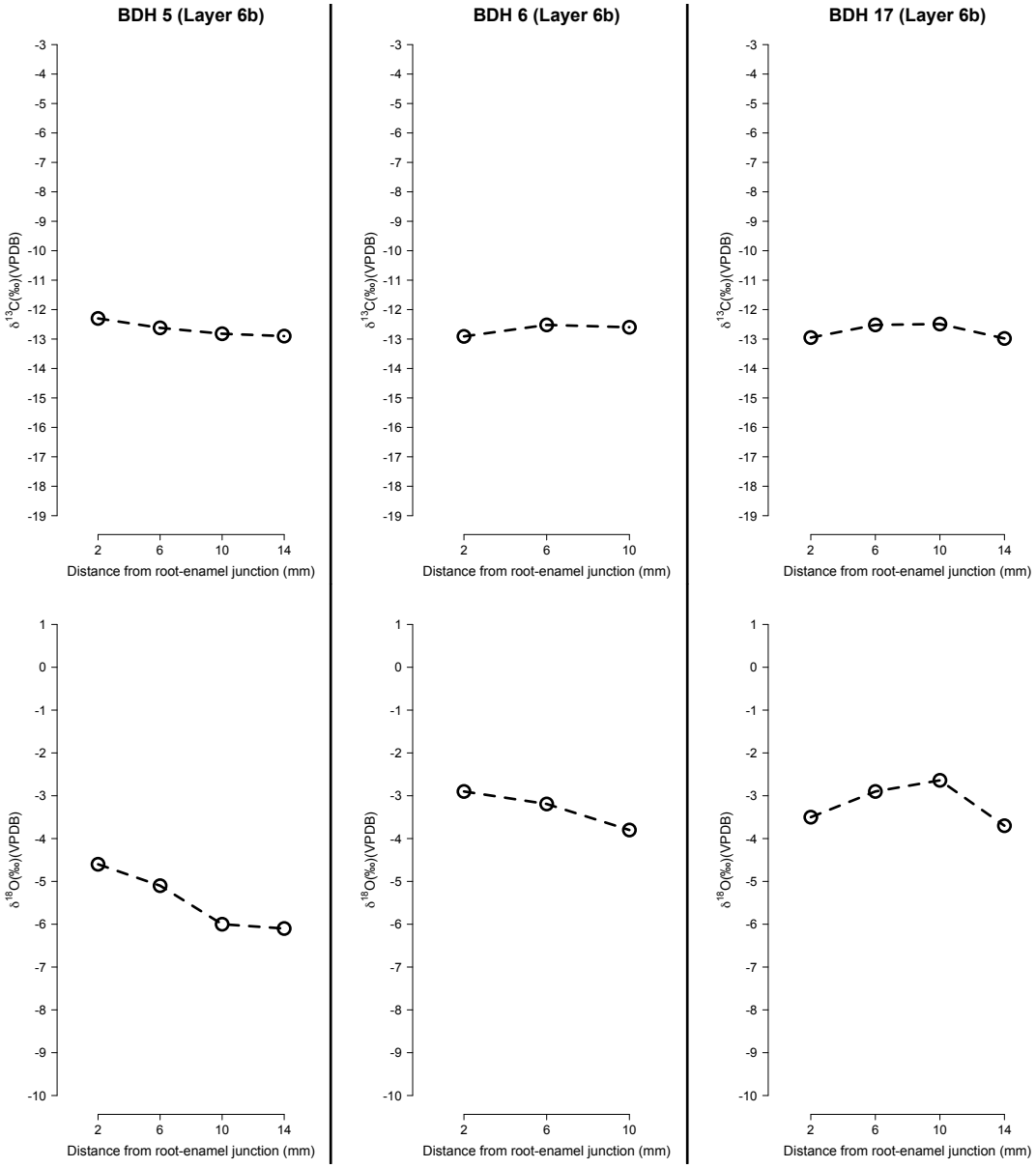


Figure 6.22. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BDH 5, BDH 6, BDH 17 (all Layer 6b) from Batadomba-lena.

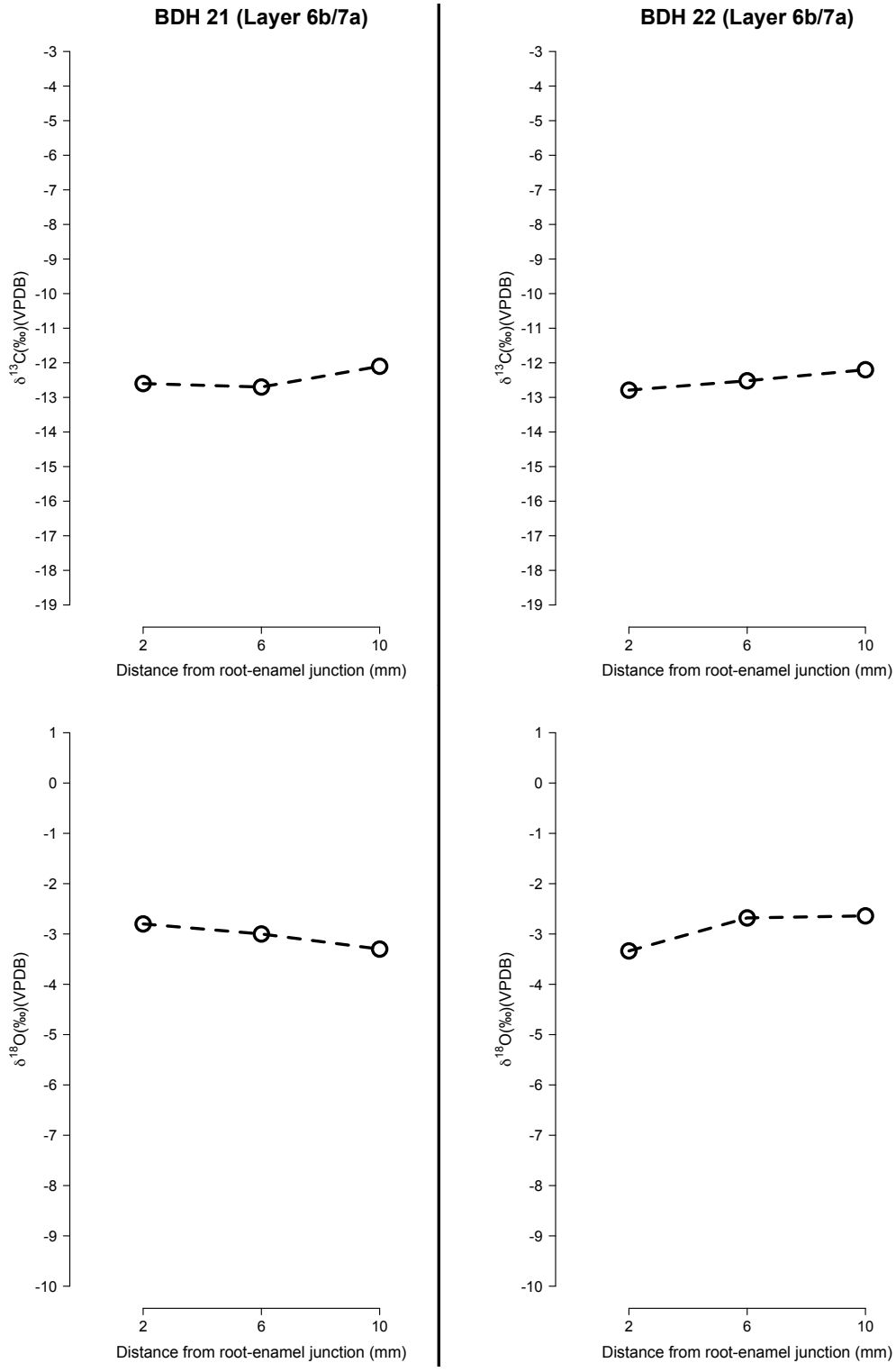


Figure 6.23. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of human samples BDH 21 and BDH 22 (both Layer 6b/7a) from Batadomba-lena.

6.5 – Human isotopic niches and ecology in Late Pleistocene/Holocene Sri Lanka

$\delta^{13}C$ and $\delta^{18}O$ measurements of humans and fauna from Sri Lanka allow the direct assessment of the degree and longevity of prehistoric human reliance on rainforest resources during one of the earliest encounters of our species with tropical forests beyond Africa. Although Terminal Pleistocene/Early Holocene human specimens from Fa Hien-lena and Balangoda Kuragala may have occupied closed rainforest, the majority of humans from this period, as well as those from Batadomba-lena dated to *c.* 20,000-16,000 cal. years BP, have $\delta^{13}C$ and $\delta^{18}O$ values indicative of long-term subsistence concentration and habitation in more-open tropical forest environments, similar to those found in the 'Intermediate' Zone of Sri Lanka today. No Late Pleistocene or Early Holocene human specimen has an isotopic composition that indicates the consumption of C_4 resources, as seen in the 'open' faunal group found at Balangoda Kuragala (Figure 6.24).

This suggests that, contrary to earlier arguments (Bailey *et al.,* 1989; Bailey and Headland, 1991), Sri Lankan human foragers concentrated on the exploitation of forest environments rather than using them as part of more-diverse seasonal subsistence strategies which would have resulted in higher $\delta^{13}C$, in the direction of the two Iron Age agricultural specimens from Balangoda Kuragala. Rainforest specialisation reaches back to the earliest human fossil in Sri Lanka, and South Asia, which demonstrates a preference for closed canopy rainforest resources, and continues beyond the introduction of agriculture to the tropical forest zone of Sri Lanka. Not only does this demonstrate the ability of the earliest members of our species to reach South Asia's rainforests to specialise in their exploitation, but it also indicates the effectiveness and

desirability of this subsistence strategy even in the face of agricultural food production (Figure 6.24).

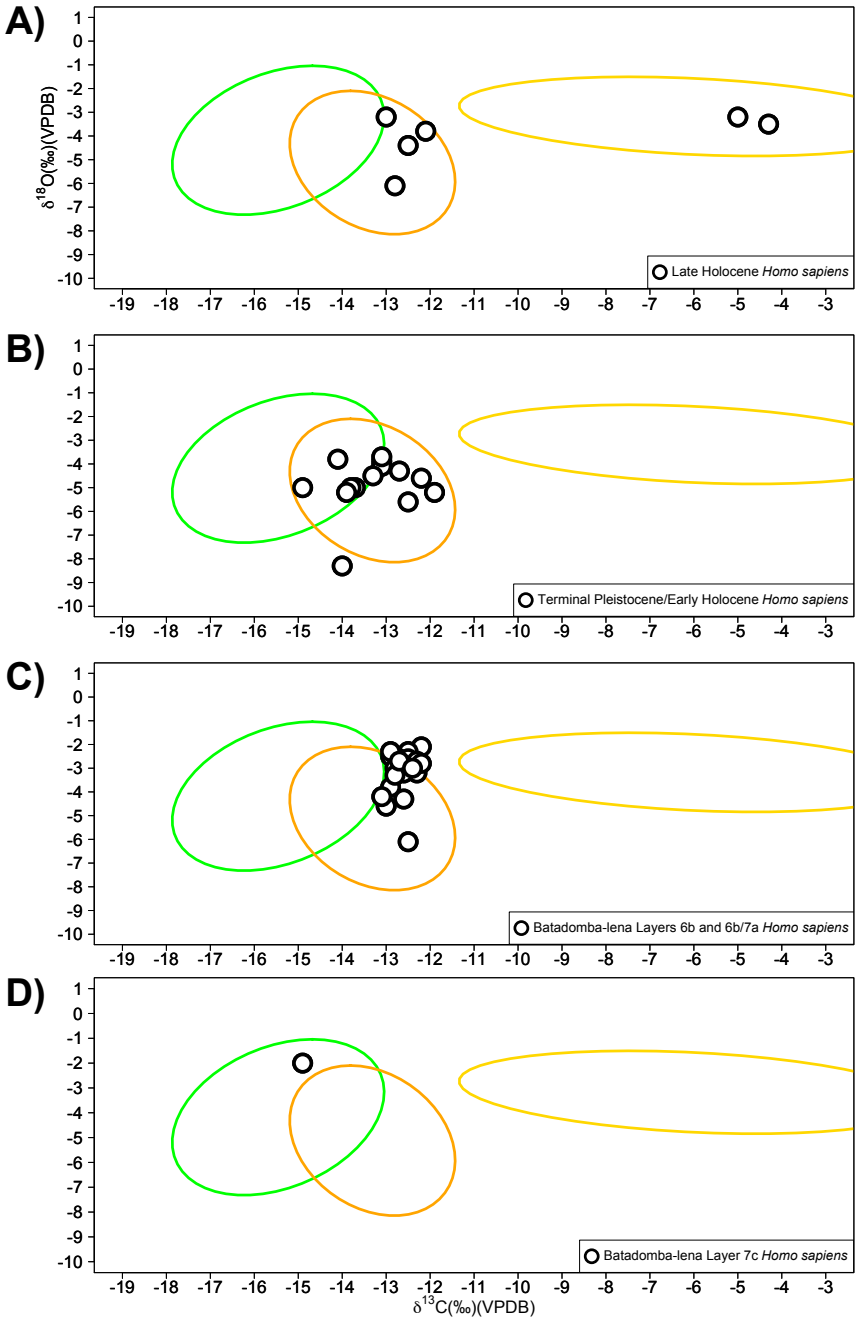


Figure 6.24. 90% confidence ellipses of Wet Zone rainforest, Intermediate rainforest, and Open conditions from Figures 6.16 and 6.17 with A) Late Holocene human $\delta^{13}C$ and $\delta^{18}O$ measurements from Balangoda Kuragala, B) Terminal Pleistocene/Early Holocene human $\delta^{13}C$ and $\delta^{18}O$ measurements from Balangoda Kuragala and Fa Hien-lena, C) Layer 6b and 6b/7a human $\delta^{13}C$ and $\delta^{18}O$ measurements from Batadomba-lena (c. 20,000-17,000 *cal. years BP), and D) Layer 7c human $\delta^{13}C$ and $\delta^{18}O$ measurements from Batadomba-lena (c.* 36,000-29,000 *cal. years BP) over-plotted.*

The temporal stability of Sri Lankan tropical forest environments is indicated by the consistency of faunal $\delta^{13}C$ and $\delta^{18}O$ throughout the Terminal Pleistocene/Holocene sequences of Fa Hien-lena and Balangoda Kuragala. Faunal $\delta^{13}C$ and $\delta^{18}O$ from Batadomba-lena Layer 6 indicates that rainforest within Sri Lanka's Wet Zone was more open before and during the LGM *c.* 20,000-16,000 cal. years BP (Figures 6.25 and 6.26). This is confirmed by ANOVA and post-hoc Tukey pair-wise comparison of faunal $\delta^{13}C$ that demonstrates that Batadomba-lena differs from Fa Hien-lena, Balangoda Kuragala and Bellan-bandi Palassa ($F(3,326)=48.848$, $p<0.05$) (Catalogue Tables B51 and B52). Batadomba-lena also differs from Balangoda Kuragala and Bellan-bandi Palassa, but not Fa Hien-lena in $\delta^{18}O$ ($F(3,326)=15.406$, $p<0.05$) (Figure 6.25) (Catalogue Tables B53 and B54).

More open rainforest in the Wet Zone of Sri Lanka during the LGM fits with evidence for changes in rainforest structure and extent elsewhere in the tropics at this time (*c.* 25,000-18,000 cal. years BP) (Chapter 3 – Section 3.2) (e.g. Mercader *et al.,* 2000; Thompson *et al.,* 2000; Mayle *et al.,* 2004; Haberle *et al.,* 2012). Yet the opening of the rainforest in Sri Lanka seems to have encouraged rather than altered human foragers' general preference for slightly open 'Intermediate' rainforest resources in Sri Lanka (Figures 6.24 and 6.26), and they continue to demonstrate clear reliance on rainforest resources throughout this period of climatic flux and environmental change. Arguments for the potential mosaic nature of Sri Lanka's rainforest during MIS 4-2 (Boivin *et al.,* 2013) are borne out by the spread of faunal $\delta^{13}C$ and $\delta^{18}O$ values in Layer 7c of Batadomba-lena *c.* 36,000-29,000 cal. years BP. Even here, however, Sri Lanka, and South Asia's, oldest human fossil demonstrates evidence for and closed-canopy rainforest resource reliance (Figure 6.26).

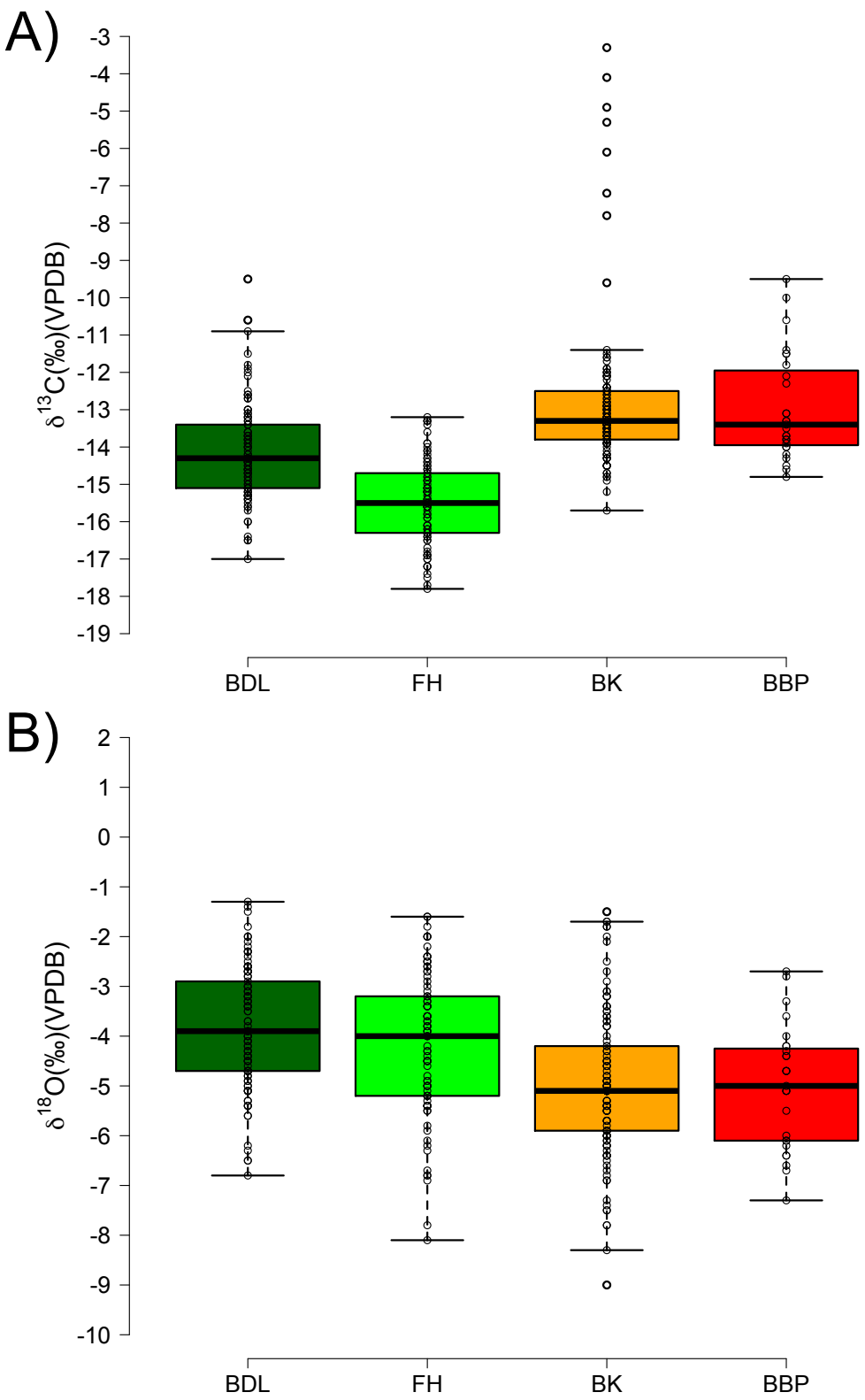


Figure 6.25. Boxplots of A) $\delta^{13}C$ and B) $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena (FH), Balangoda Kuragala (BK), and Bellan-bandi Palassa (BBP) and the Late Pleistocene deposits of Batadomba-lena (BDL).

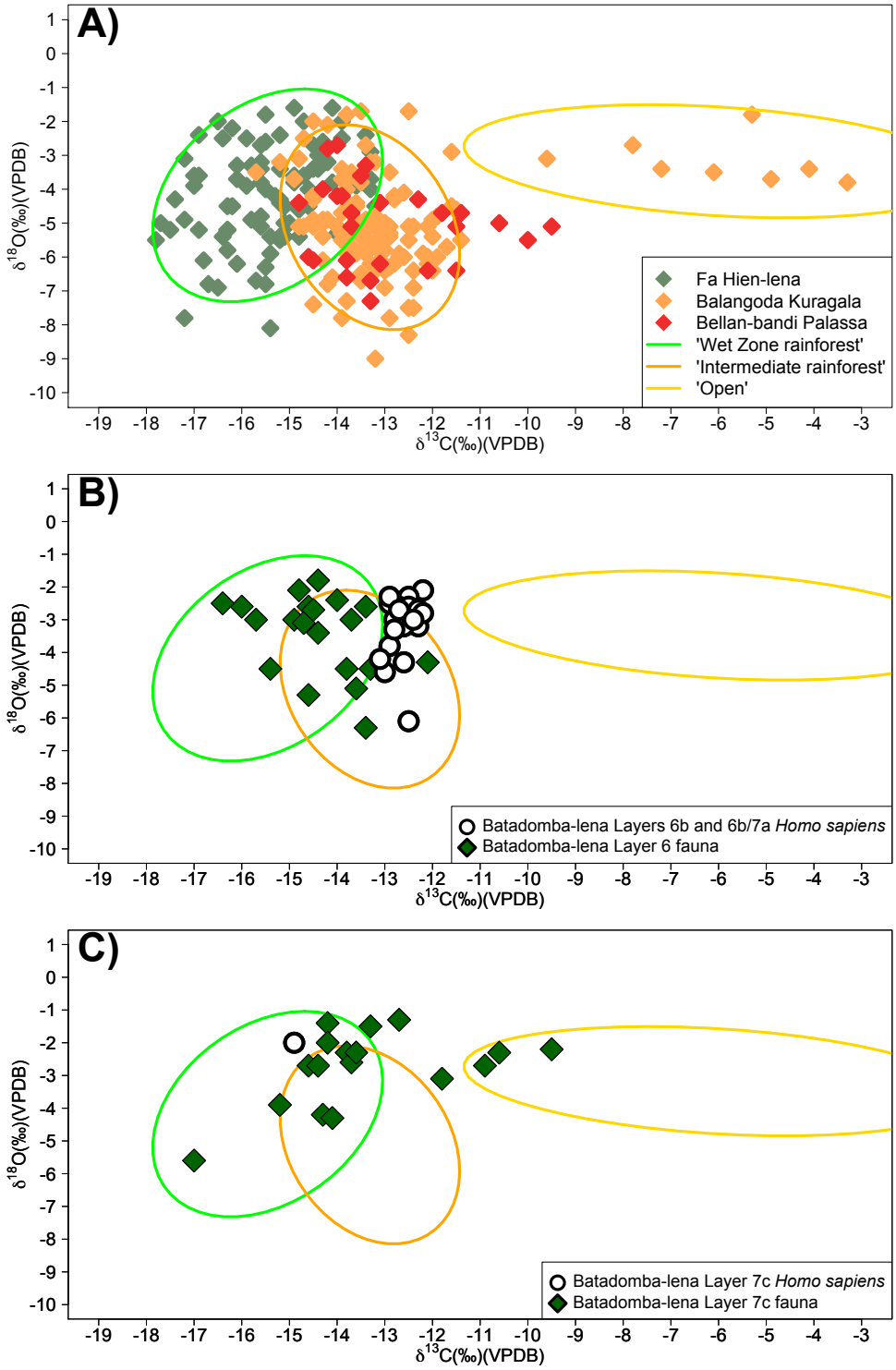


Figure 6.26. A) $\delta^{13}C$ and $\delta^{18}O$ measurements of fauna from the Terminal Pleistocene/Holocene deposits of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa with 90% confidence ellipses representing Wet Zone rainforest, Intermediate rainforest, and Open conditions (see Figures 6.16 and 6.17), B) $\delta^{13}C$ and $\delta^{18}O$ values of human specimens from Layers 6b and 6b/7a and faunal specimens from Layer 6 at Batadomba-lena, C) $\delta^{13}C$ and $\delta^{18}O$ values of human and faunal specimens from Layer 7c at Batadomba-lena.

The specialised nature of this rainforest adaptation may have been supported by the hunting strategies and social networks implied by the early and ongoing presence of microlithic toolkits, bone technologies, and personal ornamentation evidenced at sites in Sri Lanka's Wet Zone and Intermediate Zone forests from *c.* 36,000-29,000 cal. years BP, through the LGM and Terminal Pleistocene/Holocene transition, until the Iron Age *c.* 3,000 cal. years BP (S.U. Deraniyagala, 1992, 2007; Wijeyapala, 1997; Perera, 2010; Perera *et al.,* 2011*,* in press; Lewis *et al.,* 2014; Roberts *et al.,* 2015a, 2015b). Indeed, in contrast to other regions of the world in which early human rainforest occupation has been suggested (Mercader, 2002a, 2002b; Barker *et al.,* 2007; Summerhayes *et al.,* 2010; Barker, 2013), it is only Sri Lanka that demonstrates such an early, persistent, and intensive exploitation and occupation of its rainforests throughout the Late Pleistocene (Roberts and Petraglia, 2015) (Chapter 2 – Section 2.2).

The persistence of this adaptation may also, in part, be a result of the stability of extent, if not structure, of the rainforests of Sri Lanka's Wet Zone and Intermediate Zone throughout periods of climatic change. This resilience, in the face, of considerable variability in rainfall, temperature, and CO_2 concentrations, ensured the consistent provision of a diverse array of plant and animal communities for human groups (Whitmore, 1998; Barboni *et al.,* 2003; Farooqui *et al.,* 2010). Indeed, it is clear that the Late Pleistocene and Early Holocene occupants of Sri Lanka's Wet and Intermediate Zones were very capable of exploiting a variety of microhabitats *within* rainforest ecologies in order to maintain their forest specialisation. I now turn to one of these exploitation strategies, primate hunting, in order to gain a more detailed handle on the diverse and stable resource strategies that have allowed humans to rely upon South Asia's rainforests for at least the last 36-29,000 years.

Chapter 7 – Late Pleistocene-Holocene and modern primate stable isotope ecology in Sri Lanka

This chapter revisits the stable carbon and oxygen isotope data from the fossil primates presented in Chapter 6 in order to evaluate the ecological relevance of these results for primate ecology, and then the potential importance of these niche differences for prehistoric human rainforest subsistence in Sri Lanka. Stable carbon, oxygen and nitrogen isotope results analysed from the modern vegetation, as well as stable carbon and oxygen isotope results from modern primate enamel samples, from the Polonnaruwa Nature Sanctuary and Archaeological Reserve are discussed as baselines to evaluate interpretations of Sri Lankan primate isotope ecology and niche distinctions past and present. Niche distinctions between *Macaca sinica*, *Tracypithecus vetulus*, and *Semnopithecus priam thersites* are discussed in detail. Finally, broader issues with using stable isotope analysis of primate tissues to obtain high-resolution ecological information in primatology are discussed.

7.1 – Stable isotope ecology of Late Pleistocene-Holocene Sri Lankan primates

Fossil enamel $\delta^{13}C$ and $\delta^{18}O$ data for Late Pleistocene-Holocene specimens of *Macaca sinica*, *Tracypithecus vetulus*, and *Semnopithecus priam thersites* were presented in Chapter 6 and the full list of results can be found in Catalogue Table B13. At each of the sites of Fa Hien-Lena, Balangoda Kuragala, Bellan-bandi Palassa and Batadomba-lena more than one of these primate species is present. However, contrary to the set of expectations outlined in Chapter 4 (Section 4.4), obvious stable isotope niche distinctions between these species do not always exist at each site.

Fa Hien-lena

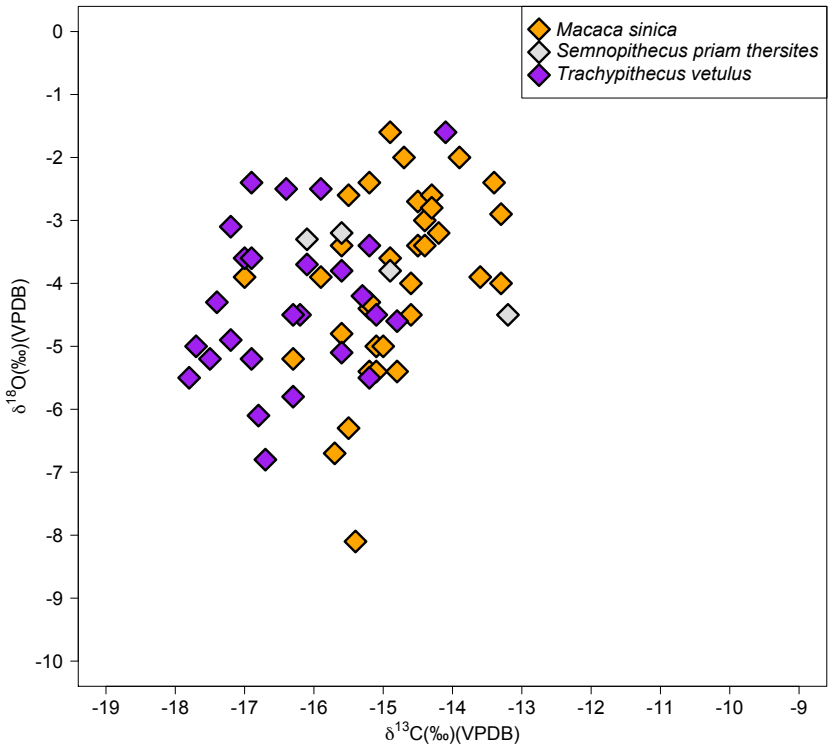


Figure 7.1. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena.

At the site of Fa Hien-lena all three species of monkey found in modern Sri Lanka have been identified. The four *Semnopithecus priam thersites* individuals are unusual in that the modern species do not occur in the Wet Zone rainforests of Sri Lanka today. This either implies that this species occupied a wider ecological niche in the past or that the Wet Zone rainforests today were more open during the Terminal Plesitocene/Early Holocene. This latter possibility would, however, appear to be ruled out by the fact that the other faunal identifications, and their $\delta^{13}C$ and $\delta^{18}O$, are indicative of closed Wet Zone rainforest at the site. The primary monkey niche distinction observed at the site is between *Trachypithecus vetulus* and *Macaca sinica* (Figure 7.1). Figure 7.1 shows that *Trachypithecus vetulus* has lower $\delta^{13}C$ values (mean= -16.3 ± 0.9‰) than *Macaca sinica* (-14.9 ± 0.8‰). By contrast, no discernible $\delta^{18}O$ distinction is observable

between the species. These trends are more easily observable when primate $\delta^{13}C$ and $\delta^{18}O$ values are plotted by stratigraphic layer (Figure 7.2). In every layer where both species are present, *Macaca sinica* show higher $\delta^{13}C$ relative to *Trachypithecus vetulus*. No consistent $\delta^{18}O$ trend is evident between the species throughout the sequence.

