

Persistent tropical foraging in the Highlands of Terminal Pleistocene-Holocene New Guinea

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Introductory paragraph

The Terminal Pleistocene-Holocene boundary (*c.* 12-8 ka) represented a major ecological threshold for humans, both as a significant climate transition and due to the emergence of agriculture around this time. In the Highlands of New Guinea, climatic and environmental change across this period have been highlighted as potential drivers of one of the earliest domestication processes in the world. Here we present a Terminal Pleistocene-Holocene palaeoenvironmental record (12-0 ka) of carbon and oxygen isotopes in small mammal tooth enamel from the site of Kiowa. The results show that tropical highland forest and open mosaics, and the human subsistence focused on these environments, remained stable throughout the period in which agriculture emerged at nearby Kuk Swamp. This suggests the persistence of tropical forest foraging among highland New Guinea groups and highlights that agriculture in the region was not adopted as a unilinear or dramatic, forced event but was locally and historically contingent.

Introduction

The transition from the Terminal Pleistocene to the Holocene witnessed increasingly intensive human manipulation of plant and animal resources that resulted in genetic and phenotypic changes in various species as part of what has been termed the ‘origins of agriculture’ (Denham et al., 2003). This process has been cited as one of the most significant ecological moments in human evolutionary history (Bocquet-Appel, 2011; Larson et al., 2014), representing a shift in human interactions with the natural world that was to have significant, global environmental ramifications (Fuller et al., 2011; Boivin et al., 2016). The emergence of this new form of subsistence has elsewhere been linked to dramatic climatic and environmental processes witnessed across the Terminal Pleistocene/Holocene transition and into the Holocene (Bar-Yosef and Belfer-Cohen, 1989; Richerson et al., 2011), yet the horticulture-style cultivation seen in the tropics is often ignored in such discussions. This is despite the fact that active human manipulation of plants and animals, including deliberate anthropogenic burning of forests to encourage plant growth (Summerhayes et al., 2010; Hunt et al., 2012) and the deliberate translocation of small mammals (Gosden and Robertson, 1991), occurred in tropical forest environments as early as 45 ka and 20 ka, respectively.

It is now clear that one of the clearest and earliest examples of the mutualistic relationship between humans and their plant-foods comes from Kuk Swamp in the tropical Highlands of New Guinea (Denham et al., 2003; Golson, 1977; Harris, 1995). Here, in a montane tropical rainforest and grassland ecotone, Terminal Pleistocene human foragers moved and tended the tropical plants of yam (*Dioscorea* sp.), banana (*Musa musa* sp.), and taro (*Colocasia* sp.) taxa until these species were fully ‘domesticated’ during the Early-Mid Holocene (Denham et al., 2003; Golson, 1977; Denham et al., 2004). While decades of research has described the archaeological sequence of Kuk Swamp, little is known of foraging behaviour elsewhere in the New Guinea Highlands, and the drivers behind the intensification of tropical plant manipulation at this time. As in other regions, it has been suggested that this process was stimulated by climatic fluctuation across the Pleistocene-Holocene boundary (Denham et al., 2003; Haberle and Lusty, 2000). However, there are currently no detailed, well-dated, ‘on-site’ palaeoenvironmental records, directly associated with forager behaviour, in this region to support or refute such ideas.

We applied stable carbon and oxygen isotope analysis to small mammal tooth enamel from the site of Kiowa (SI Text 1) (Table S1-S2), which is located at a similar ecological and altitudinal position to Kuk Swamp in the Central Highlands of New Guinea (Fig. 1-2), to produce a well-dated, palaeoenvironmental sequence associated with Terminal Pleistocene-Holocene forager behaviour (12-0 ka) (Gaffney et al., 2015; Gaffney et al., 2016) (SI Table 1). Large core tools and small retouched flakes are found throughout the sequence associated with a large faunal assemblage interpreted to represent the hunting of small mammals, especially fruit bats (*Aproteles bulmerae*), cuscus (Phalangeridae), ring-tailed possum (Pseudocheiridae) and macropods (Macropodidae) (SI Text 1, 2). Unlike at Kuk Swamp there is no evidence for local landscape modification or a shift towards plant cultivation during the Holocene, with the presence of these fauna remaining stable throughout the duration of site occupation (SI Text 1). Isotope analysis of archaeological small mammalian fauna such as these is an increasingly popular method of local palaeoenvironmental reconstruction due to their high frequency (and therefore large sample sizes), small home ranges, and high habitat discrimination (Grimes et al., 2008; Jeffrey et al., 2015).

