**Late Pleistocene to Holocene human palaeoecology in the tropical environments of coastal eastern Africa**

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**Abstract**

While dispersals of our species beyond Africa apparently began as early as *c.* 200 ka, genetic and archaeological evidence highlights an increased intensity of human migration during the Late Pleistocene. The ecological conditions and adaptations that supported this expansion are a key topic for palaeoanthropological and archaeological research, providing potential insights into the novel capacities of *Homo sapiens*. It has been traditionally argued that an adaptive focus on coastal resources or savanna biomes drove human dispersals into Asia. However, little direct evidence for such adaptations exists, particularly in eastern Africa, which represents a key point of access to the Arabian Peninsula and the Indian Ocean rim of Asia for populations in southern, eastern, central, and western Africa. Here, we present chronologically resolved, detailed zooarchaeological analysis and stable isotope data from human and faunal tooth enamel, from the site of Panga ya Saidi (*c.* 78-0.4 ka), Kenya. These records provide a novel palaeoenvironmental record for Late Pleistocene-Holocene coastal eastern Africa, where dated, ‘on-site’ archives have been generally lacking. Moreover, they yield direct insights into human palaeoecology from the Late Pleistocene into the Late Holocene. Our results demonstrate that humans consistently utilized tropical forest and grassland biomes throughout the period of occupation of the site, through a transition from Middle Stone Age to Later Stone Age technological industries and the arrival of agriculture in the region. By contrast, while coastal resources were obtained for use in symbolic material culture, there is limited evidence for consumption of marine resources until the Holocene. We argue that the ecotonal or heterogeneous environments of coastal eastern Africa may have represented an important refugium for populations during the increasing climatic variability of the Late Pleistocene and Holocene, and that tropical environments were one of a diverse series of ecosystems exploited by *H. sapiens* in Africa at the dawn of global migrations.

**1. Introduction**

The discovery of early *Homo sapiens* fossils from northern (Hublin et al., 2017; Richter et al., 2017) and eastern Africa (McDougall et al., 2005; White et al., 2003), and proposed technological correlates in many parts of the continent (Brooks et al., 2018; McBrearty and Brooks, 2000; Mercader, 2002; Scerri, 2017; Tryon and Faith, 2013), suggest that our species gradually emerged across Africa from 300 ka onwards (Scerri et al., 2018). Recent fossil evidence outside of Africa hints that populations of our species may have left the continent as early as 210-100 ka (Bae et al., 2017; Groucutt and Petraglia, 2012; Harvati et al., 2019; Hershkovitz et al., 2018), though the longevity of these movements remains debated. Rather, it is during the Late Pleistocene (125-12 ka) that ancient and modern DNA (Posth et al., 2018; Prüfer et al., 2017), material culture (Clarkson et al., 2017; Groucutt et al., 2015; Scerri et al., 2018), and fossil evidence (Bae et al., 2017; Groucutt et al., 2018; Li et al., 2017; Westaway et al., 2017) converge to suggest an increased intensity of human dispersals beyond Africa into a huge diversity of environmental settings across Asia, Australasia, and Europe (Groucutt et al., 2015; Scerri et al., 2018). Understanding human cultural and ecological adaptations during this period is essential if we are to determine how our species began to colonize every continent, becoming the last hominin on the planet.

In Africa and beyond, scholars have argued that intensified use of coastal habitats, and possible competition for rich sources of protein, facilitated the emergence of cultural and technological complexity in the Late Pleistocene (Marean, 2016). Material culture and subsistence evidence from sites proximate to the coast, such as Blombos Cave in South Africa (Henshilwood et al., 2011; Henshilwood et al., 2018; Henshilwood et al., 2002; Vanhaeren et al., 2013) and Taforalt in Morocco (Bouzouggar et al., 2007), have seemingly confirmed the association between marine habitats and the emergence technological complexity, as well as early art and symbolism. In an influential theory, Mellars (2006) proposed that coastal settings stimulated a rapid dispersal that enabled *H. sapiens* to reach Australia via a ‘southern route’ by at least 45 ka. Other scholars stress the importance of terrestrial grassland biomes, which support large and medium sized game, as settings for human technological experimentation and corridors for dispersal within and beyond Africa (Ambrose, 2002; Boivin et al., 2013b; Faith et al., 2015; Shea and Sisk, 2010). However, coast or grassland landscapes have often been treated as homogeneous, with little room for environmental complexity as part of the human story.

In the last decade it has become increasingly apparent that the Late Pleistocene palaeoecology of our species in Africa was more complex than has often been considered (Roberts and Stewart, 2018; Will et al., 2019). Research in the Sahara, Kalahari, and Namib Deserts has suggested our species may have inhabited these now arid environments at varying points in the past (Dewar and Stewart, 2012; Thomas and Burrough, 2012; Vogelsang et al., 2010), and not only during humid phases (Nash et al., 2016). Recent work in Ethiopia and Lesotho has demonstrated human adaptation to relatively cold and ecologically patchy high-altitude environments from 80 ka onwards (Brandt et al., 2012; Ossendorf et al., 2019; Stewart et al., 2012). It has also long been argued that tropical forests in western and central Africa supported Pleistocene human foragers throughout the Late Pleistocene (Barham, 2001; Brooks et al., 1995; Clark, 1967; Clark, 1969; Mercader, 2002), though this remains debated (Cornelissen, 2013; Scerri, 2017). The spectrum of eastern African environments, from arid grassland habitats to mesic coastal tropical forests, offers an important opportunity to further investigate the diversity of Late Pleistocene human paleoecology. Yet, despite fossil, genetic, and archaeological evidence indicating the region was a crucial place for human origins (McDougall et al., 2005; White et al., 2003), subsequent population dispersal (Nielsen et al., 2017), and technological change (Blinkhorn and Grove, 2018; Tryon and Faith, 2013; Tryon and Faith, 2016), detailed palaeoecological studies have remained somewhat limited, particularly beyond the semi-arid grasslands of the interior.

The cave site of Panga ya Saidi (PYS), Kenya offers a unique opportunity to broaden our understanding of ecological diversity of human behavioural change in Late Pleistocene eastern Africa, sitting in a coastal tropical forest-grassland ecotone. Here, we build on the work of Shipton et al. (2018) by extending the zooarchaeological analysis and stable carbon (δ13C) and oxygen (δ18O) isotope analysis of mammalian fauna at the site in several new directions. We present new taxonomic identification and ecological association data for PYS from *c.* 78-0.4 ka, providing the first well-dated insights into human prey choices across the Late Pleistocene and Holocene in an often-neglected portion of eastern Africa. We also add new stable carbon and oxygen isotope analysis of fauna from the lowest levels of the site (n=18) to existing datasets to build a more resolved record of the dominance of forest and grassland prey, and water dynamics, during this period of occupation. By weighting the isotopic data with new faunal taxonomic identifications and ecological insights, we produce a more accurate record of palaeoenvironmental change at the site through time (as per Leichliter et al., 2017; Robinson et al., 2017). Finally, we present new stable carbon and oxygen isotope analysis of two human teeth from PYS: one from the oldest MSA levels (*c.* 78 ka) and one from the Later Iron Age, in order to directly study human resource reliance during the earliest known period of site occupation and during late Holocene agricultural expansion (as per Roberts et al., 2015; Roberts et al., 2017). This analysis represents one of the first long-term ‘on-site’ palaeoenvironmental investigations for Late Pleistocene through Holocene eastern Africa, and also one of the most detailed assessments of palaeoecology for this period and region to date.

**2. Background**

**2.1. Late Pleistocene and Holocene human environments in eastern Africa and the potential of Panga ya Saidi**

Prior to the recent reports from Jebel Irhoud, Morocco (Hublin et al., 2018), eastern Africa was home to the earliest fossil evidence for our species, from the Middle Pleistocene at Omo Kibish 1 (195 ka) (McDougall et al., 2005) and Herto (160 ka) (White et al., 2003) in Ethiopia. Archaeological evidence indicates that the earliest appearance of Middle Stone Age (MSA) technologies can be found in the region, dating to *c.* 300 ka at Olorgesailie (Brooks et al., 2018). Eastern Africa has also gained attention as a key region of Late Pleistocene human cultural and technological change. Sites such as Porc-Epic, Goda Buticha, and Mochena Borago in Ethiopia, Enkapune ya Muto in Kenya, and Kisese II, Magubike, Mumba, and Nasera in Tanzania have yielded evidence for the emergence of backed stone tools, symbolic beads, and an intensification of organic tool production over the last 60-40,000 years (Ambrose, 1998a; Assefa et al., 2008a; Brandt et al., 2012; Diez-Martín et al., 2009; Miller and Willoughby, 2014; Pleurdeau et al., 2014; Ranhorn and Tryon, 2018; Tryon et al., 2018). There has also been an increasing focus on the transition from MSA to Later Stone Age (LSA) technological traditions which appears to be characterized by significant regional variability (Tryon and Faith, 2013) and a persistence of older MSA technologies, such as Levallois cores, alongside the development of backed artefacts and blade production (Shipton et al., 2018).