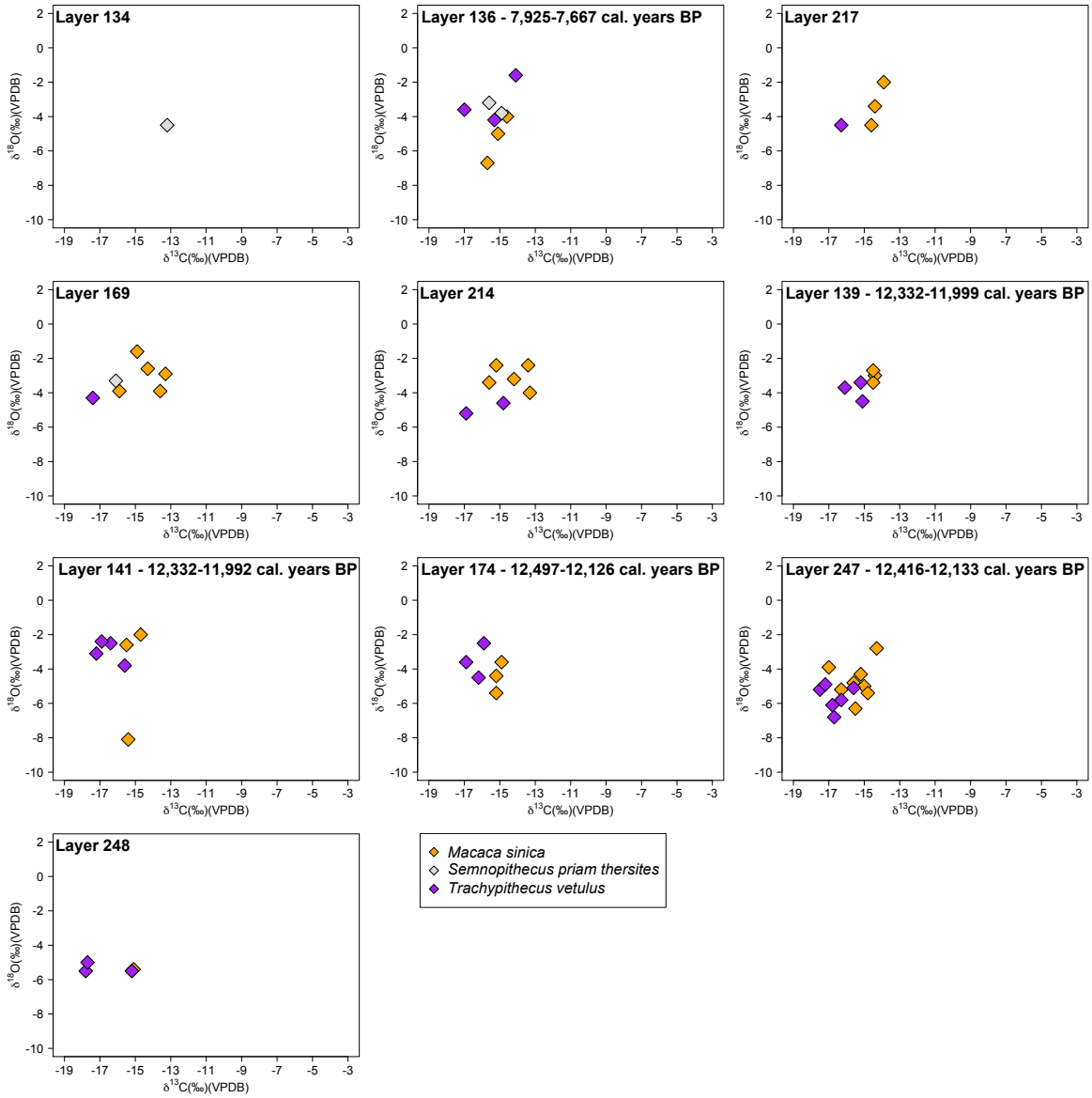


Figure 7.2. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer.

ANOVA testing and post-hoc Tukey pair-wise comparison supports these observations and draws out *Trachypithecus vetulus* and *Macaca sinica* as being distinct from each other in terms of $\delta^{13}C$ ($F(9,74)=6.191$, $p<0.05$) (Catalogue Tables B17 and B18). No distinction is found between the $\delta^{13}C$ of *Semnopithecus priam thersites* and *Macaca sinica* or *Semnopithecus priam thersites* and *Trachypithecus vetulus*, though this could be a result of small sample size in the case of the former ($p>0.05$) (Catalogue Tables B17 and B18). ANOVA testing failed to draw out a $\delta^{18}O$ distinction between any of the primate species ($F(9,66)=1.237$, $p>0.05$) (Catalogue Tables B19 and B20). Lower $\delta^{13}C$ values in *Trachypithecus vetulus*, when compared to *Macaca sinica*, could *either* indicate a greater predominance of leaves in the diet of the former *or* that *Trachypithecus vetulus* was inhabiting more closed areas of the forest than *Macaca sinica*. Following Krigbaum *et al.* (2013), *Trachypithecus vetulus* would also have been expected to have higher $\delta^{18}O$ due to its feeding higher in the canopy than *Macaca sinica*. However, such an interpretation is confounded by the fact that *Macaca sinica* will drink from open, potentially evaporated, water sources on the ground (Fooden, 1979; Dittus, 1984), while *Trachypithecus vetulus* is a non-obligate drinker obtaining the majority of its water from foliage. The lack of distinction in $\delta^{18}O$ between the species could therefore be a consequence of different feeding and drinking behaviours as much as it is an indicator of canopy feeding height.

Further resolution into the mechanism behind this difference might be visible in boxplots of *Macaca sinica* and *Trachypithecus vetulus* $\delta^{13}C$ and $\delta^{18}O$ values by layer (Figures 7.3-7.4). *Macaca sinica* $\delta^{13}C$ and $\delta^{18}O$ values exhibit *no* trend through time, possibly reflecting (1) a diverse diet and drinking strategy that eclipses ecological variability, (2) dietary variation not associated with isotopic variation, or (3) the absence

of ecologically relevant environmental change (Figure 7.3). An ANOVA test demonstrates that stratigraphic layer played no role in structuring *Macaca sinica* $\delta^{13}C$ ($F(8,25)=1.552$, $p>0.05$) or $\delta^{18}O$ ($F(8,25)=1.745$, $p>0.05$) (Catalogue Tables C1 and C2). *Trachypithecus vetulus*, by contrast, appears to demonstrate a trend towards lower $\delta^{18}O$ values from the Holocene to the Terminal Pleistocene layers at the site (Figure 7.4). While the effect of layer on *Trachypithecus vetulus* $\delta^{13}C$ values is not statistically significant (Catalogue Table C3) ($F(8,17)=1.078$, $p>0.05$), ANOVA testing and subsequent post-hoc Tukey pair-wise comparison indicates statistical differences among stratigraphic layers for *Trachypithecus vetulus* $\delta^{18}O$ values ($F(8,17)=5.748$, $p<0.05$) (Catalogue Tables C4 and C5). Lower $\delta^{18}O$ values in the oldest part of the Fa Hien-lena sequence are also observed in the faunal assemblage as a whole (Chapter 6 – Section 6.2). Although these inter-layer analyses are based on very small sample sizes, the fact that *Trachypithecus vetulus* records this environmental signal in $\delta^{18}O$ and *Macaca sinica* does not may further indicate the fact that the non-obligate drinker *Trachypithecus vetulus* is obtaining the majority of its water from humidity-sensitive leaves (Chapter 4 – Section 4.4).

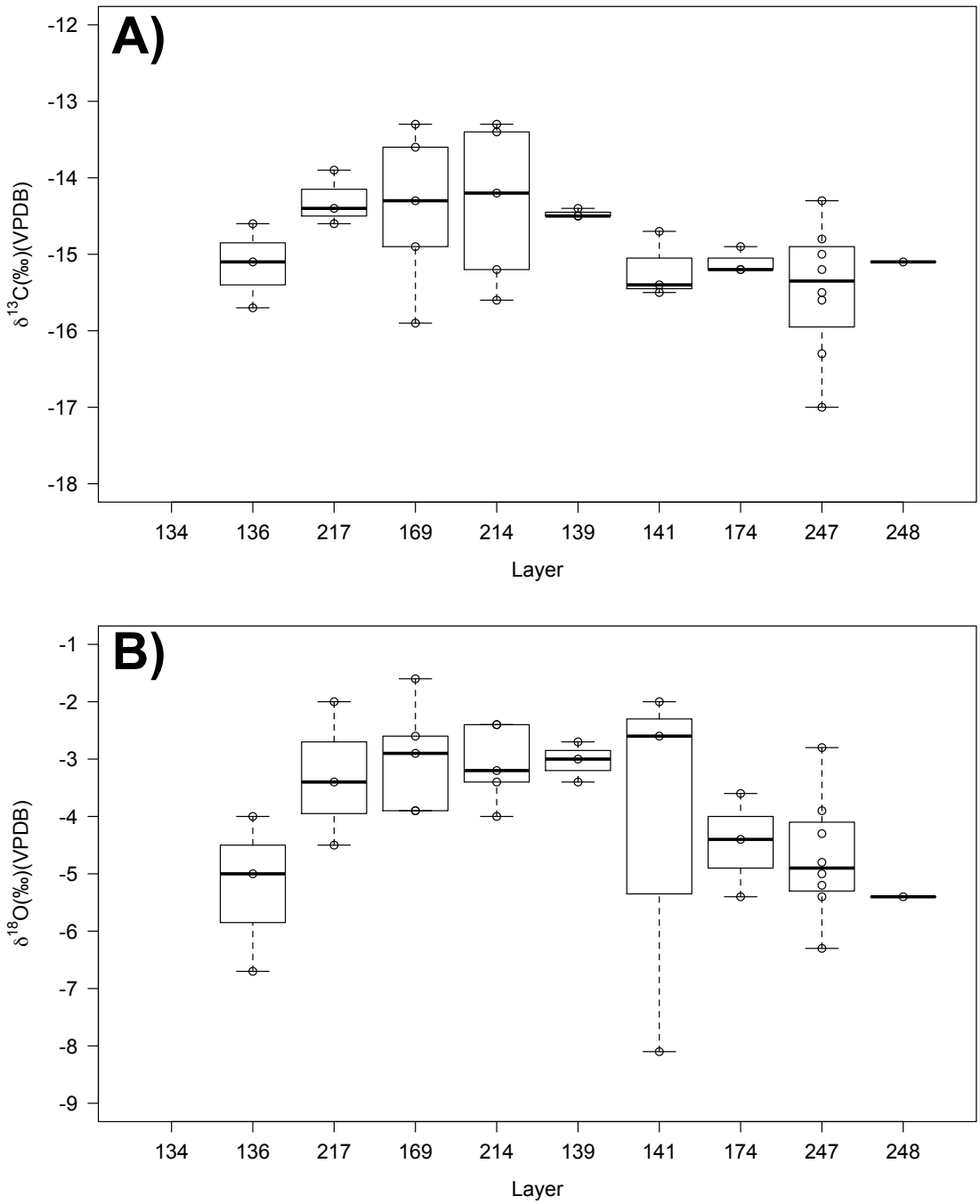


Figure 7.3. Boxplots of Macaca sinica *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer.*

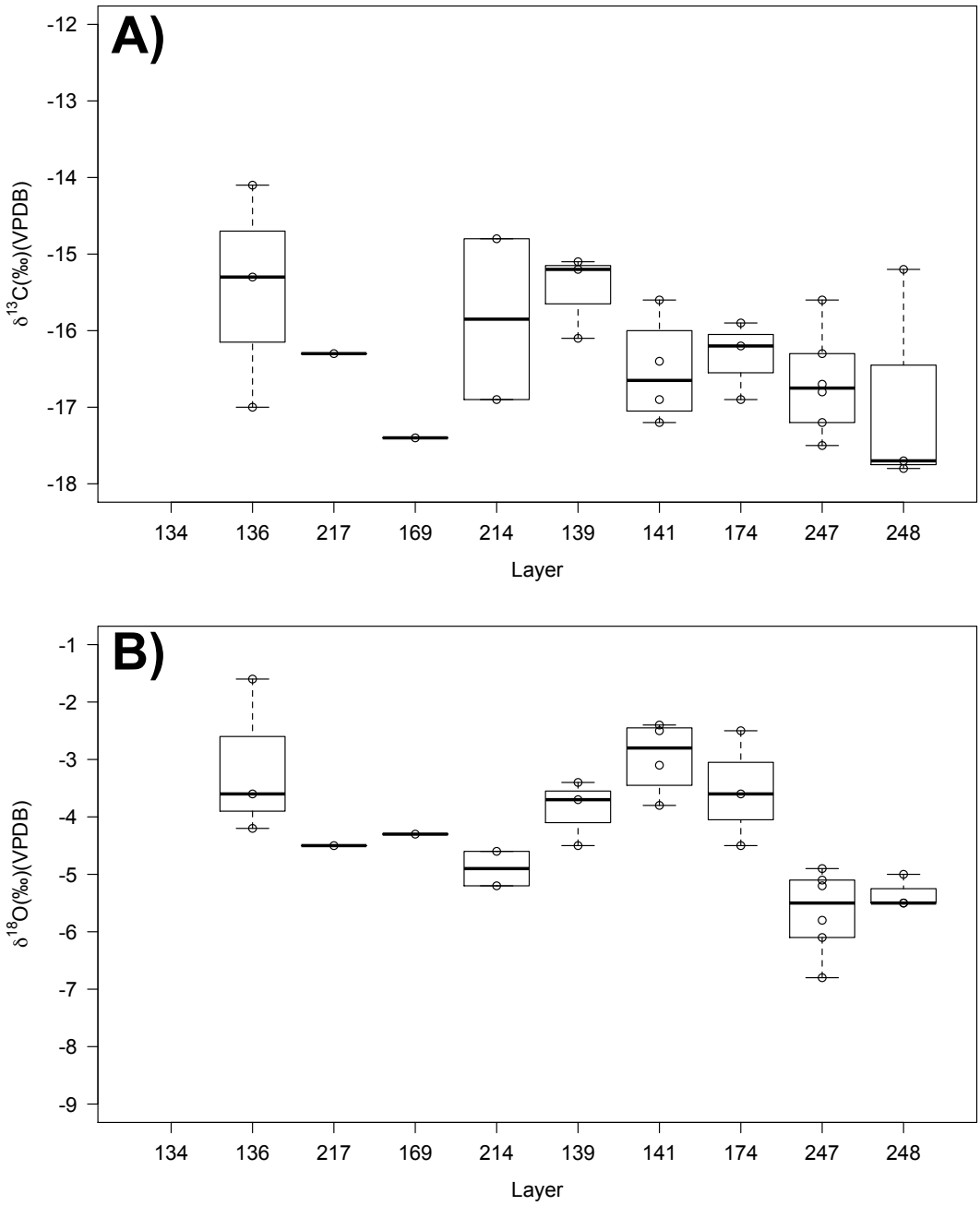


Figure 7.4. Boxplots of Trachypithecus vetulus *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Fa Hien-lena shown by stratigraphic layer.*

Balangoda Kuragala

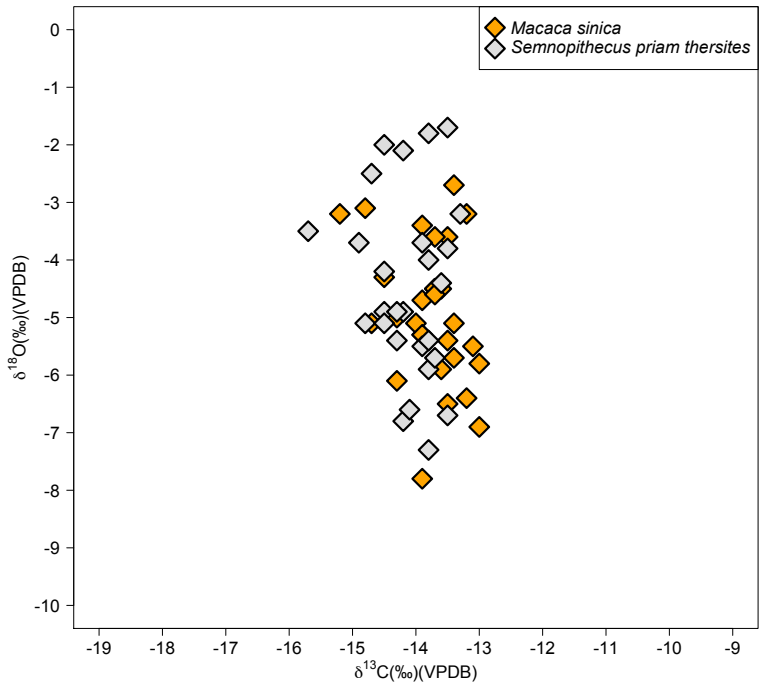


Figure 7.5. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala.

Macaca sinica and *Semnopithecus priam thersites* were the only monkey species found in the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala, further supporting the information in Chapter 6 that indicates this site retained more open 'Intermediate' rainforest cover across its period of occupation. As might be expected for two dietary generalists there are no obvious distinctions between these species in either $\delta^{13}C$ or $\delta^{18}O$ at the site (Figure 7.5). Although Figure 7.5 shows a group of *Semnopithecus priam thersites* that have higher $\delta^{18}O$ than their con-specifics and *Macaca sinica*, they do not influence the overall trend and post-hoc Tukey pair-wise comparison failed to draw out any distinctions between the species in either $\delta^{13}C$ ($p>0.05$) (Catalogue Tables B30 and B31) or $\delta^{18}O$ ($p>0.05$) (Catalogue Tables B32 and B33) (Chapter 6 – Section 6.2). The lack of any consistent $\delta^{13}C$ or $\delta^{18}O$ pattern

between *Macaca sinica* and *Semnopithecus priam thersites* persists when the data are plotted by stratigraphic layer (Figure 7.6), with the relative position of each species in $\delta^{13}C$ or $\delta^{18}O$ space changing through time. Although modern ecological information and existing stable isotope ecologies for primates outlined in Chapter 4 might suggest that *Semnopithecus priam thersites* would have lower $\delta^{13}C$ and higher $\delta^{18}O$ (as a result of leaves being a more major component of their diet and their feeding at a greater height, respectively) than *Macaca sinica,* this is not borne out here.

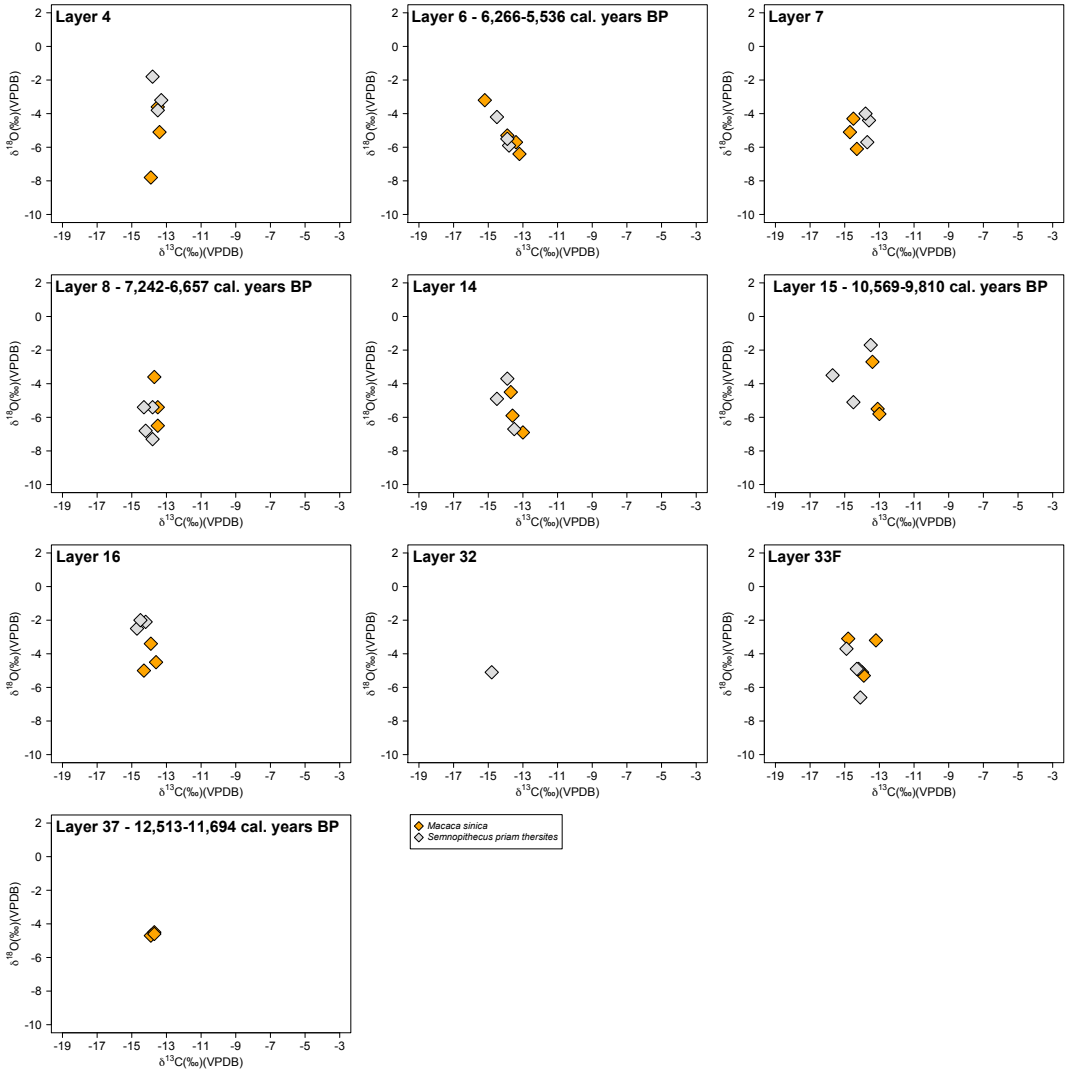


Figure 7.6. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer.

The generalist strategies of both these primates are further indicated by analysis of their $\delta^{13}C$ and $\delta^{18}O$ by stratigraphic layer (Figures 7.7-7.8). Although again based on a small sample, inter-layer comparison suggests that there is no consistent pattern in the structuring of *Macaca sinica* $\delta^{13}C$ and $\delta^{18}O$ by layer. This is further supported by ANOVA tests that fail to draw out any distinctions in $\delta^{13}C$ ($F(8,20)=1.945$, $p>0.05$) or $\delta^{18}O$ ($F(8,20)=0.543$ $p>0.05$) through time (Catalogue Tables C6 and C7). The $\delta^{13}C$ of *Semnopithecus priam thersites* appears equally variable on an intra-layer basis, with ANOVA testing indicating that it accounts for more variability than inter-layer variation ($F(8,18)=1.848$, $p>0.05$) (Catalogue Table C8). By contrast, *Semnopithecus priam thersites* $\delta^{18}O$ demonstrates some structuring by stratigraphic layer ($F(8,18)=41.98$, $p<0.05$) (Catalogue Tables C9 and C10). Post-hoc Tukey pair-wise comparison indicates that Layers 16 and 8 are distinct from each other (Catalogue Table C10), as was also demonstrated in the overall faunal dataset from Balangoda Kuragala ($F(9,94)=4.121$, $p<0.05$)) (Catalogue Table B33). That said, the sample size currently remains far too small to provide definitive conclusions and a lack of definitive niche separation in $\delta^{13}C$ may highlight the generalist dietary tendencies in *Semnopithecus priam thersites,* confounding purely environmental interpretation.

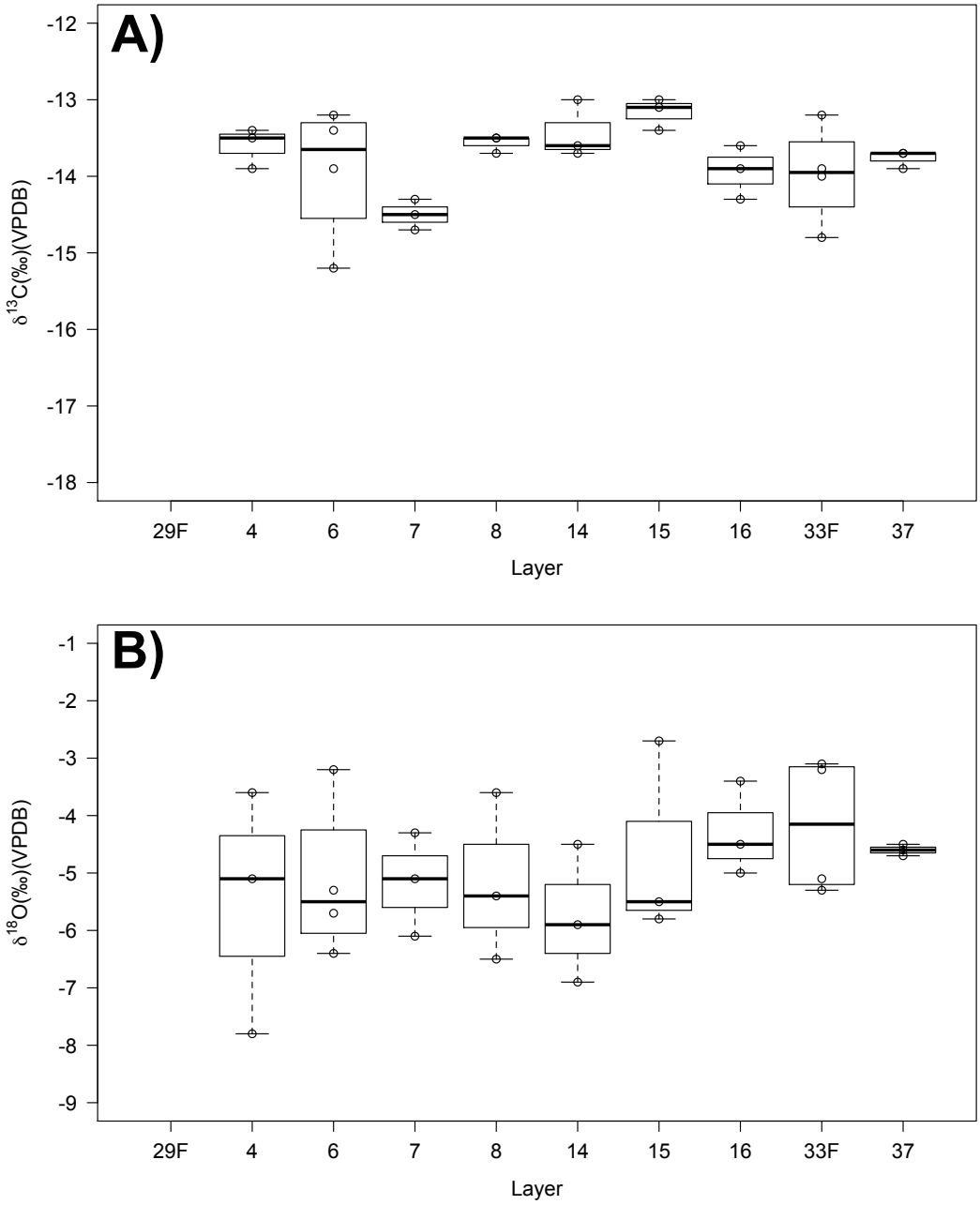


Figure 7.7. Boxplots of Macaca sinica *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer.*

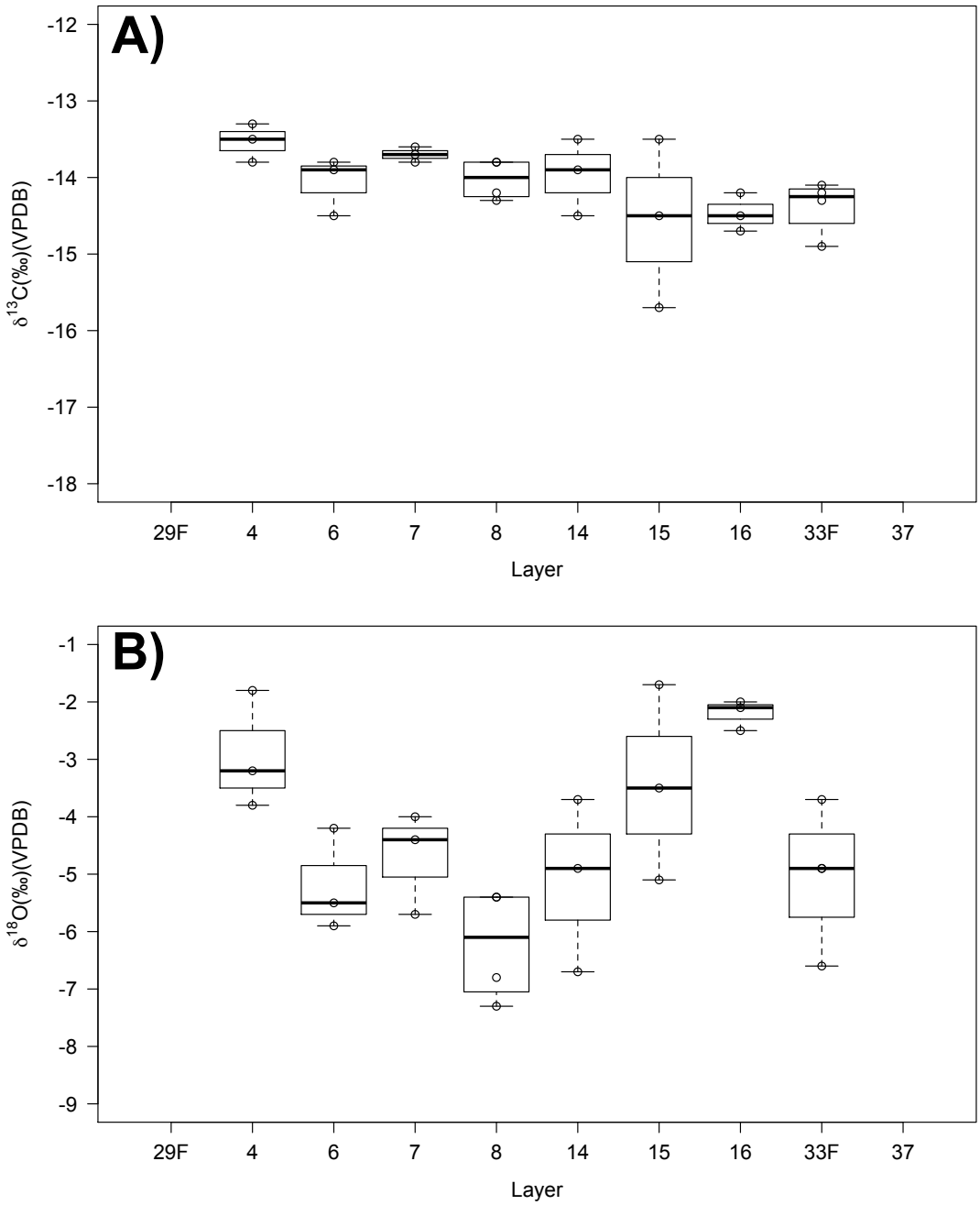


Figure 7.8. Boxplots of Semnopithecus priam thersites *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Balangoda Kuragala shown by stratigraphic layer.*

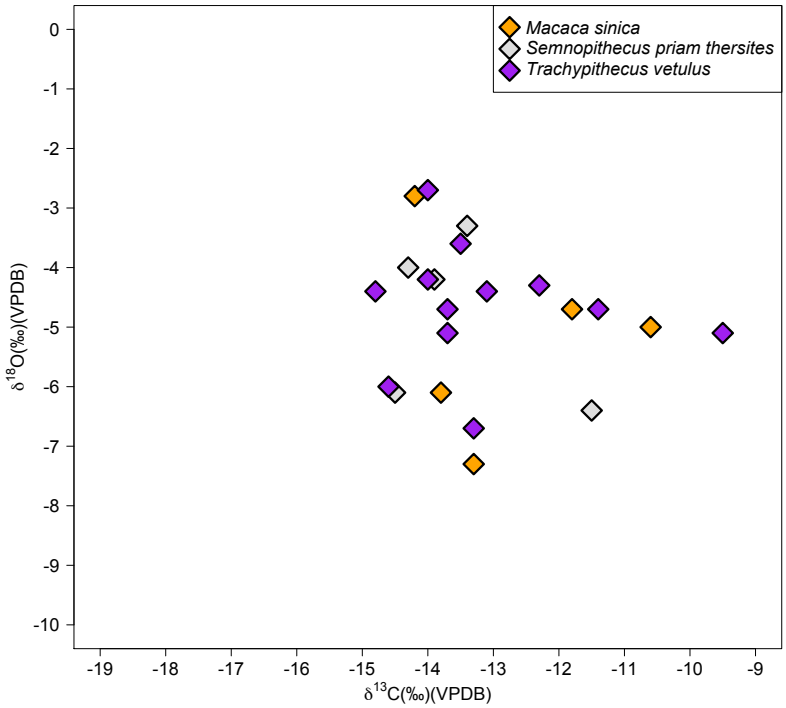


*Figure 7.9. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Layer 10 (*c. *12-11,000 cal. years BP) of Bellan-bandi Palassa.*

All three monkey species, *Trachypithecus vetulus*, *Semnopithecus priam thersites*, and *Macaca sinica*, were identified in Layer 10 (*c.* 12,000 cal. years BP) of the Dry Zone site Bellan-bandi Palassa. The $\delta^{13}C$ and $\delta^{18}O$ values of all three species overlap (Figure 7.9) and ANOVA testing failed to draw out a distinction in either $\delta^{13}C$ ($F(7,19)=1.020$, $p>0.05$) or $\delta^{18}O$ ($F(7,19)=0.708$, $p>0.05$) between any of the species (Chapter 6 – Section 6.2) (Catalogue Tables B36 and B37). The $\delta^{13}C$ values of *Trachypithecus vetulus* individuals at Bellan-bandi Palassa (-14.8 to -9.5‰) are, however, consistently higher compared to individuals of the same species at Fa Hien-lena (-17.8 to -14.1‰). This could suggest that this same species occupied a wide ecological niche at this time, ranging from closed 'Wet Zone' rainforests to more open 'Intermediate' rainforests *c.*

12,000 cal. years BP. Alternatively, this evidence could be indicative of the fact that the modern day Dry Zone subspecies, *Trachypithecus vetulus philbricki* (Phillips, 1926, 1980) (Chapter 4 – Section 4.4), was already occupying the denser forests of the Intermediate and Dry Zone *c.* 12-11,000 cal. years BP, at the same time as other *Trachypithecus vetulus* subspecies were specialising in the closed Wet Zone rainforests of Sri Lanka. Regardless, *Trachypithecus vetulus* individuals show no niche distinction, in either $\delta^{13}C$ or $\delta^{18}O$, to *Macaca sinica* or *Semnopithecus priam thersites* individuals at Bellan-bandi Palassa, indicating 1) similar, generalist dietary strategies across the three species or 2) niche differentiation that is not associated with isotopic variability.