Stable carbon isotopes of mammalian faunal enamel primarily reflect the proportions of C₃ and C₄ biomass in the diet in the tropics and subtropics ; low faunal $\delta^{13}\text{C}$ indicates reliance on ^{13}C -depleted C₃ resources relative to ^{13}C -enriched C₄ resources available in open areas ((Lee-Thorp and van der Merwe, 1987; Cerling et al., 2004; Levin et al., 2008). In dense C₃ forest, very low $\delta^{13}\text{C}$ values for C₃ plants are attributed to the “canopy effect”, in which vegetation growing under closed forest canopy is markedly ^{13}C -depleted due to low light (Farquhar et al., 1989) and recycled CO₂ (van der Merwe and Medina, 1991). These environmental factors can be tracked into mammalian tooth enamel following an established dietary fractionation factor of between *c.* 12-14‰ (Lee-Thorp and van der Merwe, 1987; Cerling and Harris 1999). Tooth enamel $\delta^{18}\text{O}$ values primarily reflect water consumed, either as drinking water or plant water, as well as some input from bound oxygen in food (O’Grady et al., 2012; Zazzo et al., 2015). In the tropics, imbibed water $\delta^{18}\text{O}$ will be dictated by the amount of rainfall (Gonfiantini et al., 2001) or evapotranspiration in plants that, in turn, can be associated with forest coverage. Tropical forests are thought to have retreated during cooler glacial periods when pCO₂ was low, giving way to more open C₃/C₄ grasslands and shrublands, particularly at higher altitudes (Jolly and Haxeltine, 1997; Mayle et al., 2004), with corresponding impacts on faunal diets and ingested water.

Results

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results for all small mammal faunal groups (cuscus, ringtail possum, bat, and macropod) from the site of Kiowa are shown in Fig. 3 and can also be found in Table S3.

$\delta^{13}\text{C}$ values cover a wide range (-14.5 to -8.7‰). Based on comparison with stable isotope analysis of modern faunal tooth enamel corrected for the fossil fuel effect (using the relationship in Francey et al., 1999), the data show an environmental range from closed forest environments (\leq -14.0‰) to open-woodland mosaic C₃ habitats (*c.* -12.0 to -9.0‰) (Lee-Thorp et al., 1989; Cerling et al., 2004; Levin et al., 2008; Leichliter et al., 2016).

This range fits with the modern ecological preferences of the faunal groups sampled (SI Text 2). The $\delta^{13}\text{C}$ range remains broadly consistent across the Terminal Pleistocene and Holocene levels at the site with some elements of dense forest habitat and more open C₃ environments present throughout the period of human occupation. ANOVA testing indicates that there is no difference in overall faunal $\delta^{13}\text{C}$ values between the levels ($F(6,130)=1.61$, $p>0.05$) (Table S4).

$\delta^{18}\text{O}$ data from the Kiowa fauna show a similarly large range (-12.6 to -6.4‰). Low $\delta^{18}\text{O}$ is expected in the tropics as a result of the high intensity of rainfall (Gonfiantini et al., 2001). All of the fauna analysed are obligate drinkers and therefore this range is likely indicative of variability in precipitation values, in open drinking water sources in the vicinity of the site, and in food. The faunal groups sampled have varying reliance on open water sources, while cuscus, ringtail possums, and bats are known to drink nocturnally, which likely contributes to the size of this range (SI Text 2). As with $\delta^{13}\text{C}$, the $\delta^{18}\text{O}$ values and range also remain consistent across the Terminal Pleistocene and Holocene periods of site activity, suggesting little change in the influences that govern hydrological isotope values in the tropics during human occupation at the site (D’Angela and Longinelli, 1990; Gehler et al., 2012; Jeffrey et al., 2015). An ANOVA test demonstrates that there is no significant difference between overall fauna $\delta^{18}\text{O}$ values from the different levels ($F(6,130)=1.008$, $p>0.05$) (Table S5).

