



# Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments



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## ABSTRACT

The Wallacea Archipelago provides an extraordinary laboratory for the study of human colonisation and adaptation, yet few detailed archaeological studies have been conducted in the region that span the earliest phase of human settlement. Laili Cave, in northern Timor-Leste, preserves the oldest human occupation in this insular region with a cultural sequence spanning 11,200 to 44,600 cal BP. Small-bodied vertebrates and invertebrates were recovered to the lowest excavated levels, associated with highly concentrated stone artefacts. We report on human behavioural adaptations within the context of Pleistocene environments and changing landscapes using zooarchaeological, stone artefact, bathymetric, and experimental isotopic analyses. Results indicate that Pleistocene humans used the abundant local chert liberally and engaged in mobile broad-spectrum exploitation of invertebrates and fishes from marine, estuarine, and freshwater environments within close proximity of Laili Cave. The faunal assemblage indicates heterogeneous but relatively stable environments during the late Pleistocene. Variability in subsistence strategies over time appears to be a response to changing landscapes and concomitant local resources. This record contrasts with marine specialisations evident from other sites in Timor-Leste and within the broader Wallacean region.

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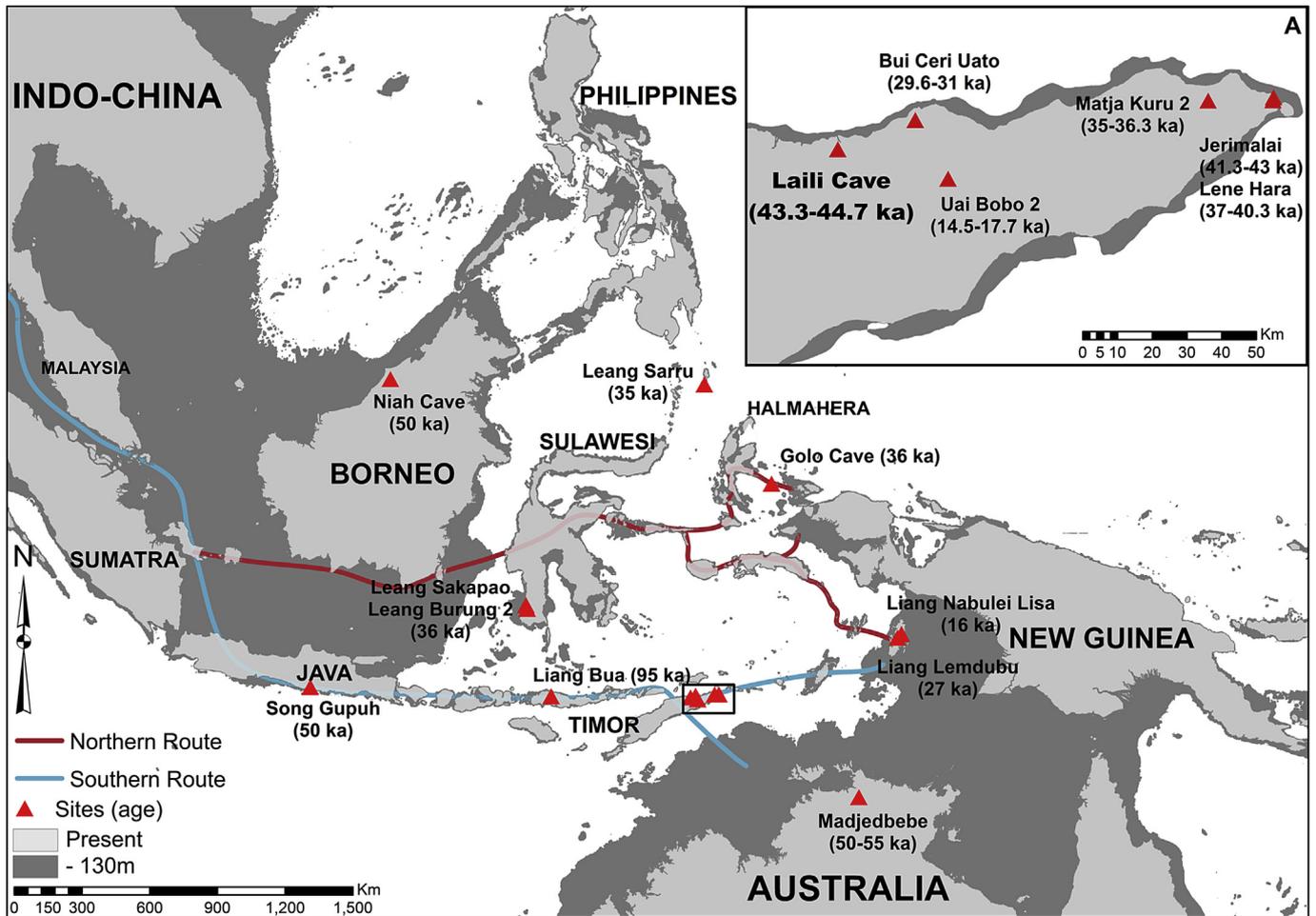
## 1. Introduction

One of the most enduring questions in modern human migration studies concerns the timing, route and ecological and/or behavioural impetus for maritime migration and subsequent adaptation in Island Southeast Asia (ISEA) en route to Sahul (the landmass consisting of New Guinea, Australia, and associated small, currently offshore islands). Two main routes, one via the south and onto the expanded northwest Australian coastline, and the other via the northern islands of Wallacea and into New Guinea, have been suggested (Fig. 1), based largely on bathymetric reconstructions (Birdsell, 1977; Kealy et al., 2015). These models are predicated on the earliest dates that have emerged from Sahul's archaeological record that has pushed back the antiquity of initial

colonisation beyond the radiocarbon window, with optical luminescence dates in the order of 50–60 ka (Clarkson et al., 2015; Hamm et al., 2016; Hiscock et al., 2016). These ages are significantly older than the oldest dates for modern human occupation in Wallacea, represented by the cave deposits of Jerimalai, Timor-Leste (41,310–43,000 cal BP; O'Connor, 2007). This disparity likely results from sampling and preservation constraints in ISEA, with continuing research seeking to close this gap.

Reasons for the apparently rapid movement of modern humans through the Wallacean islands are subject to considerable debate, invoking behavioural responses to changing sea levels and insular maritime environments (e.g., Anderson, 2017; Kealy et al., 2015; O'Connell and Allen, 2012, 2015). Optimal foraging models have been used to predict that during low sea levels and periods of increased island inter-visibility, rapid exploitation and depression of initially abundant coastal resources would have driven modern human populations in Wallacea to mobile foraging, rapid migration, and thus extensive onward island colonisations (O'Connell and Allen, 2012, 2015). These patterns of movement and island

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**Fig. 1.** Island Southeast Asia, early hominin archaeological sites, and Laili Cave, Timor-Leste, Wallacea, in relation to sea levels (both modern and during the height of the Last Glacial Maximum), showing northern and southern migration routes.

colonisation have been criticised on several grounds, including likely low population densities during the initial migration phase, differences in timing of maritime skill developments worldwide, and most pertinently, the lack of data available to test such predictions (e.g., Anderson, 2017; Kealy et al., 2015).

How humans then adapted to insular environments has engendered further discussion. Early technological records from Jerimalai Shelter at the eastern end of Timor-Leste reveal innovative stone reduction involving the production of truncated faceted flakes and Levallois-like cores, which Marwick et al. (2016) describe as emphasising the efficient production of relatively large flakes from proportionately small cores. Marwick et al. (2016) also drew parallels between the Jerimalai reduction sequences and early modern human assemblages from Flores (e.g., Brumm et al., 2006). The presence of these new technological systems indicates adaptation and innovation following initial island migration. The manufacture of significant socio-cultural items from local marine and native terrestrial fauna also demonstrates rapid adaptation to locally available resources (Brumm et al., 2017; Langley and O'Connor, 2016; Langley et al., 2016). The development of distinctive human subsistence strategies to local island specific faunal resources is also evident. On the relatively faunally diverse island of Sulawesi, large-bodied native mammals such as babirusa and anoa as well as shellfish from rivers were exploited at Leang Burung 2 and Leang Sakapao 1 (Bulbeck et al., 2004; Glover, 1981). On small

Wallacean islands, subsistence appears to have been focused on maritime faunal resources (O'Connor et al., 2011; Ono, 2010; Samper Carro et al., 2016; Szabó and Amesbury, 2011). On these islands, limited terrestrial faunal diversity appears to have resulted in only a minor terrestrial contribution to human subsistence, which probably included large fruit bats and giant rats (Aplin and Helgen, 2010; Hawkins et al., 2016, 2017).