Batadomba-lena

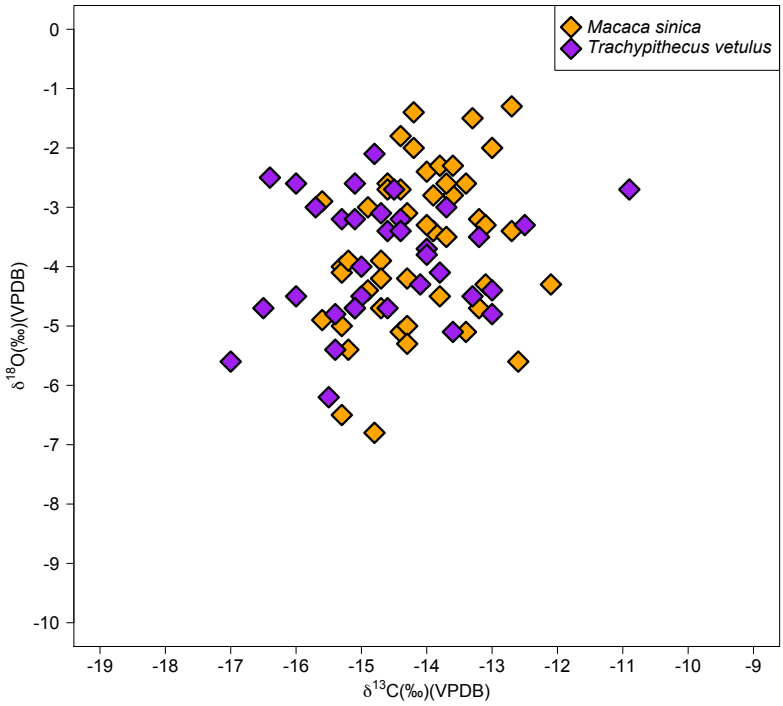


Figure 7.10. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Late Pleistocene site of Batadomba-lena.

Only the monkey species *Trachypithecus vetulus* and *Macaca sinica* have been identified at the Late Pleistocene Wet Zone site of Batadomba-lena. Although Figure 7.10 demonstrates that some members of *Trachypithecus vetulus* have lower $\delta^{13}C$ (range= -17.0 to -10.9‰), the values of other individuals of the same species fall right across the *Macaca sinica* range (-15.6 to -12.1‰). Indeed, post-hoc Tukey pair-wise comparison indicates that neither species can be distinguished from each other in terms of either $\delta^{13}C$ ($p>0.05$) or $\delta^{18}O$ ($p>0.05$) (Catalogue Tables B42-B45) (Chapter 6 – Section 6.4). This overlap is maintained when enamel $\delta^{13}C$ or $\delta^{18}O$ values from the two species are plotted by stratigraphic layer for the site (Figure 7.11). The breadth of the $\delta^{13}C$ range for *Trachypithecus vetulus* is dictated by Layer 7c (*c.* 36-29,000 cal. years BP) at a time when other faunal stable isotope information indicates the presence of an

environmental spectrum from closed forest to open ecosystems (Chapter 6 – Section 6.4). Batadomba-lena *Trachypithecus vetulus* $\delta^{13}C$ values range between -17.0 and -10.9‰ (-14.6±1.2‰), indicating the exploitation of rainforest habitats in the 'Wet' Zone that were slightly more open than those occupied by the same species at Fa Hien-lena subsequently (-17.8 to -14.1‰ (-16.3±1.0‰)).

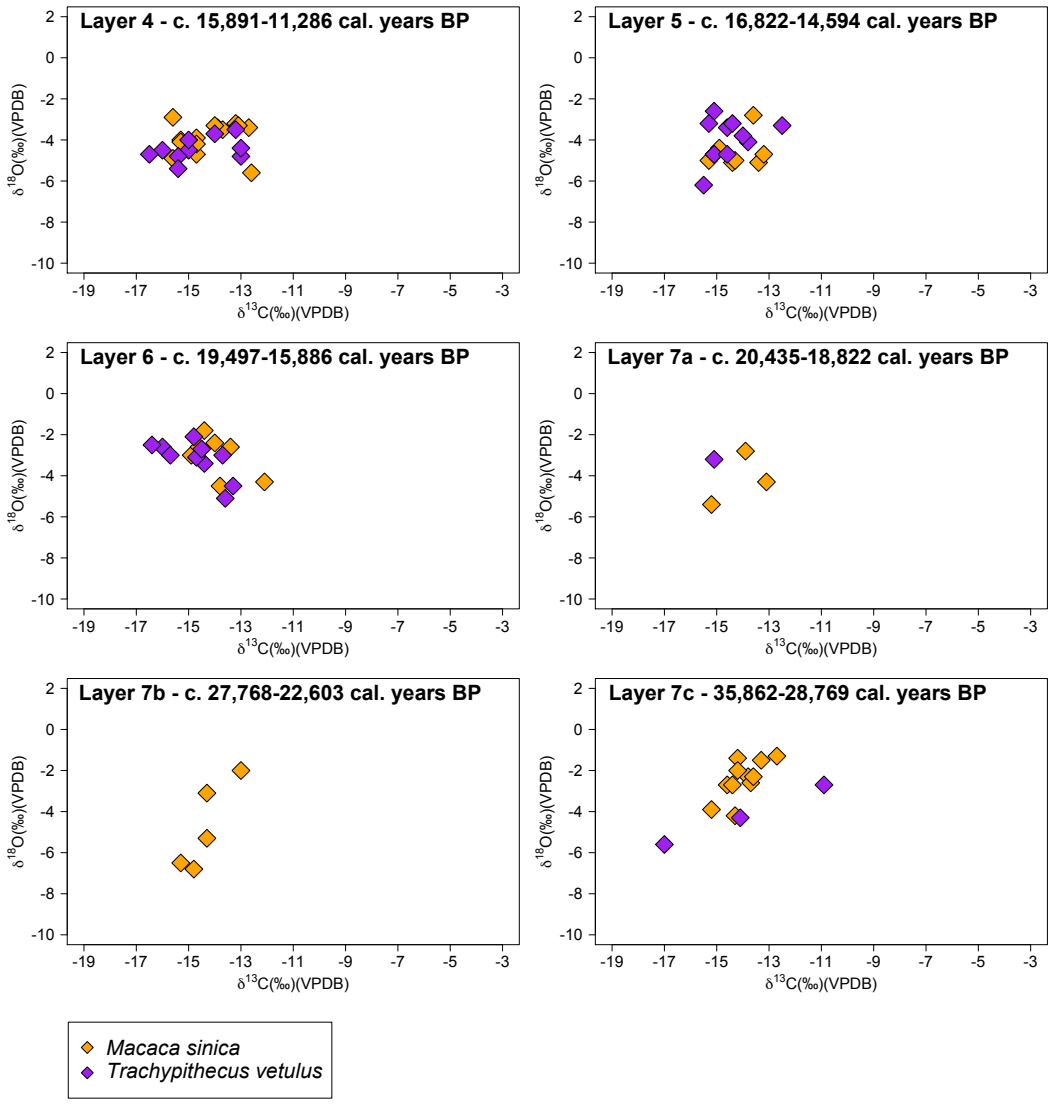


Figure 7.11. Primate $\delta^{13}C$ and $\delta^{18}O$ from the Terminal Pleistocene-Holocene sequence of Batadomba-lena shown by stratigraphic layer.

Analysis of the $\delta^{13}C$ and $\delta^{18}O$ datasets for *Macaca sinica* and *Trachypithecus vetulus* by stratigraphic layer reveals the large intra-layer variation in both $\delta^{13}C$ and $\delta^{18}O$ for both species (Figures 7.12-7.13). Large sample sizes for the primates from each layer enable more effective statistical analysis of stable isotope trends through time. Layer provenance has no influence on *Macaca sinica* $\delta^{13}C$ variation ($F(5,41)=0.233$, $p>0.05$) (Catalogue Table C11) but does effect $\delta^{18}O$ in the enamel of this primate species ($F(5,41)=5.536$, $p<0.05$)) (Catalogue Tables C12 and C13). Post-hoc Tukey pair-wise comparison suggests that this trend is primarily driven by Layer 7c (Figures 7.12-7.13) (Catalogue Table C13). Higher $\delta^{18}O$ in *Macaca sinica* individuals in Layer 7c (-2.5±0.9‰) perhaps further supports suggestions in Chapter 6 that open, evaporative environments were present in the vicinity that this species was exploiting for drinking water (Chapter 4 – Section 4.4). ANOVA testing of the effects of layer on *Trachypithecus vetulus* $\delta^{13}C$ ($F(4,30)=0.223$, $p>0.05$) and $\delta^{18}O$ ($F(4,30)=2.536$, $p>0.05$) suggests that there is no variation through time (Catalogue Tables C14 and C15) though intra-layer variation in $\delta^{13}C$ is particularly high in Layer 7c (*c.* 6‰ – Figures 7.11 and 7.13). Faunal $\delta^{13}C$ and $\delta^{18}O$ presented in Chapter 6 (Section 6.4) indicates more open rainforests in the Wet Zone of Sri Lanka between 36-29,000 cal. years BP and the LGM, perhaps suggesting that climate change encouraged *Trachypithecus vetulus* to make use of more open rainforest environments at this time when compared to individuals of the same species at Terminal-Pleistocene/Holocene Fa Hien-lena.

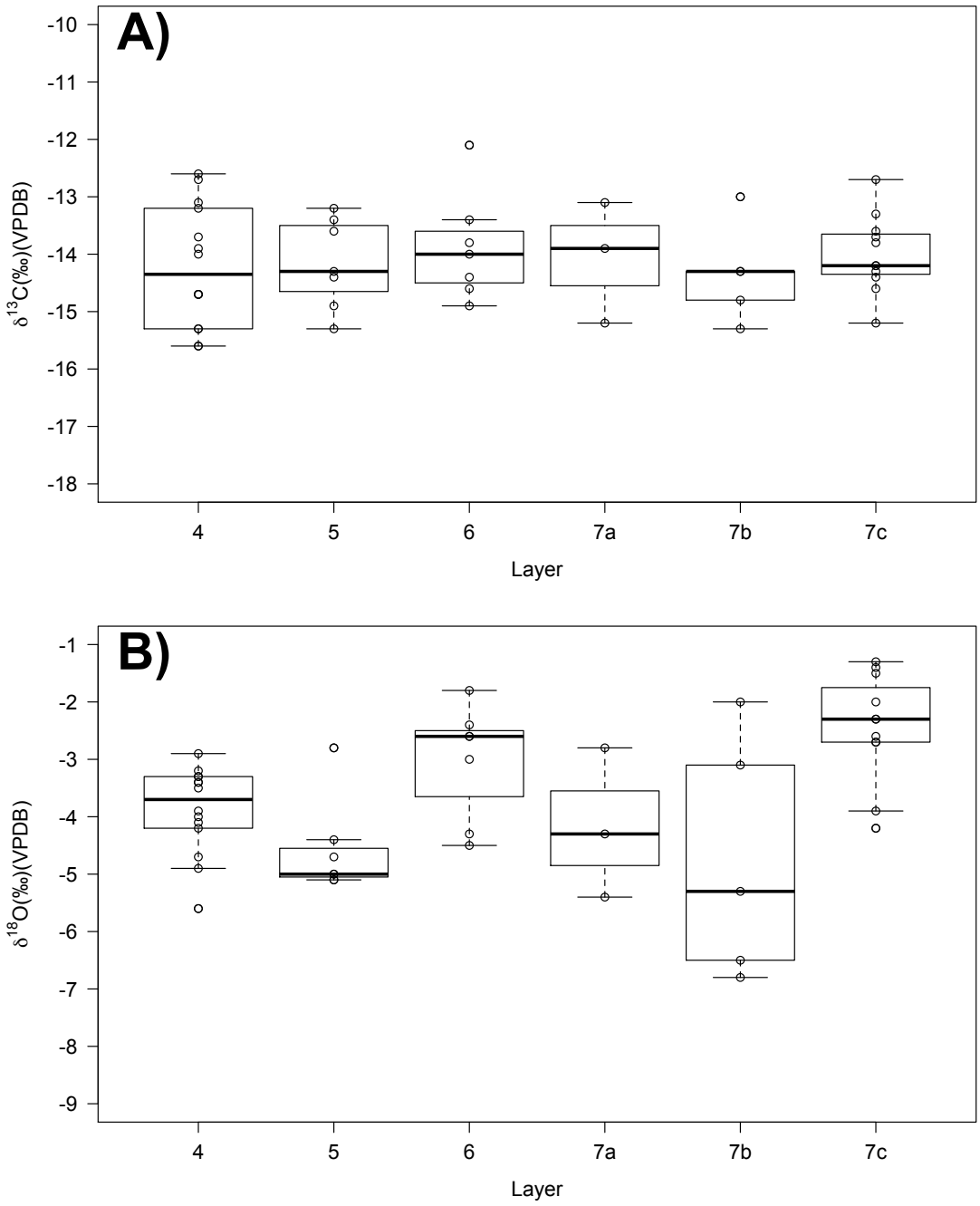


Figure 7.12. Boxplots of Macaca sinica *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Late Pleistocene sequence of Batadomba-lena shown by stratigraphic layer.*

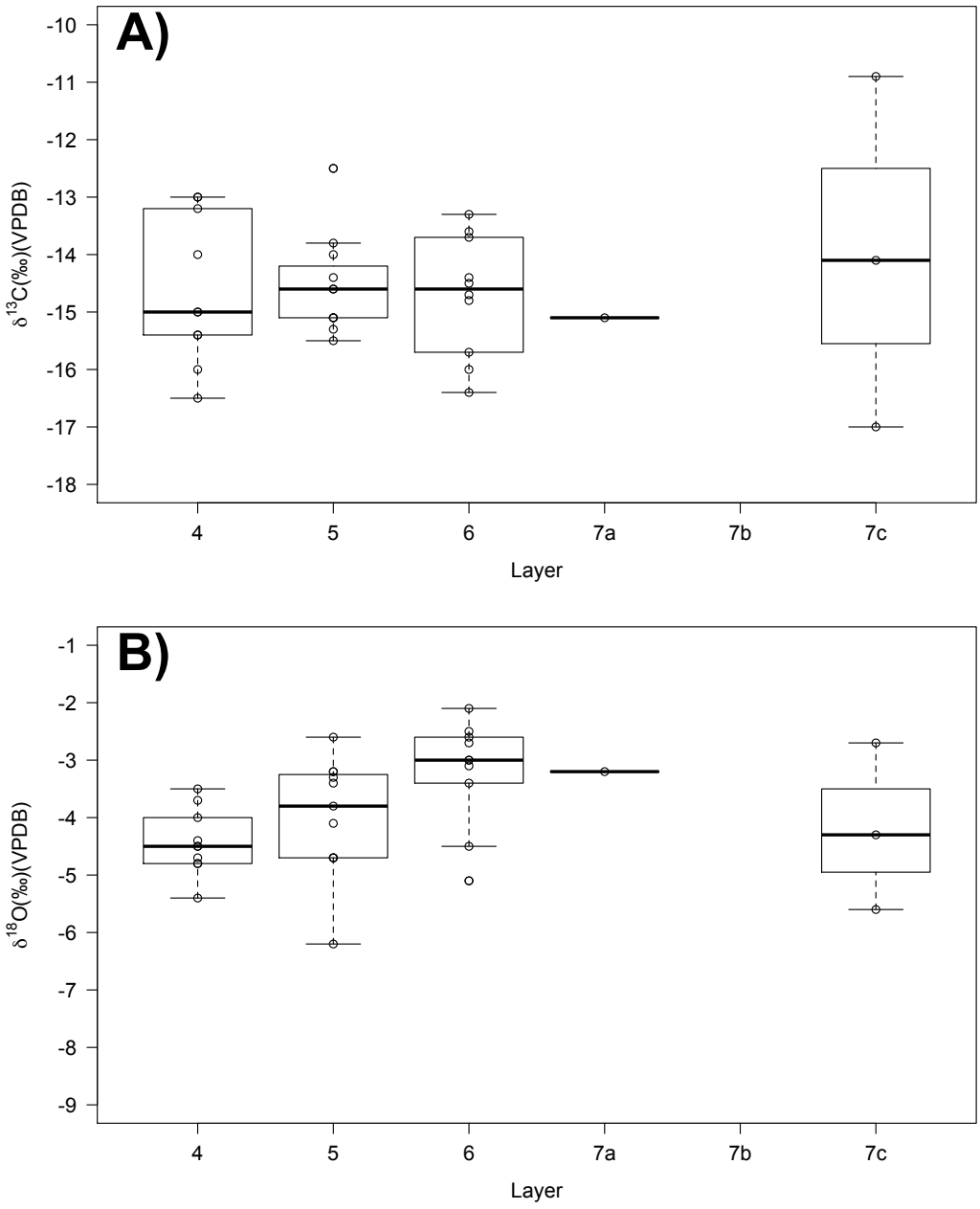


Figure 7.13. Boxplots of Trachypithecus vetulus *A) $\delta^{13}C$ and B) $\delta^{18}O$ from the Late Pleistocene sequence of Batadomba-lena shown by stratigraphic layer.*

An overview of Late Pleistocene-Holocene Sri Lankan primate niche distinctions

A number of studies on modern primate groups have suggested that $\delta^{13}C$ and $\delta^{18}O$ of their tissues can be used to explore niche differences between species (Chapter 4 – Section 4.3). Low $\delta^{13}C$ in primate tissues has been argued to be indicative of greater leaf versus fruit consumption (Oelze *et al.,* 2014), increased focus on more shaded or forested areas of a given forest or environmental spectrum (Macho and Lee-Thorp, 2014), or indicative of life at the base of the canopy (Cerling *et al.,* 2004). Similarly, higher primate $\delta^{18}O$ could imply a higher feeding height exposed to increased evapotranspiration (Krigbaum *et al.,* 2013; Carter and Bradbury, 2015; Crowley *et al.,* 2015), an increased consumption of evaporation-stressed leaves (Cernusak *et al.,* 2002), non-obligate drinking versus obligate drinking (Cerling *et al.,* 2004), or the exploitation of more open water sources in more open regions of the forest. As I highlighted in Chapter 4 (Section 4.3), the potential overlapping effects of these factors may confound highly resolved interpretations of primate niche differentiation. Indeed, the combination of these factors may be why the niche distinctions expected to be obvious in the Sri Lankan fossil primates are largely absent isotopically.

Even where significant stable isotope distinctions between primate species are present in the Sri Lankan fossil record, interpretation is complex. *Trachypithecus vetulus* has lower $\delta^{13}C$ values than *Macaca sinica* at the site of Fa Hien-lena. Given what we know regarding the digestive tract of the former and generalist diet of the latter, this could be linked to an increased focus on leaf consumption in *Trachypithecus vetulus* versus *Macaca sinica*. However, it could also be a result of *Trachypithecus vetulus* feeding in more shaded forest areas/parts of the canopy transect. This is further complicated by the fact that no niche distinction exists between the two in terms of $\delta^{18}O$. While this might

be used by some to suggest that both primates are feeding at the same canopy height or feeding equally on evapotranspiration-stressed leaves, modern ecological observation indicates that *Macaca sinica* is likely to be obtaining most of its water from open, potentially evaporation-stressed, water sources (Fooden, 1979; Dittus, 1984). As a result, high $\delta^{18}O$ could be an equifinal product of high feeding height, increased leaf consumption and obtaining the majority of drinking water from foliage by *Trachypithecus vetulus* and evaporative, open water source, obligate drinking by *Macaca sinica*.

Carter and Bradbury (2015) suggested confident environmental interpretations of primate tissue $\delta^{18}O$ might only be possible where we know that a species is primarily folivorous. Indeed, at both Fa Hien-lena and Balangoda Kuragala it is the colobines, and non-obligate drinkers, *Trachypithecus vetulus* and *Semnopithecus priam thersites*, respectively, that follow the environmental signal identified in the $\delta^{18}O$ of the site fauna as a whole. By contrast, $\delta^{18}O$ of the dietary generalist, and obligate drinker, *Macaca sinica,* does not follow these patterns. However, even changes in diet or drinking behaviour *within* the same species can cause problems in the interpretation of $\delta^{13}C$ and $\delta^{18}O$ data. At both the Dry Zone site of Bellan-bandi Palassa and Batadomba-lena the colobine *Trachypithecus vetulus* demonstrates considerable variability in the openness of the environments it is utilising, compared to individuals of the same species at Fa Hien-lena. This ranges from the use of more open 'Intermediate' forests at Bellan-bandi Palassa to occupation of a patchwork of open-closed environments at Batadomba-lena *c.* 36-29,000 cal. years BP. At both of these sites, this causes *Trachypithecus vetulus* $\delta^{13}C$ and $\delta^{18}O$ to overlap that of the dietary generalists *Semnopithecus priam thersites* and *Macaca sinica* (where they are present).

7.2 – Modern vegetation baseline results from the Polonnaruwa Nature Sanctuary

$\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) analysis of modern plant samples from the Polonnaruwa Nature Sanctuary and Archaeological Reserve, where all three of the identified monkey species are present today, was designed so as to provide information regarding the impact of different environmental and behavioural factors on the interpretation of Sri Lankan primate $\delta^{13}C$ and $\delta^{18}O$. Catalogue Tables C16 and C17 show the $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ measurements of each plant sample collected during the dry season and wet season, respectively. $\delta^{13}C$ measurements on the two standards (IAEA-CH-6 and IAEA-CH-7) used in two-point calibration of the plant sample $\delta^{13}C$ are shown in Tables C18 and C19. For CH-6 the average measurements were within 0.1‰ of the certified value for this standards (IAEA-CH-6 ($\delta^{13}C$=-10.4‰, SD=0.2; n=76) (Catalogue Table C18). For CH-7, the measured $\delta^{13}C$ average was 0.6‰ off from the certified value, with low standard deviation suggesting a consistency in this measurement across the runs (IAEA-CH-7 ($\delta^{13}C$=-31.6‰, SD=0.2; n=76)) (Catalogue Table C19).

$\delta^{15}N$ measurements on the two standards (IAEA-N_2 and IAEA-600) used in two-point calibration of the plant sample $\delta^{15}N$ are shown in Catalogue Tables C20 and C21. For both IAEA-N_2 and IAEA-600 the average $\delta^{15}N$ measurements were within 0.2‰ of the certified values (IAEA-N_2 ($\delta^{15}N$=20.1‰, SD=0.6; n=50); IAEA-600 (($\delta^{15}N$=1.1‰, SD=0.2; n=50)), although the standard deviation for IAEA-N_2 indicates some measurement variability across the runs. $\delta^{18}O$ measurements on the two standards (EMA-P1 and EMA-P2) used in two-point calibration of the plant sample $\delta^{18}O$ are shown in Catalogue Tables C22 and C23. The average $\delta^{18}O$ measurements of EMA-P1 and EMA-P2 are within 0.1‰ of their certified values, with lower standard deviations

across runs than are certified (EMA-P1 ($\delta^{18}O$=21.0‰, SD=0.3; n=50); EMA-P2 ($\delta^{18}O$=27.0‰, SD=0.7; n=50). Levels of isotopic variation within the plant samples themselves were analysed by taking ten separate $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ subsample measurements (and their standard deviations) from the two single bulk samples PL 183 and PL 178 (Tables 7.1-7.2). In all cases isotopic variation (standard deviation) within a sample is minimal (PL183: $\delta^{13}C$=0.1, $\delta^{15}N$=0.2, $\delta^{18}O$=0.2; PL178: $\delta^{13}C$=0.1, $\delta^{15}N$=0.2, $\delta^{18}O$=0.2).

*Table 7.1. $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ measurements of ten subsamples taken from PL 183 (*Ficus benghalensis *fruits).*

Sample	**PL 183**	**PL 183 A**	**PL 183 B**	**PL 183 C**	**PL 183 D**	**PL 183 E**	**PL 183 F**	**PL 183 G**	**PL 183 H**	**PL 183 I**	**Mean**	**S.D.**
$\delta^{13}C$ (‰) (VPDB)	-32.4	-32.6	-32.6	-32.4	-32.4	-32.4	-32.5	-32.6	-32.6	-32.6	-32.5	0.1
$\delta^{18}O$ (‰) (VSMOW)	23.2	23.5	23.1	23.4	23.2	23.3	23.3	23.3	23.5	23.0	23.3	0.2
$\delta^{15}N$ (‰) (AIR)	5.1	5.4	5.1	5.1	5.4	5.0	5.5	4.9	5.5	5.0	5.2	0.2

*Table 7.2. $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$ measurements of ten subsamples taken from PL 178 (*Manilkara hexandra *leaves).*

Sample	**PL 178**	**PL 178 A**	**PL 178 B**	**PL 178 C**	**PL 178 D**	**PL 178 E**	**PL 178 F**	**PL 178 G**	**PL 178 H**	**PL 178 I**	**Mean**	**S.D.**
$\delta^{13}C$ (‰) (VPDB)	-27.4	-27.7	-27.7	-27.4	-27.5	-27.7	-27.6	-27.5	-27.4	-27.6	-27.6	0.1
$\delta^{18}O$ (‰) (VSMOW)	24.7	25.0	24.6	24.6	25.1	24.5	24.7	24.9	24.7	24.6	24.7	0.2
$\delta^{15}N$ (‰) (AIR)	7.3	7.5	7.2	7.2	7.0	7.1	7.1	7.0	7.2	7.4	7.2	0.2

Principal components analysis (PCA)

PCA analysis was used to determine whether $\delta^{13}C$, $\delta^{18}O$ or $\delta^{15}N$ had the greatest impact on variance in the data. Skewness, centre and scale transformations were applied to standardise the variables prior to the application of PCA. The analysis produced three principal components (Catalogue Table C24). Principal Components 1 and 2 together explain 80% of the variance in the data. As can be seen in Figure 7.14 (and Catalogue Table C24), Principal Component 1 gives the most weight to $\delta^{13}C$, followed by $\delta^{18}O$, in a positive direction, with both operating in the same direction along this component. Principal Component 1 accounts for 42% of the variance in the data. Principal Component 2 gives almost equal weight to $\delta^{15}N$ and in a negative direction. Principal Component 2 accounts for 38% of the data. As can be seen in Figure 7.14, however, Principal Component 1 is affected by a cluster of plant samples at the far end of the positive scale. These samples are Cyperaceae spp. sedges that come from an open, waterlogged area beyond the forest ecology and were used to provide a control for 'open' resources in the region. They greatly extend the $\delta^{13}C$ scale of the plant dataset (Cyperaceae spp. average= -12.3‰, SD=0.5; Rest of plants average $\delta^{13}C$ = -29.1‰, SD=2.0).

To analyse the impact of $\delta^{13}C$, $\delta^{18}O$ or $\delta^{15}N$ on plant data variance solely *within* the forest plants, PCA analysis was repeated with the Cyperaceae spp. samples removed (Figure 7.15, Catalogue Table C25). Principal Components 1 and 2 together explain 78% of the variance in the data. As seen in Figure 7.15 (and Catalogue Table C25), Principal Component 1 gives the most weight to $\delta^{13}C$ and $\delta^{18}O$ in a negative direction, with both operating in the same direction along this component. Principal Component 1

accounts for 43% of the variance in the data. Principal Component 2 gives the most weight to $\delta^{15}N$ in a positive direction, discriminating it from $\delta^{13}C$ that operates in the opposite direction along this component. Principal Component 2 accounts for 35% of the data. While the trends remain broadly the same across the two analyses, it is clear that these Cyperaceae spp. outliers affect the weighting of $\delta^{13}C$ and $\delta^{18}O$ in Principal Components 1 and 2. They have consequently been removed from all further statistical analyses.

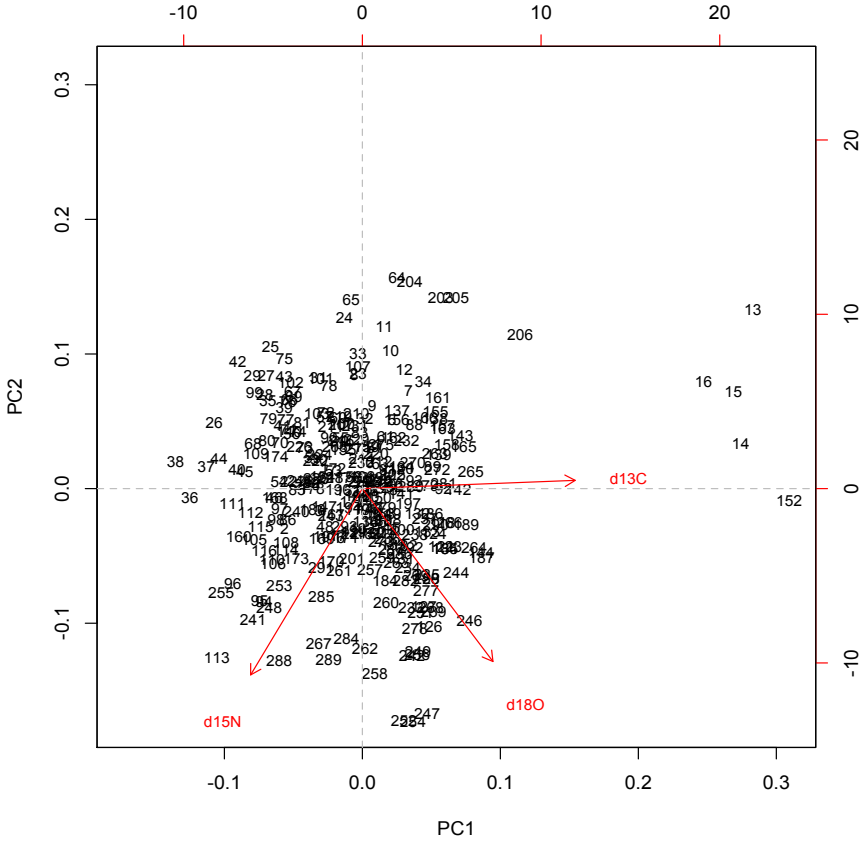


Figure 7.14. Plot of the first two components of PCA analysis, and the observation location of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$, of modern plant samples (with Cyperaceae spp. included).