Reconstruction of Middle and Late Pleistocene human paleoecology in eastern Africa has focused on the Rift Valley and adjacent areas. Faunal and speleothem datasets have been used to argue that the Herto and Omo Kibish 1 fossils are best associated with dry grassland habitats supported by local aquatic environments, including riparian forest (Assefa et al., 2008b; Vaks et al., 2007). The Late Pleistocene faunal record at Porc-Epic similarly indicates exploitation of grasslands near a perennial water source (Assefa, 2006). Palaeontological, sedimentological, and biogeochemical evidence from Late Pleistocene MSA sites near Lake Victoria have also highlighted semi-arid environments, seasonal precipitation, and a dominance of C4 grasslands (Faith et al., 2015; Garrett et al., 2015; Tryon et al., 2010). This pattern has been used to argue that the expansion of arid grasslands, and the game they support, may have provided key corridors for MSA human expansion (Tryon et al., 2010). The MSA-LSA transition itself has been suggested to be associated with climatic instability and rapid aridification events, perhaps linked with the Toba eruption *c.* 74 ka (Ambrose, 1998b; but see Lane et al., 2013) or ‘mega-droughts’ recorded in eastern African lakes *c.* 70 ka (Cohen et al., 2007). Some researchers have hypothesized the existence of Late Pleistocene environmental refugia in eastern Africa that buffered against dramatic climate shifts seen in the interior and farther south in tropical Africa, allowing populations to persist prior to subsequent expansion (Basell, 2008; Blome et al., 2012). Indeed, a recent study suggests much broader engagement with the diverse habitats of eastern Africa during MIS 5 may represent such an expansion under interglacial conditions (Blinkhorn and Grove, 2018). By MIS 3, this habitat diversity included alpine environments, as recently shown at Fincha Habera rockshelter in Ethiopia (Ossendorf et al., 2019). However, discussions of environmental change and its influence on Pleistocene human behaviour in eastern Africa are currently reliant on palaeoenvironmental records limited to the interior, despite the fact that our species likely utilized far more diverse settings (see also Basell, 2008; Robinson, 2017; Wright et al., 2017).

PYS cave lies 15 km from the present-day coastline in the Zanzibar-Inhambane tropical coastal forest mosaic (Fig. 1A). Formed within the Dzitsoni limestone hills, PYS today straddles an ecotone between lowland tropical forest and savanna environments (Fig. 1B). As presented by Shipton et al. (2018), the site preserves evidence for human activity between *c.* 78-0.4 ka (Fig. 2; Table 1), including a transition between lithic forms associated elsewhere with the MSA and LSA. Following an initial phase of occupation *c.* 78-73 ka, the intensity of human occupation appears to increase from *c.* 67 ka into the Holocene, alongside the appearance of marine shell beads, ostrich eggshell beads, worked bone artefacts, and miniaturized backed artefacts. The site also spans the terminal Pleistocene-Holocene transition, a time of increased humidity across much of the continent (DeMenocal et al., 2000). Faunal records from this period in the eastern African interior suggest intensification of lacustrine and riverine fishing and foraging (e.g., Prendergast and Beyin, 2017; Prendergast and Lane, 2010), and a reduction of grassland biomes and their dependent fauna, such as oryx (*Oryx gazella*) and Grevy’s zebra (*Equus grevyi*) (Faith, 2014; Faith et al., 2015). Coastal faunal records are rare for this timeframe – limiting comparisons with PYS – but those from the site of Kuumbi Cave suggest major biotic shifts as islands like Zanzibar became isolated by rising seas (M.E. Prendergast et al., 2016).

During the last 1,300 years of occupation at PYS, major economic, demographic, and cultural shifts were already occurring on the coast, as agropastoral communities expanded and marine trade networks developed (Boivin et al., 2013a; Crowther et al., 2018). Coastal faunal and botanical records testify to growth of fishing and farming economies (e.g., Crowther et al., 2016; Prendergast et al., 2017b; Quintana Morales and Prendergast, 2017). Ancient DNA analysis of a male adult buried at PYS during the Later Iron Age (human remains directly dated to 388 ± 27 bp, 496-322 cal BP, OxA-30803) indicates that this individual had a strong genetic affinity with both ancient and recent eastern African foragers (Skoglund et al., 2017). This affinity, together with the PYS faunal record discussed below, implies long-term persistence of foragers in the area. Indeed, coastal indigenous communities in Kenya such as Aweer, Dahalo, and Waata have continued to forage in recent times.

**2.2. Zooarchaeology, stable isotope analysis, and tropical human palaeoecology**

Long-term, well-dated zooarchaeological records in direct association with records of human behaviour that span the last 80 ka are sparse for eastern Africa. PYS is a notable exception, and detailed zooarchaeological analysis, alongside the δ13C and δ18O analysis of faunal tooth enamel, jointly offer the possibility of elucidating the complexity of tropical environments in this part of the world during the Late Pleistocene and Holocene. Identified bovid, suid, and primate remains can be informative about the types of African environments in which PYS occupants pursued game during the Late Pleistocene through Holocene. African bovid tribes in particular have been categorized by feeding behaviour and habitat based on modern dietary and stable isotopic data, although these studies also stress variability and caution against oversimplification (Fig. 3) (Cerling et al., 2015; Cerling et al., 2003; Gagnon and Chew, 2000). Within some bovid tribes – notably Antilopini, Neotragini, and Tragelaphini – there is considerable variation, and this is also true of suids. Additionally, while there is a broad correlation between body mass and diet so that, generally, larger bovids are grazers and smaller ones are browsers or frugivores (Gagnon and Chew, 2000), this dichotomy masks some important variation.

Broadly speaking, Alcelaphini (examples in eastern Africa include *Alcelaphus* [hartebeest], *Damaliscus* [topi/tsessebe], *Connochaetes* [wildebeest]) and Hippotragini (*Oryx* [oryx] and *Hippotragus* [roan and sable antelopes]) can be considered ‘hyper-grazers’, feeding in open grasslands. Reduncini (*Redunca* [reedbuck], *Kobus* [waterbuck, kob]) and Bovini (*Syncerus* [buffalo]) are less extreme grazers, preferring open and semi-open habitats. Aepycerotini (*Aepyceros* [impala]) and Antilopini (*Nanger/Eudorcas* [gazelle], *Ourebia* [oribi; formerly Neotragini]) are mixed feeders but tend toward grazing. Among suids, *Phacochoerus* sp. (warthog) are generally grazers (Cerling et al., 2015). At the other end of the continuum, bovid tribes Tragelaphini (*Tragelaphus* [bushbuck, kudu], *Taurotragus* [eland]), Neotragini (*Madoqua* [dik-dik]*, Neotragus* [suni]*, Raphicerus* [steenbok]), and Cephalophini (*Sylvicapra* [bush duiker], *Cephalophus* [numerous duikers]) browse in semi-closed to closed environments, and *Cephalophus* are predominantly frugivores. Other frugivores considered in Fig. 3 include monkeys of the Cercopithecini and Colobini tribes. Among suids, *Potamochoerus* sp. (bushpig) are highly variable but are generally browsers (Cerling et al., 2015).

In the context of stable isotope analysis, in tropical settings, the isotopic distinction between C3 and C4 biomass is useful for studying the relative proportion of C4 and C3 plants in faunal and human diets and, indirectly, the structure of their inhabited environments (e.g. C4 grassland versus C3 woodland and forest) (Codron et al., 2012; Crowley et al., 2012; Roberts et al., 2015; Roberts et al., 2017). Inside tropical forest settings, C3 vegetation found beneath a closed forest canopy is depleted in 13C, due to low light (Farquhar et al., 1989) and large amounts of respired CO2 (van der Merwe and Medina, 1991). This ‘canopy effect’ causes CO2, soils, and vegetation within a closed canopy to have low δ13C values that are also reflected in the tissues of animals feeding in the same habitats (Cerling et al., 2004; van der Merwe and Medina, 1991). In faunal diets, prior to the impact of significant fossil fuel emission from the 18th and 19th centuries on atmospheric δ13C, tooth enamel with δ13C lower than -14‰ represents reliance on dense or closed canopy forest, while average herbivore values for C3 and C4 reliance are *c.* -12‰ and 0‰, respectively (Lee-Thorp et al., 1989a; Lee-Thorp et al., 1989b; Levin et al., 2008).