Here, we report on an archaeological sequence from Laili, a partially collapsed cave, situated in the modern village of Laleia, about 4.3 km from the north coast of Timor-Leste (Fig. 1a). Formed in a limestone outcrop ~86 m above sea level, the cave overlooks the braided plain of the Laleia River about 350 m to the east (Fig. 2a). The local environment consists of open savannah woodlands and grasslands in a broad floodplain valley through which the Laleia River flows. We discuss the implications of this site in relation to early human movement into Sahul, and in light of the broader Wallacean archaeological record, paying particular attention to human adaptations to changing ecological conditions during the Pleistocene. To this end we conducted a range of archaeological and environmental analyses (bathymetric, stable isotope, stone artefact, and zooarchaeological) in order to provide proxies for sea level and climatic changes, unequivocal evidence of human presence in the cave, technological aspects of human behavioural adaptations, evidence of changing human foraging behaviour, and general palaeoecological conditions (marine, mangrove, riverine,

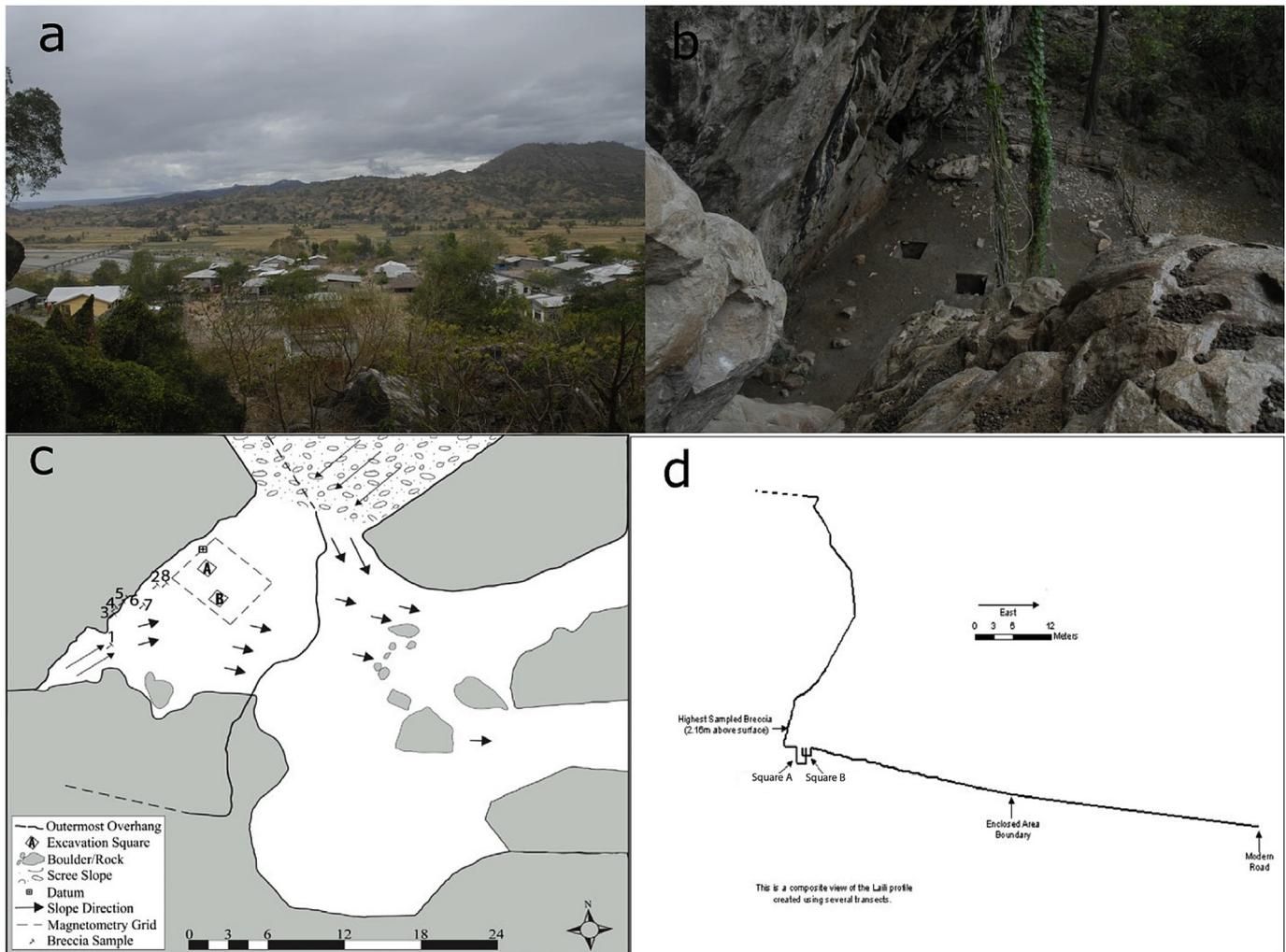


Fig. 2. Laili Cave (a) view facing east towards the Laleia River Basin; (b) excavated squares (c) excavation site plan; (d) profile showing topography.

forest, and grassland), over the course of Late Pleistocene human settlement of Timor.

## 2. Materials and methods

### 2.1. Excavation and radiocarbon dating methods

Two 1 m<sup>2</sup> excavation squares, squares A and B, were excavated in the centre of the cave platform in June and July 2011 (Fig. 2). Excavation was carried out in spits (average = 4.93 cm, range = 2.2–8 cm). Where stratigraphic change was evident, spits followed the stratigraphy. While square A provided a deep and largely undisturbed stratigraphic sequence c. 2.2 m deep (Fig. 3), square B appeared heavily disturbed by burrows and termite nests. Excavation of this square was abandoned at c. 80 cm depth and in view of this disturbance (e.g., O'Connor et al., 2010) square B materials were excluded from diachronic analysis. Each bucket of excavated sediment was weighed before sieving, while rocks recovered *in situ* were weighed separately before being discarded. All excavated sediments were wet screened through 1.5 mm screens. Recovered materials were sorted into general classes (e.g., vertebrate, crustacean, mollusc and stone artefacts) in the field. They were later re-sorted and analysed in the Australian National University (ANU) Archaeological and Natural History departmental

laboratory. Spits 14 and 21 are missing from the analysis. Unfortunately, the sacks containing the dried cultural material from these spits were stolen from the site and only a single marine turtle bone collected from spit 21 can be included. However, since this represents only 5% of the sequence, it is likely this will not affect our analyses and we have not included these spits in our statistical tests. All data (stone artefacts, vertebrates, molluscs, crustaceans) are summarized by spit in Fig. 4 and Table S1. *In situ* marine shell and charcoal were dated at the Australian National University Radiocarbon Dating Centre (Fallon et al., 2010). All dates were calibrated in Oxcal 4.2, using ShCal 13 (Hogg et al., 2013) and Marine13 (Reimer et al., 2013) to 95.4%. Marine shell dates are presented in Table S2 both with ( $59 \pm 31$  calculated from average Northwest Australian coast values obtained from [calib.qub.ac.uk/marine/regioncalc.php](http://calib.qub.ac.uk/marine/regioncalc.php)) and without  $\Delta R$ .