There are, however, consistent $\delta^{13}\text{C}$ distinctions evident between the faunal groups sampled when ANOVA tests are performed ($F(3,130)=30.79$, $p<0.05$) (Table S4). When post-hoc Tukey pairwise testing is applied, statistically significant differences are found between macropods and bats, ringtail possums and bats, macropods and cuscus, and ringtail possums and cuscus (Table S6). Bats and cuscus sit at the higher end of the $\delta^{13}\text{C}$ range, relative to the ringtail possums, while macropods span the whole range (SI Figure 3). As bats are known to travel large distances to obtain food (Fleming et al., 1993; Segers and Broders, 2015), the contribution of resources from open C_3 environments is unsurprising. The distinction between the cuscus and ringtail possums and macropods may suggest that cuscus can survive in more open forest mosaics than these other taxa (SI text 2). ANOVA testing also demonstrates differences in $\delta^{18}\text{O}$ values between the groups of taxa sampled ($F(3,130)=6.015$, $p<0.05$). (Table S5). When post-hoc Tukey pairwise testing is applied, statistically significant differences were observed between macropods and bats, and ringtail possums and macropods (Table S7). These differences may be linked to the nocturnal habits of bats and ringtail possums while macropods feed and drink diurnally (SI Text 2).

Nevertheless, there remains no variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ between stratigraphic levels when ANOVA tests were performed on individual faunal groups (Fig. 4). Ringtail possums show no variation in $\delta^{13}\text{C}$ ($F(6,28)=0.860$, $p>0.05$) (Table S8) or $\delta^{18}\text{O}$ by level ($F(6,28)=1.582$, $p>0.05$) (Table S9). The same is true for cuscus ($\delta^{13}\text{C}$: ($F(6,28)=0.738$, $p>0.05$) (Table S10), $\delta^{18}\text{O}$: ($F(6,28)=2.127$, $p>0.05$) (Table S11)) and bats ($\delta^{13}\text{C}$: ($F(6,29)=1.568$, $p>0.05$) (Table S12), $\delta^{18}\text{O}$: ($F(6,29)=1.273$, $p>0.05$) (Table S13)). No variation in $\delta^{13}\text{C}$ by level was also found for macropods ($F(6,27)=0.710$, $p>0.05$) (Table S14). However, there was found to be a significant difference in macropod $\delta^{18}\text{O}$ by level ($F(6,27)=2.636$, $p<0.05$) (Table S15). This may be a result of macropods feeding and drinking diurnally, and therefore more strongly reflecting palaeoenvironmental evapotranspiration-linked changes in $\delta^{18}\text{O}$, than then other taxa sampled. That said, when post-hoc Tukey pairwise testing is applied, no specific inter-level $\delta^{18}\text{O}$ differences were found for this taxon group (Table S16).

Discussion

Overall, the results indicate stability in faunal diets and drinking water sources, and their associated environments, from the Terminal Pleistocene into the Holocene in the vicinity of Kiowa. The data presented here is consistent with other palaeoenvironmental evidence from South Asia (Premathilake and Risberg, 2003; Roberts et al., 2015), Southeast Asia (Hunt et al., 2012; Sun et al., 2000), and the New Guinea Highlands themselves (Hope and Haberle, 2005), that suggest the persistence of tropical forests, albeit of varying structure, in this part of the world between 12 and 5 ka. Significant, rapid climate fluctuations, particularly in the form of sub-montane tropical forest encroachment under the warmer conditions of the Holocene, have been argued for in the Highlands of New Guinea across the Terminal-Pleistocene boundary (Haberle, 1998; Haberle, 2003; Haberle et al., 2001), and have been suggested to coincide with a peak in human forest burning around Kuk Swamp *c.* 10-9 ka (Hope and Haberle, 2005; Haberle et al., 2012). However, major changes in vegetation do not appear to have occurred in the vicinity of the site of Kiowa, or at least not significantly enough to alter the isotope values in typically hunted prey. Since an ecotone of tropical forest and open C_3 environments remains present within the hunting range of Kiowa's human occupants, it seems unlikely that palaeoclimatic and palaeoenvironmental change drove the intensification of plant use and landscape modification witnessed at nearby Kuk Swamp during this period.