δ18O measurement of mammalian tissues provides additional palaeoecological information about water and food. In tropical ecosystems δ18O of vegetation reflects either evaporative potential or the source-effect of rainfall (Buchmann and Ehleringer, 1998; Buchmann et al., 1997; McCarroll and Loader, 2006). Notably, the relationship between plant δ18O and evaporative potential may be used to infer canopy density in a forest environment. CO2 and vegetation δ18O have also been shown to differ depending on height within the canopy, and between different plant parts, given changing evaporative potentials (Buchmann and Ehleringer, 1998; Buchmann et al., 1997; da Silveira et al., 1989). Animals that obtain the majority of their water requirements from plants will most effectively record environmental factors that influence plant transpiration and plant δ18O (Carter and Bradbury, 2016; Kohn et al., 1996; Levin et al., 2006). Tooth enamel is the archaeological material of choice for isotopic analysis in the tropics over longer timescales (Krigbaum, 2005). The apatite of tooth enamel differs from that of bone and dentine in having fewer substitutions, less distortion and larger crystals (LeGeros, 1991), making it more resistant to post-mortem diagenetic substitution and degradation (Lee-Thorp, 2008; Lee-Thorp et al., 1989a). Tooth enamel will record an isotopic ‘whole-diet’ sequence for the period of enamel formation, a period that will vary depending on species and tooth sampled (Passey et al., 2005).

**3. Materials and Methods**

**3.1. Zooarchaeological sample and analytical methods**

Excavations at PYS in 2011 and 2013 produced abundant, highly fragmented faunal remains. Tetrapod remains (mammals, birds, and reptiles) from Trenches 3 and 4 (6.4 kg and 14.7 kg of bone, respectively) were analysed at the National Museums of Kenya (NMK) in Nairobi. Remains of microfauna and terrestrial molluscs have been reported elsewhere, and marine molluscs and fish are rare (Prendergast et al., 2017a; Shipton et al., 2018). Faunal remains from more recent PYS excavations have not yet been analysed, except for 18 teeth selected for isotopic analysis from the deepest contexts in Trench 8 (see below). These latter samples were explicitly selected to increase the isotopic dataset from the latest layers and are not included as part of the taxonomic abundance evaluations.

During analysis, all maximally identifiable specimens (teeth, and bone fragments preserving highly diagnostic features; *c.* 10% of assemblage) were identified. In a subsample from Trench 4, minimally identifiable specimens such as limb shaft, rib, and vertebral fragments were also analysed. All identified faunal specimens were examined with 10x-20x hand lenses under strong oblique light to identify bone surface modifications such as cut marks, carnivore tooth marks, and rodent gnaw marks; burnt bone was also recorded. Taxonomic identification was aided by NMK osteological collections, supplemented by photographs of reference collections and published guides such as Walker (1985). Particular attention was paid to dental morphology as an indicator of bovid tribe (e.g., Gentry and Gentry, 1978). Due to fragmentation, identification to taxon was frequently impossible, especially for postcrania. Thus size classes for bovids and mammals were often used, adapting Brain’s (1981) categories to eastern African fauna (Supplementary Table 1).

Estimation of the minimum number of individuals (MNI) was derived from the database, considering laterality, body size, and where relevant, estimated age (Supplementary Table 2). The Number of Identified Specimens (NISP) and MNI for Trenches 3 and 4 together are presented using the temporal groupings of Layers 1-3 (Iron Age), Layer 4 (mid-Holocene), Layers 5-6 (terminal Pleistocene), Layers 7-8 (Last Glacial Maximum), Layer 9 (late MIS 3), Layers 10-12 (early-mid MIS 3), Layers 13-16 (MIS 4), and Layers 17-19 (MIS 5), based on chronometric and stratigraphic data reported in Shipton et al. (2018). Each of these archaeological groupings was presumed to be a discrete unit for the purposes of calculating MNI, so that specimens of the same taxon in separate temporal grouping were considered to come from separate individuals. The MNI figures are thought to be conservative underestimates: limb shafts were excluded from this analysis due to time constraints, which might otherwise have led to a higher and more accurate MNI in an assemblage with strong density-mediated attrition (e.g., Marean and Spencer, 1991).

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

Two human tooth samples were sampled for stable carbon and oxygen isotope analysis: one from the Iron Age burial of a male in Layer 1 mentioned above, a burial that has also been analysed for ancient DNA (Skoglund et al., 2017), and one isolated tooth from Layer 18 (MIS 5). These teeth were identified as a permanent maxillary molar (Layer 1) and a mandibular deciduous 2nd molar (Layer 18) (Supplementary Table 3). Whereas permanent molars develop slightly later, the deciduous second molar begins forming *in utero* and finishes developing between 2.5-3.5 years of age (AlQahtani et al., 2010). Due to the influence of breastfeeding, the isotopic signal from the latter individual will likely primarily reflect the diet of the mother (Tsutaya and Yoneda, 2015).

A total of 132 faunal teeth were analysed from the site throughout the sequence and divided based on existing chronometric and material culture information (Table 1) into the same temporal groupings used for the zooarchaeological analysis. Some faunal isotopic data were reported in a previous study (Shipton et al., 2018), but here we have enriched the dataset from the MSA layers by adding new samples (Supplementary Table 3). Our detailed zooarchaeological analysis has also enabled the re-classification of some of the specimens sampled for isotopic analysis by Shipton et al. (2018) (see Supplementary Table 3).

We also combine the isotopic data with detailed discussion of taxonomic faunal representation and detailed statistical analysis of isotopic changes through the sequence for the first time. Palaeoenvironmental reconstruction based on stable isotope analysis of faunal remains can often face the problem that isotopic shifts through time will be influenced by the presence or absence of certain taxa, which may or may not be reflective of real environmental change. As a result, here we follow Leichliter et al. (2017) and Robinson et al. (2017) by ‘weighting’ the isotopic data by meaningful ecological categories, e.g. ‘grazer’ and ‘browser’ based on observational dietary and skeletal stable isotope data (Cerling et al., 2015; Cerling et al., 2003; Gagnon and Chew, 2000) (Supplementary Tables 3 and 4). Comparison of temporal isotopic variation *within* these categories enables more accurate palaeoenvironmental reconstruction, less biased by species representation.

Human and other faunal teeth were chosen for isotopic analysis on the basis of archaeological context, tooth completeness, and identifiability. All teeth were photographed prior to analysis and are currently housed either at the NMK or on temporary loan at the Max Planck Institute for the Science of Human History (MPI-SHH) in Jena, Germany. Sampling took place at both NMK and MPI-SHH, where teeth or tooth fragments were cleaned using air-abrasion to remove any adhering external material. Enamel powder was obtained using gentle abrasion with a diamond-tipped drill along the full length of the buccal surface in order to maximize the period of formation represented by the bulk sample. Enamel powders were pre-treated to remove any organic or secondary carbonate contaminates. This consisted of a wash 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 (per Lee-Thorp et al., 2012; Roberts et al., 2017; 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 MPI-SHH. δ13C and δ18O values were compared against International Standards (IAEA-603 (δ13C = 2.5; δ18O = -2.4); IAEA-CO-8 (δ13C = -5.8; δ18O = -22.7); USGS44 (δ13C = -42.2)) and in-house standard (MERCK (δ13C = -41.3; δ18O = -14.4)). Replicate analysis of MERCK standards suggests that machine measurement error is *c.* ± 0.1‰ for δ13C and ± 0.2‰ for δ18O. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard (n = 20, ± 0.2‰ for δ13C and ± 0.3‰).

**3.3. Statistical analysis**

All statistical analyses were conducted using the free R software (R Core Team, 2013). For zooarchaeological data, NISP values for selected taxonomic groups on which this study focuses (bovids, suids, and primates) were tested to examine whether or not there are differences in taxonomic representation across the layer groupings. NISP data in a contingency table were analysed using chi-square and Fisher exact tests, but the latter was seen as more reliable, given the small sample sizes and the fact that some taxa are not represented (i.e., have empty values) in some temporal groupings. For both tests, p-values were computed using Monte Carlo simulation, replicated 2000 times.

For stable isotope data, Shapiro-Wilk tests found that the faunal enamel δ13C and δ18O values were non-normally distributed. We therefore performed Kruskal-Wallis tests on the data to determine the influence of species and temporal period on isotopic variation. Where variance was found to be significant, this was combined with a pairwise Wilcox test (padj = bonferroni) to determine which taxa or stratigraphic layers were distinct from each other. We also performed Kruskal-Wallis tests to determine whether there were distinct variations between the ‘weighted’ groups of ‘browsers’ and ‘grazers’ and whether the δ13C and δ18O within these categories varied through time. Finally, we performed a linear regression on the data to determine whether δ13C and δ18O were statistically correlated.