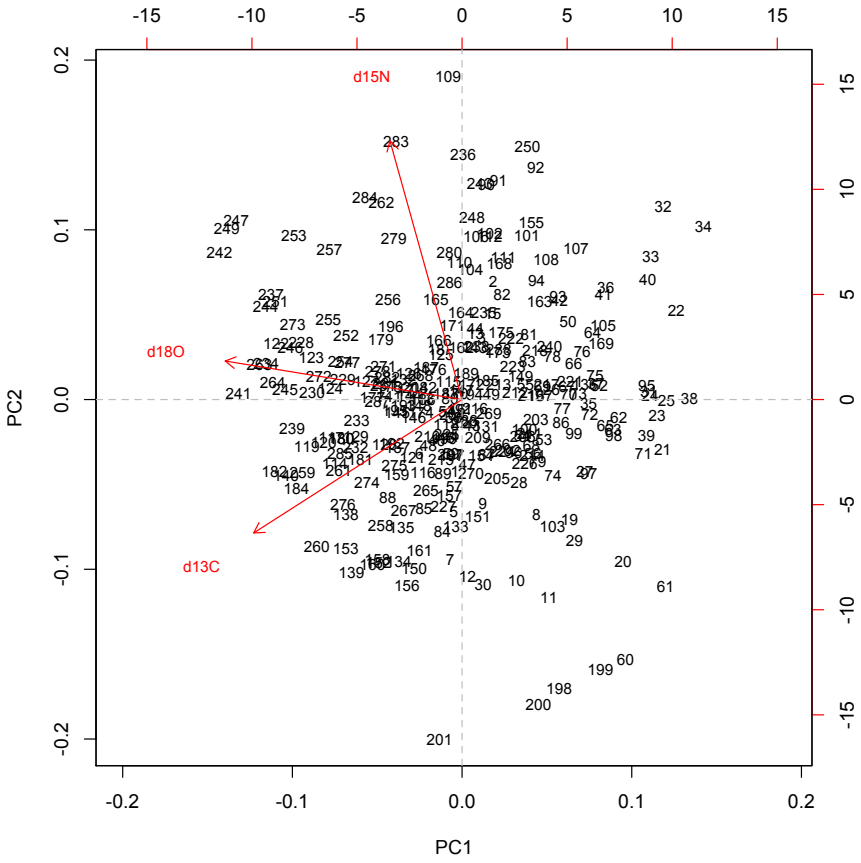


Figure 7.15. Plot of the first two components of PCA analysis, and the observation location of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$, of modern plant samples (with Cyperaceae spp. excluded).

Stable carbon and oxygen isotope variation

ANOVA testing on linear models of the effects of species (those taxa considered to be of significance to primate diets (Catalogue Tables A8-A11)), plant part (fruits, flowers, leaves, and young leaves where of relevance to primate diets (Catalogue Table A8-A11)), insolation (as a categorical variable of low, medium, high), height (as a categorical variable of low (0-5m) middle (5-15m), upper (15-30m)) and season (dry or wet) on $\delta^{13}C$, as well as their interaction effects, demonstrate that species ($F(17,191)=18.993$, $p<0.05$), plant part ($F(5,191)=31.606$, $p<0.05$), insolation

($F(2,191)=99.707$, $p<0.05$), and season ($F(1,191)=78.328$, $p<0.05$), but not height ($p>0.05$), significantly influenced plant $\delta^{13}C$ within the Polonnaruwa Nature Sanctuary (Catalogue Tables C26-C28). Interaction effects are observed between species and plant part ($F(21,191)=3.037$, $p<0.05$), species and insolation ($F(27,191)=1.757$, $p<0.05$), species and height ($F(13,191)=1.960$, $p<0.05$), and species and season ($F(10,191)=11.294$, $p<0.05$), suggesting that different species respond differently to the effects of plant part, insolation, height in the canopy and season (Catalogue Tables C26-C27). Plant species is therefore arguably the most important influence on sample $\delta^{13}C$. Post-hoc Tukey pair-wise comparison supports this point and demonstrates 32 species distinctions in $\delta^{13}C$ ($p<0.05$) (Catalogue Table C29). Plant part also significantly influences $\delta^{13}C$, with leaves and flowers, leaves and fruits, unripe fruit and fruit, unripe fruit and leaf shoots, unripe fruit and leaves, and young leaves and unripe fruit all being found to be significantly different from each other by post-hoc Tukey pair-wise comparison tests ($p<0.05$) (Catalogue Table C29). Plants grouped as experiencing low versus high, medium versus high, and medium versus low insolation were also found to be significantly different from each other in terms of $\delta^{13}C$ while plant $\delta^{13}C$ sampled during the wet and dry season are also distinct from each other (Catalogue Table C29) ($p<0.05$).

ANOVA testing on linear models of the environmental effects on $\delta^{18}O$ found species ($F(17,227)=27.877$, $p<0.05$), plant part ($F(5,227)=11.651$, $p<0.05$), insolation ($F(2,227)=3.651$, $p<0.05$) and season ($F(1,227)=217.639$, $p<0.05$) to also significantly effect plant sample $\delta^{18}O$ (Catalogue Tables C30-C33). In addition, the height at which the plant sample was collected in the canopy also has a significant impact on measured $\delta^{18}O$ ($F(2,227)=11.860$, $p<0.05$) (Catalogue Tables C30-C33). Interaction effects

between species and plant part ($F(21,227)=5.069$, $p<0.05$) and species and season ($F(12,227)=5.299$, $p<0.05$) were also found, again suggesting that different species respond differently to the impacts of plant part and season on their $\delta^{18}O$ values (Catalogue Table C32). That species has a significant impact on plant sample $\delta^{18}O$ is further demonstrated by a post-hoc Tukey pair-wise comparison, which demonstrates 50 species distinctions in $\delta^{18}O$ ($p<0.05$) (Catalogue Table C34). As with $\delta^{13}C$, plant part impacts $\delta^{18}O$, with post-hoc Tukey pair-wise comparison testing finding differences between fruits and flowers, young leaves and flowers, leaf shoots and fruit, leaves and fruit, and young leaves and leaf shoots ($p<0.05$) (Catalogue Table C34). Although both insolation and height were found to significantly impact plant sample $\delta^{18}O$ in ANOVA testing, no specific distinctions were found in post-hoc Tukey pair-wise analysis ($p>0.05$) (Catalogue Table C34). By contrast, a significant $\delta^{18}O$ distinction was found between plants collected in the dry season versus those collected in the wet season ($p<0.05$) (Catalogue Table C34).

The impacts of the different environmental factors are also seen in plots of $\delta^{13}C$ by $\delta^{18}O$. Figure 7.16. Plants collected within the forest (excluding the Cyperaceae spp.) during the dry season tend to have higher $\delta^{13}C$ (-32.8 to -23.5‰, mean=-28.4±1.8‰) and $\delta^{18}O$ (23.2 to 35.4‰, mean=28.1±2.7‰) values than those collected within the forest during the wet ($\delta^{13}C$: -34.7 to -25.6‰, mean=-30.1±1.7‰, $\delta^{18}O$: 19.9 to 30.5‰, mean=24.7±2.4‰) season (Figure 7.16). These trends are expected given that during the dry season, lower rainfall and higher temperatures cause the Polonnaruwa forest to become more open (Chapter 5 – Section 5.4), resulting a reduction in the 'canopy effect' and therefore higher $\delta^{13}C$. This fits with larger-scale studies that have found relationships between plant $\delta^{13}C$ and climate parameters, including precipitation amount

(Tieszen, 1991; Heaton, 1999; Kohn, 2010). Simultaneously, a more open forest leads to increased irradiation and thermal stress on plants during evapotranspiration that, in turn, is expected to result in higher plant $\delta^{18}O$ values. These effects are evidently tracked into the bulk organic matter of the plant parts sampled. The six samples that sit between -14‰ and -11‰ are all Cyperaceae spp. collected from beyond the forest region as a control for 'open' resources available in the immediate region. As discussed above, they have not been included in statistical analyses due to the strong pull this 'open' signal has on $\delta^{13}C$ measurements. However, as can be seen in Figure 7.16, season of collection also plays a role in the $\delta^{18}O$ values of these plants, with higher $\delta^{18}O$ visible in the sample collection from the dry (33.4‰) versus the wet (25.5 to 28.7‰) season.

Figures 7.17 and 7.18 show modern plant $\delta^{13}C$ and $\delta^{18}O$ plotted by species. Although there is some overlap, species groups separate out in $\delta^{13}C$ and $\delta^{18}O$ space when their means and standard deviations are plotted, as supported by ANOVA and post-hoc Tukey pair-wise comparison testing (Figure 7.18) (Catalogue Tables C28 and C29, C33 and C34). This is particularly the case during the wet season, implying that species differences are more pronounced during periods of increased humidity and increased forest closure. Two of the three species that dominate the Polonnaruwa forest canopy, *Schleichera oleosa* and *Vitex pinnata* (Dittus, 1977a) (Chapter 5 – Section 5.4) have relatively low mean $\delta^{13}C$ and $\delta^{18}O$, especially during the wet season (*Schleichera oleosa*: $\delta^{13}C$=-30.0±0.9‰, $\delta^{18}O$=22.4±0.8‰; *Vitex pinnata*: $\delta^{13}C$=-30.1±1.0‰, $\delta^{18}O$=23.3±1.6‰), indicating that they form closed areas of forest with less irradiation and increased influence of the 'canopy effect'. By contrast, the other main component of the canopy, *Drypetes sepiaria*, has higher mean $\delta^{18}O$ values than these species,

particularly in the wet season (28.9±0.6‰), implying that it may form part of the emergent canopy at this time.

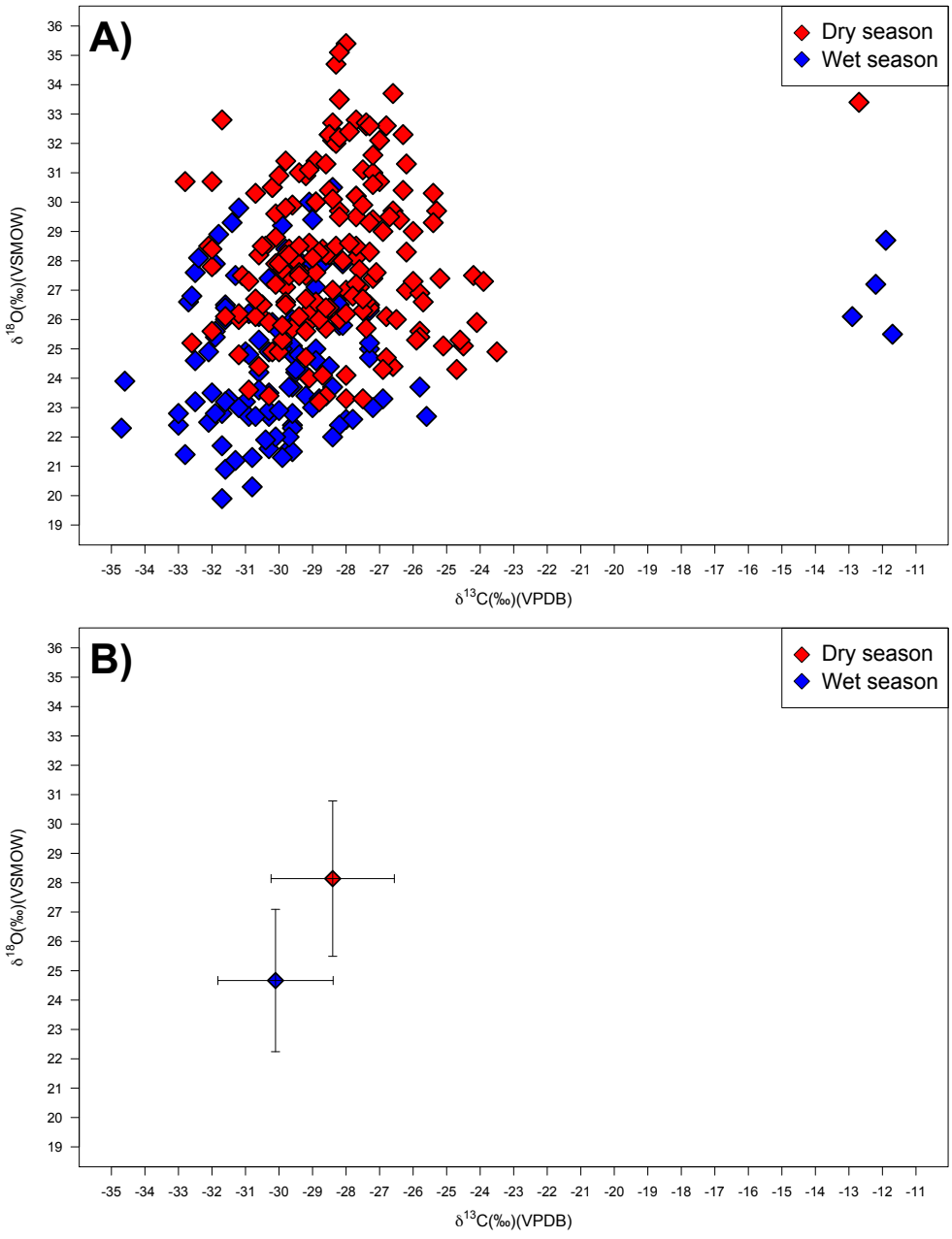


Figure 7.16. A) Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ values from the Polonnaruwa Nature Sanctuary shown by the season in which they were collected B) the means and standard deviations of wet and dry season $\delta^{13}C$ and $\delta^{18}O$ excluding Cyperaceae spp.

Manilkara hexandra is also known to form part of the emergent canopy during the wet season. However, in this species this appears to correspond with higher mean $\delta^{13}C$ (-28.3±0.9‰) rather than $\delta^{18}O$ (25.1±0.9‰) (Figures 7.17-7.18). *Mimosa pudica* and *Tamarindus indica* form part of the understory in the Polonnaruwa forest. While the $\delta^{13}C$ and $\delta^{18}O$ of these species are broadly spread during the dry season (*Mimosa pudica*: $\delta^{13}C$=-30.2 to -27.7‰; $\delta^{18}O$=24.9 to 29.5‰; *Tamarindus indica*: $\delta^{13}C$=-30.6 to -23.9‰; $\delta^{18}O$=26.0 to 32.6‰), their understory position is demonstrated by some of the lowest $\delta^{13}C$ values of the sample during the wet season (*Mimosa pudica*: -32.5 to -31.0‰; *Tamarindus indica*: -32.7 to -31.6‰) (Figures 7.17-7.18). *Szygium cumini* has high mean $\delta^{18}O$ in both the dry (31.0±3.4‰) and wet (28.9±2.0‰) seasons, likely due to it being found in more open, irradiated, and water-stressed forest during sampling (Figures 7.17-7.18). Cyperaceae spp. show persistently elevated $\delta^{13}C$ values (wet season: -12.9 to -11.7‰; dry season: -12.7‰) relative to the other species as they are sedges sampled from open, waterlogged conditions with no influence of the 'canopy effect'.

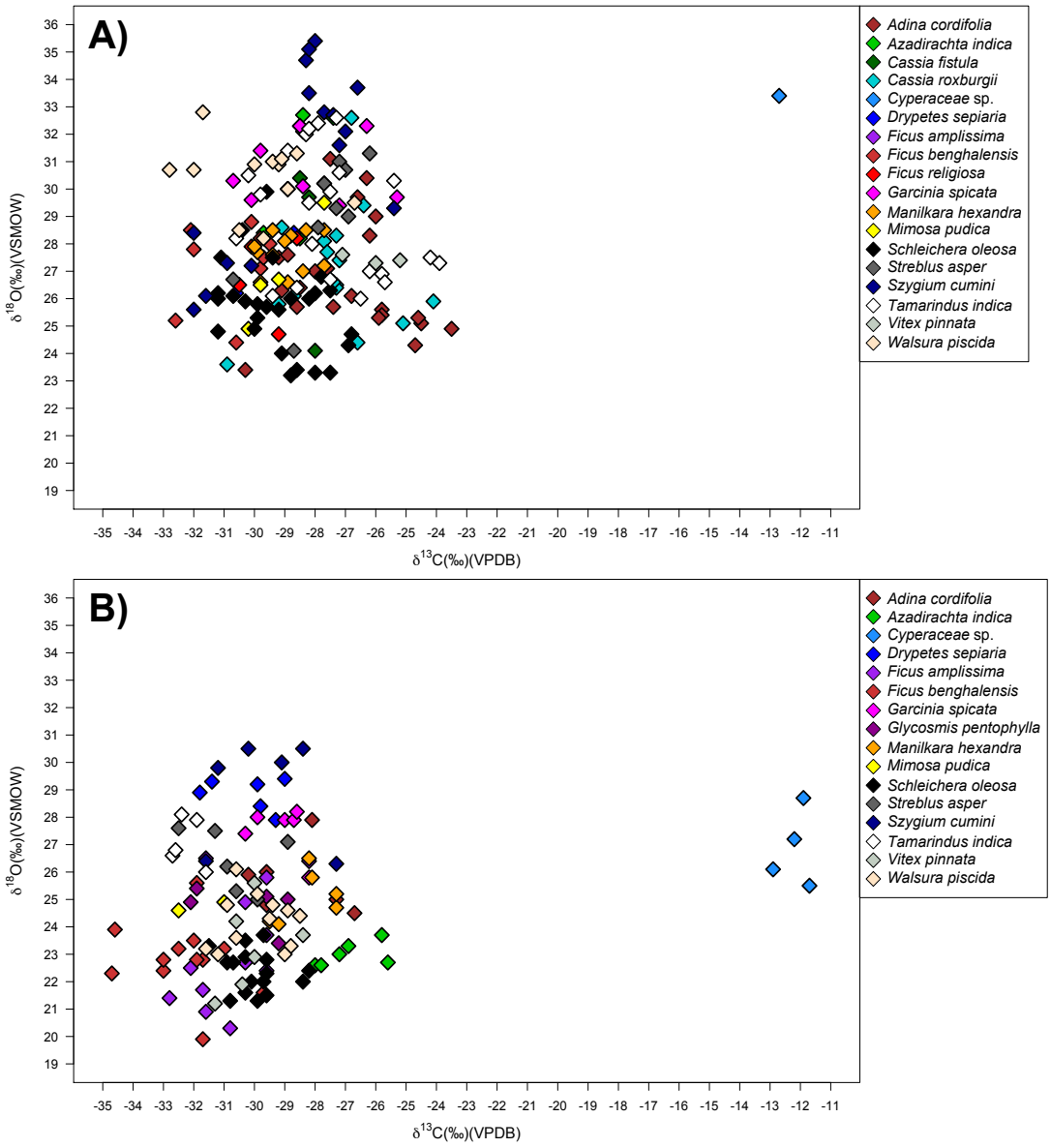


Figure 7.17. Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ plotted by species for A) the dry season and B) the wet season.

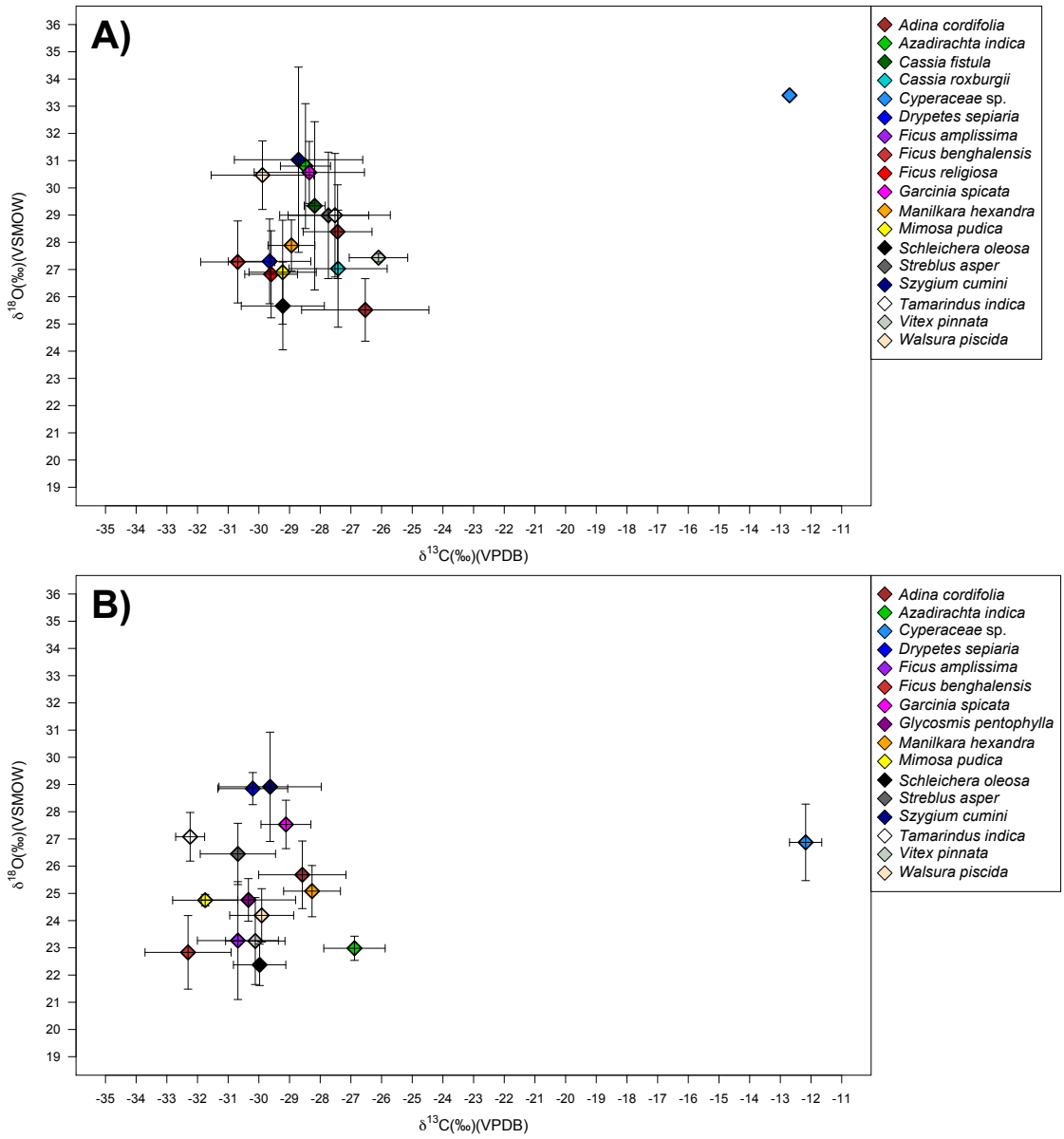


Figure 7.18. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for each modern plant species sampled during A) the dry season and B) the wet season.

Figures 7.19 and 7.20 show modern plant $\delta^{13}C$ and $\delta^{18}O$ plotted by plant part. Despite ANOVA and post-hoc Tukey pair-wise comparison testing indicating that plant part has a significant effect on both $\delta^{13}C$ and $\delta^{18}O$ (Catalogue Tables C28 and C29, C33 and C34) it is not easy to distinguish between plant parts in Figure 7.19. Plotting $\delta^{13}C$ and $\delta^{18}O$ means and standard deviations for each plant part in Figure 7.20 demonstrates that fruits and flowers have higher $\delta^{13}C$ relative to leaves and leaf shoots during the dry season. This trend is reversed, however, during the wet season where fruits appear to broadly have lower $\delta^{13}C$ than leaves, flowers and leaf shoots (though it should be noted that only *Ficus amplissima* and *Ficus benghalensis* yielded fruits and leaves from both seasons of collection – Catalogue Tables A10-A11). This could be a result of the fact that fruits were forming during periods of increased 'canopy effect' during the wet season, relative to mature leaves. Indeed, mature leaves have the highest $\delta^{18}O$ values of all the plant parts during the wet season, implying that they formed a long time before sampling when more open forest and increased irradiation was present. Nonetheless, fruit also has lower $\delta^{18}O$ relative to leaf shoots and flowers (Figure 7.20). Young leaves during the dry season have higher $\delta^{18}O$ relative to the other plant parts, perhaps indicative that they are forming from ^{18}O-enriched plant water during a period of increased water stress and evapotranspiration. Within Sri Lanka, subtle $\delta^{18}O$ differences between source water of different monsoonal systems could also impact the $\delta^{18}O$ of plant parts growing at different times of year. However, such distinctions are muted in the northeast of the island where the majority of rain is brought from the Bay of Bengal during the northeastern monsoon.

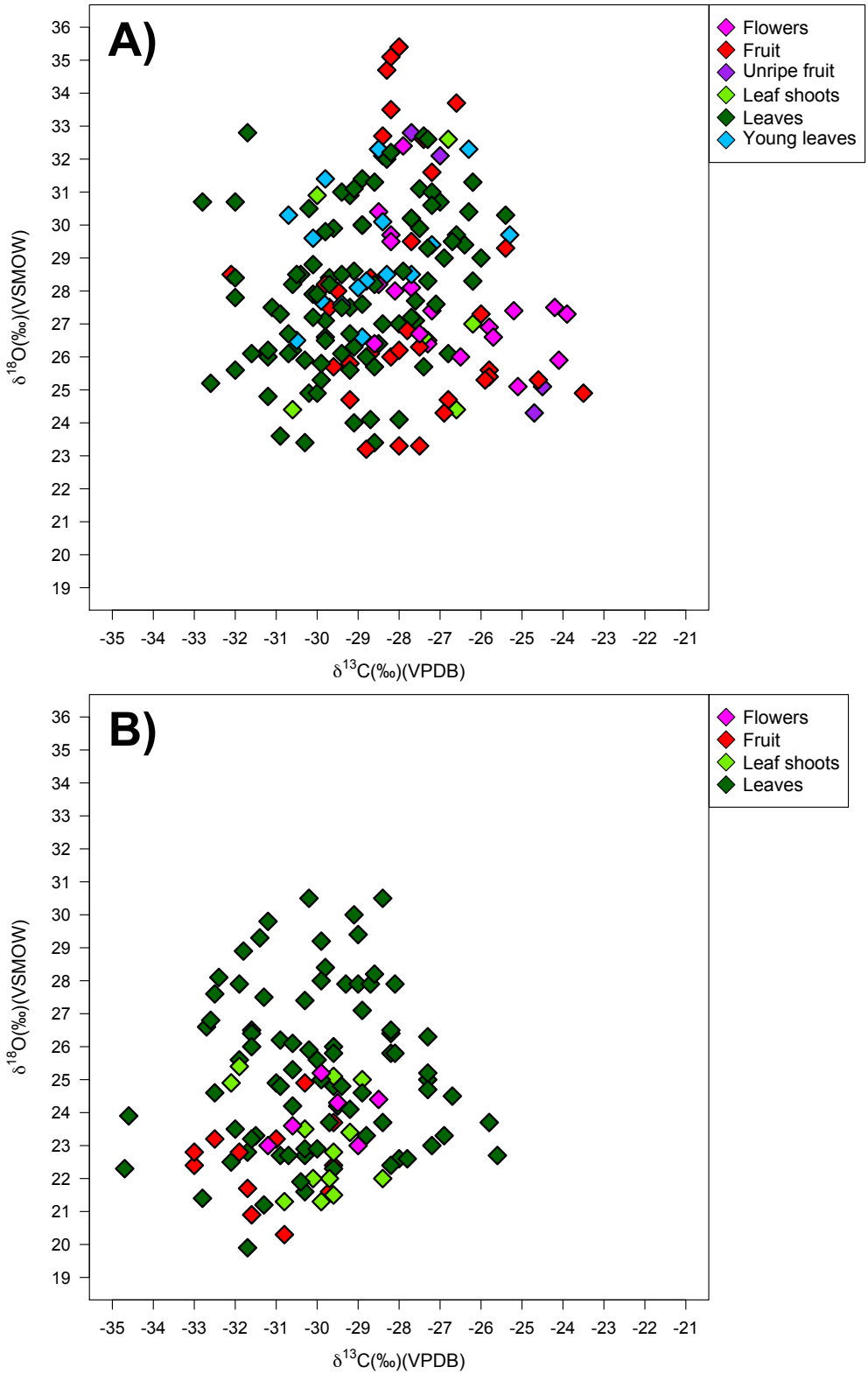


Figure 7.19. Modern plant sample $\delta^{13}C$ by $\delta^{18}O$ plotted by plant part for A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

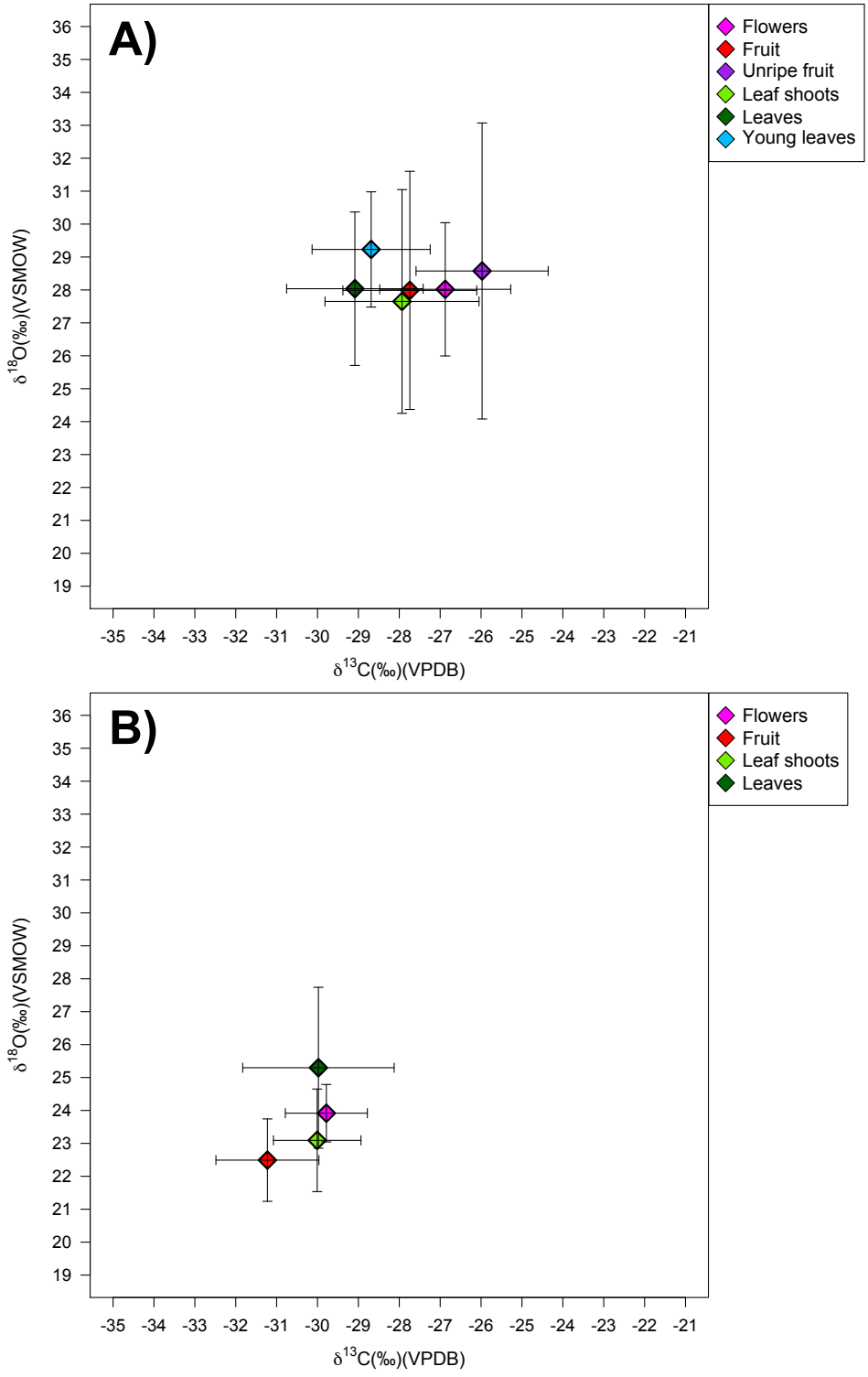


Figure 7.20. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for modern plant parts sampled during A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

Figures 7.21 and 7.22 plot the $\delta^{13}C$ and $\delta^{18}O$ of different plant parts by species for the dry season and wet season, respectively. These plots demonstrate the great influence species has on the interpretation of plant part differences, as was indicated in the ANOVA testing of interaction effects between species and plant part in the structuring of variance in $\delta^{13}C$ and $\delta^{18}O$ (Catalogue Tables C27, C32). For the dry season, fruit has higher (*c.*1-4‰) $\delta^{13}C$ relative to leaves from the *same* species. The one exception is *Cassia roxburghii*. However, the fruits of this tree were collected from the ground where they had been lying in robust pods, which could have initially formed during a period of more closed forest relative to the leaves and flowers that had formed more recently. The fruits of *Azadirachta indica* and *Szygium cumini* are higher in $\delta^{18}O$ relative to leaves from the same species, though this trend is not seen across the fruiting plants (Figure 7.21). Flowers of *Azadirachta indica*, *Cassia roxburghii*, *Tamarindus indica*, and *Vitex pinnata* also demonstrate higher $\delta^{13}C$ relative to leaves from the same species during the dry season (Figure 7.21). Figure 7.22 demonstrates that, whereas fruits have relatively low $\delta^{13}C$ and $\delta^{18}O$ for samples in the wet season as a whole (Figure 7.19), when viewed on a species by species basis they have similar or higher $\delta^{13}C$ relative to leaves from the same plant. Nevertheless, the $\delta^{13}C$ separation between fruits and leaves during the wet season is much smaller relative to the dry season (*c.* 0-1‰). The same can be said for the flowers of *Walsura piscida*, which appear to have only slightly higher $\delta^{13}C$ relative to leaves during the wet season.