### 2.2. Bathymetric and sea level modelling

Current bathymetric data of Timor's seas, obtained from the General Bathymetric Chart of the Oceans (GEBCO\_14) dataset (Smith and Sandwell, 1997); in combination with data on sea-level fluctuation (Lambeck and Chappell, 2001) and local uplift rates (Cox, 2009), were used to model the changing coastline north of Laili. We produced an estimate of what the northern Timor

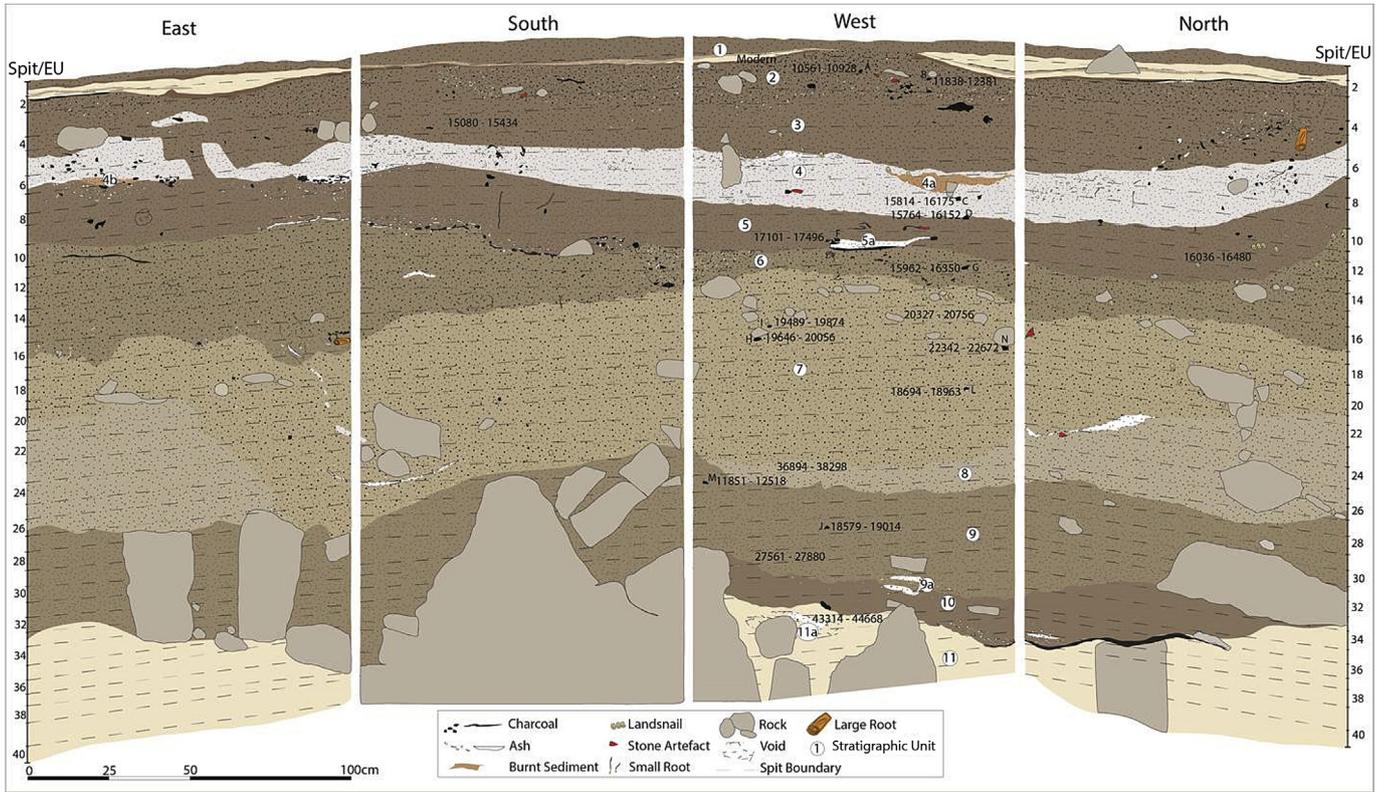


Fig. 3. Laili Cave, square A, chronostratigraphic profile.

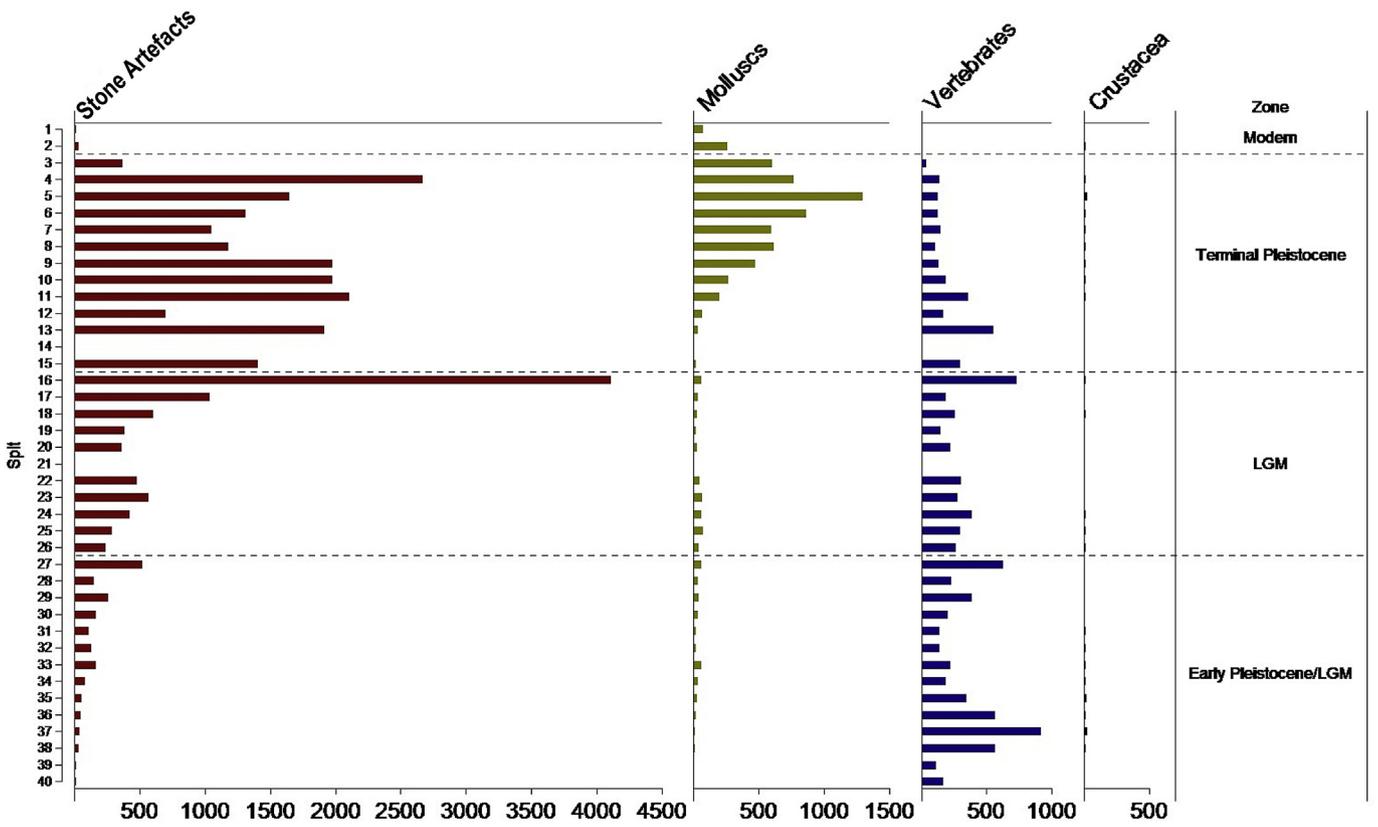


Fig. 4. Stone artefacts, molluscs, vertebrates and crustacean Number of Identified Artefacts/Specimens per spit, square A, Laili Cave.

palaeocoast would have looked like during the earliest period of Pleistocene settlement (c. 44.6 ka), during the height of the Last Glacial Maximum (LGM) (c. 18 ka), as well as at current sea stand. This provided information on the changing distance of Laili from the coast as well as the steepness of access to the marine coastal resource zone (Fig. 5). The model does not consider sedimentation and erosion processes, although the general trends in land shape and slope are clear (e.g., Robles et al., 2015).

### 2.3. Stable isotope analysis

Stable oxygen isotope ratios ( $\delta^{18}\text{O}$ ) in aquatic mollusc shell carbonate are commonly used to estimate palaeoenvironmental conditions (e.g., Colonese et al., 2012; Ingram et al., 1996).  $\delta^{18}\text{O}$  values in mollusc shell are determined by the  $\delta^{18}\text{O}$  values and temperature of surrounding seawater during shell formation (Böhm et al., 2000):

$$T = (20.0 \pm 0.2) - (4.42 \pm 0.10) \times (\delta^{18}\text{O}_s - \delta^{18}\text{O}_w)$$

where T is temperature (in °C) and  $\delta^{18}\text{O}_s$  and  $\delta^{18}\text{O}_w$  are oxygen isotope values for shell and seawater, respectively. As this equation shows, a change in  $\delta^{18}\text{O}_w$  has more than four times the impact on  $\delta^{18}\text{O}_s$  than does an equivalent change in temperature. Due to the preponderance of low  $\delta^{18}\text{O}$  values in ice sheets, marine  $\delta^{18}\text{O}$  values increased by up to 2‰ across the Last Glacial Maximum (Lisiecki and Raymo, 2005). In the tropics, where temperature is relatively stable, this change in  $\delta^{18}\text{O}_w$  is therefore likely to control  $\delta^{18}\text{O}_s$ . We

therefore measured  $\delta^{18}\text{O}_s$  in shell obtained throughout the Laili square A excavation to identify marine changes and corresponding palaeoenvironmental patterns.