**4. Results**

**4.1. Panga ya Saidi faunal assemblage overview and formation**

In total 5,239 nonhuman faunal bone and tooth fragments were identified (Number of Identified Specimens, NISP) in Trenches 3 and 4, representing a minimum number of 358 individuals (MNI) (Table 2, Supplementary Table 2). The highest MNI values are found in the lowermost and uppermost layers, inflated by the presence of bats, rodents, and shrews (Fig. 4A). During these most ancient and most recent parts of the sequence, the cave appears to have been less intensively occupied, as was previously argued based on artefact density, and for the lower part of the sequence, on geomorphology and magnetic susceptibility (Shipton et al. 2018).

At various points in the sequence, potential bone-accumulating and bone-modifying agents such as carnivores, raptors, snakes, and primates also occupied or were brought into the cave, and may be partially responsible for faunal assemblage formation (Supplementary Table 2). Large carnivores, including leopard (*Panthera pardus*; NISP = 1) and hyena (Hyaenidae; NISP =2) are represented by few elements, found in the MIS 4 and early-middle MIS 3 temporal groupings. Remains of small carnivores (NISP = 23) are found scattered throughout the sequence, and include, minimally, a small felid (*Felis* cf. *serval*) and two genera of mongoose (Herpestidae). Primates, too, can accumulate bones, and monkeys (Cercopithecini and Colobini, total NISP=45), baboon (*Papio* sp., NISP =5) and greater galago *(Otolemur* sp., NISP = 2) are present at PYS, and are abundant in the earliest parts of the sequence. Nevertheless, primates are also found throughout the sequence and cut marks on remains of a colobus monkey (*Colobus* sp.) deposited during the early MIS3 (Layer 11) suggests that at least some of them were brought in as human prey. Likewise, the presence of cut marks on the remains of hyrax (Hyracoidea) indicates that at least some other small fauna also entered the cave as prey.

Other potential bone-accumulating agents include raptors, such as owls (Strigiformes), and snakes (Serpentes), both primarily documented in the Iron Age layers – potentially explaining the abundance of rodent remains in the site at this time. Prior to the Iron Age, however, bird remains are rare at PYS, are more frequently identified as ground-dwelling fowl (Phasianidae), while snake remains are few and scattered throughout the sequence. Rodent remains are also rare prior to the Iron Age, suggesting a minimal role for raptors and snakes in earlier assemblage formation.

Despite these potential biogenic inputs, it appears that humans were the main accumulators of the macrofaunal assemblage at PYS based on analysis of bone modifications (Supplementary Figure 1). Burnt bone is relatively common, affecting 9% of the macromammalian bone assemblage, with more than a fifth of macromammalian bone being burnt in the MIS 4 deposits for example (Layers 13-16). The presence of multiple hearths and ash dumps in the sequence suggests such burning is anthropogenic (Shipton et al. 2018). Clear, unambiguous cut marks occur on 2.1% of macromammalian bone, a frequency that rises to 3.2% if ambiguous cut marks are included (these were identified cautiously, given the presence of confounding marks from trampling and biochemical damage). Cut marks vary across the sequence, being most abundant in the LGM (5%, if including ambiguous marks) and MIS 5 (6%) deposits. The paucity of cut marks might be partially explained by the fact that the assemblage is biased toward small fauna, with small bovids being abundant throughout and particularly in the earliest and latest layer groupings where they form more than half of all bovid remains (Fig. 4B). These would require minimal butchery, a pattern observed at other coastal eastern African sites where cut marks are relatively infrequent and small bovids dominate (M. Prendergast et al., 2016; Prendergast et al., 2017b).

Evidence for nonhuman modification of bone is rare, with tooth pits (likely made by carnivores) and gnawing (likely made by rodents) occurring sporadically across the sequence, affecting about 1% of the macromammalian bone assemblage overall. Notches along limb fracture planes clearly identifiable as carnivore-made are nearly completely absent (NISP = 2). At maximum, carnivore tooth pits are found on up to 2.4% of macromammalian bone in the late MIS 3 deposits (if ambiguous tooth marks are included), and rodent gnawing affects up to 3.4% of bone in the MIS 5 deposits. While the PYS faunal assemblage has clearly been overall impacted by density-mediated attrition – where durable bones such as limb shafts, carpals, tarsals, phalanges dominate – there is no convincing evidence to suggest that carnivores are the primary cause of this pattern, though they may be contributors.

**4.2. Macromammalian remains at Panga ya Saidi and environmental implications**

PYS archaeofauna are mostly indicative of semi-closed to closed environments, as illustrated in Fig. 3 and Supplementary Table 4. There is a complete absence of grazers like Hippotragini and Aepycerotini, as well as grazing non-bovids such as zebra. Instead, small, browsing bovids – especially Cephalophini and Neotragini – dominate the assemblage. However, there are pronounced diachronic shifts in relative taxonomic abundance along the sequence. These shifts can be illustrated in several ways, each using a different sample of identified remains: one can consider all fauna identifiable to major groups such as bovids, suids, primates, hyraxes, bats, rodents, and shrews (Fig. 4A, Table 2); all bovid remains according to body size class (Fig. 4B); or all bovids identifiable to tribe, an analysis limited by small sample size (Fig. 5A). One can also compare absolute abundances of five groups of mostly browsing or frugivorous taxa (Neotragini, Cephalophini, Tragelaphini, *Potamochoerus*, Cercopithecini/Colobini) *versus* five groups of mostly grazing taxa (Antilopini, Bovini, Reduncini, Alcelaphini, *Phacochoerus*) (Fig. 5B).

As seen in Fig. 4 and Fig. 5, the earliest and most recent occupations at PYS are marked by exploitation of small, bush- and forest-dwelling bovids. During the initial MIS 5 (L17-19) occupation, all identified bovids are browsing taxa (Cephalophini, Neotragini, Tragelaphini); in the final Iron Age (L1-3) occupation, Cephalophini and Neotragini form 80-100% of identified bovids. In both of these temporal groupings, small bovids form more than half of all bovid NISP. Monkeys, generally preferring closed environments, are also relatively more abundant during MIS5 and the Iron Age, although this may be partly due to their use of the cave. By contrast, in the rest of the sequence, there is greater diversity: from MIS 4 (L13-16) through the middle Holocene (L4), grazing fauna are relatively more abundant than browsing fauna. This is particularly so for the middle of the sequence, with hyper-grazing Alcelaphini present during MIS 3 (L10-12, L9) and the LGM (L8), alongside other grazers such as Bovini and Reduncini. While few suid remains could be identified to genus due to fragmentation, the tentative trend follows that of the bovids (Table 2): *Phacochoerus* remains are particularly abundant during MIS 3 and the LGM, while *Potamochoerus* remains are relatively more abundant in the Iron Age deposits.

A chi-square test yielded significant differences (*χ*2 = 228.66, df = 63, p<2.2e-16) across temporal groupings in terms of the representation of ten major taxonomic groups (Neotragini, Cephalophini, Tragelaphini, Antilopini, Bovini, Reduncini, Alcelaphini, *Potamochoerus*, *Phacochoerus*,Cercopithecini/Colobini) (Supplementary Table 5). A randomized Fisher test, applied to the same ten groups, also yielded a significant difference (p<0.001). The same Fisher test was then applied to only the seven bovid groups, again finding a significant difference in representation of tribes (p<0.001). Finally, another Fisher test was applied after separating the ten groups into mainly browsers/frugivores and mainly grazers; this test also found a significant difference across temporal groupings (p<0.001).

**4.3. Faunal stable carbon and oxygen isotope results from Panga ya Saidi**

The full dataset of δ13C and δ18O measurements of faunal teeth is shown in Supplementary Table 3. Identifications of some of the specimens presented in Shipton et al. (2018) have now been altered following more detailed zooarchaeological analysis. The δ13C range of the measured samples (-16.7 to 3.4‰) indicates that fauna likely exploited by humans at the site utilised a variety of terrestrial environments (Fig. 6, Supplementary Figure 1), ranging from closed tropical forest, through more open woodland, to C4 grassland biomes. Primates identified as Cercopithecini (range = -14.5 to -9.9‰; mean = -12.3 ± 1.8‰), *Colobus* sp. (-11.2‰), or *Papio* sp. (range = -11.5 to -9.2‰; mean = -10.3 ± 1.0‰), as well as browsing Neotragini (range = -11.4 to -10.1‰; mean = -10.8 ± 0.7‰), persistently occupy the lower end of this δ13C range. Meanwhile, grazers identified as *Alcelaphus* sp. and/or *Damaliscus* sp.(range = -4.2 to 3.4‰; mean = 0.1 ± 2.7‰), *Connochaetes taurinus* (-0.9‰), *Kobus ellipsiprymnus* (range = -0.3 to 3.3‰; mean = 1.2 ± 1.2‰), *Ourebia ourebi* (range = -3.7 to 0.2‰; mean = -1.2 ± 1.8‰), or *Syncerus caffer* (range = -2.9 to 2.3‰; mean = -0.3 ± 3.7‰) lie at the higher end. The suid identified as *Phacochoerus* sp.(range = -6.9 to 2.1‰; mean = -1.4 ± 2.0‰) also appears to feed in primarily C4 environments throughout the sequence. Other animals show wide variation in δ13C, seemingly occupying the diversity of environments available in the region. These include suids identified as *Potamochoerus* cf. *larvatus* (range = -16.6 to -2.9‰; mean = -9.1 ± 4.7‰) or simply as ‘indeterminate suid’ (range = -14.4 to -5.6‰; mean = -10.9 ± 3.4‰), as well as the cephalophine *Sylvicapra grimmia* (range = -12.7 to -9.0‰; mean = -11.1 ± 1.2‰) and the tragelaphine *Tragelaphus scriptus* (range = -11.4 to -11.3‰; mean = -11.4 ± 0.1‰).