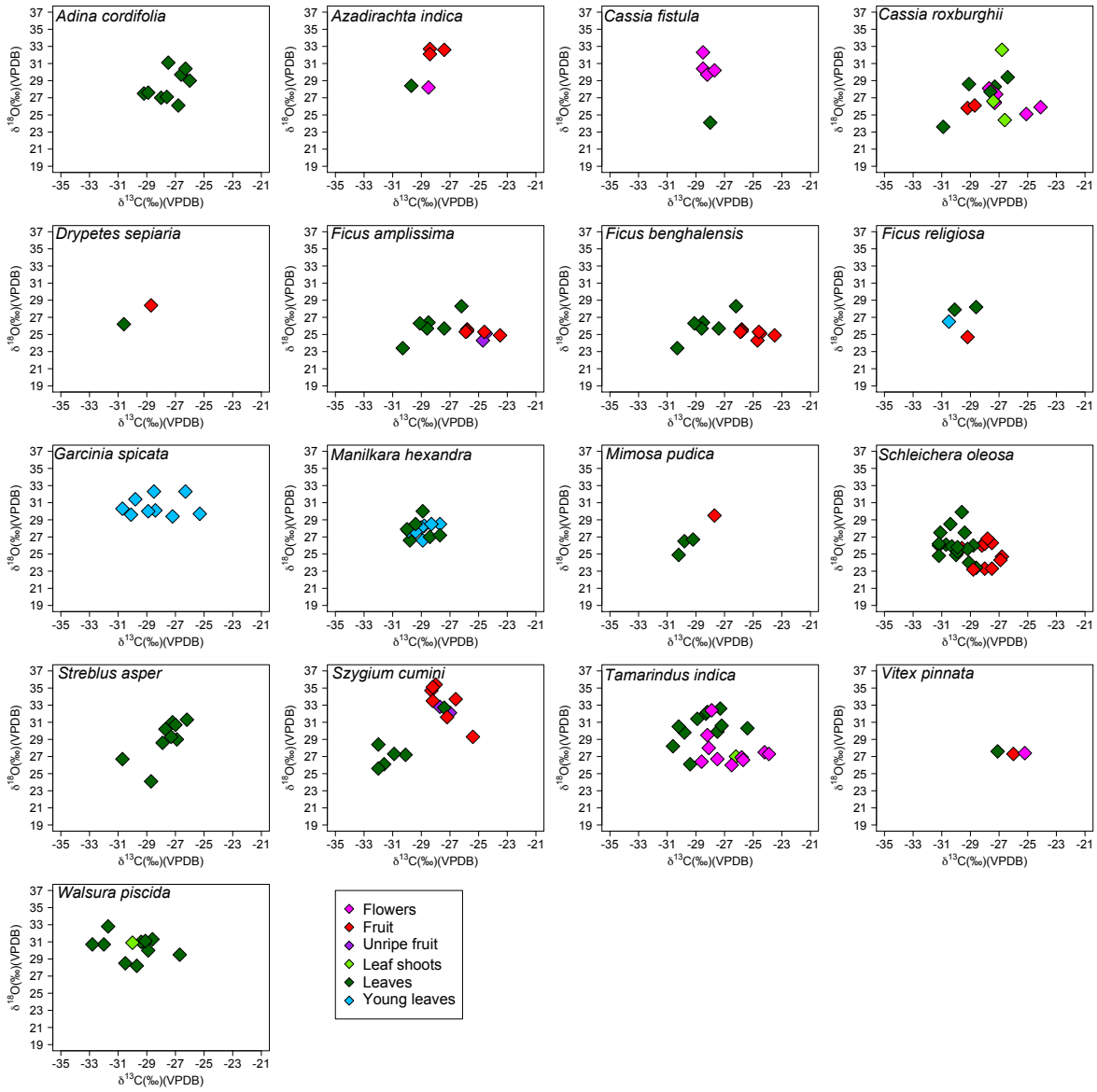


Figure 7.21. $\delta^{13}C$ by $\delta^{18}O$ of modern plant samples collected in the dry season plotted by species and plant part (Cyperaceae spp. are excluded).

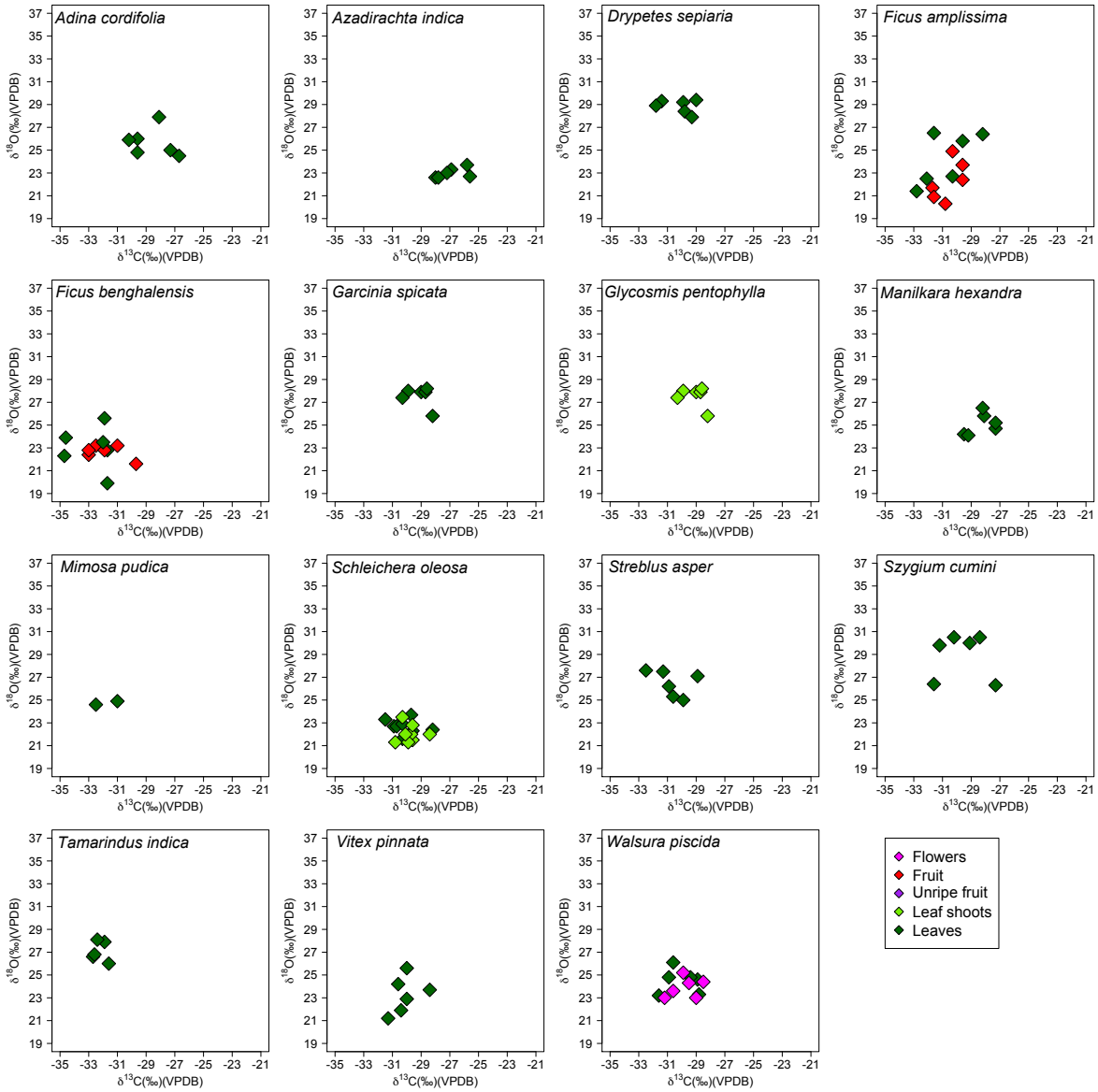


Figure 7.22. $\delta^{13}C$ by $\delta^{18}O$ of modern plant samples collected in the wet season plotted by species and plant part (Cyperaceae spp. are excluded).

Figures 7.23-7.26 show modern plant sample $\delta^{13}C$ and $\delta^{18}O$ plotted by degree of insolation and height collected in the canopy. Similar trends were found for both parameters. The degree of insolation experienced by a sample was found to have significant effects on $\delta^{13}C$ during ANOVA and post-hoc Tukey pair-wise comparison testing (Catalogue Tables C28 and C29). These effects are apparent in Figures 7.23 and 7.24 where greater insolation is associated with higher $\delta^{13}C$ values during both the wet and dry seasons. Insolation was also found to have an effect on $\delta^{18}O$ during ANOVA testing although there is no obvious trend (Catalogue Tables C33 and C34). Although height appears to demonstrate higher $\delta^{13}C$ at higher positions in the canopy (Figures 7.25 and 7.26), ANOVA testing found height to only have a significant effect on $\delta^{18}O$ (Catalogue Tables C28 and C29, C33 and C34). Higher $\delta^{18}O$ in the 'upper' group during the dry season is likely linked to increase water stress affecting plant evapotranspiration higher in the canopy (Sternberg *et al.,* 1989; Krigbaum *et al.,* 2013). However, this trend is apparently reversed during the wet season. Overall, the statistically significant impacts of insolation and height on plant $\delta^{13}C$ and $\delta^{18}O$ do not appear as strong as that of species, plant part and season. It is possible that the collection of more refined, quantitative assessments of insolation and height in the future could enable more detailed testing of the impacts of these parameters on plant $\delta^{13}C$ and $\delta^{18}O$ in the Polonnaruwa forest.

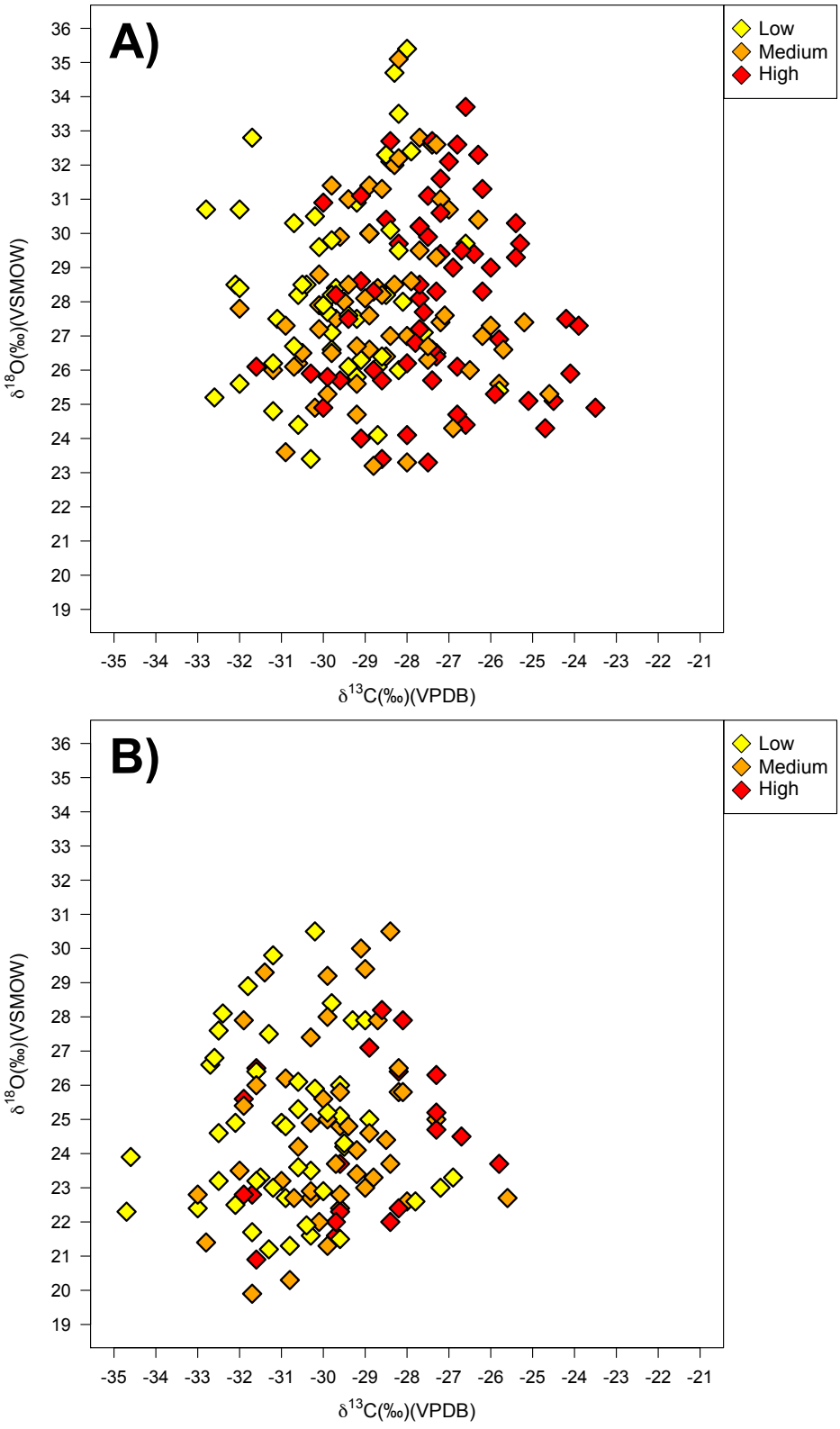


Figure 7.23. Modern plant sample $\delta^{13}C$ and $\delta^{18}O$ plotted by qualitatively assigned insolation groupings (low, medium or high) for A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

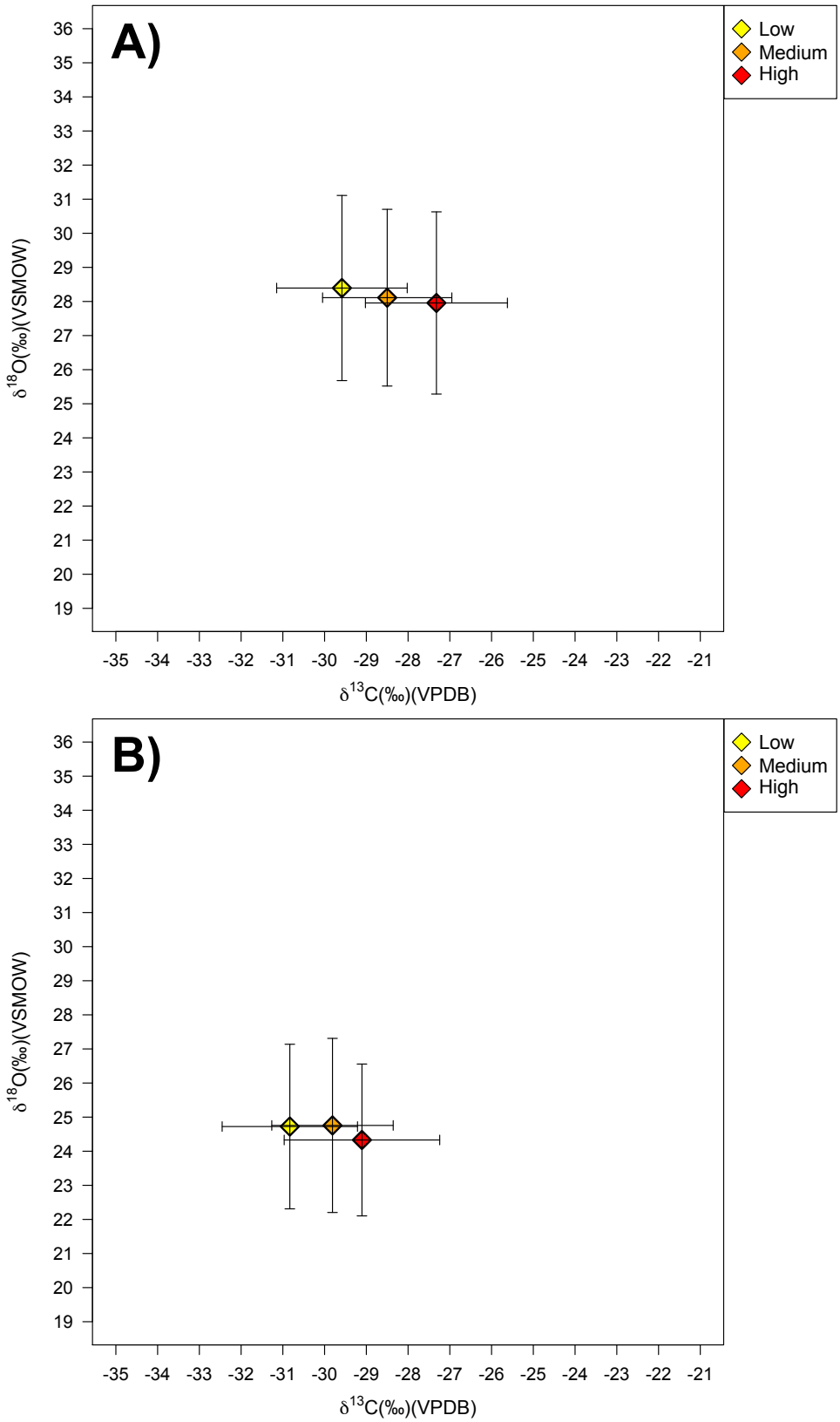


Figure 7.24. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of qualitatively assigned insolation groupings (low, medium or high) (Cyperaceae spp. are excluded).

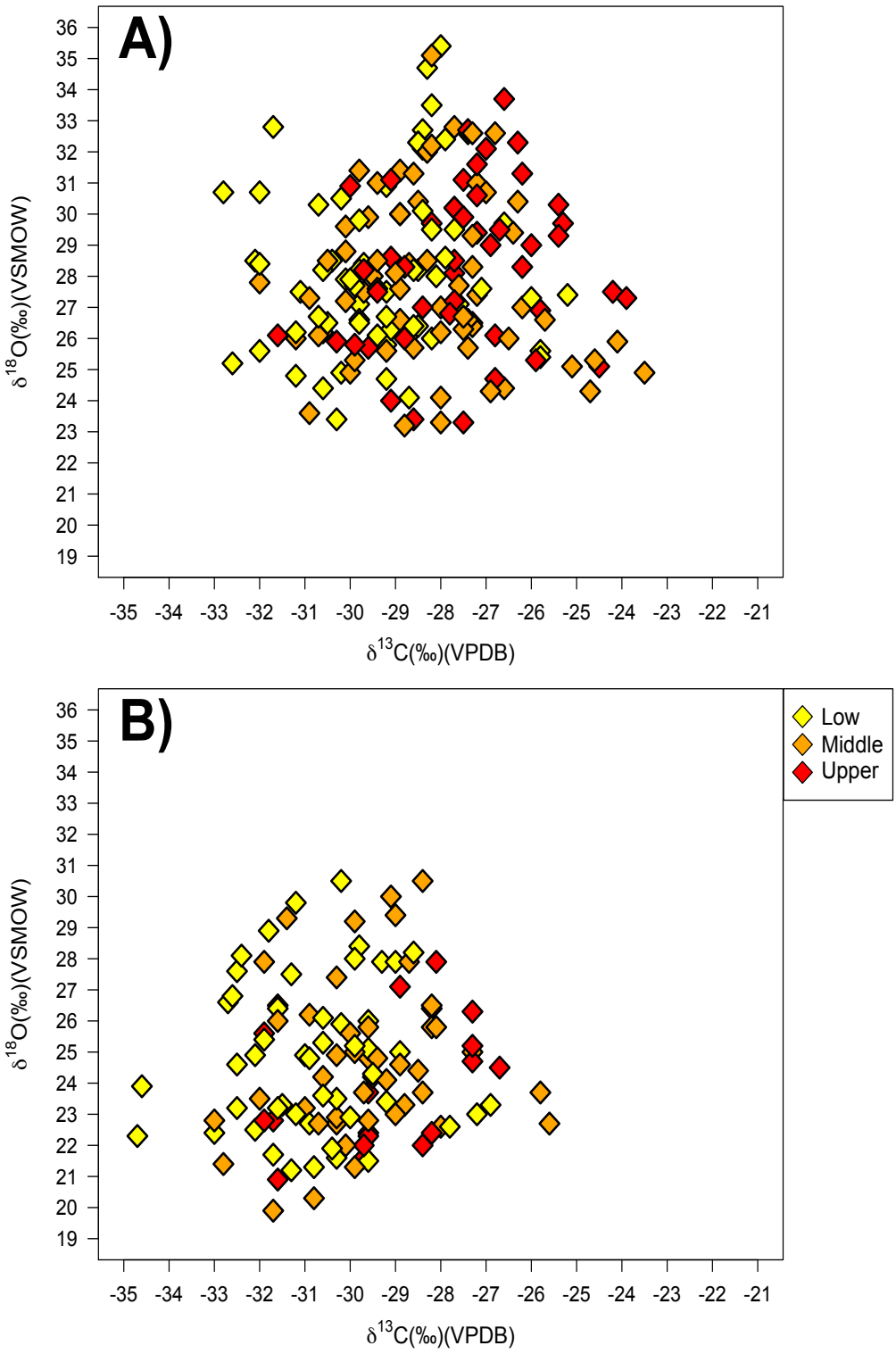


Figure 7.25. Modern plant sample $\delta^{13}C$ and $\delta^{18}O$ plotted by canopy height groupings (floor, low, middle or upper) for A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

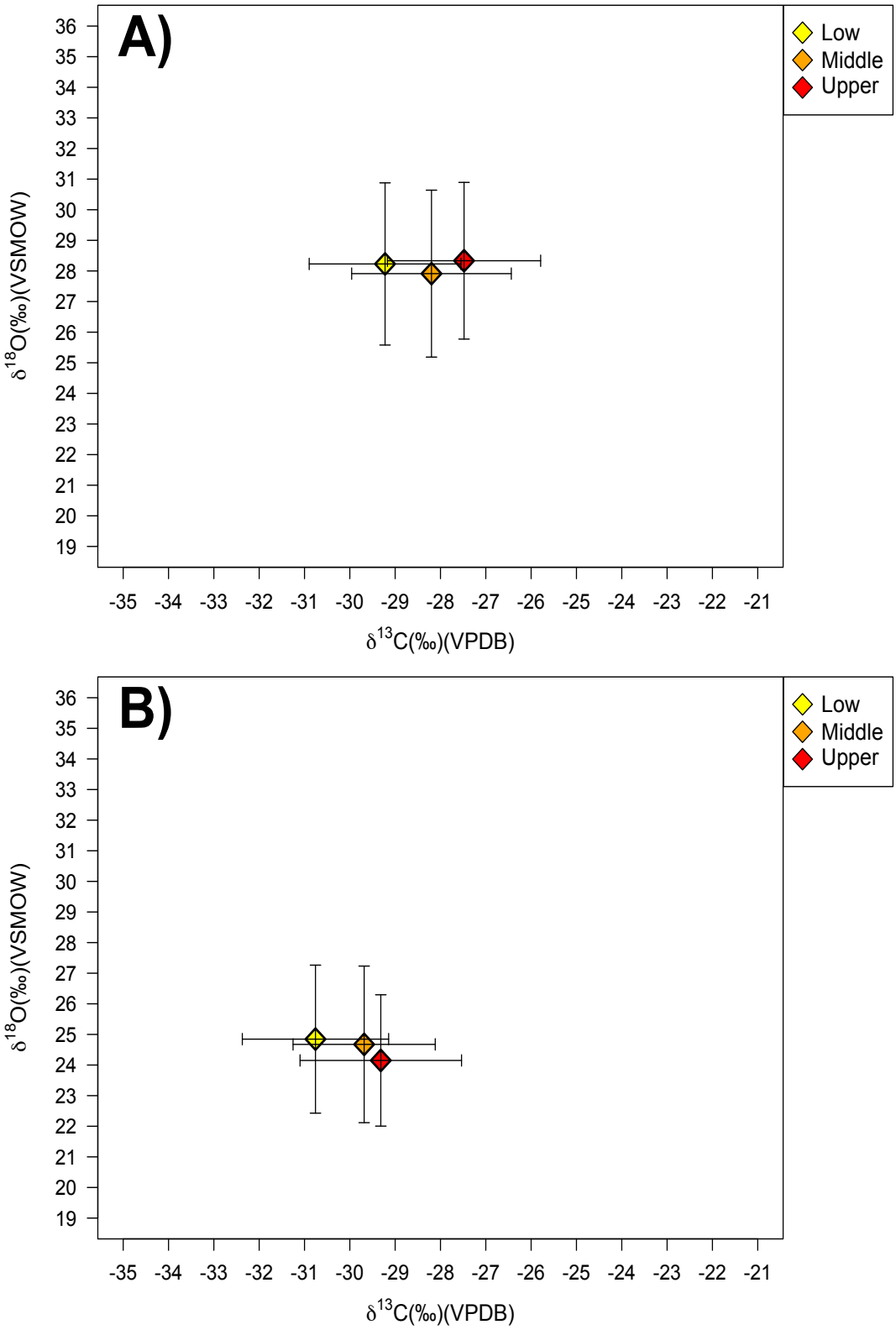


Figure 7.26. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of canopy height groupings (floor, low, middle or upper) for A) the dry season and B) the wet season.

Stable nitrogen isotope variation

Although of less immediate interest to the study of fossil primate tooth enamel, the modern plant $\delta^{15}N$ data from Polonnaruwa are also influenced by certain environmental parameters that may be of importance for interpretations of primate organic tissue $\delta^{15}N$ in the region in future. ANOVA testing on linear models of the effects of species, plant part, insolation, height and season on $\delta^{15}N$, as well as their interaction effects, demonstrate that species ($F(17,231)=17.663$, $p<0.05$) and plant part ($F(5,231)=2.458$, $p<0.05$), but not season, height or insolation, significantly influenced plant $\delta^{15}N$ within the Polonnaruwa forest (Catalogue Tables C35-C37). Interaction effects are observed between species and plant part ($F(21,231)=2.250$, $p<0.05$) and species and season ($F(12,231)=4.719$, $p<0.05$), suggesting that different species respond differently to the effects of plant part and season (Catalogue Tables C35-C36). As for $\delta^{13}C$ and $\delta^{18}O$, plant species is therefore arguably also the most important influence on sample $\delta^{15}N$. Post-hoc Tukey pair-wise comparison supports this point and demonstrates 31 species distinctions in $\delta^{15}N$ ($p<0.05$) (Catalogue Table C38). The effect of plant part on $\delta^{15}N$ disappears when a linear model that includes just species and plant part is performed, and post-hoc Tukey pair-wise comparison test was consequently not performed on this parameter ($p>0.05$) (Catalogue Tables C37 and C38).

Although it has been suggested that in tropical ecosystems there should be a trend towards decreasing $\delta^{15}N$ measurements with increasing rainfall (Austin and Vitousek, 1998; Austin and Sala, 1999; Handley *et al.,* 1999; Amundson *et al.,* 2003; but see Craine *et al.,* 2009) this is not seen in a distinction between the dry season and wet season at the Polonnaruwa Nature Sanctuary (Figure 7.27). Similarly, although previous

studies have highlighted differences in plant part $\delta^{15}N$ (Blumenthal *et al.,* 2012, 2015), this is not observed in the Polonnaruwa dataset, with the exception of flowers that demonstrate higher $\delta^{15}N$ values during the wet season (Figures 7.28 and 7.29). This remains the case when plant part is plotted by species and no obvious plant part $\delta^{15}N$ distinctions are observed for either the dry season or wet season (Figures 7.30 and 7.31). The only exceptions are the higher values for the flowers of *Walsura piscida* (Figure 7.31). While this could indicate that flowers growing in the wet season are ^{15}N-enriched compared to other plant parts, the fact that such a distinction does not exist for the dry season, and the identification of an interaction effect between species and plant parts in ANOVA testing, suggests that this distinction is likely to be species-driven. The lack of plant part distinctions found in this study, relative to existing research, is likely due to the fact that previous studies highlighted nitrogen isotope composition distinctions between woody parts (stems and bark), which were not collected in this study due to limited importance to the primate diets under study, and non-woody parts (leaves and fruit) (Blumenthal *et al.,* 2012, 2015). Figures 7.32 and 7.33 also support the ANOVA results in indicating a lack of impact of either insolation or height on plant $\delta^{15}N$, respectively.

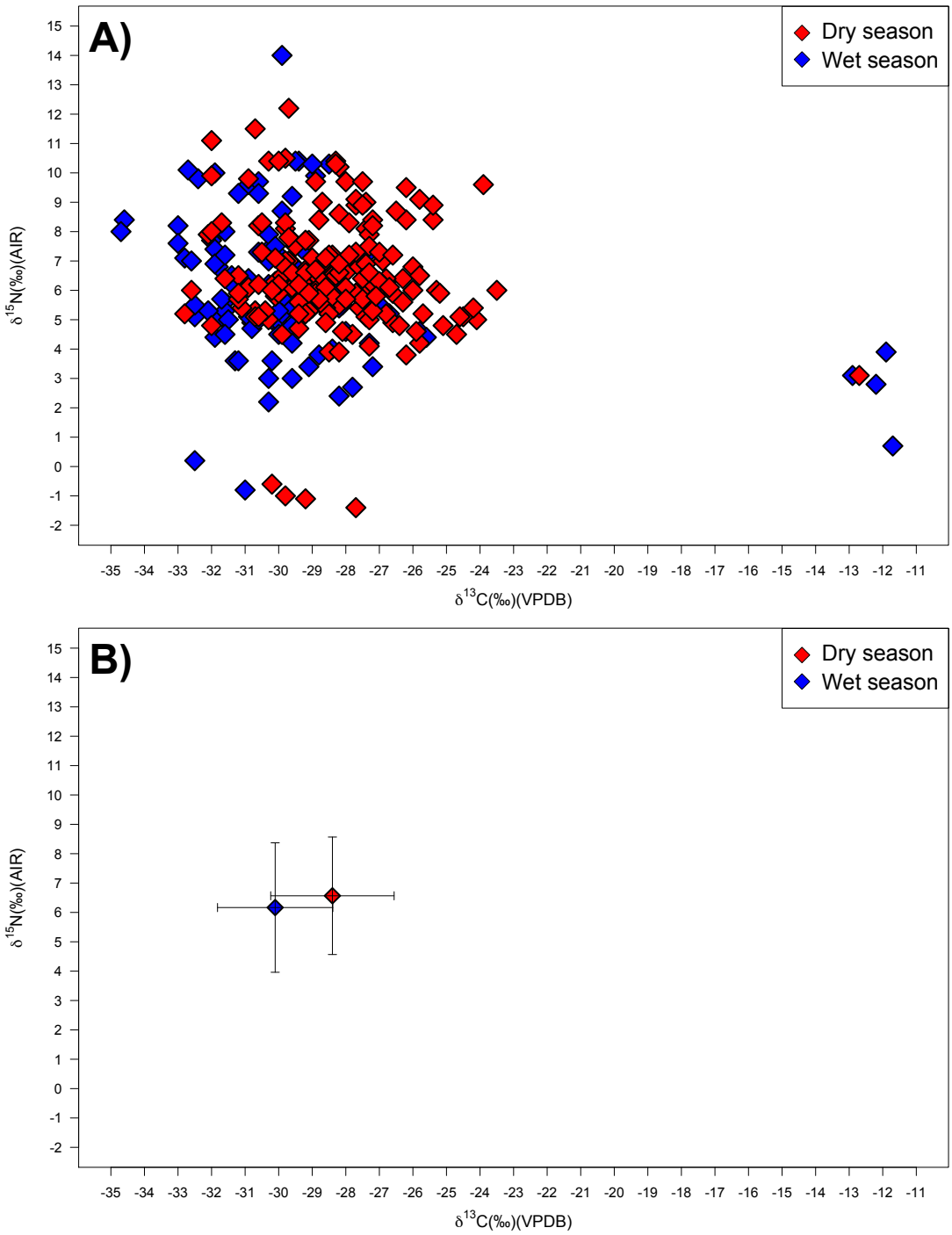


Figure 7.27. A) Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ values from the Polonnaura Nature Sanctuary shown by the season in which they were collected B) the means and standard deviations of wet and dry season $\delta^{13}C$ and $\delta^{15}N$ excluding Cyperaceae spp..