Chiton shell was found in almost all excavation spits, so sample selection focused on chiton shells identified to genus (*Acanthopleura* sp.) and in visibly good condition across the inner surface of the shell. Two shells from every third spit and five shells from two spits (5 and 29) were selected to evaluate intra-spit variation. Carbonate in fresh chiton shell is nearly 100% aragonite (Treves et al., 2003), so the presence of calcite carbonate would indicate post-depositional carbonate conversion and possibly diagenesis of  $\delta^{18}\text{O}$  values. Therefore, shells were ultrasonically cleaned and then cut in half, with shell from the face of one half tested for the presence of calcite using Meigen's solution (Suzuki et al., 1993). Seven shells identified as containing calcite (LA12-1, LA12-2, LA29-5, LA31-2, LA33-1, LA36-1, LA36-2) were not included in subsequent analyses. Fifty-five chiton samples passed the aragonite test; for these shells, powdered samples were obtained from along the face of the second, previously un-sampled shell face. These shell samples were sent to the Stable Isotope Facility at the Research School of Earth Sciences, ANU, for Isotope Ratio Mass Spectrometry (IRMS) analysis of carbonate  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ .

Statistical tests were conducted using Statistical Package for the Social Sciences (SPSS) version 22. The data were examined for outliers (greater than 1.5\*Interquartile Range from the median); the three outliers found ( $\delta^{13}\text{C}$  in LA6-2;  $\delta^{18}\text{O}$  in LA1-1, LA2-1) were removed from subsequent analyses. When assessing trends, data from spits with multiple measurements were averaged across the

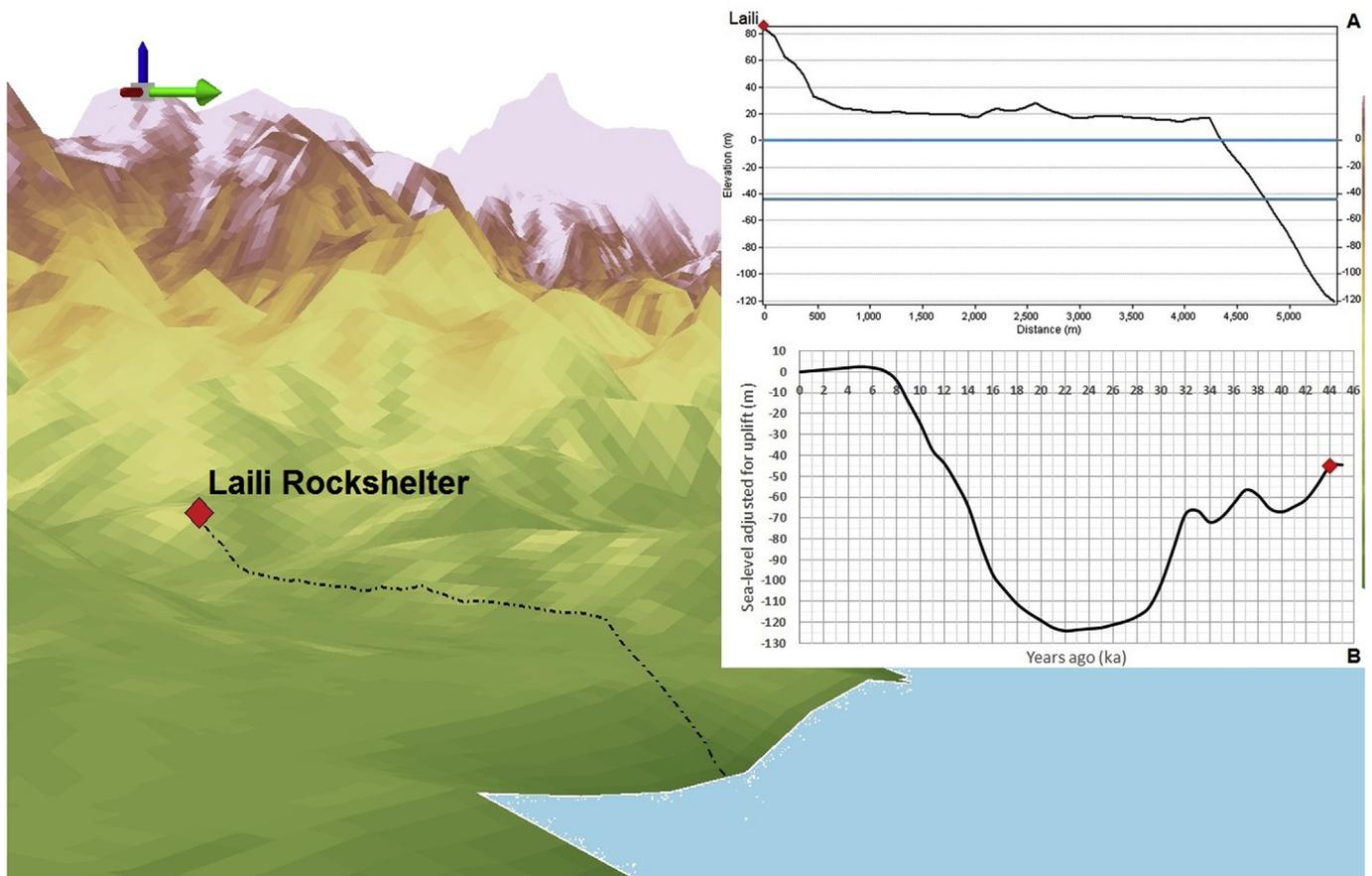


Fig. 5. 3D reconstruction of the topography surrounding Laili Cave showing the river valley and LGM coastline. Graph inset shows the cross-section of the dotted line on the 3D image, with present sea-level (0 m) and 44.5ka (–63 m) sea-levels drawn in bold.

spit and a three-point centred moving average for each element computed.

#### 2.4. Stone artefacts

Analyses of stone artefacts included a count of the total number of artefacts as well as the Minimum Number of Flakes (MNF) (Hiscock, 2002). The MNF equation tallies the number of complete flakes with the greater number of proximal or distal fragments, plus the greater number of left or right longitudinal cone split fragments. The MNF therefore provides a technique of assessing artefact frequency throughout the deposit that excludes heat shatter, and other artefacts such as flaked pieces and medial flake fragments, which may inflate or bias artefact numbers (Hiscock, 2002). Statistical tests used to examine artefact frequencies were conducted using SPSS version 22, and included a Shapiro-Wilk test of normality and Wilcoxon Signed Rank test.

#### 2.5. Fauna

Tetrapod skeletal elements were identified to the lowest taxonomic level possible. Fish and reptile remains were identified by comparison with the ANU Archaeology and Natural History Osteology Laboratory reference collection. In addition, murid skeletal material was identified to taxon by comparison with extinct archaeological and fossil specimens collected from previous ANU expeditions. The identifications were made on maxillae and mandibular tooth rows with and without teeth, as well as loose teeth. Consideration was given to distinctive tooth and tooth row morphology and size. Chiropteran skeletal material was identified by comparison with reference specimens housed at the Australian Museum. Typically, chiropteran cranial and mandibular material can be identified to taxon based on distinctive tooth morphology (Cranbrook, 1966; Hand and Grant-Mackie, 2012). This approach was followed but with the addition of identifying distinctive distal humeri from insectivorous bats following Stimpson (2012). Pteropodids are quite distinctive from insectivorous bats, but their long bones are considered morphologically conservative within the family (Stimpson, 2012). In the absence of teeth these were identified simply as pteropodids. The avifauna material was identified through comparisons with collections housed at the Australian National Wildlife Collection of the Commonwealth Scientific and Industrial Research Organization (CSIRO) National Facilities and Collections, to genus or family when possible, and in some cases species identifications were based on size comparisons with avifauna still extant on Timor.