A Kruskal-Wallis test confirms that species significantly influences δ13C at PYS (chi-squared = 92.421, df = 23, p-value = <0.05 (0.000). However, subsequent pairwise Wilcox tests failed to draw out a number of specific differences between taxa (p = >0.05) (Supplementary Table 6). Given the clear distinctions visible in Figure 6, this is likely a product of issues of taxa representation, as a number of comparisons are not possible due to absences among temporal groupings (Supplementary Table 6), furthering the need for the ‘weighting’ methodology below. The two exceptions are the significant difference found between *Potamochoerus* cf. *larvatus* and *Phacochoerus* sp.(p = <0.05), confirming the differences in feeding behaviours between these two suids, and the significant difference between *Sylvicapra grimmia* and *Phacochoerus* sp (p = <0.05). The PYS fauna also documents a wide range in δ18O (range = -10.7 to 0.8‰; mean = -2.7 + 1.9‰). A Kruskal-Wallis test confirms that there are species differences in terms of δ18O (chi-squared = 62.614, df = 23, p-value = <0.05 (0.001). However, once again, subsequent pairwise Wilcox tests failed to draw out specific differences among taxa (p = >0.05), beyond that between *Potamochoerus* cf. *larvatus* and *Phacochoerus* sp.(p = <0.05) (Supplementary Table 7).

In terms of variation in δ13C and δ18O through time, Figure 7A suggests that MIS 5 has fauna with lower δ13C prior to an increase in MIS 4 to MIS 2, followed by a gradual return to lower values in the terminal Pleistocene and Holocene. This pattern is mirrored in δ18O suggesting that the same factors are driving both isotopic systems (Fig. 7B). Kruskal-Wallis testing confirms that variation in δ13C (chi-squared = 30.564, df = 7, p-value = <0.05 (0.000) through time is significant, with pairwise Wilcox tests confirming a significant difference in faunal δ13C between MIS 5 and early-mid MIS 3 and between MIS 5 and the terminal Pleistocene (p = <0.05) (Supplementary Table 8). A Kruskal-Wallis test also identified significant differences in δ18O by layer grouping (chi-squared = 34.040, df = 7, p-value = <0.05 (0.000). Pairwise Wilcox tests identified MIS 5 and early-mid MIS 3, MIS 4 and early-mid MIS 3, early-mid MIS 3 and the Iron Age, the mid-Holocene, and the terminal Pleistocene to be significantly distinct from each other in terms of δ18O (p = <0.05) (Supplementary Table 9). A linear regression shows δ13C and δ18O to be positively correlated (p = 0.000) albeit relatively weakly (Multiple R-squared: 0.260; Adjusted R-squared: 0.254).

Variation in species representation through the sequence (Figs. S1 and S2) makes it important to ‘weight’ the isotopic data into larger, more robust groups that are present throughout the sequence (browser, grazer), to provide higher resolution into the observed palaeoenvironmental shifts. Figure 8 demonstrates an obvious increase in δ13C for browsers from MIS 4 to early-middle MIS3, before subsequent decrease by late MIS3 and the terminal Pleistocene and Holocene. Comparison with modern data corrected for the fossil fuel effect taken from Cerling et al. (2015) highlights that, while some fauna from Layers 17-19 and Layers 13-16 have values below -14‰ indicative of closed forest at this time, even during these early occupations the majority of browsers align with the median of modern eastern African browsers (Fig. 8). This suggests that there was always a mixture of some elements of closed forest and open woodland in the vicinity of the site. Temporal changes in δ13C are not seen prominently in grazers at PYS, with a subtle increase perhaps visible from MIS 4 to the LGM prior to increased variation in the terminal Pleistocene. This suggests, that the environmental shifts primarily impacted browsing animals and that grazers possibly moved more widely to obtain their preferred vegetation sources. Distinctions between browser and grazer δ13C (Kruskal-Wallis chi-squared = 487..9, df = 1, p-value = <0.05 (0.000)) and δ18O (Kruskal-Wallis chi-squared = 20.609, df = 1, p-value = <0.05 (0.000)) are backed up by Kruskal-Wallis and pairwise Wilcox tests. For δ18O, there is a clear increase in browser δ18O from MIS 4 to MIS 3 prior to a decline in the terminal Pleistocene and Holocene (Fig. 9). The same trend is, albeit more subtly, also visible among grazers, with an increase in δ18O between MIS4 and MIS3 prior to a decline from the LGM/terminal Pleistocene to the Holocene (Fig. 9). Kruskal-Wallis and pairwise Wilcox tests found no distinctions in δ13C or δ18O between the layer groupings to be significant for both browsers (>0.05) and grazers (>0.05) indicating the relatively limited amplitude of the palaeoenvironmental changes effecting these feeding groups at PYS, as well as likely the wide range of variability within relatively small sample sizes and the conservative bonferroni adjustment methods used in the R Package.

**4.4. Human stable carbon and oxygen isotope result from Panga ya Saidi**

The deciduous second molar in Layer 18 (MIS 5) dating to *c.* 78 ka had measured δ13C and δ18O of 11.4‰ and -4.3‰, respectively (Supplementary Table 3). Given that the sampled tooth would have formed between just before birth and ~2.5 years (AlQahtani et al., 2010), the δ13C signal is indicative of a full reliance on C3 resources by the individual’s mother (with the signal transferred through breastfeeding) and of any diet the child may have been weaned onto during this time. This is supported by a lack of fauna with δ13C values indicative of C4 environments in Layers 17-19 and a preponderance of browsing fauna with preferences for tropical forest and woody habitats **(**Figs. 6, and S1-3). The permanent molar from the Iron Age human burial in Layer 1 produced δ13C and δ18O measurements of -11.1‰ and -3.2‰, respectively. As can be seen in Figures 6 and S1, this places this person towards the lower end of the δ13C range of associated fauna, overlapping with fauna considered to be primarily occupying forest or woodland environments. These results are consistent with an interpretation that he was reliant on the wild fauna excavated at PYS from the time period of the burial (Later Iron Age, *c.* 400 BP), with no evidence for the significant consumption of C4 crops such as millet. Associated fauna appear to come from a variety of environments – including more closed forest, open woodland, and open C4 grassland – but this person demonstrated a preference for resources sourced from forested settings. While the sample size is small, the results from the two human individuals sampled hint at a persistent reliance on forested/wooded resources by Late Pleistocene and Holocene human populations living at the site.

**5. Discussion**

**5.1. A new palaeoenvironmental record for Late Pleistocene and Holocene eastern Africa**

Our zooarchaeological and stable isotopic data represent a novel, multi-proxy record for Late Pleistocene and Holocene palaeoenvironments in eastern Africa. The combined use of these methodologies provides high-resolution insights into assemblage formation and composition, as well as deviations in feeding preferences as a product of environmental or behavioural change through time (see Chritz et al., 2019). Overall, the taxonomic composition of the PYS assemblage, dominated by small bovids, flexible suids, and some primates, is broadly consistent with fauna found in Holocene and present-day faunal assemblages in the coastal mosaic forests of eastern Africa (Prendergast et al., 2017b; M.E. Prendergast et al., 2016; Walsh, 2007). This suggests the relative stability of a mixture of closed forest and open woodlands, alongside the sporadic appearance of open grasslands, in the region over a long period of time. The stable isotope data supports this, documenting the persistence of carbon isotope values consistent with minor elements of closed forest alongside open woodland throughout the majority of the sequence, but also demonstrates, after the initial phase of occupation, the persistent use of fauna feeding on open C4 grasslands by human prey. This is also visible in the zooarchaeological record, albeit more subtly and based on small samples in some cases. Remains of small bovids, primates, and bushpigs relying on closed habitats are more common in the earliest portion of the sequence, with increases in remains of grazing bovids and suids with preferences for open settings beginning in MIS 4 and continuing until the Holocene, when there is a return to dominance of forest- and woodland-adapted species. Meanwhile, the isotope data demonstrate environmental shifts from more humid, wooded settings to more open, drier environments, affecting both grazers and browsers, from MIS 5 into MIS 4 and again into MIS 3, before a return to more wooded conditions in the terminal Pleistocene and Holocene.