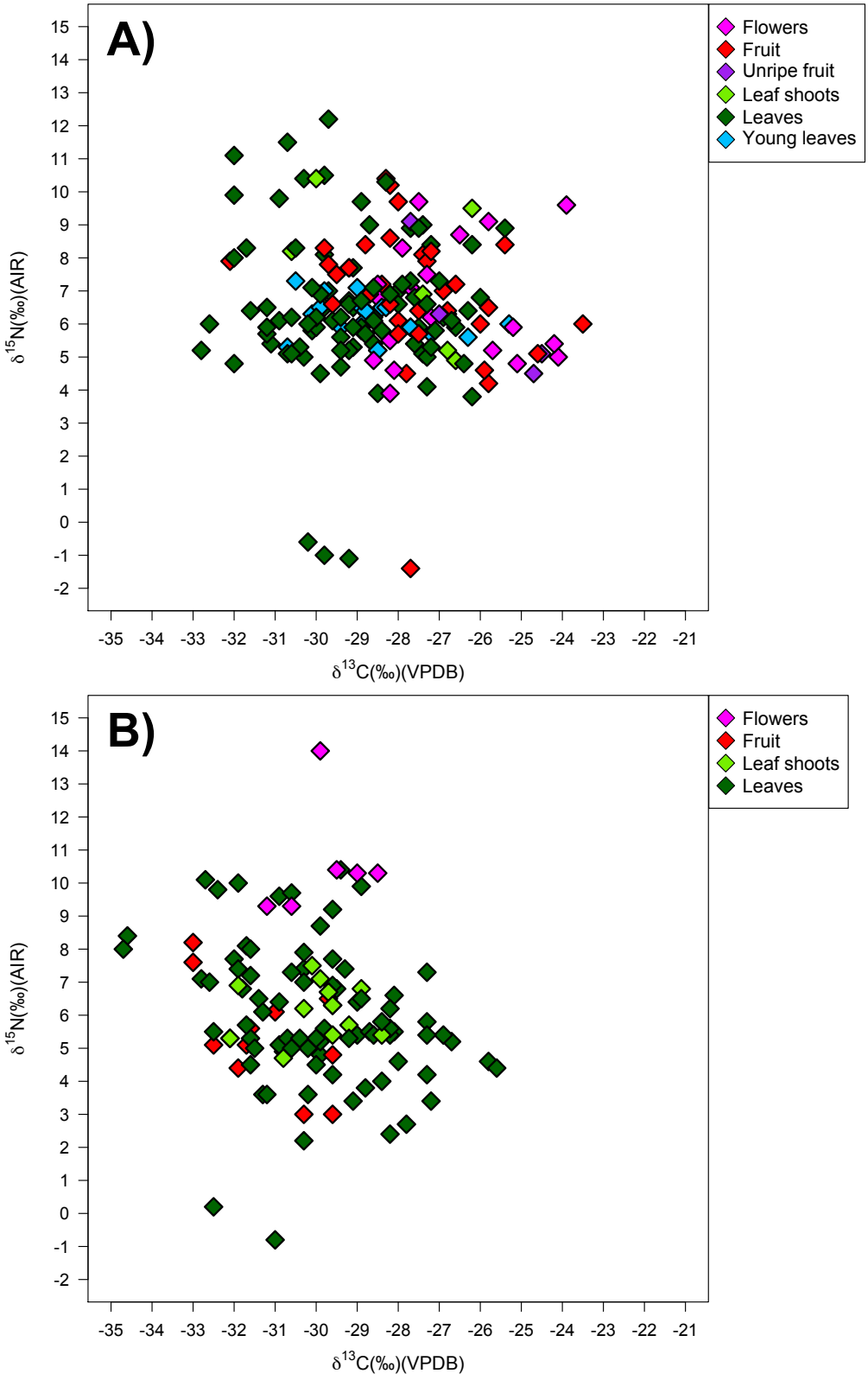


Figure 7.28. Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ plotted by plant part for A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

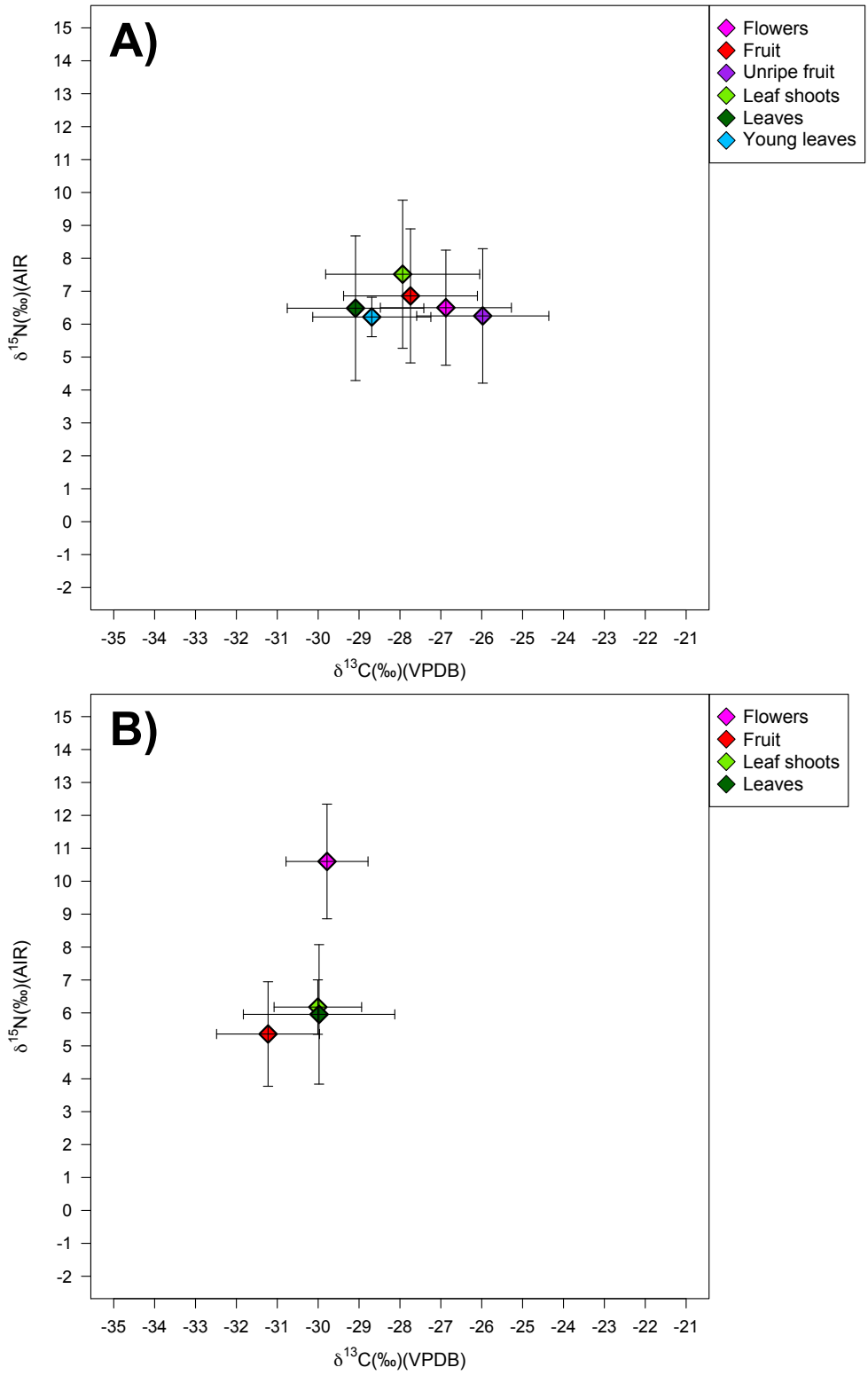


Figure 7.29. Mean and standard deviations of $\delta^{13}C$ by $\delta^{18}O$ for modern plant part sampled during A) the dry season and B) the wet season (Cyperaceae spp. are excluded).

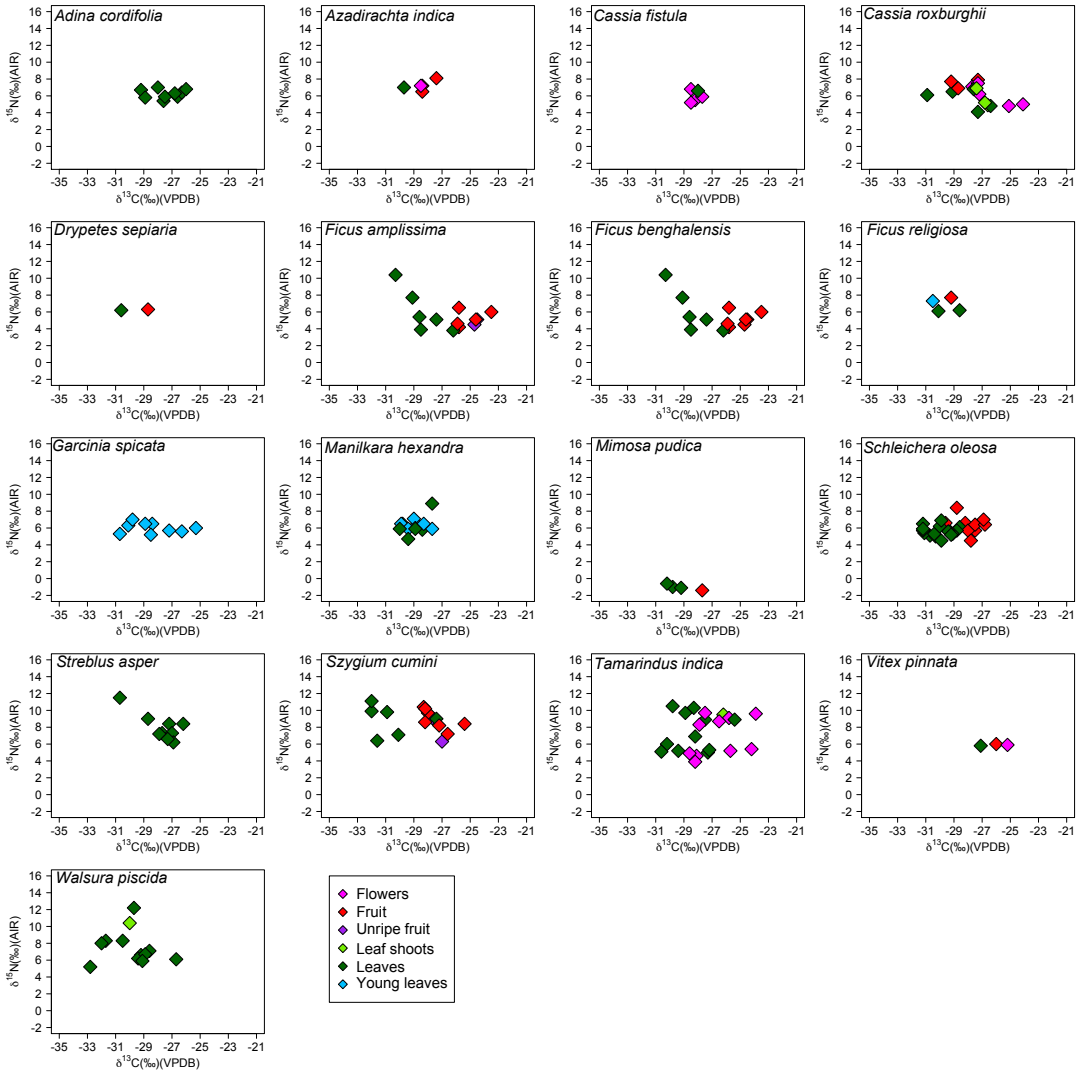


Figure 7.30. $\delta^{13}C$ by $\delta^{15}N$ of modern plant samples collected in the dry season plotted by species and plant part (Cyperaceae spp. are excluded).

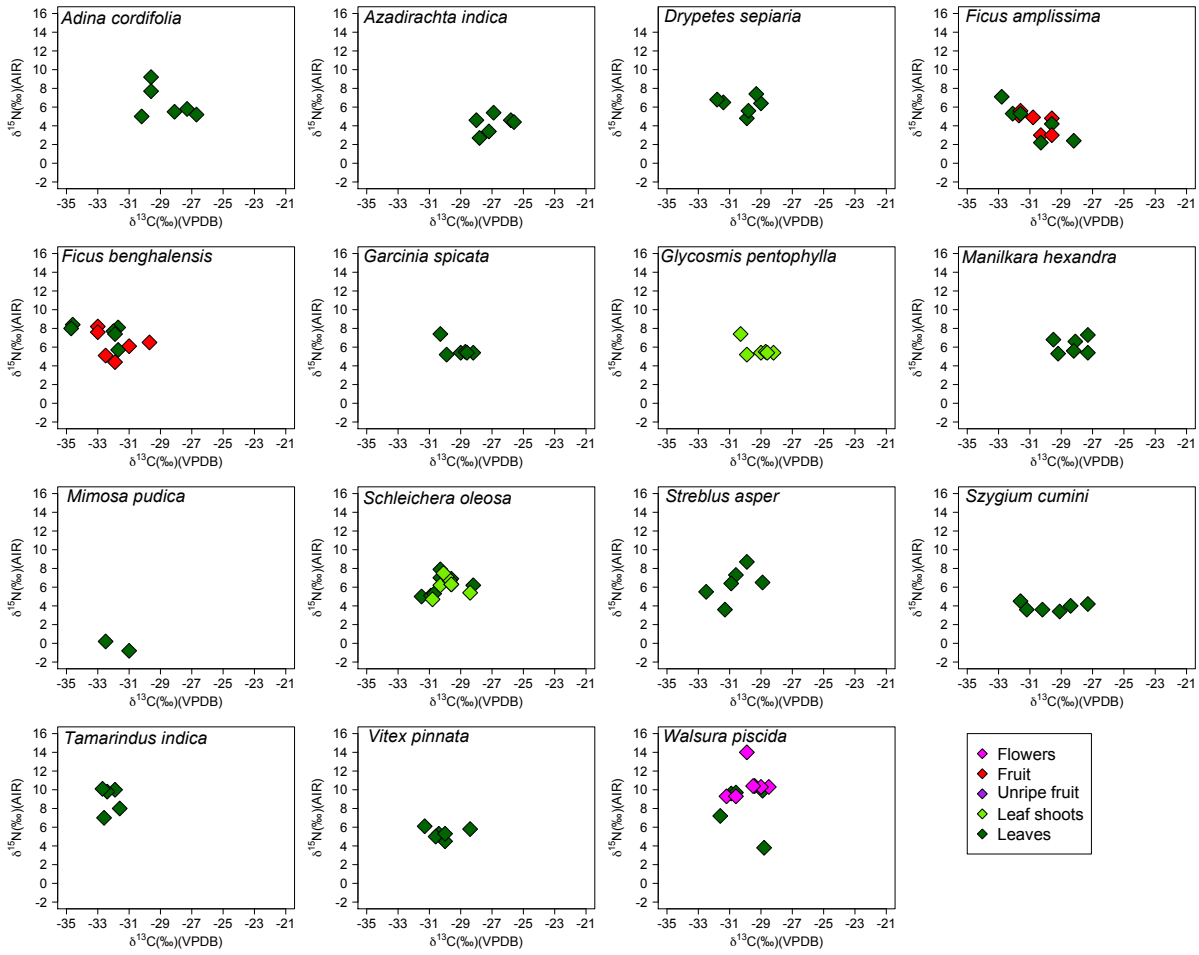


Figure 7.31. $\delta^{13}C$ by $\delta^{15}N$ of modern plant samples collected in the wet season plotted by species and plant part (Cyperaceae spp. are excluded).

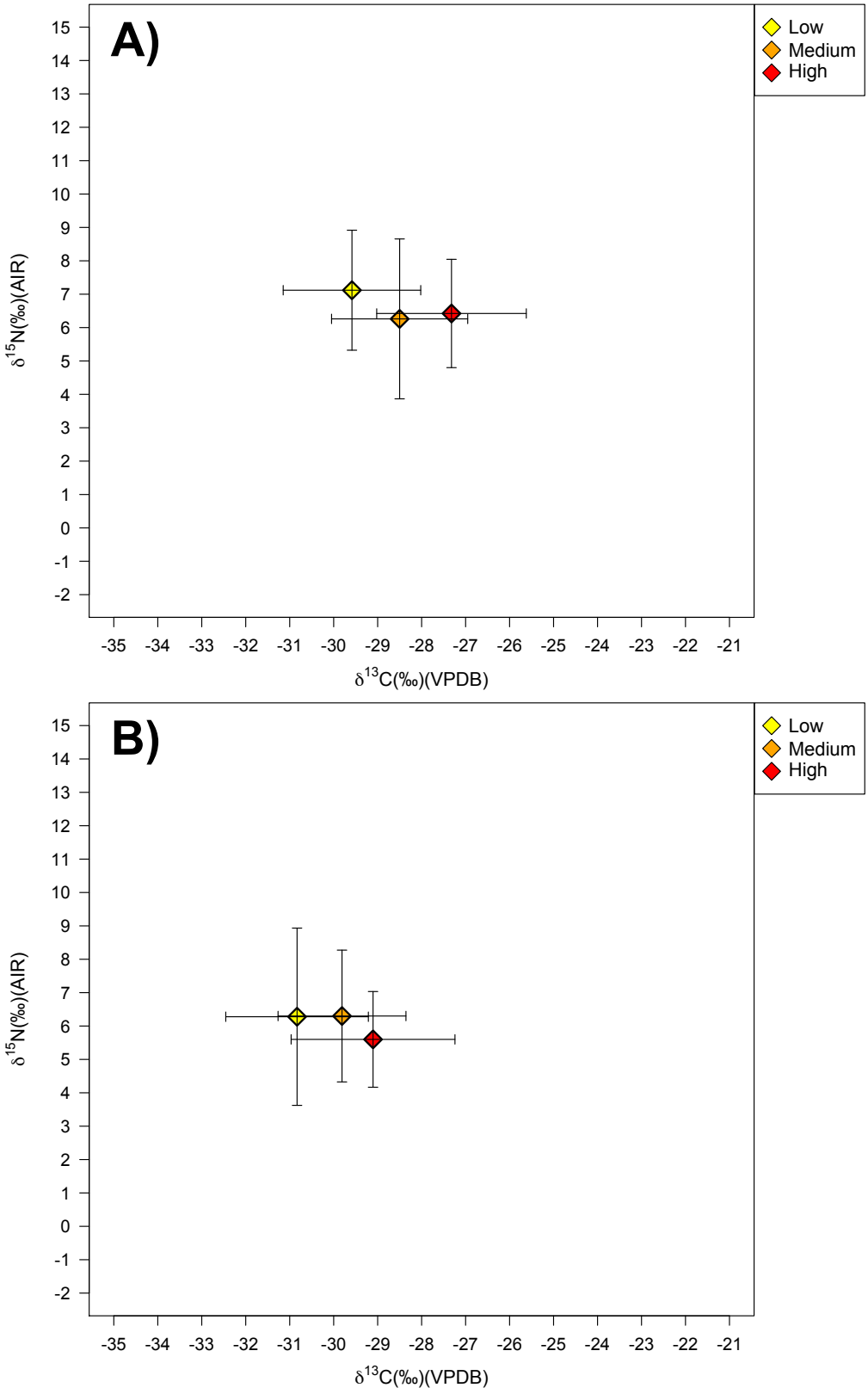


Figure 7.32. Mean and standard deviations for $\delta^{13}C$ and $\delta^{15}N$ of qualitatively assigned insolation groupings (low, medium or high) (Cyperaceae spp. are excluded).

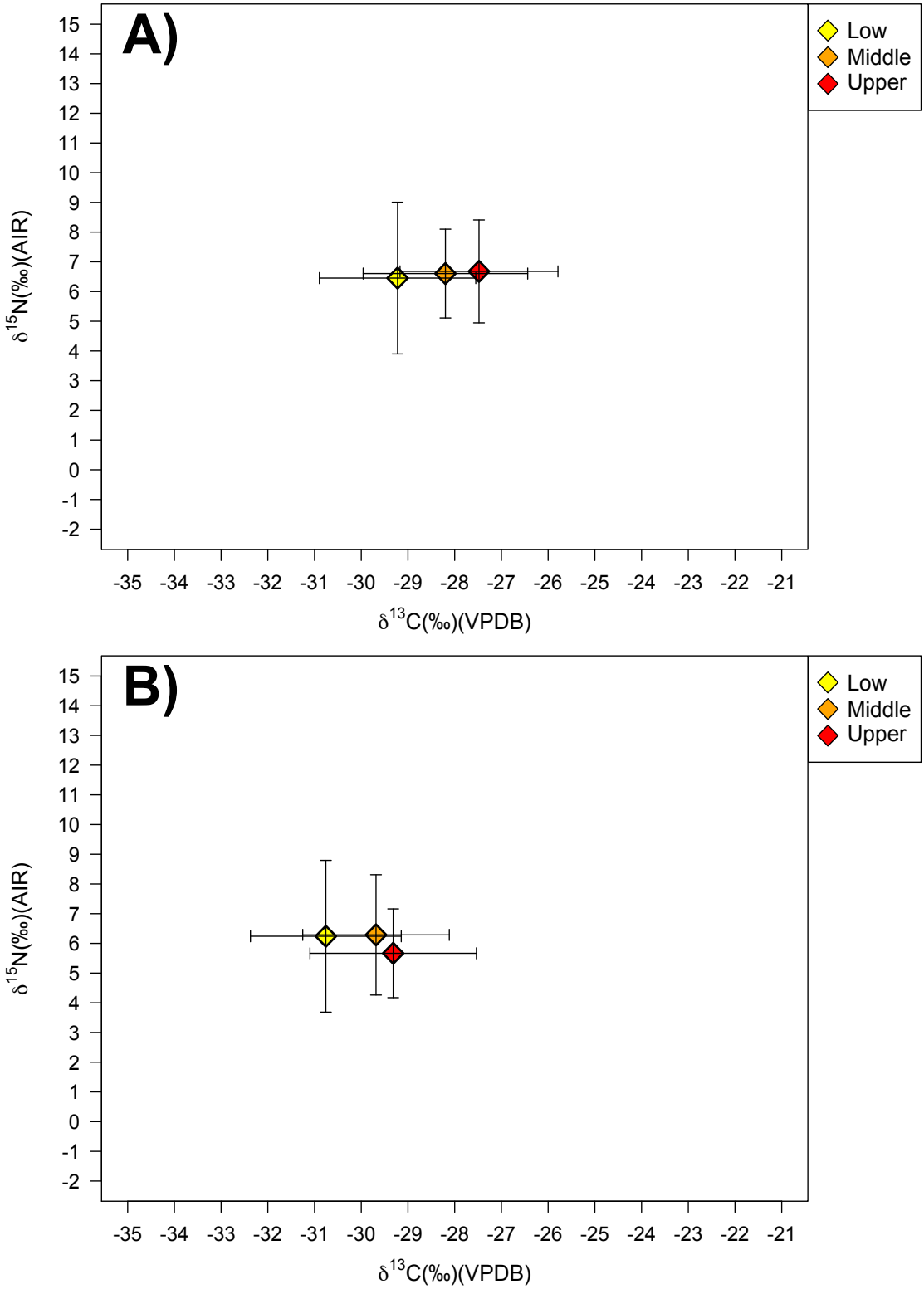


Figure 7.33. Mean and standard deviations for $\delta^{13}C$ and $\delta^{15}N$ of canopy height groupings (floor, low, middle or upper) (Cyperaceae spp. are excluded).

Plots of plant $\delta^{13}C$ and $\delta^{15}N$ by species demonstrate the role that this parameter plays in $\delta^{15}N$ variation (Figures 7.34 and 7.35). The Cyperaceae spp. sedges have some of the lowest $\delta^{15}N$ values in both seasons (wet: 0.7 to 3.9‰; dry: 3.1‰). This may be linked to the fact that these plants were collected from waterlogged settings near rivers. Codron *et al.* (2013) noted low $\delta^{15}N$ values for plants growing in riverine settings, which they linked to lower rates of ^{15}N-enrichment processes such as nitrification and de-nitrification in wetter habitats (Handley *et al.,* 1994). Samples from *Mimosa pudica* are significantly low in $\delta^{15}N$, relative to the rest of the sample, in both the dry (-1.4 to -0.6‰) and wet (-0.8 to 0.2‰) season. The roots of *Mimosa pudica* create carbon disulphide that prevents certain fungi from growing within the plant's rhizosphere. This facilitates the formation of nodules on the roots of the plant that fix atmospheric nitrogen and convert it into a form usable by the plant (dos Reis *et al.,* 2010; Azim *et al.,* 2011). ^{15}N depletion has been noted elsewhere in connection to nodular N-fixing capabilities in plants (Ambrose, 1991).

In the dry season other species distinctions remain relatively muted, although *Szygium cumini* samples appear to demonstrate higher $\delta^{15}N$ values (8.8±1.5‰) than other species. In the wet season more species distinctions are apparent with *Walsura piscida* (9.5±2.4‰), *Tamarindus indica* (9.0±1.4‰) and, to some extent, *Adina cordifolia* (6.4±1.7‰) have higher $\delta^{15}N$ and *Ficus amplissima* (4.4±1.5‰), *Szygium cumini* (3.9±0.4‰), and *Azadirachta indica* (4.2±1.0‰) have lower $\delta^{15}N$ values. Although the impact of species on plant $\delta^{15}N$ has been noted elsewhere (Oelze *et al.,* 2014), the dominance of its effect on plant $\delta^{15}N$ in this study urges caution in the interpretation of $\delta^{15}N$ distinctions in mainly vegetarian primates as being reflective of local environmental variation (Macho and Lee-Thorp, 2014), plant part choice (Oelze *et al.,*

2014), or indeed studies that have used $\delta^{15}N$ as a proxy for physiological processes such as weaning (Fahy *et al.,* 2014).

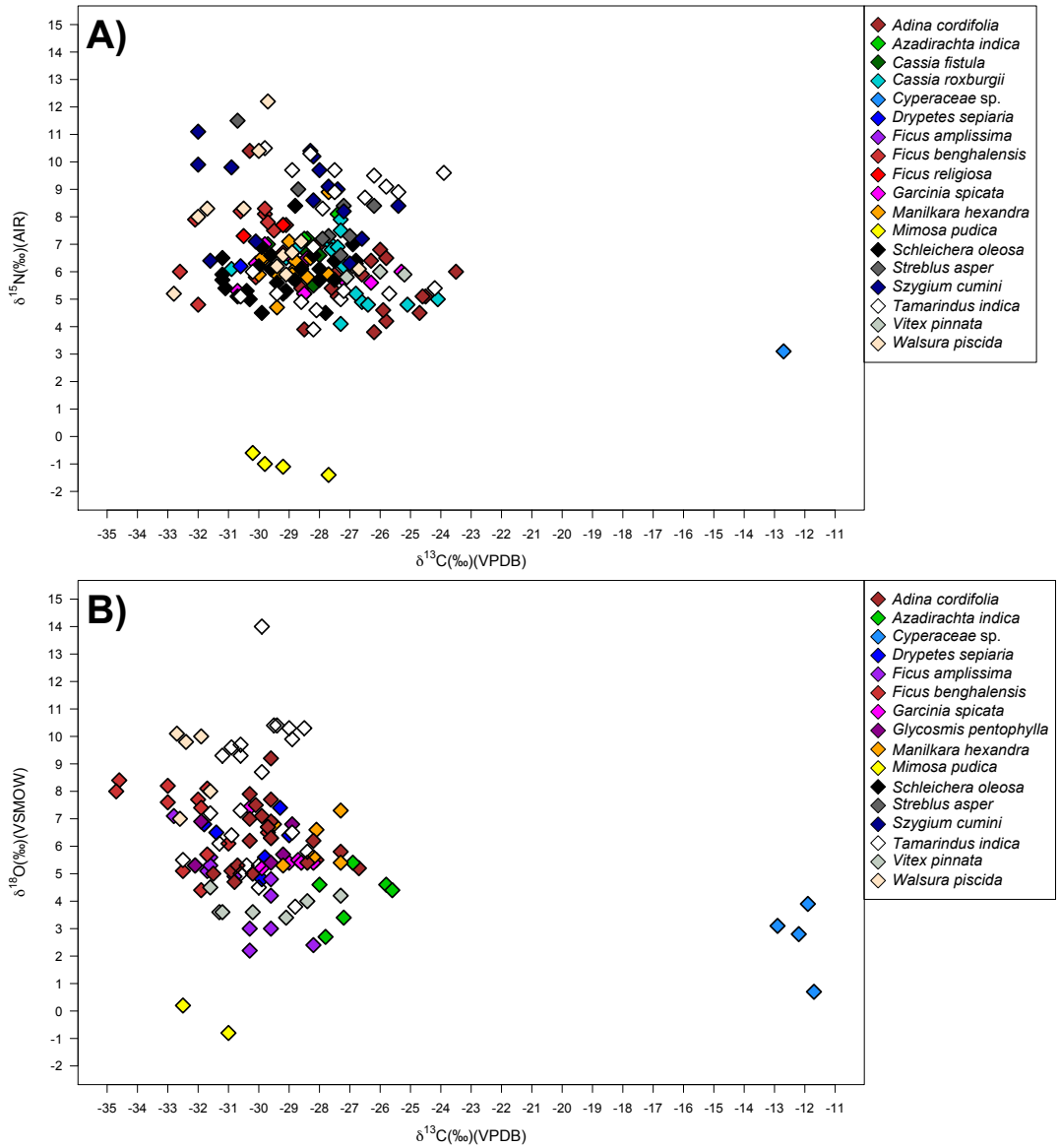


Figure 7.34. Modern plant sample $\delta^{13}C$ by $\delta^{15}N$ plotted by species for A) the dry season and B) the wet season.

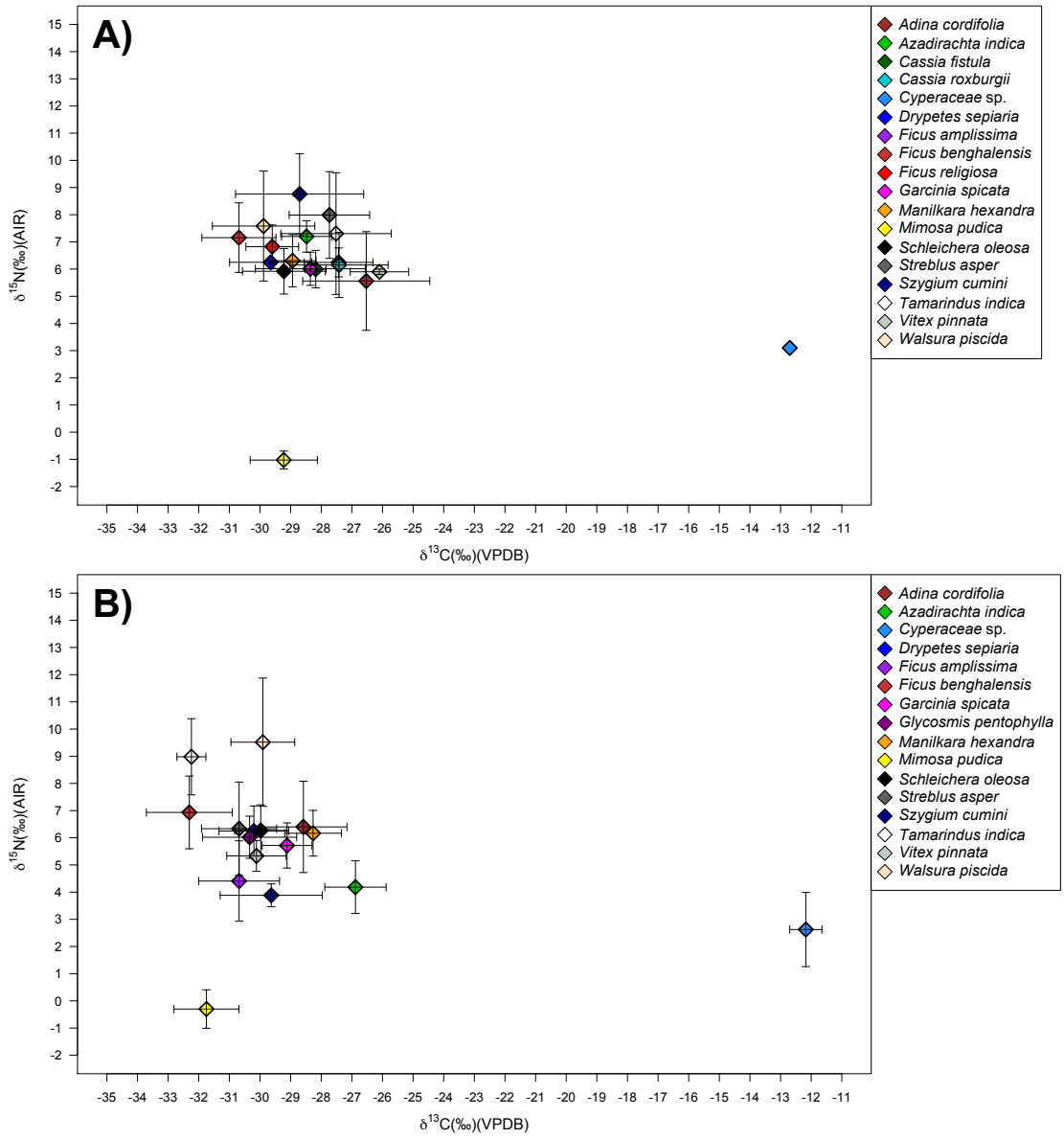


Figure 7.35. Mean and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for each modern plant species sampled during A) the dry season and B) the wet season.