The vertebrate assemblage was quantified using Number of Identified Specimens (NISP) as NISP typically tracks Minimum Number of Individuals (MINI) closely with respect to measuring relative abundance and avoids issues of aggregation, interdependence, and sample size (Lyman, 2008). The taphonomy of the vertebrate assemblage was assessed by observing bone surface modifications under light magnification ( $\times 10$ ) followed by the use of a binocular microscope (Zeiss Stemi, 2000-C W-PI, 10  $\times$ /23 magnification) for more detail. Bone modifications examined included the distinctive pitting from owl digestion and signs of butchery via cut marks and fracture patterns.

Molluscs were identified using the malacology collections of the Museum and Art Gallery of the Northern Territory (MAGNT) and the ANU Archaeology and Natural History reference collections. Mollusc remains were quantified by recording the Number of Identifiable Specimens (NISP), Minimum Number of Individuals (MNI) and weight of each taxon per spit. The MNI was calculated by selecting the most frequently occurring non-repetitive element for each identified taxon, this element was then recorded consistently

throughout all spits. The NISP has been selected for illustrating species representation at Laili as use of the MNI indicates an absence of molluscs in some spits otherwise recorded as present by other measures (NISP and weight).

Crustacean (subphylum Crustacea) specimens of the Decapoda were identified through comparison with the marine invertebrate collections at the Muséum National d'Histoire Naturelle in Paris, France. Crustaceans have five pairs of legs with terminating chelipeds (pincers) and a calcified exoskeleton. While exoskeleton fragments are only identifiable to subphylum, identification of the mandibles and the cheliped elements to lower taxonomic levels was possible. The pollex and dactyl hand are robust and therefore well preserved and they have distinctive "teeth", characteristics that can be used as a distinguishing morphological criterion.

### 3. Results

#### 3.1. Chronostratigraphic sequence at Laili

Forty spits were excavated to an average depth across square A of c. 220 cm, when large rocks covered most of the square in plan and excavation was discontinued. Nineteen charcoal samples from the deposit, collected during excavation, or from the sections at the completion of the excavation, were subjected to AMS radiocarbon dating (Fig. 3; Table S2). Breccia deposits containing cultural remains such as marine shell and stone artefacts were cemented to the walls of the cave at heights well above the current floor of the deposit. Marine shell samples recovered from these breccia deposits have been dated to between 2000 and 8600 cal BP, demonstrating that the cave was occupied during the Holocene (Table S2) and the Holocene deposits subsequently removed, at least from the area near square A (O'Connor et al., 2016). The square A deposit was divided into eleven stratigraphic units (1–11), based on sedimentary characteristics. The relationships between the stratigraphic units and the excavation spits are shown in Fig. 3. The stratigraphic units are described in the Supplementary Information (SI) with reference to the radiocarbon dates. Three main chronostratigraphic periods were defined on the basis of these units and the radiocarbon dates. The youngest is terminal Pleistocene (stratigraphic units 2–6; spits 3–15) dated between 11,161 and 17,468 cal BP. The second period represents the globally important LGM (stratigraphic unit 7; spits 16–26), and is dated between 18,500 and 22,500 cal BP. The earliest period recovered includes the pre-LGM deposits (stratigraphic units 8–11; spits 27–40), dated to between 27,000 and 44,631 cal BP.

#### 3.2. Modelling of sea level change

Fig. 5 illustrates the sharp drop-off of Timor's northern continental shelf, differences in sea level, and distance from the coast to Laili during human site use. During the time of initial site use the coast was c. 4700 m distant from Laili, that is, about 450 m further than it is today. During this time a sea level lowering of approximately 63 m would have presented a much steeper coastline. During the peak of the LGM c. 18 ka sea levels were significantly lower, approximately 130 m below current levels, representing an even steeper cliff access to the shore, and increasing the distance from Laili to the coast to about 5 km.

#### 3.3. Stable isotope analysis

All submitted shell samples produced valid results (Table S3). Using 19 NBS-19 measurements, the 1- $\sigma$  instrument analysis uncertainty for  $\delta^{13}\text{C}$  is 0.02‰ and for  $\delta^{18}\text{O}$  is 0.07‰. The moving average shows a slight decrease in  $\delta^{18}\text{O}$  with depth, but that is only

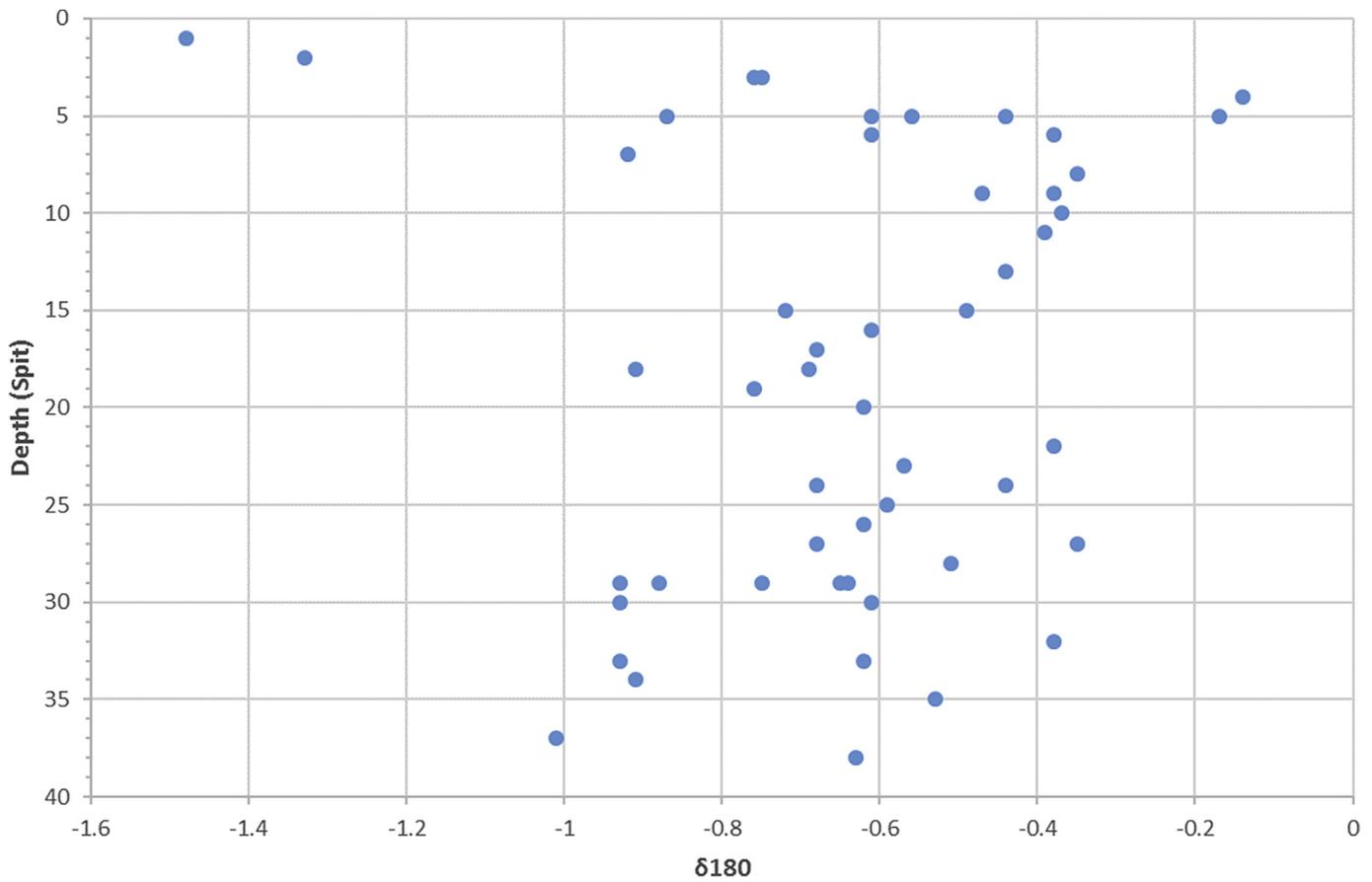


Fig. 6. Laili  $\delta^{18}\text{O}$  stable oxygen isotope values of chiton (*Acanthopleura* sp.) shell samples by depth (spit).

because of two particularly low values for spits 34 and 37 (Fig. 6). There is a significant but very weak correlation between depth and  $\delta^{18}\text{O}$  ( $R = -0.314$ ,  $p = 0.04$ ,  $n = 45$ ). Given the large amount of variability across adjacent spits (and within spits per previous charts),  $\delta^{18}\text{O}$  does not seem to provide a useful environmental signal. Carbon isotopes also display a lot of variability among adjacent spits (and within spits); however, with this stable isotope a more significant pattern emerges (Fig. 7).  $\delta^{13}\text{C}$  averages  $3.8 \pm 0.9\text{‰}$  for spits 38–15, is hypervariable for spits 13, 11 and 10, then settles in around a new average of  $2.5 \pm 1.0\text{‰}$  for spits 9–3. The two groups on either side of the hypervariable region are significantly different ( $p = 0.001$ ,  $df = 20.358$ , equal variance not assumed).