The lack of marked climate and environmental shifts in our data suggest that plant manipulation and domestication at Kuk Swamp is best seen as active anthropogenic modification of the landscape rather than an environmental response. It could be argued that other reasons, including demographic change or an increase in social network densities (Binford, 1968; Hayden, 1992), should be used to explain one of the earliest global experiments with ‘agriculture’. However, given the paucity of evidence elsewhere in the region for ‘domestication’ processes at this time (Gaffney et al., 2015; Summerhayes et al., 2016) it is perhaps best to see Kuk Swamp as part of a diversity of stable, successful tropical forest foraging adaptations in the region, that extend back to 45 ka (Summerhayes et al., 2010; 2016), through the Last Glacial Maximum (Pavlidis, 2004; Leavesley, 2006), and into the Holocene (Denham et al., 2003; 2004). Evidence for an increasingly intensive relationship between human foragers and tropical forests across the Sahul Indeed, in the Terminal Pleistocene and Holocene includes an increase in burning to stimulate plant growth (Fairbairn et al., 2006) and the deliberate translocation of animal protein between tropical forest islands (Gosden and Robertson, 1991). Instead of a dramatic, forced event, plant management at Kuk Swamp is part of long-term relationships between hunter-gatherer communities and tropical forest habitats that have characterised this part of the world from the Late Pleistocene.

Tropical forests are currently undergoing a rehabilitation in the archaeological and anthropological literature as productive environments for human foraging (Mercader, 2002; Roberts and Petraglia, 2015; Denham, 2016), and also for the development and spread of agricultural practices (Denham et al., 2003; Harris, 1995; Bellwood, 2004; Denham, 2011). Yet, rather than reinforcing the familiar dichotomies of ‘hunter-gatherer’ and ‘farmer’, human subsistence strategies within these habitats challenge our perceptions of the unilinear movement of *Homo sapiens* towards agricultural production and sedentary populations (Denham et al., 2007). Tropical forest foraging has apparently provided diverse and stable resources for humans in Melanesia since their arrival c. 45 ka, and through periods of climatic perturbation and the appearance of what might be termed ‘agriculture’ in certain localities (Golson, 1977; Bellwood, 2004). Effective niche construction (Boivin et al., 2016) by human populations from 45 ka, including the burning of forest vegetation (perhaps to maintain ecotonal environments and promote useful plant growth) and the movement of animals between habitats, blur the lines between foragers and farmers. Our results show that the development of farming, in this region at least, was unlikely to have been sparked by climate change, and is part of complex, long-term human modifications of the landscape and its wildlife that defy simplistic categories of ‘agricultural’ origins.

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Author contributions

P.R., D.G., J.L.T., and G.S. designed research, performed research, analysed data, and wrote the paper.

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Methods

We sampled molar teeth from small mammal taxa that made up a consistently high portion of human mammalian kill assemblages throughout the sequence of Kiowa (Gaffney et al., 2015; Bulmer, 1964a,b; Sutton et al., 2009) (SI Text 1). Faunal remains were identified by Jim Menzies and David Bulmer using a modern reference collection housed in the Zoology Department at the University of Papua New Guinea. Molar teeth were taken from bats (*Dobsonia magna*), cuscus (*Phalanger carmelitae*), ringtail possums, (*Pseudocheirus corinnae*/*P. cupreus*/*P. forbesi*), and macropods (*Dendrolagus/Thylogale*). Where possible, all specimens were selected from the large East Extension, in levels directly associated with radiocarbon determinations to ensure secure stratigraphic control. Level designations follow Gaffney and colleagues (Gaffney et al., 2015) therefore Level 10A-B and Level 12B-12A are grouped simply as Level 10 and 12. No fauna was sampled from Level 12C that has been argued elsewhere to be potentially representative of a natural accumulation of small mammal fauna by birds of prey, prior to human occupation (Gaffney et al., 2015) (SI Text 1).