7.3 – Modelling modern primate diet $\delta^{13}C$ and $\delta^{18}O$ at the Polonnaruwa Nature Sanctuary

As outlined in Chapter 5, the $\delta^{13}C$ and $\delta^{18}O$ plant data presented above were estimated into 'diets' for each of the monkey species at the Polonnaruwa Nature Sanctuary and Archaeological Reserve based on qualitative observations of the importance of each of the measured species and plant parts in their diets during the dry and wet seasons (Catalogue Tables A8 and A9). This was done firstly for only those species/plant parts ranked for dietary importance as '1' for each monkey species in Catalogue Tables A8 and A9 (Figure 7.36). To remove the impact of different sample sizes for each species/plant part, an average $\delta^{13}C$ and $\delta^{18}O$ value was obtained for each species/plant part prior to inclusion in an overall calculation of the mean and standard deviation for the whole 'diet'. ANOVA tests were performed to see whether these 'diets' significantly affected $\delta^{13}C$ and $\delta^{18}O$.

Although subtle distinctions in $\delta^{18}O$ appear to be present between the modelled diets in Figure 7.36, with *Trachypithecus vetulus* and *Macaca sinica* having slightly higher $\delta^{18}O$ (*Trachypithecus vetulus*= 24.4 to 33.3‰; *Macaca sinica*= 25.0 to 33.3‰) relative to *Semnopithecus priam thersites* (24.4 to 29.0‰), ANOVA analysis indicated that there was no distinction in either $\delta^{13}C$ ($F(2,10)=0.260$, $p>0.05$) or $\delta^{18}O$ ($F(2,10)=0.418$, $p>0.05$) for the dry season modelled diets (Catalogue Tables C39 and C40). In the wet season, there appears to be less variability in the three modelled diets and there seems to be a subtle trend from lower $\delta^{13}C$ values for the *Macaca sinica* diet (-31.2±0.9‰) to higher $\delta^{13}C$ in the *Trachypithecus vetulus* diet (-29.2±0.9‰). Nevertheless, once again, there was found to be no distinction in either $\delta^{13}C$ ($F(2,4)=2.700$, $p>0.05$) or $\delta^{18}O$ ($F(2,4)=0.545$, $p>0.05$) for these modelled diets (Catalogue Tables C41 and C42).

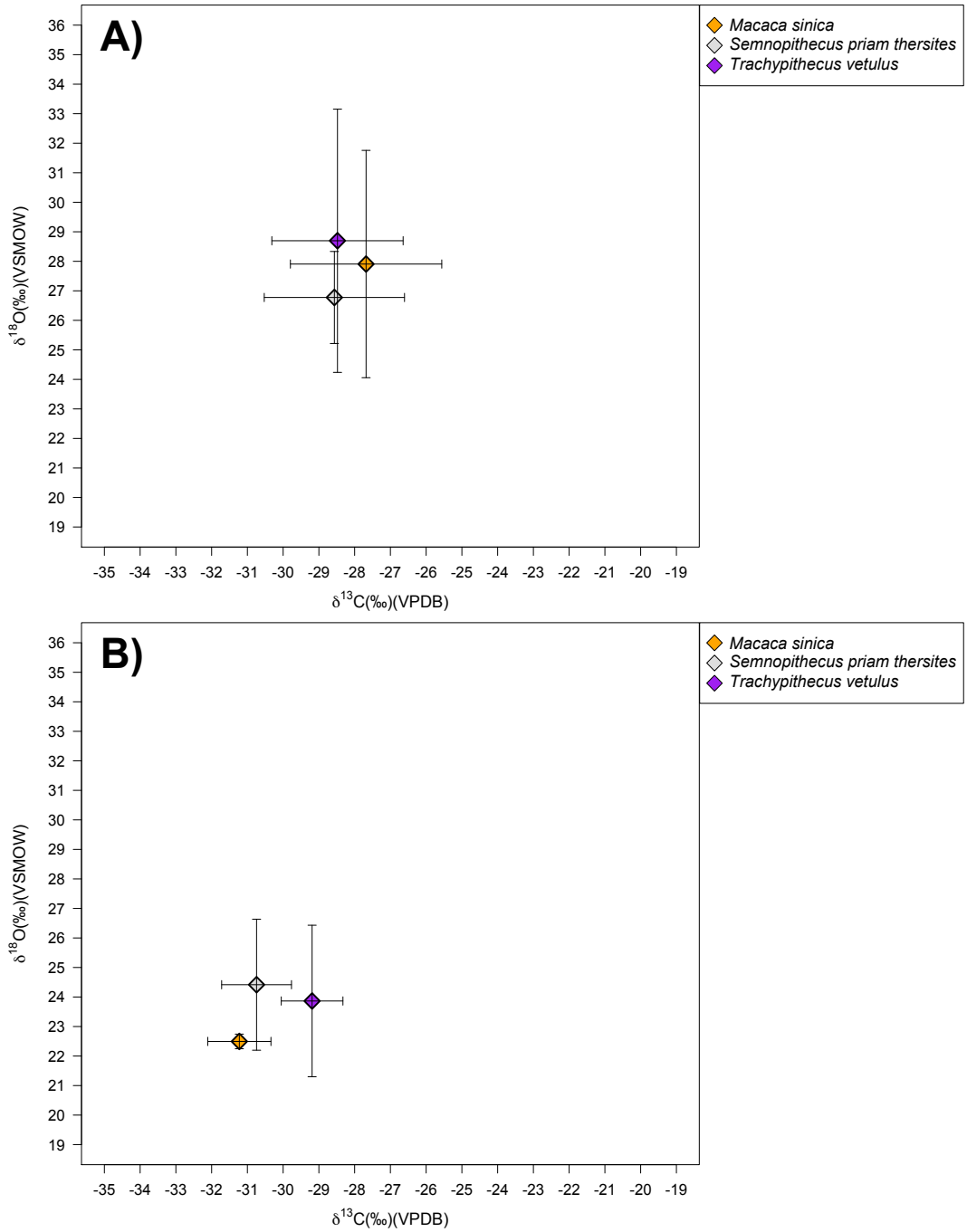


Figure 7.36. Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of modelled monkey diets (for Trachypithecus vetulus, Semnopithecus priam thersites*, and* Macaca sinica*) for A) the dry season and B) the wet season when species and plant parts of importance '1' are included (see Catalogue Tables A8 and A9). To remove the impact of different sample sizes an average $\delta^{13}C$ and $\delta^{18}O$ value was obtained for each species/plant prior to inclusion in an overall calculation of the mean and standard deviation for the whole 'diet'.*

A slightly different picture emerges when the plant $\delta^{13}C$ and $\delta^{18}O$ data are modelled into 'diets' based on those species and plant parts ranked for dietary importance as '1' and '2' for each monkey species in Catalogue Tables A8 and A9 (Figure 7.37). For both the dry and wet season, the main change is that the $\delta^{18}O$, and particularly $\delta^{13}C$, range of the *Macaca sinica* modelled diet greatly increases (dry season: $\delta^{13}C$=-30.3 to -12.7‰, $\delta^{18}O$= 25.0 to 33.4‰; wet season: $\delta^{13}C$= -31.9 to -12.2‰, $\delta^{18}O$= 22.3 to 26.9‰) This shift is driven by the inclusion of 'open', ground-dwelling plants, namely the Cyperaceae spp. sedges and demonstrates the highly generalist diet of this monkey species. *Trachypithecus vetulus* (wet season: $\delta^{13}C$= -29.5±1.7‰, $\delta^{18}O$= 23.7±1.4‰; dry season: $\delta^{13}C$= -28.1±1.6‰, $\delta^{18}O$= 28.7±1.8‰) and *Semnopithecus priam thersites* (wet season: $\delta^{13}C$= -30.2±1.7‰, $\delta^{18}O$= 23.9±1.5‰; dry season: $\delta^{13}C$= -28.2±1.5‰, $\delta^{18}O$= 28.2±2.7‰), by contrast, demonstrate much smaller standard deviations for their model diets with means that are lower in $\delta^{13}C$ than the model diet of *Macaca sinica* (wet season: $\delta^{13}C$= -26.2±9.4‰, $\delta^{18}O$= 24.2±2.1‰; dry season: $\delta^{13}C$= -26.0±5.6, $\delta^{18}O$= 29.3±3.6‰). This is perhaps indicative of more specialised folivory in these two monkeys. However, ANOVA testing fails to note any statistically significant differences in $\delta^{13}C$ (dry season ($F(2,41)=2.088$, $p>0.05$); wet season ($F(2,41)=0.394$, $p>0.05$) or $\delta^{18}O$ (dry season ($F(2,14)=0.982$, $p>0.05$); wet season ($F(2,14)=0.110$, $p>0.05$) (Catalogue Tables C43-C46).

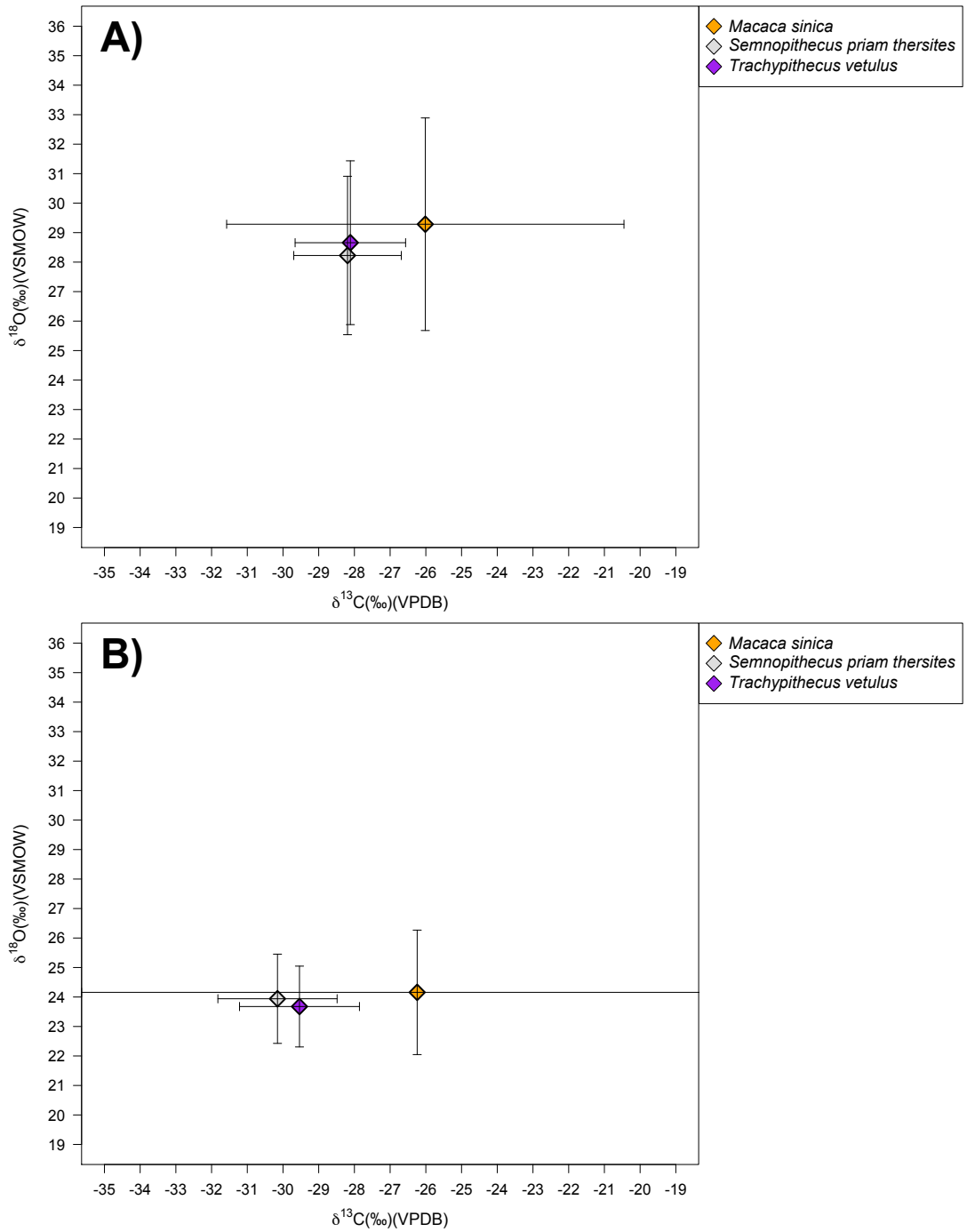


Figure 7.37. *Mean and standard deviations for $\delta^{13}C$ and $\delta^{18}O$ of modelled monkey diets (for* Trachypithecus vetulus, Semnopithecus priam thersites*, and* Macaca sinica*) for A) the dry season and B) the wet season when species and plant parts of importance '1' and '2' are included (see Catalogue Tables A8 and A9). To remove the impact of different sample sizes an average $\delta^{13}C$ and $\delta^{18}O$ value was obtained for each species/plant prior to inclusion in an overall calculation of the mean and standard deviation for the whole 'diet'.*

From this dietary modelling it should be clear that, based on the modern plant dataset studied, modern niche distinctions between *Trachypithecus vetulus*, *Macaca sinica* and *Semnopithecus priam thersites* are difficult to track isotopically at Polonnaruwa. When species and plant parts of importance '1' are included, despite *Macaca sinica* being more frugivorous than *Trachypithecus vetulus* and *Semnopithecus priam thersites,* there is no statistically significant difference in $\delta^{13}C$ between the modelled diets. Therefore, although I have shown there to be a $\delta^{13}C$ distinction between leaves to fruits of the same plant within the plant dataset, increased fruit relative to leaf consumption is not visible between these primate diets isotopically. This is likely due to the confounding effect of plant species on plant, and monkey diet, $\delta^{13}C$ values. A similar situation exists when species and plant parts of importance '1' and '2' are included in the model diets. While *Macaca sinica* does show, on average, higher $\delta^{13}C$ values than *Trachypithecus vetulus* and *Semnopithecus priam thersites* this is primarily linked to the incorporation of 'open' growing sedge plants in the diet. Indeed, it is the isotopic variation of the generalist strategy of *Macaca sinica* that is most obvious in Figure 7.37 rather than any absolute dietary distinction.

This modelling does not include the potential impacts of height in the canopy and insolation on species/plant part, and monkey diet, for $\delta^{13}C$ and $\delta^{18}O$ (Krigbaum *et al.,* 2013; Carter and Bradbury, 2015). However, the effects of these parameters on $\delta^{13}C$ and $\delta^{18}O$ were found to be minimal in Figures 7.23-7.26. Furthermore, it should be noted that the plant sampling undertaken in this thesis does not cover the whole diets of any of the monkey species, which could include things like woody plant parts, other plant species, or invertebrates (particularly in the case of *Macaca sinica*). Nonetheless, $\delta^{13}C$ and $\delta^{18}O$ measurements of tooth enamel from a modern sample set of

Trachypithecus vetulus, *Semnopithecus priam thersites*, *Macaca sinica* indicate similar difficulties of interpretation (Figure 7.38) (Catalogue Table C47). Although the sample size is very small, the broad $\delta^{13}C$ range of *Macaca sinica* (-17.2 to -11.9‰) relative to the other two monkeys is apparent in modern samples. *Trachypithecus vetulus* (-17.4 to -16.2‰) and *Semnopithecus priam thersites* (-16.2 and -15.7‰) have more uniform $\delta^{13}C$ relative to the three *Macaca sinica* samples, perhaps indicative of greater dietary specialisation. *Trachypithecus vetulus* (-2.3 to -0.5‰) and *Semnopithecus priam thersites* (-3.1 to -1.5‰) also appear to have slightly elevated $\delta^{18}O$ relative to *Macaca sinica*, (-4.0 to -3.6‰), potentially indicative of feeding height in the canopy. Alternatively it could be a result of *Trachypithecus vetulus* and *Semnopithecus priam thersites* being non-obligate drinkers and *Macaca sinica* being an obligate drinker (Cerling *et al.,* 2004) (Chapter 4 – Section 4.4). However, the high $\delta^{18}O$ values of one obligate drinker, *Cervus* sp., indicates the equifinality of interpreting elevated $\delta^{18}O$ as feeding higher in the canopy, non-obligate versus obligate drinking, or feeding and drinking in more open, evaporative environments.

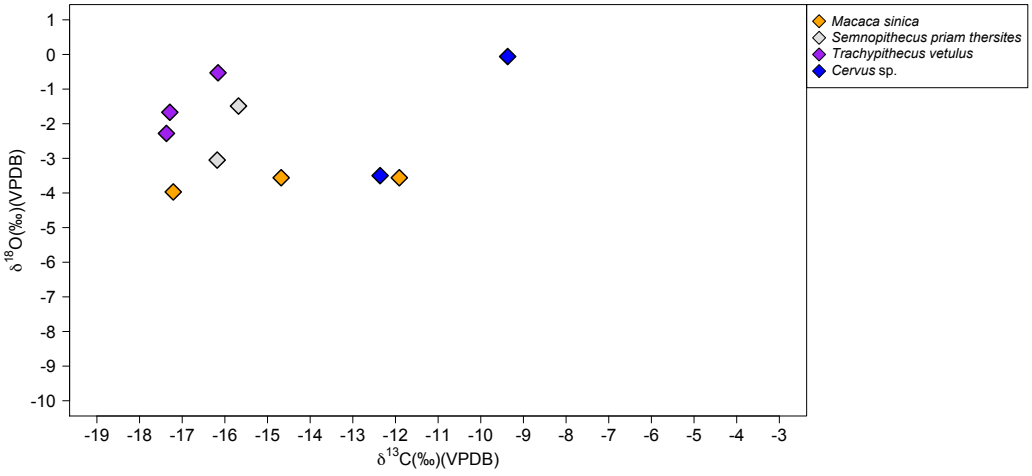


Figure 7.38. $\delta^{13}C$ and $\delta^{18}O$ values of modern monkey and Cervus *sp. samples from a collection of Wolfgang Dittus collected at the Polonnaruwa Nature Sanctuary during the 1980s.*

7.4 – Sri Lankan primate isotopes, past and present

The three monkey species present in Sri Lanka today, *Trachypithecus vetulus* (purple-faced leaf monkey), *Semnopithecus priam thersites* (grey crested langur), and *Macaca sinica* (toque macaque), are all present in the Sri Lankan archaeological record. Yet, despite four decades of observations suggesting these species occupy distinct niches (Chapter 4 – Section 4.4), few differences were visible in the stable carbon and oxygen isotope measurements of the fossil tooth enamel of these primates suggesting that ecological niche distinctions, if they exist, are not tracked into isotopic space. On the basis of agreement between records of $\delta^{18}O$ change in *Trachypithecus vetulus* at Fa Hien-lena and *Semnopithecus priam thersites* at Balangoda Kuragala and that of the faunal assemblage at large, I have suggested that these colobine monkeys likely focused on leaf consumption in contrast to the generalist diets of *Macaca sinica*. However, the only potential clear-cut observation of this are the lower $\delta^{13}C$ values for *Trachypithecus vetulus*, when compared to *Macaca sinica*, at the Terminal Pleistocene-Holocene sequence of Fa Hien-lena, possibly indicating increased specialisation in the consumption of ^{13}C-depleted leaves relative to ^{13}C-enriched fruits. This distinction does not, however, exist where the two species co-occur in the Late Pleistocene sequence at Batadomba-lena.

It has been argued that primates living and feeding higher in a tropical forest canopy will demonstrate higher $\delta^{18}O$ values in their tissues than those feeding on the ground (Krigbaum *et al.,* 2013; Carter and Bradbury, 2015). In addition, higher $\delta^{18}O$ values might be expected in a species consuming evapotranspiration-stressed leaves versus fruits (Krigbaum *et al.,* 2013) or in non-obligate drinkers versus obligate drinkers (Cerling *et al.,* 2004). Based on modern observation this should lead to *Trachypithecus*

vetulus demonstrating higher $\delta^{18}O$ enamel values than *Semnopithecus priam thersites* and *Macaca sinica* (Chapter 4 – Section 4.4). Nevertheless, no distinction exists between any of the monkey species in terms of $\delta^{18}O$ isotope space where they co-occur archaeologically. While this may lead to the conclusion that all primates are feeding at the same canopy height or feeding equally on leaves, *Macaca sinica* is likely obtaining most of its water from open, potentially evaporation-stressed, water sources. As a result, high feeding height, increased leaf consumption, and non-obligate drinking by *Trachypithecus vetulus* and open water source use by *Macaca sinica* could lead to an equifinal increase in $\delta^{18}O$.

Few modern stable isotope studies have been conducted on primate ecosystems in Asia, and no modern plant studies have analysed the impact of environmental parameters on plant $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$ values. Although modern plant samples from the Polonnaruwa Nature Sanctuary and Archaeological Reserve do not come from exactly the same environments as those being explored archaeologically in Sri Lanka, they do provide a regionally-specific baseline for interpreting variation of plant, and therefore primate, $\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) in South Asia. Although eco-physiological studies have tended to focus on $\delta^{18}O$ of leaf water or leaf cellulose more specifically, bulk organic matter $\delta^{18}O$ presented here appears to reliably track seasonal changes in precipitation. Weaker $\delta^{18}O$ trends in relation to insolation and height than suggested elsewhere could be a result of bulk organic matter providing a less-refined environmental signal than leaf water or cellulose (Sternberg *et al.,* 1989; Barbour, 2007). Nevertheless, bulk organic matter arguably provides a more reliable proxy for overall primate food $\delta^{18}O$ contribution. Where a significant influence on primate $\delta^{18}O$ comes from open water (e.g. for *Macaca sinica*) this may, however, confound

environmental and dietary interpretations based on bulk organic matter $\delta^{18}O$. $\delta^{18}O$ measurement of available local water could help to resolve this issue further in future.

With regard to $\delta^{13}C$ distinctions, although fruits were found to be elevated by *c.* 1-4‰ relative to leaves from the same plant during the dry season, this was reduced to a difference of *c.* 0.5-1‰ during the wet season. Given that bulk tooth enamel samples represent more than one season, these seasonal distinctions potentially impact the overall extent of the $\delta^{13}C$ difference one would expect to see between the enamel of frugivorous and folivorous primates. Nevertheless, even when a *Macaca sinica* diet including 100% fruit was estimated against a *Trachypithecus vetulus* diet including 100% leaves and leaf shoots, no $\delta^{13}C$ or $\delta^{18}O$ distinctions were found. This is due to the significant, and usually dominant, impact plant *species* has on determining $\delta^{13}C$ and $\delta^{18}O$. Similarly, while growing season and insolation (and height for $\delta^{18}O$) were also found to have a significant influence on plant $\delta^{13}C$ and $\delta^{18}O$ it is clear that these effects are minor when compared to the impact of species. Plant species has thus far been little emphasised in stable isotope interpretations of modern primate niche (Krigbaum *et al.,* 2013; Macho and Lee-Thorp, 2014; Oelze *et al.,* 2014; Carter and Bradbury, 2015) (but see Codron *et al.,* 2013; Blumenthal *et al.,* 2015). This dataset suggests it may, in fact, be the defining factor of primate tissue $\delta^{13}C$ and $\delta^{18}O$, particularly where diets are primarily vegetarian.

In a modern context, observational data may help in the narrowing down of niche interpretations. For example, a very small modern sample dataset indicates that modern *Trachypithecus vetulus* and *Semnopithecus priam thersites* may have higher $\delta^{18}O$, and generally more uniform $\delta^{13}C$, than *Macaca sinica* in the Polonnaruwa Nature Sanctuary.

Based on modern primate stable carbon and oxygen isotope literature, and modern observation (Krigbaum *et al.,* 2013; Carter and Bradbury, 2015), this would likely be interpreted as higher feeding heights and folivory in the first two species and ground-dwelling and fruit consumption in the latter species. However, the modern plant dataset suggests that this could equally be a result of different species preferences amongst these monkeys, the consumption of more evaporatively-active leaves, or the exploitation of more open areas on the ground. This is particularly problematic in the study of prehistoric primates when we have no direct observational data and no direct measurements on their dietary components. If we can assume that a primate species is folivorous in the past, then it may be possible to interpret trends in $\delta^{13}C$ and $\delta^{18}O$ as environmentally linked. That said, as is indicated by the diverse niches of the folivore *Trachypithecus vetulus*, and its subspecies, in the past and present (Dela, 2007), the observation of this preference is rarely straightforward and may have varied through time.

In the context of the Sri Lankan Microlithic tradition, the stable carbon and oxygen isotope analysis of primate tooth enamel can tell us, in association with other fauna, the degree of closure in the forests they occupied, as discussed in Chapter 6. The high percentages (*c.* 70-80%) of primates within the mammalian assemblages at Batadomba-lena and Fa Hien-lena (Perera, 2010; Perera *et al.,* 2011; Roberts *et al.,* 2015a) indicate that humans had sophisticated hunting technologies specialised in the exploitation of these prey that facilitated the reliable capture of significant protein resources. These species live in social groups and often co-exist together, as at Polonnaruwa, making them a particular attraction for foragers hunting in protein-poor rainforest ecosystems. Modern observations suggest that the capture of *Trachypithecus vetulus* would necessitate projectile technologies to shoot this species from high in the canopy and

traps to capture the semi-arboreal and highly mobile *Macaca sinica*. Stable carbon and oxygen analysis of these fossil primates, and a modern plant dataset, indicates that these niche distinctions cannot be definitively verified isotopically. Nevertheless, the basic identification of these three species at different Late Pleistocene-Holocene sequences implies the existence of complex exploitation strategies that could be investigated further through use-wear analysis of the microlith and bone tool technologies found in great abundance at these sites.

7.5 – Stable isotopes and primate ecology

The last two decades have witnessed a vastly expanding literature of stable carbon, nitrogen, and oxygen isotope analysis of modern primates. Stable isotope analysis of hair, bone collagen, bone carbonate, and tooth enamel of various primate groups has been considered to provide long-term records of dietary distinctions that can complement observational data (Cerling *et al.,* 2004; Oelze *et al.,* 2011, 2014; Krigbaum *et al.,* 2013; Macho and Lee-Thorp, 2014). These methodologies have also been used to investigate social distinctions within and between different primate groups and species (Loudon *et al.,* 2007; Macho and Lee-Thorp, 2014). In recent years, there has been a growing drive to verify previous interpretations of primate $\delta^{13}C$ and $\delta^{15}N$ distinctions using modern plant datasets as a reference (Blumenthal *et al.,* 2012*,* 2015; Oelze *et al.,* 2014). However, although these studies have highlighted that stable isotope distinctions do exist between plant parts ($\delta^{13}C$ - fruit versus leaves, $\delta^{15}N$ - woody versus non-woody), they have largely neglected the significant stable isotope variation caused by plant species. The modern plant data from the Polonnaruwa tropical forest emphasise that plant species can be the most significant 'effect' on plant $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$ and

needs to be taken into account when dietary or environmental interpretations of primate tissue $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$ are attempted.

In a fossil, or historical, context, $\delta^{13}C$ of primate tissues can be used to track the degree of closure in habitats occupied by a species through time (Crowley *et al.,* 2014). As seen here and in Chapter 6, $\delta^{13}C$ of the likely-folivorous *Trachypithecus vetulus* and dietary generalist *Macaca sinica*, when compared with that of associated fauna, demonstrate clear changes between the closed Wet Zone rainforests, more open Intermediate rainforest, and the open Dry Zone of Sri Lanka. However, more detailed interpretation of primate niches within a given environmental context is complicated by equifinality of the potential impacts of plant part, plant species, height in the canopy, insolation, and local clearances. For example, while Nelson (2007) argued that high $\delta^{18}O$ values in the Miocene ape, *Sivapithecus*, indicate that it fed arboreally, in a more recent publication she acknowledges that the same effect could be caused by it feeding higher in the canopy, feeding in a less continuous canopy, or relying more on leaves (Nelson, 2013). A similar scenario has been demonstrated here whereby lower $\delta^{13}C$ in the monkey *Trachypithecus vetulus*, as opposed to *Macaca sinica*, in the Terminal Pleistocene-Holocene sequence of Fa Hien-lena could indicate increased reliance on leaves versus fruits, or it could suggest the inhabitation of more closed forest regions.

It is possible, as Nelson (2013) notes, that $\delta^{13}C$ and $\delta^{18}O$ can be used together to aid interpretation. For example, high primate $\delta^{18}O$ as a result of feeding in more open forest clearings should correspond with increased $\delta^{13}C$. Yet, this will only work where the primate diet can be assumed to be purely folivorous, as generalist diets, such as that of *Macaca sinica*, can lead to huge variation in $\delta^{13}C$ and $\delta^{18}O$, as a result of plant part,

species, or occupation of clearings. Such an assumption cannot be made for extinct species such as *Sivapithecus* and *Ardipithecus ramidus.* As a result, while stable carbon, oxygen, and nitrogen isotope analysis of modern primate tissues provide useful long-term dietary and environmental information, at least within restricted spatial and temporal contexts (Schoeninger *et al.,* 1997; Cerling *et al.,* 2004; Loudon *et al.,* 2007), and fossil primate tissues can provide information regarding shifts in forest closure through time (Crowley *et al.,* 2014), more detailed interpretations of primate niches will be complex, if not impossible, without the assistance of observational data. In a fossil context, beyond the interpretation of large shifts in forest extent and composition, it seems unlikely that primate $\delta^{13}C$ and $\delta^{18}O$ (and possibly also $\delta^{15}N$) can provide definite identification of reliance on different plant parts, different plant species, different feeding heights in the canopy, or different local clearing use with any degree of certainty.

Chapter 8 – Conclusions

This thesis endeavoured to evaluate the status of Sri Lanka as a region of Late Pleistocene-Holocene human rainforest adaptation. Previous research on early human rainforest interactions has had to largely rely on coarse zooarchaeological and palaeobotanical datasets, or indirect correlation between 'off-site' records of rainforest presence and archaeological sequences (Chapter 2 – Sections 2.1, 2.2 and 2.3). I employed stable carbon and oxygen isotope analysis of fossil faunal and human tooth enamel from Late Pleistocene-Holocene sites in Sri Lanka in order to produce a *direct* record of human rainforest resource reliance and a human stable isotope ecology for the rainforests of this region. This is the first time this methodology has been applied to questions of Late Pleistocene human rainforest adaptations (Chapter 4 – Section 4.2). Such an approach is important in that it allows us to not only investigate the adaptive flexibility of our species on its expansion beyond Africa, but it also facilitates the testing as to whether populations of *Homo sapiens* were able to specialise, at this early stage, in the exploitation of an environment that has often been perceived as a 'barrier' to long-term human occupation and complexity (Hart and Hart, 1986; Bailey *et al.,* 1989; Bailey and Headland, 1991; Gamble, 1993; Bird *et al.,* 2005; Dennell and Roebroeks, 2005).