The increased presence of grassland alongside increasing aridity occurs at a time (*c.* 70 ka) when faunal and lacustrine records from the interior have been used to argue for an expansion of semi-arid, seasonal, C4 grasslands (Faith et al., 2015; Tryon et al., 2010). Indeed, the MSA-LSA transition has been argued to occur around this time in eastern Africa *c.* 65 ka (Shipton et al., 2018), when changes in equatorial insolation led to drier conditions (Blome et al., 2012; Trauth et al., 2003). Some have argued for additional extreme environmental changes in eastern Africa as a product of the Toba eruption *c.* 74 ka (Ambrose, 1998b; but see Lane et al., 2013) or ‘mega-droughts’ recorded in tropical African lakes *c.* 70 ka (Cohen et al., 2007). Recent isotopic work and faunal analysis has also highlighted climate fluctuations at the terminal Pleistocene/Holocene boundary in the interior of eastern Africa, with the onset of more humid conditions at this time (Faith, 2014; Prendergast and Beyin, 2017; Robinson et al., 2016). This aligns with the increase in the representation of forested/wooded environments in the vicinity of PYS during this period. In the later Holocene, such environments at PYS may have been isolated from wider regional changes, including land clearance, brought about by shifts to food production (Marchant et al., 2018). Together, the PYS zooarchaeological and human isotopic records also suggest continuity of foraging, despite dramatic economic, cultural, and demographic shifts along the coast at this time (Crowther et al., 2018). Overall then, the PYS dataset suggests that while some environmental changes are recorded in the vicinity of the cave from *c*. 78 to 0.4 ka, these are of low amplitude and appear to be buffered by a mesic maritime influence, relative to fluctuations in aridity witnessed in the interior. A mixture of fauna reliant on open forest, woodland, and grassland biomes were utilized by humans at PYS throughout the period of human occupation, with isotopic evidence from two human samples highlighting a general preference for resources from wooded environments.

The PYS data conforms with recent work emphasising the need for local and regional resolution in the context of eastern African palaeoenvironmental change of relevance to human behaviour (Robinson, 2017), something that is becoming increasingly possible with the expansion of high-resolution archaeological sequences and multivariate palaeoenvironmental proxies (e.g., Chritz et al., 2019). In Figs. 10 and 11 we group our δ13C and δ18O data for browsers and grazers at PYS, respectively, into MSA and LSA categories (based on Shipton et al. (2018)) in order to compare them to δ13C and δ18O for browsers, grazers, and mixed feeders published by Robinson (2017) in MSA and LSA levels at Porc-Epic (Ethiopia), Lukenya Hill (Kenya), and Kalemba Rockshelter (Zambia). PYS, like Kalemba Rockshelter, shows some faunal δ13C values indicative of the presence of closed forest or woodland (<-14‰) during the LSA. PYS is, however, the only site with no identified grazers in its MSA levels, highlighting the potential distinctiveness of this setting (Fig. 10). The majority of δ13C data for PYS MSA browsers align with that from the Kalemba Rockshelter MSA and LSA browsers, interpreted as more wooded, riverine settings, shifting to higher, but also variable, browser δ13C during the LSA comparable with browsers present at the semi-arid Porc-Epic and Lukenya Hill (Robinson, 2017), indicating a shift towards more open settings in the vicinity of the site (Fig. 10). In terms of δ18O, PYS browsers are similar to browsers from the MSA and LSA Kalemba Rockshelter, with both sites having much lower δ18O than Lukenya Hill and Porc Epic (Fig. 11). While this could indicate the presence of humid forest/woodland in the vicinity of PYS and Kalemba, relative to the more arid Lukenya and Porc-Epic (Fig 11), more sophisticated comparison of obligate and non-obligate drinker taxa δ18O (as per Levin et al., 2006; Blumenthal et al., 2017; Roberts et al., 2018) would be required, which is not possible based on the existing small sample sizes of these sites.

Robinson (2017) has recently highlighted the significant temporal and spatial variation in aridity and vegetation distributions across Pleistocene tropical Africa. PYS only further adds to this picture, representing a region where shifts in vegetation, from more wooded to more grassland environments, are closely driven by changes in rainfall. Moreover, when zooarchaeological and isotope analyses are combined at PYS, we can see that while similar shifts in aridity are seen at PYS when compared to other Late Pleistocene records from Kenya and Ethiopia, they remain subtle, and are not accompanied by a complete shift in the representation of different fauna (notably browsers and grazers). Alongside work by Mercader et al. (2013) and Wright et al. (2017) in Mozambique and Malawi, as well as reviews by Basell (2008) and Blome et al. (2012) for Africa more widely, the PYS data highlight the importance of fluctuating mosaic environments, consisting of forest patches and more open grassland, for human expansion and persistence during periods of climatic change. While subtle climatic and environmental shifts may have acted as a backdrop to the MSA-LSA transition in some regions, the PYS zooarchaeological and isotopic record fits with a growing body of work highlighting that: a) climatic variations are unlikely to be viable one-size-fits all explanations for changes in human technology or material culture anywhere in Pleistocene eastern Africa (as also noted by Jacobs et al. (2008) and Roberts et al. (2016) in southern Africa) and b) that mosaic or ecotonal environments combining forest, woodland, and grassland biomes may have provided highly attractive settings for human persistence of occupation and experimentation.

**5.2. Strength in diversity: Late Pleistocene human palaeoecology in eastern Africa and beyond**

This latter point highlights the major role that tropical coastal Africa may have played as an environmental ‘refugium’ for human populations facing the increasing climatic instability of the Late Pleistocene. In the context of Pleistocene *H. sapiens* evolution and behavioural change, it is often coastal and grassland environments that have been seen as reliable sources of high protein marine resources and large game, respectively (Marean et al., 2007; Shea and Sisk, 2010). However, more recently, increasing attention has been paid to environmental ‘mosaics’. For example, the development of ochre working, shell bead production, and technological changes with the Still Bay and Howiesons Poort at sites such as Blombos Cave and Klipdrift Shelter on the southern Cape coast of South Africa have been set against a background of not just marine resources (van Niekerk, 2011) but also small and large game on the broader coastal plain (Copeland et al., 2016; Reynard and Henshilwood, 2019). Here, ecotonal settings are seen as buffering any shifts in specific resources that might occur as a result of sea-level change or climatic impacts on terrestrial environments (Reynard and Henshilwood, 2019). Similar arguments have been made in tropical Malawi and Mozambique where researchers have highlighted that archaeological sites and MSA technologies followed woodland-grassland mosaics whose extent and composition fluctuated between MIS 5 and MIS 3 (Mercader et al., 2013; Thompson et al., 2012). Access to both forest animal and plant resources, as well as larger grassland game, is seen as providing a diversity of options in the face of external instability.

Such a perspective has also been proposed for the movement and emergence of *H. sapiens* populations across Africa more generally (Basell, 2008; Blome et al., 2012; Scerri et al., 2018) and encourages a reconfiguration of research away from environments assumed as being homogeneously attractive to hunting and gathering populations. In the case of PYS, the unique conditions of the tropical coastal forest ecotone, where vegetation and animal resources vary within a relatively small area even today, were resilient to the more extreme effects of fluctuations in water availability seen in the interior. As Shipton et al. (2018) suggested, the mesic coastal environments, as in southern Africa (see also Roberts et al., 2016), seemingly buffered such changes, enabling the resilience of both moist forest and moist grassland settings when compared to the regions surrounding Lake Malawi and Lake Turkana (Faith et al., 2015; Tryon et al., 2010). Indeed, rather than dramatic shifts in climate and environment, it appears to be the persistence of heterogeneous environments that facilitated technological and cultural experimentation by hunter-gatherers at PYS in the form of an early appearance of shell ornamentation and organic material culture (Shipton et al., 2018). It is worth noting that while a number of sites in the eastern African interior have an occupational hiatus during the Last Glacial Maximum, human use of PYS continues throughout this period (Ambrose, 1998a; Gliganic et al., 2012; Mehlman, 1989; Tribolo et al., 2017).