#### 3.4. Stone artefacts

Laili square A produced 28,324 flaked stone artefacts, making this the largest excavated collection of stone artefacts per unit volume from Pleistocene ISEA (Balme and O'Connor, 2014). Artefacts were identified throughout the sequence, with the highest frequencies found between stratigraphic units 2–6 (spits 4–16), and dating from the end of the LGM to the onset of the Holocene (Fig. 4; Table S2). Artefacts continue to the base of the excavation, with two complete flakes recovered from a hearth feature in the basal spit (spit 40), thus precluding the possibility of vertical movement of these from higher deposits. The assemblage is dominated by high quality, locally abundant chert in a variety of colours (Fig. 8). Chert nodules can be found in eroding terraces within 5 km of the cave and most likely makes up a sizable portion

of the Laleia River gravels.

Despite the size of the stone artefact assemblage, square A contains only 42 retouched flakes and 17 flake fragments with evidence for retouch. The few retouched artefacts were only minimally modified (Fig. 8A and B), and none conform to any formal tool morphologies such as those previously described from Timor (e.g., Glover, 1986:171–179), or the nearby island of Flores (Brumm et al., 2006:627, Fig. 4; Brumm and Moore, 2012:38). Flakes were used without extensive efforts to extend their use life with retouch. Additionally, 28 flakes were observed to have edge damage likely produced from use wear, including two with marginal gloss. The assemblage included 128 cores, some of which are radial cores, as well as a range of truncated faceted flakes (Fig. 8C and D), similar to artefacts identified from the coastal shelter Jerimalai (Marwick et al., 2016), as well as Mata Menge in Flores (Brumm et al., 2006:626, Fig. 3; Marwick et al., 2016).

Notably, the assemblage has a high frequency of heat shattered flakes and cores displaying features such as crenulations, crazing, and pot-lids (Fig. 8A, B, C). A total of 6472 heat shattered pieces (23.8% of total assemblage) and 2236 pot lids (7.9% of total assemblage) were identified in the assemblage. The heat-shattered material derives from the same high-quality chert and no change in the frequency of heat shattered pieces was seen throughout the sequence. The minimum number of flakes (MNF) is significantly correlated with the count of the total number of artefacts (TNA) which included the heat shattered pieces and pot lids ( $W = 0.827$ ,  $p = <0.001$ ;  $Z = -5.737$ ,  $p = 0.001$ ). This indicates that the trends in artefact abundance are related to occupation and discard rather than heat-shatter related fragmentation.

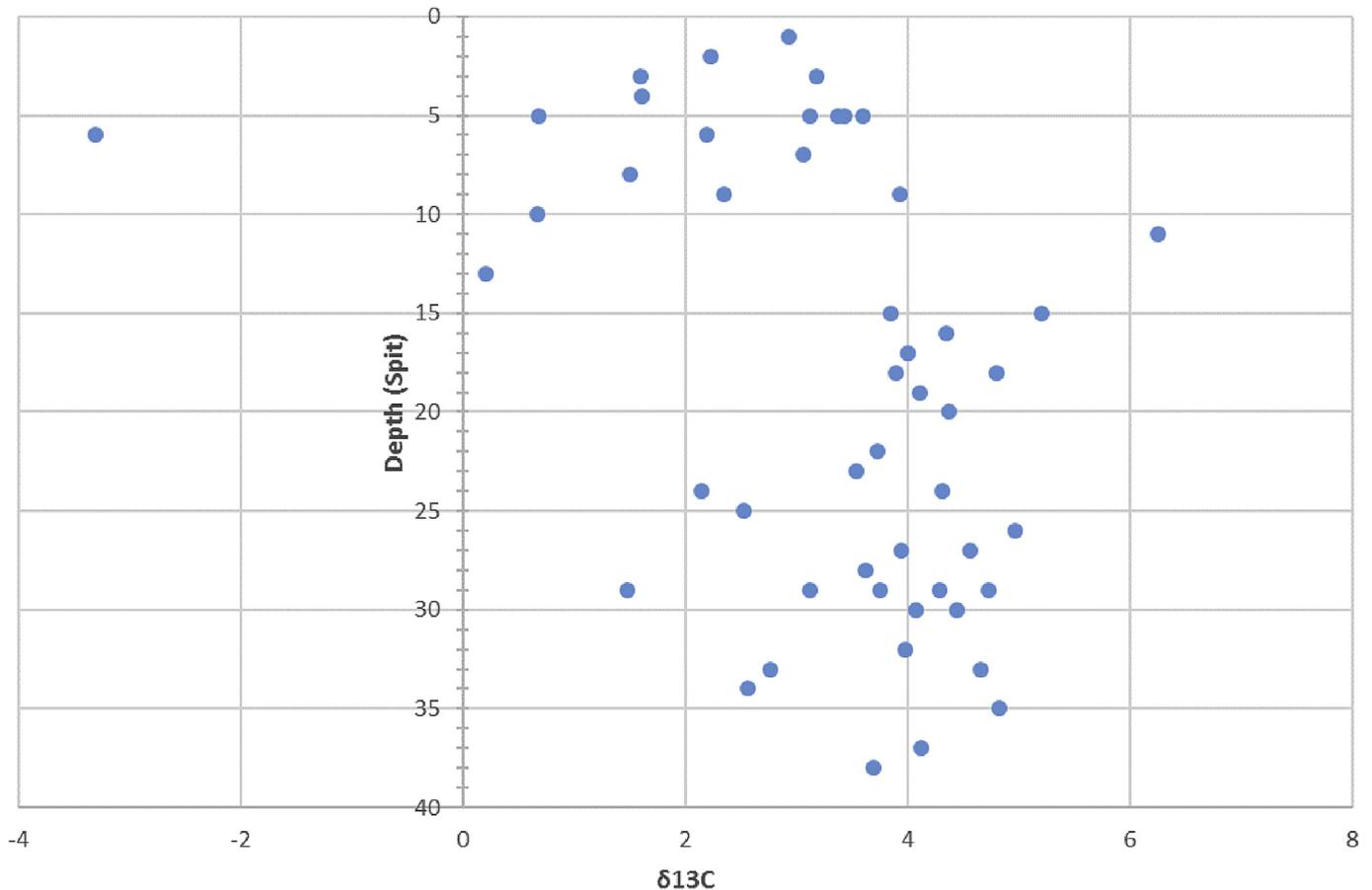


Fig. 7. Laili  $\delta^{13}\text{C}$  stable carbon isotope values of chiton (*Acanthopleura* sp.) shell samples by depth (spit).

### 3.5. Faunal remains

#### 3.5.1. Vertebrates

Vertebrate NISP (square A total NISP = 10,016) are most abundant during the early history of site use and appears to decline over time (Fig. 9; Tables S4–S5). At least sixteen distinct mammal taxa were identified, including human (*Homo sapiens*), juvenile dog (*Canis familiaris*), four extinct small rat species (Muridae; *Komodomyx* small, *Komodomyx* large, *Melomys* small, *Melomys* large), four extinct giant rats (Muridae; Glover's (1986) Genus A, B, and C; *Coryphomys* sp.), at least one fruit bat (Pteropodidae), and at least six insectivorous bat taxa (Vespertilionidae, *Taphozous*, *Rhinolophus* small, *Rhinolophus* large, *Hipposideros*, cf. *Chaerephon*). Seven bird taxa were identified (*Coturnix* cf. *ypsilophora*, *Turnix maculosus*, Passeriformes 1, 2, 3, *Ducula* sp., and cf. Anatidae). A least one species of frog/toad (*Anura*) was identified. Four reptile taxa were represented by small lizard (Lacertilia), sea turtle (Chelonioidae), freshwater turtle (Testudines) and snake (Serpentes). Finally, Osteichthyes were represented by two taxa, freshwater eels (Anguillidae) and parrotfishes (Scaridae) in small quantities.