I have emphasised in Chapters 1 to 3 that archaeological analysis of rainforest environments needs to take into account a significant degree of temporal and geographical complexity in these environments. This thesis therefore also sought to use stable isotope analysis to examine the particularities of the impacts of climate on Sri Lanka's rainforest ecosystems through time, as well as the particular strategies exploited by human foragers in these tropical forests. Stable carbon and oxygen isotope

analysis of fossil fauna was performed on sequences spanning the LGM and the Terminal Pleistocene-Holocene boundary, periods known to have effects on rainforest ecologies elsewhere (Chapter 3 – Section 3.2), to assess the stability of Sri Lankan rainforest ecologies across the Late Pleistocene and into the Holocene. Stable carbon and oxygen isotope analysis was also applied to fossil primates in order to determine the niche positioning, and subsistence strategies necessary, to hunt monkey species that make up between *c.* 70 and 80% of the mammalian faunal assemblages at the Sri Lankan rainforest sites (Chapter 2 – Section 2.2). The development of a modern stable carbon and oxygen (and nitrogen) isotope reference of modern plant species and parts, known to be of dietary importance to these monkey species in the present day, represents a solid attempt to examine the impacts of species, plant part, insolation, canopy height, and season on these isotopic parameters in this region of the world (Chapter 4 – Section 4.4).

Chapters 6 and 7 presented the results of these stable isotope applications. This chapter sets out to evaluate how these results address the three research areas presented in Chapter 1 (Section 1.2), relating to prehistoric human rainforest resource reliance in Late Pleistocene-Holocene Sri Lanka, fluctuations in Sri Lanka's vegetation boundaries during the LGM and Terminal Pleistocene/Holocene transition, and the complexity of hunting strategies employed during the Sri Lankan Microlithic tradition to consistently obtain large numbers of primate species, in turn. In each case I assess how stable isotope methodologies have, to varying degrees of success, tested the relevant hypotheses associated with these research areas. Finally, I examine how the resulting information can inform us with regards to the distinctiveness of Sri Lanka's 'rainforest prehistory' and the broader desirability of rainforests as ecologies for long-term human forager exploitation and occupation.

8.1 – Stable carbon and oxygen isotope analysis of fossil humans and fauna as a direct test of human rainforest resource reliance in Late Pleistocene-Holocene Sri Lanka

Stable carbon and oxygen isotope analysis of fossils humans and fauna from the Late Pleistocene site of Batadomba-lena and the Terminal Pleistocene-Holocene sites of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa presented in Chapter 6 supports the hypothesis that:

1. *Sri Lankan human foragers relied on rainforest resources back to at least c. 36-29,000 years ago, well beyond the Holocene, and through periods of climatic and environmental flux when the productivity, stability and spatial organisation of global forest environments are known to have changed dramatically.*

The most likely date range for Layer 7c of Batadomba-lena, and the earliest human sample analysed in this study has been shown here to be *c.* 36,000-29,000 cal. years BP (Chapter 5 – Section 5.1). This human sample has $\delta^{13}C$ values that indicate that it relied on resources from closed canopy rainforests at the Wet Zone site of Batadomba-lena even when more mixed forest-open habitats were available. Other individuals from Batadomba-lena, dated to *c.* 20,000-16,000 cal years BP have $\delta^{13}C$ and, to a weaker extent, $\delta^{18}O$ values most likely interpretable as indicative of long-term subsistence concentration and habitation in more open rainforests throughout the LGM similar to the modern 'Intermediate' rainforests of Sri Lanka.

While Terminal Pleistocene/Early Holocene humans from Fa Hien-lena and Balangoda Kuragala may have occupied closed rainforest, the majority of humans from this period have $\delta^{13}C$ and $\delta^{18}O$ that demonstrate a preference for these 'Intermediate' rainforest resources. Significantly, no Late Pleistocene or Holocene human specimen, spanning

the period *c.* 36-29,000 to 3,000 cal. years BP has $\delta^{13}C$ and $\delta^{18}O$ values akin to those of the open faunal group found at Balangoda Kuragala. The two exceptions are individuals dated to *c.* 3,000 cal. years BP, a time when the Sri Lankan Iron Age, and accompanying agriculture, was moving into the region (Chapter 6 – Sections 6.2 and 6.3) (S.U. Deraniyagala, 1992; 2007). Even then though, other individuals from the same date at Balangoda Kuragala demonstrate clear, continued reliance on rainforest resources even in the face of agricultural arrivals into the region.

These results emphatically demonstrate that, contrary to earlier arguments (Bailey *et al.,* 1989; Bailey and Headland, 1991), Sri Lankan human foragers exploited rainforest resources from the Late Pleistocene through to the Holocene. Furthermore, they persisted in this adaptation even during the appearance of domesticated resources in the region. In contrast to previous methodologies employed in the context of human rainforest prehistory (though see Krigbaum, 2001, 2003, 2005), stable carbon and oxygen isotope analysis of fossil Sri Lankan human also establish that Microlithic tradition foragers *specialised* in the exploitation of forest environments from *c.* 36-29,000 cal. years BP to 3,000 cal years BP, rather than using them as part of more-diverse seasonal subsistence strategies which would have resulted in higher bulk $\delta^{13}C$ being seen in the human samples or $\delta^{13}C$ fluctuations in intra-tooth sampling. Not only is this consistent with the ability of the earliest members of our species to reach South Asia's rainforests to specialise in the exploitation of these ecologies, but it also indicates the persistent effectiveness of this subsistence strategy even when the option of agricultural food production appears.

These data sit well with the archaeological evidence from Sri Lanka's cave and rockshelter sites for the early and consistent presence of microlith toolkits, bone

technologies, personal ornamentation, and rainforest plant and animal procurement from *c.* 38-35,000 cal. years BP, through the LGM and Terminal Pleistocene/Holocene transition down to the Iron Age (S.U. Deraniyagala, 1992, 2007; Wijeyapala, 1997; Perera, 2010; Perera *et al.,* 2011, in press; Lewis *et al.,* 2014; Roberts *et al.,* 2015a, 2015b). Whereas other regions where early human rainforest adaptation has been suggested (Mercader, 2002a, 2002b; Barker *et al.,* 2007; Summerhayes *et al.,* 2010; Barker, 2013) have only sparse early evidence, or evidence for the exploitation of mosaic habitats, prior to later intensification (Chapter 2 – Section 2.1), the Sri Lankan record implies rainforest adaptation and specialisation from initial human arrival in these ecologies *c.* 38-35,000 cal. years BP. While there is the hint at a potential earlier coastal hominin presence in Sri Lanka (S.U. Deraniyagala, 1992) (Chapter 2 – Section 2.2), this remains poorly dated and no other Late-Terminal Pleistocene sites have been found beyond the Wet Zone of Sri Lanka. The two exceptions, Balangoda Kuragala (Intermediate Zone) and Bellan-bandi Palassa (Dry Zone), studied here demonstrate that they were most likely surrounded by 'Intermediate' rainforest during the period of occupation and are not indicative of deviation from this pattern.

The perception of rainforests as 'green deserts' (Bailey and Headland, 1991) is clearly out-dated. Chapter 3 (Section 3.4) explored the wealth of evidence for the ethnographic exploitation of carbohydrate-rich tubers and fruits, the use of plant parts for structures, the medicinal benefits of rainforest plants, and the use of plants in baiting animal prey by rainforest foragers. Chapter 3 (Section 3.4) also highlighted how, while large mammalian fauna can be limited, the sophisticated exploitation of fauna through projectile technologies, trapping, net hunting, and the exploitation of rainforest rivers and insects can provide a consistent and stable source of protein, particularly where groups of sympatric primate species exist. In Sri Lanka this broad-spectrum approach,

albeit with a specialised focus on primate hunting, can still be seen today in the context of the forest Veddas, who still employ projectile hunting to catch primates and other varied fauna, and collect sugar-rich honey, tubers, and palm toddy (Chapter 3 – Section 3.4). This evidence, alongside the stable isotope data reported here, demonstrates that tropical forests *can* provide stable and rich subsistence opportunities, sufficient for human subsistence even without the input of resources from other ecologies or food-systems.

It is also clear that, if a successful rainforest adaptation can be developed, rainforest foraging can be resilient in the face of climate change. Stable isotope evidence for Sri Lankan human forager preference for 'Intermediate' rainforest resources does not appear to be linked to a mixed exploitation of forest and open environments, given intra-tooth evidence for stable $\delta^{13}C$ and $\delta^{18}O$ through time. Rather specialisation in slightly more open Intermediate rainforest visible in individuals from Balangoda Kuragala facilitated access to an abundance of arboreal and semi-arboreal primates, potential access to suids and other large game utilising forest fringes on an occasional basis, and the exploitation of riverine resources. The opening of the 'Wet Zone' rainforest during the LGM, *c.* 20,000-16,000 cal. years BP, may have helped this strategy further, and individuals at Batadomba-lena from this date show a clear preference for 'Intermediate' rainforest resources. This is not to say that humans could not exploit closed 'Wet Zone' rainforest in Sri Lanka, as indicated by human $\delta^{13}C$ and $\delta^{18}O$ data from Fa Hien-lena and Batadomba-lena. However, general preference for more open 'Intermediate' rainforest subsistence would leave hunter-gatherers well-placed to deal with fluctuations in the extent and structure of Sri Lanka's rainforests.

8.2 – Stable carbon and oxygen isotope analysis of fossil fauna as a palaeoenvironmental proxy for rainforest environments in Late Pleistocene-Holocene Sri Lanka

Stable carbon and oxygen isotope analysis of fossil fauna from the Late Pleistocene site of Batadomba-lena and Terminal Pleistocene-Holocene sites of Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa presented in Chapter 6 also supports the hypothesis that:

2. *The extent of the closed 'Wet Zone' rainforest of Sri Lanka waxed and waned in the past, especially across the significant climatic transitions of the LGM (c. 20,000 years ago) and the Terminal Pleistocene/Holocene boundary (c. 12,000-8,000 years ago).*

Faunal $\delta^{13}C$ and $\delta^{18}O$ from Batadomba-lena indicates that the extent and structure of Sri Lanka's 'Wet Zone' rainforest changed significantly over the last 36-29,000 years. Although the one human individual sampled from this time period indicates a clear preference for closed 'Wet Zone' rainforest resources (Chapter 6 – Section 6.4), at the stage of earliest occupation of the rainforests of this region, there appears to have been a mosaic of closed canopy rainforest, more open rainforest, and mixed forest-open environments available to human populations. Evidence for more open rainforest at Batadomba-lena persists across the LGM, though mosaic forest-open habitats appear to disappear from *c.* 12,000 cal. years BP. This fits with vegetation modelling performed by Boivin *et al.* (2013) that, although indicating a persistence of tropical forest, suggest a more fragmented, mosaic landscape in the tropical forest regions of South Asia for MIS 4-2.

An abundance of evidence for the persistence, but alteration in extent and structure, of rainforests during the LGM (*c.* 25,000-18,000 years ago) now exists for Africa, South

America, Southeast Asia, and Melanesia (Chapter 3 – Section 3.2). Less evidence exists for South Asia (Farooqui *et al.,* 2010), although palaeoenvironmental proxy evidence from Bay of Bengal and Arabian Sea marine cores indicate significant fluctuations in the intensity and position of the palaeo-monsoon throughout the Late Pleistocene (Schulz *et al.,* 1998; Prabhu *et al.,* 2004; Caley *et al.,* 2011; Rashid *et al.,* 2011; Deplazes *et al.,* 2014) that would have had significant impacts on regional vegetation distributions (Chapter 3 – Section 3.3). Stable carbon and oxygen isotope evidence presented here provides the first evidence for changes in rainforest extent and structure, of immediate relevance to human rainforest adaptations, in South Asia. While to some extent these data agree with the pollen record from the Horton Plains highlands, that 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), they highlight that rainforest persisted in locales occupied and exploited by human foragers.

In contrast to this earlier period, the Terminal Pleistocene-Holocene transition appears to represent a remarkably stable period in the context of Sri Lanka's rainforests. Faunal $\delta^{13}C$ and $\delta^{18}O$ from Fa Hien-lena, Balangoda Kuragala, and Bellan-bandi Palassa potentially suggest that the climate and vegetation boundaries of modern Sri Lanka, namely 'Wet Zone' closed rainforest, 'Intermediate Zone' intermediate rainforest, and 'Dry Zone' grasslands and open jungles, were present in the past. These data also indicate an increase in rainforest presence and closure in the 'Wet Zone' of Sri Lanka, compared to earlier periods, during the Terminal Pleistocene-Holocene (as noted elsewhere in the world: Chapter 3 – Section 3.2). Furthermore, the closed rainforest conditions at Fa Hien-lena and 'Intermediate' rainforest conditions at Balangoda Kuragala fluctuated little over the periods of *c.* 12,500-7,500 cal. years BP and *c.*

12,500-3,000 cal. years BP, respectively. At Balangoda Kuragala, the minimal presence of isotopically 'open' fauna throughout the sequence could be a result of human choice, or could be representative of the limited presence of open ecologies in this region during this period. Indeed, the possibility that forest extent was greater during the Terminal Pleistocene/Holocene boundary, even compared to the present day, is suggested by faunal taxa, and their $\delta^{13}C$ and $\delta^{18}O$, from Bellan-bandi Palassa (*c.* 12-11,000 cal. years BP) being indicative of Intermediate rainforest presence in a Dry Zone locale that is currently characterised by grassland surrounding a stream.

The lack of change in rainforest structure and extent throughout the Terminal Pleistocene-Holocene also suggests that, unlike in areas of Southeast Asia and Melanesia, human groups did not burn or remove the rainforests of Sri Lanka, despite long-term presence and intensive exploitation. Although the earlier evidence for forest fragmentation in the Sri Lankan Wet Zone could be seen as potentially indicating human influence, a lack of charcoal evidence from the Late Pleistocene Horton Plains highlands pollen sequence (Premathilake and Risberg, 2003; Premathilake, 2006, 2012; Premathilake and Gunatilaka, 2013), as well as a lack of evidence for human restructuring of the forest during the Terminal Pleistocene-Holocene, suggests that foragers of the Sri Lankan Microlithic tradition did not actively seek to open rainforests through burning or deforestation. This would fit with an ongoing, persistent focus on different primate species that live together only in dense forest environments, the hunting of a variety of fauna with preferences for forest environments (Chapter 5 – Section 5.2), and the use of tree nut and fruit species rather than starch rich tubers that might benefit from burning (Perera *et al.,* 2011). Although evidence for the latter is difficult to find in rainforest taphonomies, it appears that the foragers of the Sri Lankan Microlithic tradition had a different relationship with the rainforest than Late

Pleistocene foragers in Melanesia and Southeast Asia who frequently burned local forest habitats to promote plant growth and faunal access (Fairbairn *et al.,* 2006; Denham *et al.,* 2009; Hunt *et al.,* 2012).

Stable carbon and oxygen isotope analysis of fossil faunal tooth enamel in Sri Lanka has therefore contributed significantly to our understanding of fluctuations in rainforest ecologies of immediate relevance to human behaviour in this region. It should be borne in mind, however, that the fauna sampled have been selected by people. Therefore, this palaeoenvironmental signal may be indicative of human preference rather than the real variability inherent in regional conditions. Future work using stable isotope analysis of fossil fauna as a palaeoenvironmental proxy in a rainforest environment may thus benefit from a focus on the analysis of abundant small mammal samples, if present, throughout a sequence. Limited mobility in these species will at least ensure that a local record of palaeoenvironmental change is obtained (Jeffrey *et al.,* 2015). A potential, subtle impact of species on the interpretation of fossil $\delta^{13}C$ and $\delta^{18}O$ as a palaeoenvironmental signal may also be seen between the folivorous and generalist monkey species analysed in this study (Chapter 7 – Section 7.1). Nevertheless, agreement of the isotopic records produced here with vegetation models, regional pollen and climate records, and similar changes in tropical forest extent and structure documented elsewhere would suggest that the stable carbon and oxygen isotope analysis of fossil faunal tooth enamel has provided reliable information related to Sri Lankan palaeoforest extent and structure through time.

8.3 – Stable carbon and oxygen isotope analysis of fossil and modern primate tooth enamel as an indirect indicator of human hunting strategies in Late Pleistocene-Holocene Sri Lanka

In contrast to the other research areas, stable carbon and oxygen isotope analysis of fossil primate tooth enamel was unable to test the hypothesis:

3. *Late Pleistocene and Early Holocene forest-dwelling humans in Sri Lanka practised diverse primate hunting strategies to capture the diversity of primate species present at associated archaeological sites.*

Fossil enamel $\delta^{13}C$ and $\delta^{18}O$ data were obtained for Late Pleistocene-Holocene specimens of *Macaca sinica*, *Tracypithecus vetulus*, and *Semnopithecus priam thersites.* At each of Fa Hien-Lena, Balangoda Kuragala, Bellan-bandi Palassa and Batadomba-lena there was always more than one of these primate species present. However, obvious niche distinctions expected between these species, based on modern observations and ecological information, were rarely found. In the only case where a distinction was observed, with *Trachypithecus vetulus* having lower $\delta^{13}C$ values than *Macaca sinica* at Fa Hien-lena, this can be interpreted as either increased leaf consumption or feeding in more shaded parts of the forest by the former. No niche distinction existed between the two in terms of $\delta^{18}O$.

Stable carbon and oxygen (and nitrogen) isotope analysis of modern plant samples illustrate the considerable complexity of environmental parameters influencing plant, and monkey diet, $\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) in a tropical forest environment. The influences of plant part (i.e. fruits versus leaves) on $\delta^{13}C$, impacts of canopy height on $\delta^{18}O$, and effect of insolation on $\delta^{13}C$ and $\delta^{18}O$, documented in the literature on modern primate stable isotope studies (Krigbaum *et al.,* 2013; Oelze *et al.,* 2014; Carter and

Bradbury, 2015), were verified in this dataset. However, modern plant $\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) from the Polonnaruwa Nature Sanctuary suggests that previous studies have significantly downplayed the impact species can have on these parameters. Indeed, in this case, species arguably has the greatest influence on plant $\delta^{13}C$ and $\delta^{18}O$ (and $\delta^{15}N$) and therefore the diet of any largely vegetarian primates. As a result, it is therefore perhaps unsurprising that when the modern plant dataset was used to construct hypothetical 'diets' for each of the primate species, obvious niche distinctions could not be identified isotopically, with the exception of highlighting that *Macaca sinica* is a dietary generalist and *Trachypithecus vetulus* and *Semnopithecus priam thersites* are more specialised. This is the case even though four decades of modern observation work on these primates indicate that there are clear differences in the relative consumption of fruits versus leaves and feeding height in the canopy (Chapter 4 – Section 4.4, Chapter 5 – Section 5.4).

In presenting the modern plant dataset from a tropical forest to study the impacts of plant part, species, season, height, and insolation on plant $\delta^{13}C$, $\delta^{15}N$ *and* $\delta^{18}O$, this thesis has also highlighted issues in the application of stable isotope analysis to the detailed discrimination of primate niches more broadly. Although fossil, or historical, primate $\delta^{13}C$ and $\delta^{18}O$ can be used to track broad changes in forest extent (Loudon *et al.,* 2007), as with other fauna, folivorous primates will likely track these more reliably than generalist primates (Chapter 7 – Section 7.1). Furthermore, while the application of these methodologies can potentially be used to document primate social group and primate species niche distinctions, when a large amount of observational data is present (Macho and Lee-Thorp, 2014), issues of equifinality, and the significant impact of plant species, limit the degree to which independent verification of specific niche trends, such

as feeding height in the canopy and reliance on plants versus fruits, can be gained from primate tissue $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$. This problem is exacerbated in studies of fossil primate niches where a lack of observational data, and a lack of certainty as to whether a species is consistently purely folivorous, mean that the exact reason for subtle variations in primate tissue $\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$, beyond large $\delta^{13}C$ trends in forest coverage, is impossible to resolve, despite attempts to do this with fossil primates back to *c.* 9 Ma (Nelson, 2007).

Returning to the specific hypothesis presented here, if we wish to identity the strategies used by Late Pleistocene and Early Holocene human foragers to procure large numbers of primates, we are left to rely on zooarchaeological identifications and indirect assumptions regarding the usage of the persistent microlith and bone tool technologies (Chapter 7 – Section 7.4). The high percentages of primates found within the mammalian assemblages at Batadomba-lena and Fa Hien-lena (Perera, 2010; Perera *et al.,* 2011; Roberts *et al.,* 2015a), demonstrate that these animals were not being procured casually, but that a sophisticated, reliable strategy had been developed to ensure their capture. The consistent presence of nocturnal species, such as *Hystrix indica* (porcupine), at all of the sites sampled in this study suggests that Late Pleistocene-Holocene humans may have utilised trapping technologies. Perera *et al.* (in press) have suggested that this may be one of the possible uses for the bone tool technologies at Batadomba-lena given that their frequency appears to fluctuate with the presence of small arboreal and semi-arboreal mammals such as palm civets (*Viverricula indica*) and squirrels (*Ratufa macroura*). By contrast, the procurement of large, dangerous animals such as elephants (*Elephas* sp.), wild boar (*Sus scrofa*) and muntjak

deer (*Muntiacus muntjak*) would imply the use of projectile technologies, though only the muntjak is represented in the Late Pleistocene record of Batadomba-lena.

On the basis of modern observations, and biological information, the purple-faced leaf monkey (*Trachypithecus vetulus*) is digestively and behaviourally specialised in the consumption of leaves, although in modern times its diet has diversified (Dela, 2007, 2012). While its presence at Bellan-bandi Palassa indicates that it could occupy more open 'Intermediate' rainforest, this is likely representative of the presence of the Dry Zone subspecies of this monkey at this point in time (Chapter 4 – Section 4.4) and, when found in the 'Wet Zone' forests of Sri Lanka, this species is shy and limited to greater heights in the canopy. On the basis of ethnographic observations (Chapter 3 – Section 3.4), it is highly likely that projectile technologies would be necessary to capture this species in the rainforest. Although the grey crested langur (*Semnopithecus priam thersites*) is also adapted to leaf consumption, it, like the toque macaque (*Macaca sinica*), is regularly found on the ground and both species are present across the Wet, Intermediate, and Dry Zones of Sri Lanka in the present day. The Vedda community of Sri Lanka today hunts these species using projectile technologies, using great stealth to get close to their prey (Chapter 3 – Section 3.4). However, the Raute of western Nepal use communal net hunting to procure monkeys of the same genera (Fortier, 2009).

Together, this information would imply that the earliest human occupants of the 'Wet Zone' rainforest of Sri Lanka at Batadomba-lena and Fa Hien-lena employed diverse hunting strategies to capture these various species of primate, as well as the other forest animals present. Given that the bone tools appear to have been linked to either the trapping of small, semi-arboreal mammals or the exploitation of riverine and forest molluscs (Perera *et al.,* in press), the specialised primate procurement may be best

associated with microlith technologies. Elsewhere, microlith tools have been associated with use as part of bow and arrow mechanisms (Lombard and Philipson, 2010; Shea and Sisk, 2010), and it could be that the quartz microliths of Sri Lanka were used to hunt arboreal primates, and larger ground-based mammals, as a persistent source of protein. Nonetheless, this largely remains speculation on the basis of modern primate and ethnographic observations, and stable carbon and oxygen isotope analysis of the primates themselves has been unable to definitively demonstrate niche distinctions that might be of relevance to these strategies. It is possible that use-wear studies of microlith toolkits and bone tools in future may help to resolve the usage of these technologies.

8.4 – A Sri Lankan 'rainforest prehistory'

The stable carbon and oxygen isotope data from fossil humans and fauna presented here indicate that, contrary to many regions of the world in which Late Pleistocene human rainforest adaptations have been suggested (Chapter 2 – Section 2.1), foragers of the Sri Lankan Microlithic tradition specialised in the reliance on rainforest resources from 36-29,000 to 3,000 cal. years BP, without recourse to other environments or food systems. It is possible that, in future, stable isotope analysis of early human fossils in Southeast Asia (such as the Niah Cave skull), Africa, and Melanesia will provide evidence for similar adaptations elsewhere. However, until then, the Sri Lankan stable isotope evidence, as well as early and persistent evidence for microlith toolkits, bone technologies, and the procurement of a variety of rainforest fauna and plants, makes this region distinctive in the context of early rainforest adaptations by our species. Unlike Late Pleistocene Southeast Asia, Melanesia, and potentially Africa, there is no evidence for the seasonal exploitation of mosaic environments, cursory initial occupation prior to later intensification, or evidence for the use of burning to open up tropical forests.

Instead, the rainforest of Sri Lanka appear to have provided an early, and stable, ecological home for the foragers of the Sri Lankan Microlithic tradition until the eventual appearance of agriculture in the region during the Iron Age.

This apparently unique adaptation appears to have been supported by the exploitation of arboreal and semi-arboreal primate populations. These co-existing species provided a plentiful and stable protein supply, making up the majority of mammalian kill assemblages within the rainforest rockshelter and cave sites of Sri Lanka. At the Niah Caves, Sarawak, by contrast the main source of protein appears to have come from wild boar migrating through a mosaic of tropical forest environments (Barker *et al.,* 2007), while in Melanesia terrestrial animal protein is limited to small mammals (such as the cuscus and bandicoot) that were eventually deliberately transported between island tropical forest environments from 20,000 cal. years BP onwards (Gosden and Robertson, 1991; Gosden, 2010). This may go some way to suggesting why human foragers in Sri Lanka could focus their entire subsistence, including protein procurement, on rainforest resources, while those in Southeast Asia and Melanesia required more mobile strategies. Another factor may be the generally stable climate of Sri Lanka. While forests mosaics existed during MIS 4-2 there was a consistent presence of Wet Zone and Intermediate rainforests in Sri Lanka. By contrast, foragers in the montane rainforests of Highland New Guinea were faced with fluctuating temperature extremes (Gosden, 2010; Summerhayes *et al.,* 2010) and those in Southeast Asia witnessed significant sea-level change and forest fragmentation, prior to later forest expansion (Rabett, 2012).

8.5 – Forests of plenty or 'green deserts': the desirability of rainforests for long-term human subsistence

Archaeological evidence from Sri Lanka contributes to a growing abundance of evidence for Late Pleistocene human rainforest presence and resource use (Roberts and Petraglia, 2015). It is now clear that our species had reached, and was utilising, the rainforests of Southeast Asia and Melanesia by 45,000 years ago, and those of South Asia *c.* 38-35,000 years ago. Potential evidence for even earlier rainforest occupation in Africa *c.* 200,000 years ago (Mercader, 2002a, 2002b) remains to be verified directly and should be interpreted with caution. Nevertheless, while rainforests have often been considered as 'green deserts', and barriers to the migration and long-term occupation of our species, and indeed our genus (Gamble, 1993; Dennell and Roebroeks, 2005), they were potentially some of the earliest ecologies to be exploited by *Homo sapiens* as it expanded both within and beyond Africa during the Late Pleistocene. This, alongside recent evidence for the occupation of deserts (Groucutt and Petraglia, 2012; Petraglia *et al.,* 2012; Blinkhorn *et al.,* 2013), further emphasises the flexibility and resilience of early members our species, in the face of the whole diversity of the world's environments and significant climate change through MIS 5-2. It could be this resilience and adaptive plasticity that is what defines our species and its relentless expansion and success relative to other members of the hominin clade (see also Rabett, 2012).

This picture is supported by stable carbon isotope evidence from extant and fossil apes, hominin fossils in Africa, and existing datasets from rainforest human foragers (Figure 8.1). Compared to the low $\delta^{13}C$ values in our ape relatives and their ancestors, the hominin clade in Africa shows generally higher, though diverse, $\delta^{13}C$ measurements as a result of variable contributions of C_4 resources linked to savannah ecosystems. Fossil human $\delta^{13}C$ from Sri Lanka analysed here alongside Holocene forager $\delta^{13}C$ measured

by John Krigbaum for Southeast Asia, however, indicates that populations of *Homo sapiens* can and have exploited closed forest resources intensively (Figure 8.1). While this picture could be complicated when stable carbon isotope evidence becomes available from *Homo erectus* specimens from Southeast Asia and *Homo floresiensis* in Flores, Southeast Asia, our species is currently the only hominin to demonstrate dietary specialisation in the exploitation of closed rainforest resources. This could perhaps be linked to the emergence of more complex technologies and social networks with our species, as partly demonstrated in evidence for microlith and bone technologies and long-distance exchange found in Sri Lanka (Perera *et al.,* 2011).

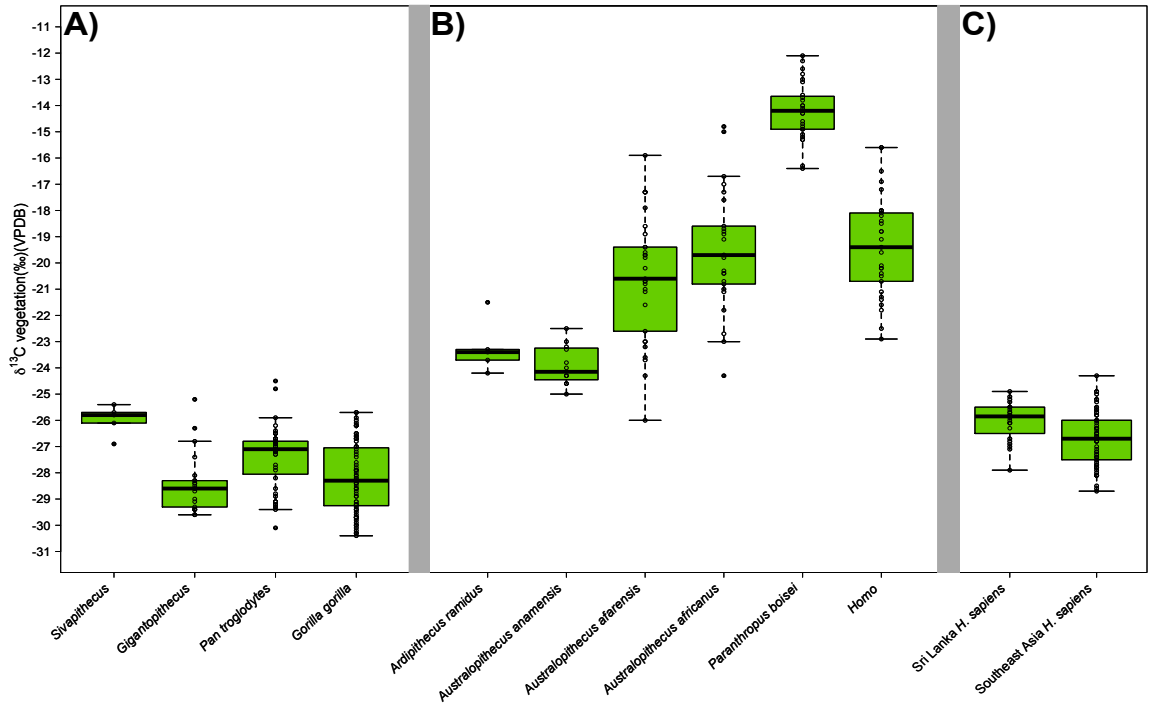


Figure 8.1. Inferred stable carbon isotope data of vegetation for a) modern chimpanzees and gorillas in western-central Africa (Oelze et al., *2014; Macho and Lee-Thorp, 2014), extinct apes (Sivapithecus-Nelson, 2007; Gigantopithecus - Nelson, 2014; Bocherens* et al., *2016), b) African hominin species (from data compiled in Sponheimer* et al., *2013) and c)* Homo sapiens *in Late Pleistocene/Holocene Sri Lanka (this thesis) and Holocene Southeast Asia (Krigbaum, 2001). A correction of -13‰ (shown in Cerling and Harris, 1999 for non-ruminant ungulates) has been applied to the fossil enamel data, while a correction of -4.5‰ has been applied to modern ape hair data. This latter value includes a correction of -3‰ for diet-hair enrichment (as in Sponheimer* et al., *2003) and a further -1.5‰ in order to correct for the fossil fuel effect.*

It is no longer viable for archaeologists to consider rainforests as 'green deserts', either in the context of nutritional requirements or in the context of human activity. These environments have been occupied and shaped by our species from at least 45,000 years ago, if not earlier (Willis *et al.,* 2004; Barton *et al.,* 2012; Roberts and Petraglia, 2015). Ongoing research is demonstrating that they not only provided the forum for some of the earliest examples of adaptive flexibility in our species but are also the site of some of the earliest experiments with resource domestication by *Homo sapiens* (Denham *et al.,* 2009) and have even supported large, complex, urban societies (Heckenberger and Neves, 2009). When exploited systematically, and with detailed knowledge of the specific plants and animals available in a given temporal and geographical rainforest context, these habitats can truly be 'forests of plenty'. As we continue to uncover the diverse rainforest prehistories of our species, it is essential that archaeologists emphasise the importance of these environments to past human adaptations, and attempt to contribute understandings of sustainable human rainforest occupation in the past, as seen in Sri Lanka, to contemporary efforts to monitor and mediate the ever-intensifying anthropogenic transformation of these environments.

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