It is becoming increasingly apparent that our species was accompanied by climatic and environmental variability as it evolved in Africa and dispersed around the planet (Graves and Weinreich, 2017; Potts, 1998, 2013; Roberts and Stewart, 2018; Scerri et al., 2018; Will et al., 2019). Rather than a focus on ‘coastal highways’ (Mellars, 2006; Mellars et al., 2013) or ‘savanna’ settings (Ambrose, 2002; Shea and Sisk, 2010; Tryon et al., 2010) it was the capacity to adapt to a variety of environmental extremes that led our species to ultimately be successful in global colonization (Roberts and Stewart, 2018). Yet, like other hominin populations that favoured combinations of lacustrine woodland and grassland settings in eastern Africa (Elton, 2006; Elton, 2008; Kingston and Harrison, 2007; Magill et al., 2013; Reed, 1997), our species also made use of productive mosaic environments, where multiple habitats could be exploited at the same time, particularly in the face of climate change. Indeed, while the ability to foster social networks and develop efficient projectile technologies undoubtedly facilitated the habitation of environments traditionally considered to be more ‘challenging’ (Shea and Sisk, 2010), more stable and varied settings could also have facilitated testing of more efficient capture and use of resources in micro-habitats, particularly as populations expanded under more favourable conditions (Reynard and Henshilwood, 2019). The PYS record contributes to the diversity of coupled palaeoenvironmental-archaeological investigations into the emergence of the behavioural traits of our species in different parts of Africa, particularly in the period of significant dispersals beyond the continent. It is by “thinking locally” (Robinson, 2017) that we can truly understand the variability behind how we became human.

**6. Conclusions**

We present new, combined zooarchaeological and stable isotope data from the site of PYS (*c.* 78-0.4 ka) situated in the coastal tropical forests of eastern Africa. The resulting palaeoenvironmental and palaeoecological data addresses problems in understanding habitats utilized by *H. sapiens* through periods of major climate and cultural change. We demonstrate that closed forest, woodland, and grassland environments were consistently available to hunter-gatherers occupying PYS. Subtle changes are evident in the faunal and isotopic data, notably a reduction in forest and increase in grassland as well as increased aridity *c.* 67 ka, followed by a return to humid, more forested conditions in the terminal Pleistocene/early Holocene. However, for the most part these environmental shifts were limited. Climate impacts noted during MIS 4 elsewhere in the interior of eastern Africa, and across tropical Africa more widely, were apparently dampened on the Kenyan coastline. We argue that the consistent presence of ecotonal or heterogeneous environments provided the ideal refugium for experimentation in technology and material culture by human populations, and that the maintenance of foraging lifestyles in the coastal tropical forest surrounding PYS persisted even beyond the arrival of agriculture in the region. As such, the PYS data urges a reconfiguration of foci on exclusive maritime and savanna adaptations in discussions of Late Pleistocene human innovation and dispersal, instead highlighting environmental diversity as key at the dawn of our species’ expansion across the planet in the Late and terminal Pleistocene.

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**Table captions**

**Table 1**. Radiometric dates from Panga ya Saidi (from Shipton et al. 2018).

|  |  |  |  |
| --- | --- | --- | --- |
| **Layer** | **Lab Code** | **Measured Age** | **Calibrated Age** |
| 1 | OxA-30803 | 388±27 | 500-300 |
| 3 | OxA-29285 | 1212±23 | 1178-1081 |
| 4 | OxA-30440 | 6797±39 | 7670-7610 |
| 5 | OxA-30441 | 12375±50 | 14570-14200 |
| **Layer** | **Lab Code(s)** | **Measured Age** | **Modelled Age** |
| 8 | OxA-29983 | 20835±75 | 25300-25050 |
| 9 | OxA-30146, OxA-29431, OSL-13 | 28970±190, 28780±180, 45900±2700 | 45650-32650 |
| 11 | Beta-368059, OxA-29984, OxA-29986, OxA-29985, OSL-11 | >39660±530, 44500±450, 45550±550, 45700±500, 49000±3000 | 49550-47550 |
| 12 | Beta-368062 | >38490±460 | 52900-49050 |
| 13 | OSL-9 | 64200±4100 | 61750-55750 |
| 15 | OSL-17 | 59900±4000 | 64700-58700 |
| 17 | OSL-5 | 74900±5100 | 76650-69400 |
| 18 | OSL-3 | 73800±5200 | 80200-72500 |

**Table 2.** Summary of identified fauna at Panga ya Saidi, Trenches 3 and 4. Taxonomic categories have been combined for brevity; for detailed identifications, see Supplementary Table 2. MIS = Marine Isotope Stage; NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals (MNI); indet. = indeterminate

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Iron Age: L1-L3 1** | | **Middle Holocene: L4** | | **Terminal Pleistocene: L5-L6** | | **Last Glacial Maximum: L8** | | **Late MIS3: L9** | | **Early-Mid MIS3: L10-L12** | | **MIS4: L13-L16** | | **MIS5: L17-L19** | | **TOTAL** | ***TOTAL*** |
| **Taxonomic Attribution** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** | **NISP** | ***MNI*** |
| **Mammalia/Artiodactyla/Bovidae** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Identified to tribe: |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Neotragini (dik-dik, steenbok, and/or suni) | 12 | *2* | 1 | *1* | 2 | *1* | 1 | *1* | 1 | *1* |  |  | 1 | *1* |  |  | **18** | ***7*** |
| Cephalophini (bush duiker, other duikers) | 13 | *3* | 1 | *1* | 3 | *1* |  |  | 1 | *1* | 1 | *1* | 3 | *1* | 2 | *1* | **24** | ***9*** |
| Antilopini (oribi) |  |  |  |  | 1 | *1* |  |  |  |  | 3 | *1* |  |  |  |  | **4** | ***2*** |
| Cf. Caprini (domestic caprine) | 4 | *1* |  |  |  |  |  |  |  |  |  |  |  |  |  |  | **4** | ***1*** |
| Reduncini (reedbuck, waterbuck) |  |  |  |  | 4 | *1* | 1 | *1* | 1 | *1* | 3 | *1* | 2 | *2* |  |  | **11** | ***6*** |
| Tragelaphini (bushbuck, kudu, and/or eland) | 4 | *1* |  |  |  |  |  |  |  |  | 3 | *1* |  |  | 1 | *1* | **8** | ***3*** |
| Alcelaphini (topi, hartebeest, wildebeest) |  |  |  |  |  |  | 1 | *1* | 2 | *1* | 14 | *2* |  |  |  |  | **17** | ***4*** |
| Bovini (buffalo) |  |  | 2 | *1* | 1 | *1* | 1 | *1* | 2 | *1* | 1 | *1* | 1 | *1* |  |  | **8** | ***6*** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Identified to size class: |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Bovid Size 1 (dik-dik/suni-sized) | 95 | *4* | 10 | *-* | 47 | *3* | 51 | *3* | 24 | *3* | 22 | *1* | 12 | *1* | 5 | *1* | **266** | ***16*** |
| Bovid Size 1-2 (bush duiker/oribi-sized) | 26 | *-* | 1 | *-* | 7 | *-* | 25 | *1* | 14 | *-* | 5 | *-* | 6 | *-* | 2 | *-* | **86** | ***1*** |
| Bovid Size 2 (bushbuck/reedbuck-sized) | 35 | *-* | 6 | *1* | 13 | *1* | 28 | *2* | 16 | *1* | 13 | *1* | 4 | *-* | 1 | *1* | **116** | ***7*** |
| Bovid Size 2-3 (reedbuck to waterbuck-sized) | 1 | *-* | 1 | *-* | 9 | *-* | 5 | *-* | 14 | *-* | 6 | *-* | 6 | *-* |  |  | **42** | ***-*** |
| Bovid Size 3 (waterbuck/wildebeest-sized) | 6 | *1* | 3 | *-* | 37 | *-* | 34 | *-* | 40 | *-* | 59 | *-* | 19 | *-* | 4 | *1* | **202** | ***2*** |
| Bovid Size 3-4 (waterbuck to buffalo sized) | 2 | *-* |  |  | 4 | *-* | 2 | *-* | 8 | *-* | 5 | *-* |  |  | 1 | *-* | **22** | ***-*** |
| Bovid Size 4 (eland/buffalo-sized) |  |  |  |  |  |  | 1 | *-* | 2 | *-* | 1 | *-* | 1 | *-* |  |  | **5** | ***-*** |
| Bovid size indet. | 1 | *-* |  |  | 3 | *-* |  |  | 1 | *-* | 21 | *-* | 2 | *-* |  |  | **28** | ***-*** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Mammalia/Artiodactyla/Suidae** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Phacochoerus* sp. (warthog) | 1 | *1* | 3 | *1* | 11 | *1* | 3 | *1* | 15 | *2* | 9 | *2* |  |  |  |  | **42** | ***8*** |
| *Potamochoerus larvatus* (bushpig) | 2 | *1* |  |  | 8 | *1* |  |  | 2 | *1* |  |  | 1 | *1* |  |  | **13** | ***4*** |
| Suid indet. | 7 | *-* | 5 | *-* | 28 | *-* | 22 | *1* | 23 | *-* | 11 | *-* | 11 | *-* | 4 | *1* | **111** | ***1*** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Mammalia/Primata** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Papio* sp. and Cf. *Papio* (baboon) |  |  |  |  | 1 | *1* |  |  |  |  | 4 | *2* |  |  |  |  | **5** | ***3*** |
| Cercopithecine and colobine monkeys | 14 | *2* | 3 | *2* | 2 | *1* | 2 | *1* | 3 | *1* | 1 | *1* | 1 | *1* | 19 | *2* | **45** | ***11*** |
| *Otolemur* sp.(greater galago) | 2 | *1* |  |  |  |  |  |  |  |  |  |  |  |  |  |  | **2** | ***1*** |
| Primate indet. |  |  |  |  | 1 | *-* |  |  |  |  | 2 | *1* |  |  | 2 | *1* | **5** | ***2*** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Mammalia/other** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Mammalia/Carnivora | 18 | *5* | 1 | *1* | 2 | *1* | 1 | *1* |  |  | 1 | *1* | 3 | *3* |  |  | **26** | ***12*** |
| Mammalia/Chiroptera | 18 | *5* | 3 | *1* | 11 | *4* | 14 | *4* | 14 | *2* | 2 | *1* | 38 | *6* | 187 | *22* | **287** | ***45*** |
| Mammalia/Hyracoidea | 9 | *2* | 2 | *1* | 11 | *2* | 23 | *3* | 13 | *2* | 22 | *3* | 3 | *1* | 2 | *1* | **85** | ***15*** |
| Mammalia/Macroscelidea | 15 | *2* |  |  |  |  |  |  |  |  |  |  | 2 | *1* | 3 | *1* | **20** | ***4*** |
| Mammalia/Pholidota |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 | *1* | **3** | ***1*** |
| Mammalia/Rodentia | 1531 | *135* | 1 | *1* | 1 | *1* | 1 | *1* | 1 | *1* | 1 | *1* | 11 | *2* | 12 | *2* | **1559** | ***144*** |
| Mammalia/Soricomorpha | 20 | *7* |  |  |  |  |  |  |  |  |  |  |  |  |  |  | **20** | ***7*** |
| Mammalia/Indeterminate | 312 | *-* | 33 | *-* | 55 | *-* | 504 | *-* | 499 | *-* | 72 | *-* | 201 | *-* | 265 | *-* | **1941** | *-* |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Other** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Aves (all birds) | 43 | *8* |  |  | 3 | *1* | 3 | *1* |  |  | 1 | *1* | 3 | *1* | 1 | *1* | **54** | ***13*** |
| Reptilia (all reptiles) | 34 | *7* | 2 | *1* | 4 | *3* | 14 | *2* | 14 | *2* | 12 | *2* | 8 | *2* | 14 | *4* | **102** | ***23*** |
| Indeterminate vertebrates | 5 | *-* |  |  | 1 | *-* | 13 | *-* | 3 | *-* | 1 | *-* | 3 | *-* | 32 | *-* | **58** | *-* |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | **2230** | ***188*** | **78** | ***12*** | **270** | ***25*** | **750** | ***25*** | **713** | ***20*** | **296** | ***24*** | **342** | ***24*** | **560** | ***41*** | **5239** | ***358*** |