#### 3.5.2. Mammalia

Mammal vertebrate remains are the most abundant class of fauna identified at Laili (square A total NISP = 4980). Four species of small murid and four species of giant murid were identified based on size and maxillary and mandibular tooth morphology. Small murids dominate the vertebrate assemblage through time (square A total small murid NISP = 4522), and the most common taxa identified were small *Komodomyx* sp. that are found throughout the

sequence. The other three small murid taxa were only present in very small numbers, with large *Komodomyx* present in the early part of the sequence (in spit 40), and small and large species of *Melomys* present in small numbers sporadically. The smaller of the *Melomys* first appears in spit 39 and up to spit 8, while the larger species first appears in spit 40 and up to spit 6. Several species of giant rat were present between spits 4–38, but in much smaller numbers (NISP = 220). Species descriptions will be provided in a future publication.

Small numbers of chiropteran bones are present in the assemblage including at least one fruit bat species and at least six insectivorous taxa. Pteropodidae appear in the sequence relatively late: during the terminal Pleistocene period and between spits 4–10. Insectivorous microbats are present in very small numbers during the earlier part of the sequence, but increase in diversity and abundance post-LGM. The six insectivorous bat taxa identified include Vespertilionidae (vesper bat), *Taphozous* sp. (tomb bat), small *Rhinolophus* (horseshoe bat), large *Rhinolophus*, *Hipposideros* sp. (roundleaf bat), and cf. *Chaerephon* sp. (free-tailed bat).

Two juvenile dog teeth (*Canis familiaris*), a mandibular canine and right deciduous fourth premolar (dp4), were recovered from spit 28, the pre-LGM period of human occupation. They were bagged separately in the field and looked fresh and uncoloured compared to other animal bones from the same level (which appeared dark brown, black, and white/grey and often encrusted with a carbonate coating). The likelihood that these teeth were intrusive in the pit during the excavation was tested by directly dating the canine. This was done at the ANU radiocarbon dating lab (Fallon et al., 2010), and returned modern collagen and carbon

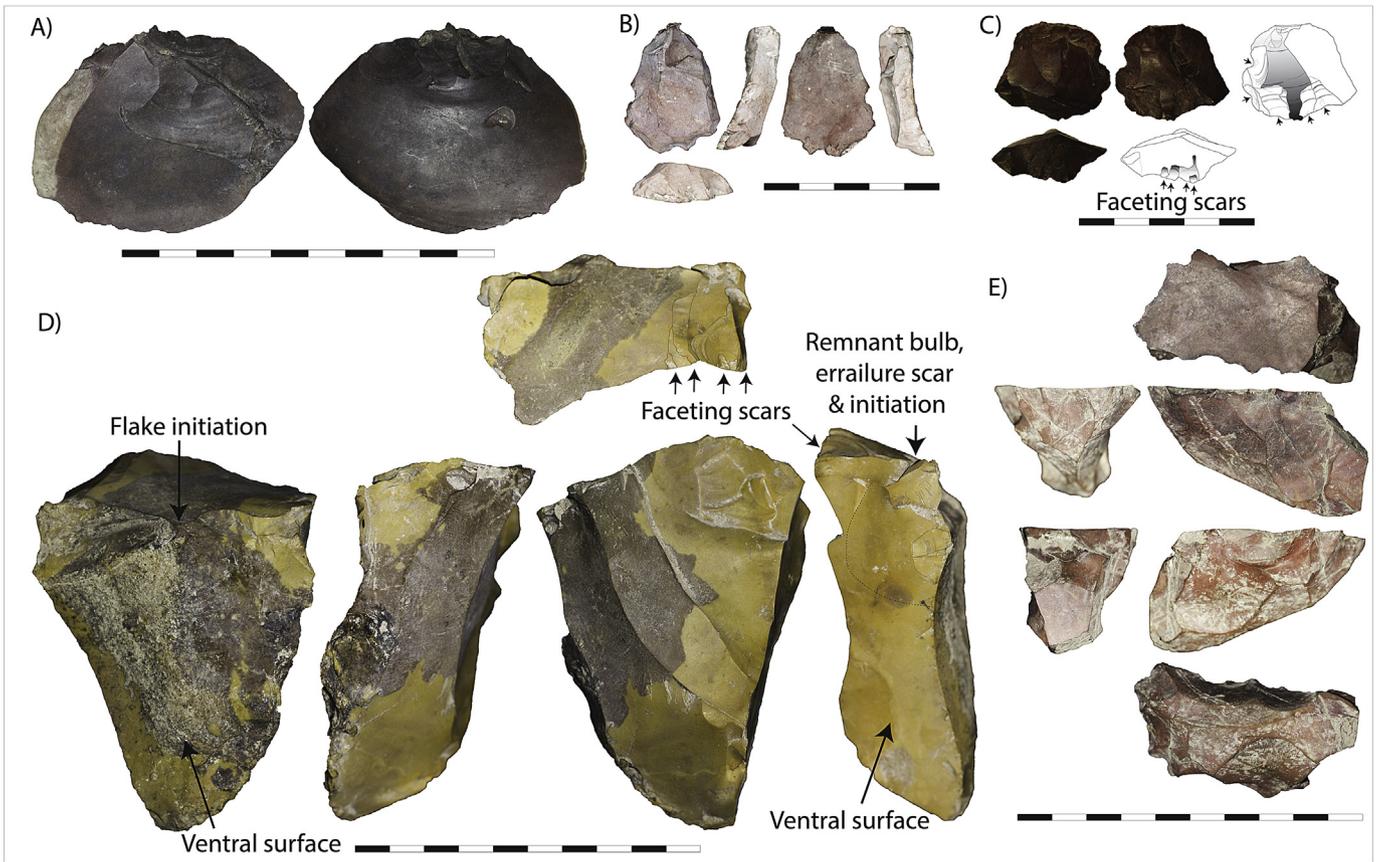


Fig. 8. Stone artefacts recovered from Laili; (A) Chert flake with marginal edge damage, gloss, and ventral pot lid scar; (B) Chert retouched flake with dorsal pot lid scar; (C) Chert truncated faceted flake, showing negative scars removing parts of ventral surface and faceting close to their initiations on the opposite surface; (D) Chert retouched flake, with multiple negative scars across a remnant ventral flake surface, with platform faceting; (E) Chert core.

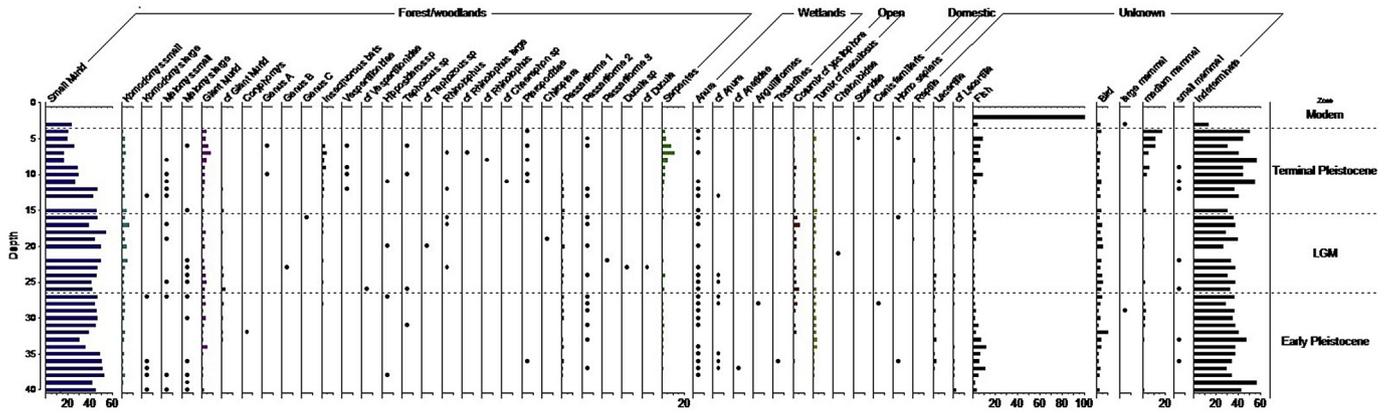


Fig. 9. Laili Cave vertebrate taxonomic relative abundance (%NISP) by spit and palaeohabitat.

values and a modern age (S-ANU 42629). These teeth are therefore not considered further.