The taxa sampled represent a diversity of environments, ecological niches, and altitudinal zones (SI Text 2) enabling a more detailed picture of local environmental change, of relevance to human hunters, to be produced throughout the sequence. Cuscus (*Phalanger carmelitae*) is a nocturnal inhabitant of primary tropical forest c. 1350-3800 m asl and the possums (*Pseudocheirus cupreus*, *Pseudocheirus corinnae*, and *Pseudocheirus forbesi*) are nocturnal and come mainly from undisturbed primary forest at c. 2000 m asl and higher. The bat species sampled (*Dobsonia magna*) is abundant in tropical forest up to 2700 m asl but is also known to range to savannah woodland at lower altitude (SI Text 2). Finally, the larger macropod individuals come from a diversity of forest habitats at different altitudes, and are also primarily nocturnal (SI Text 2).

Despite primarily being nocturnal, these taxa are extensively documented in ethnographic and archaeological hunting assemblages (Bulmer 1968; Dwyer, 1974; 1983; Flannery, 1995; Leavesley 2000; Sillitoe 2003; Sutton et al. 2009) and are clearly associated with human activity throughout the period of human occupation of Kiowa (Gaffney et al., 2015). From Level 12B (12.4-11.7kya), which contains the first material culture remains at Kiowa, the faunal assemblage notably changes from a broad array of small mammal species, to the specialised anthropogenic selection of large-medium sized bats, along with cuscus, ring-tailed possums, macropods, and some small-medium murids (see Sutton et al 2009, Zones 1B-2B).

To avoid the nursing or weaning effect, second and third molars were preferred as representing the 'adult' period of enamel formation and diet for bats, cuscus, ringtail possums, and macropods (e.g. Clout 1982). Exterior surfaces of the teeth were cleaned using air-abrasion to remove any adhering external material. The roots of the molar teeth were removed and the tooth sectioned to remove dirt from inside the tooth. Due to their small sizes, each tooth was crushed using an agate mortar and pestle following Gehler *et al.* (2012) and Jeffrey *et al.* (2015). An attempt was made to remove dentine from enamel where possible. However, as per Jeffrey *et al.* (2015), given the relatively short formation times for these

teeth we assume that dentine apatite and enamel apatite represent the same period and conditions.

All enamel powder was pretreated using a consistent technique to remove any organic or secondary carbonate contaminants. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H₂O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H₂O (Lee-Thorp et al., 2012; Sponheimer et al., 2005). 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 Department of Earth Sciences, University of Cambridge. Carbon and oxygen isotope values were compared against an international standard registered by the International Atomic Energy Agency (NBS 19) and an in-house standard (MERCK). Replicate analysis of OES standards suggests that machine measurement error is *c.* $\pm 0.1\%$ for $\delta^{13}\text{C}$ and $\pm 0.2\%$ for $\delta^{18}\text{O}$.

All $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ datasets being statistically analysed were tested for normality using the Shapiro-Wilk test and histogram observations. ANOVA tests were performed on faunal enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from Kiowa to determine the influence of species and stratigraphic level on isotopic variation overall, as well as for each faunal group (namely ringtail possums, cuscus, bats, and macropods). Where variance was found to be significant, this was combined with a post-hoc Tukey pair-wise comparison to determine which taxa or stratigraphic levels were significantly different from each other in terms of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. All statistical analyses were conducted using the free software 'R' (R Core Team, 2013).

462 **List of Figures:**

463 **Fig. 1.** Location of Kiowa and Kuk Swamp in the Central Highlands of New Guinea.

464 **Fig. 2.** a) View towards Mt Elimbari and Kiowa site in Chimbu, b) view into Kiowa NAW
465 rock shelter during excavations. Both photographs were taken by Sue Bulmer in 1960

466 **Fig. 3.** Stable carbon and oxygen isotope data for all faunal samples analysed shown by
467 stratigraphic level. Relevant dates shown come from Gaffney *et al.*¹⁵.

468
469 **Fig. 4.** Stable carbon and oxygen isotope data separated by taxonomic group: cuscus, ringtail
470 possum, bat, and macropod and shown by stratigraphic level. Relevant dates shown are from
471 Gaffney *et al.*¹⁵.