1 In Layers 1-3, microfauna were analysed in Trench 3 but not Trench 4; therefore, microfaunal NISP and MNI counts are artificially low.

**Figure captions**

**Figure 1**. Map of eastern Africa indicating locations of Late Pleistocene sites with palaeoenvironmental and/or faunal records and archaeological sequences mentioned in the text relative to A) modern precipitation (data from Hijmans et al. (2005) and B) vegetation biomes (data from Olson et al. (2001). Black star indicates the location of Panga ya Saidi, 15km from the present-day shore in the Zanzibar-Inhambane tropical coastal forest mosaic and currently experiencing more precipitation than the sites located in the Kenyan/Tanzanian Rift, in an ecotone between lowland tropical forest and savanna environments.

**Figure 2**. Stratigraphic sequence and chronology of Trenches 3 and 4 at Panga ya Saidi (after Shipton et al. 2018). Ages are based on those published in Shipton et al. (2018) and shown in Table 1.

**Figure 3**. Present-day feeding classifications for genera of bovids, suids, and select primates identified at PYS. For bovids and suids, classification is based on published modern dietary and stable isotope data, detailed in Supplementary Table 4 (Cerling et al., 2015; Cerling et al., 2003; Gagnon and Chew, 2000). All artwork is original, drawn by M.E. Prendergast.

**Figure 4.** A) Relative abundance of major mammalian groups (excluding indeterminate mammals and pangolin) in Trenches 3 and 4 at Panga ya Saidi, with archaeological layers (L) grouped temporally (Mid. Holo. = middle Holocene; Term. Pleisto. = terminal Pleistocene; LGM = Last Glacial Maximum; MIS = Marine Isotope Stage). Relative abundance is expressed as a percentage of the total Minimum Number of Individuals (MNI) for this subset of mammals in each temporal grouping. Fauna are divided into those likely living in the cave environment (grey shades) and those possibly (white) and likely (blue) brought into the cave as prey. B) Relative abundance of bovid size classes, expressed as a percentage of the total Number of Identified Specimens (NISP) for all bovids (excluding those of indeterminate size) in each temporal grouping. Small bovids include Cephalophini, Neotragini, *Ourebia*, and Bovids Size 1 and Size 1-2. Medium bovids include *Tragelaphus*, *Redunca*, and Bovids Size 2 and Size 2-3. Large bovids include Alcelaphini, Bovini, *Kobus*, large Tragelaphini, and Bovids Size 3, Size 3-4, and Size 4.

**Figure 5.** A) Spindle graph (following Lyman and Faith, 2018), illustrating the relative abundance of bovids identifiable to tribe or lower taxonomic level, expressed as a percentage of the Number of Identified Specimens (NISP) for the subset of identified bovids in each temporal grouping of archaeological layers (L). Dark green indicates bovid tribes that are mostly browsing, light green indicates tribes that are mostly grazing; see Figure 4 and Supplementary Table 4 for details of these classifications. B) Absolute abundance (NISP) of those bovids, suids, and selected primates that could be identified to tribe or genus. “Mostly browsers and frugivores” includes all identified Cephalophini, Neotragini, Tragelaphini, *Potamochoerus*, and Colobini/Cercopithecini. “Mostly grazers” includes all identified Antilopini, Reduncini, Bovini, Alcelaphini, and *Phacochoerus*.

**Figure 6**. Mean and standard deviation of δ13C and δ18O measurements by taxa at PYS with the two *Homo sapiens* specimen plotted over the top. The full scatterplot can be found as Supplementary Figure 1.

**Figure 7.** Boxplot of A) δ13C and B) δ18O measurements of faunal specimens classified by the Layer groupings defined in the main text with the individual measurements plotted on top. Boxplots show the media and interquartile range. Outliers are shown with a double circle.

**Figure 8.** Boxplot of δ13C for taxa at PYS grouped as ‘Browsers’ or ‘Grazers’ based on Cerling et al. (2003) and Cerling et al. (2015) by the Layer groupings (“L”) defined in the text (see Table 1 and Supplementary Table 3). Individual specimen values are plotted above the boxplots that represent the median values and interquartile ranges for each group. Modern taxa identified as ‘Browsers’ or ‘Grazers’ in Cerling et al. (2015), with their data corrected to pre-fossil fuel values, have also been included as a reference point.

**Figure 9.** Boxplot of δ18O for taxa at PYS grouped as ‘Browsers’ or ‘Grazers’ based on Cerling et al. (2003) and Cerling et al. (2015) by the Layer groupings (“L”) defined in the text (see Table 1 and Supplementary Table 3). Individual specimen values are plotted above the boxplots that represent the median values and interquartile ranges for each group.

**Figure 10.** Boxplots of δ13C for taxa at PYS grouped as ‘Browsers’ or ‘Grazers’ based on Cerling et al. (2003) and Cerling et al. (2015) for periods of occupation associated with MSA and LSA industries at the site (as per Shipton et al. 2018). PYS data is compared to similar data available for ‘Browsers’, ‘Grazers’, and ‘Mixed Feeders’, analysed by Robinson (2017) from MSA, MSA/LSA transitional, and LSA layers at Lukenya Hill (Kenya), Porc-Epic (Ethiopia), and Kalemba Rockshelter (Zambia).

**Figure 11.** Boxplots of δ18O for taxa at PYS grouped as ‘Browsers’ or ‘Grazers’ based on Cerling et al. (2003) and Cerling et al. (2015) for periods of occupation associated with MSA and LSA industries at the site (as per Shipton et al. 2018). PYS data is compared to similar data available for ‘Browsers’, ‘Grazers’, and ‘Mixed Feeders’, analysed by Robinson (2017) from MSA, MSA/LSA transitional, and LSA layers at Lukenya Hill (Kenya), Porc-Epic (Ethiopia), and Kalemba Rockshelter (Zambia).

**Supplementary Materials for this manuscript include:**

Supplementary Figure 1

Supplementary Tables 1-11