Small fragments of human ribs and phalanges were recovered from all three chronostratigraphic periods. This is not unusual for the region, where fragmentary human material is often recovered from cave and rockshelter deposits (e.g., Hawkins et al., 2017; Samper Carro et al., 2016).

### 3.5.3. Herpetofauna

The herpetofauna at Laili cave includes both reptiles (square A

total NISP = 257) and amphibians (square A total NISP = 93). Amphibious frog/toad bones (Anura) were consistently present in small numbers throughout the Laili sequence, and may reflect wetlands, arboreal forest, or savannah woodland environments. For the reptiles, snake bones were present in small numbers and increased in abundance during the terminal Pleistocene period (Fig. 9). Today eight species of snakes from four families [Colubridae, Typhopidae, Viperidae (*Cryptelytrops insularis*), and Pythonidae (*Liasis mackloti*)] are present on Timor. Snake bones recovered included mandibles, maxillae, proximal ribs, and

vertebra most of which appear too small to be pythons and are therefore likely to be one of the other three families. A consistent but low abundance of small lizard (Lacertilia) bones were present throughout the sequence, and these are likely to be from one of the many skink or gecko species present on Timor today.

Turtle bones are rare and include the shaft of a large sea turtle (Chelonioidae) pectoral acromion process from spit 21. A small freshwater turtle distal ulna fragment from spit 36 was identified to the order Testudines. Two freshwater turtle species occur in Timor today. *Chelodina timorensis* (Timor snake-necked turtle) is restricted to Lake Ira Lalaro in the far east of Timor-Leste, and its status as a species separate from *Chelodina mccordi* on Roti Island is controversial (Kuchling et al., 2007). The other is *Mauremys reevesii* (Chinese pond turtle) (Kaiser et al., 2011); its biogeographic range of China, Japan, Korea, and Taiwan suggests that it has recently been introduced to the island.

### 3.5.4. Avifauna

Avifauna vertebrate remains (square A total NISP = 730) were present throughout the Laili sequence. The dominant taxa were two open grassland or wetland bird species, the brown quail *Coturnix cf. ypsilophora* and the red-backed buttonquail *Turnix maculosus*. These two taxa were present between spits 4–38. In addition, three unidentified species of songbird (Passeriformes), usually forest or woodland species, were identified. Passeriforme 1 was the smallest and most abundant, followed by the medium-sized Passeriforme 2, also moderately abundant in the assemblage. The smaller, most abundant passerine was consistently present between spit 10 to 38, while Passeriforme 2 of medium size was present between spits 5 and 37. A single specimen from spit 22 represented Passeriforme 3, the largest taxon. A single small wetlands duck was tentatively identified to the family level, and is likely to be one of the six species of duck that reside on, or visit, Timor today, the smallest of which is the vagrant garganey *Anas querquedula* (Trainor et al., 2008). Imperial pigeon, a predominately forest family with two extant species (*Ducula cineracea* and *Ducula rosacea*) on Timor today (Trainor et al., 2008), was represented by two refitted specimens of a left coracoid from spit 23 associated with the LGM.

### 3.5.5. Osteichthyes

Small numbers of mostly unidentified Osteichthyes vertebrae, spines, ribs, and cranial fragments are present in the assemblage. They are mostly found in the earlier and end Pleistocene chronostratigraphic periods, and show a sharp decline during the LGM (square A total NISP = 337). Identified taxa, both represented by single specimens, include freshwater eel (Anguillidae) (spit 28) and marine parrotfishes (Scaridae) (spit 5).

### 3.5.6. Vertebrate taphonomy

The taphonomic assessment is ongoing but current data indicates that the range of microfauna was likely deposited by owls, based on distinctive pitting on many small avian skeletal elements (Hawkins et al., in press). Other fauna with digestion observed include small murids, frogs, lizards, insectivorous bats, and snakes. Discoloration including black, white and grey/blue marks, often associated with burning, were observed on some bones with digestion evidence, suggesting that such discoloration is not a reliable measure of human consumption and may instead be a result of chemical weathering processes, or inadvertent burning from human cooking events post-deposition. No cut marks or other obvious anthropogenic alterations were observed on any of the faunal remains.

### 3.5.7. Molluscs

Shellfish data are summarised in Fig. 10 (Tables S6–8). Shellfish occur from the surface to spit 38 (square A, total NISP = 6686; MNI = 1369; weight = 4150.8 g). At least 41 species of mollusc were identified from a range of habitats including marine, mudflat/mangrove and freshwater environments. Mangrove swamp and mudflat dwelling species dominate in the upper levels of Laili from spits 1–9 (dating between c. 11 and 15 ka). The dominant mangrove/mudflat-associated genus is *Terebralia* (NISP 3496, weight 1573.22 g) with smaller contributions made by the species *Telescopium telescopium*, *Geloina (Polymesoda) oviformis* and *Austriella cf. corrugata*. Mangrove-associated species continue to contribute between 27.8% and 50.9% of the mollusc assemblage between spit 9 and spit 11 (c. 15 to 16.5 ka). Mangrove-associated shellfish decline dramatically below spit 11, where they are poorly represented or entirely absent to the base of the site.

Shellfish from fresh water to brackish habitats are abundant in the assemblage between spit 4 and spit 13. The main fresh water genus exploited throughout is *Stenomelania* (square A, total NISP = 1770; MNI = 986; weight = 1093.33 g) with small contributions from *Tarebia granifera* and a freshwater Neritid, *Septaria cf. luzonica*. All freshwater species were likely gathered from the nearby Laleia River. Little or no exploitation of freshwater habitats is apparent between spits 17 and 20, where evidence for the exploitation of molluscs declines overall, suggesting a significant change in local hydrological conditions during the LGM.

Marine taxa dominate the Laili assemblage from spit 17 to 38 (NISP = 474; MNI = 156; weight = 315.43 g), and constitute the only habitat exploited in spits 19, 30, 37 and 38. The marine habitats exploited appear to be mainly open rocky coastal environments. Turbinidae and Chitonidae dominate overwhelmingly, representing 23.1% and 52.02% of the exploited marine molluscs at Laili respectively. Contributions are made by four species within the Neritidae family, with small amounts of the Trochidae, Haliotidae, and Cardiidae. Sandy marine beach taxa such as *Tegillarca (Anadara) granosa*, *Periglypta* sp. and *Strombus* sp. occur, but are rare. Deep ocean shellfish are represented by two occurrences of small fragments of *Nautilus* sp. This species is likely a post-mortem collection from the shoreline for decorative uses (e.g., Langley et al., 2016).

### 3.5.8. Crustaceans

Crustacean cheliped (NISP = 83) of the Decapoda were largely identified to family (Fig. 4; Table S9). Our analysis enabled the identification of at least three families of “true” crabs, derived from marine, mangrove, brackish, freshwater, and terrestrial environments. Strictly marine crustacean taxa identified from square A were Raninidae (cf. *Ranina*) and a lobster (Enoplometopidae), taxa living in coral reefs (Carpenter and Hiem, 1998). These single specimens were both identified from spit 16, at the end of the LGM. Several mud or mangrove crabs, common in estuaries but sometimes found in brackish to marine environments, were identified. These include remains of the Portunidae (about 12%). In this family, we identified *Scylla*. Individuals belonging to this genus are generally large crabs whose shells average widths of 20 cm (Motoh and Kuronuma, 1980). We also recorded the presence of specimens belonging to the infra-order Anomura, including the superfamily Paguroidea (about 7%), which includes coconut crabs and hermit crabs. They are mostly swimmers, but some species live in moist terrestrial environments. The most abundant crustacean in the assemblage, Gecarcinidae, accounts for nearly 46% of the assemblage. Gecarcinidae are large land crabs that are highly appreciated for their flesh today. They live in coastal areas and return to the sea to lay their eggs, but spend the day in burrows coming out only at night (Carpenter and Hiem, 1998; Guinot, 1966). Within this family,

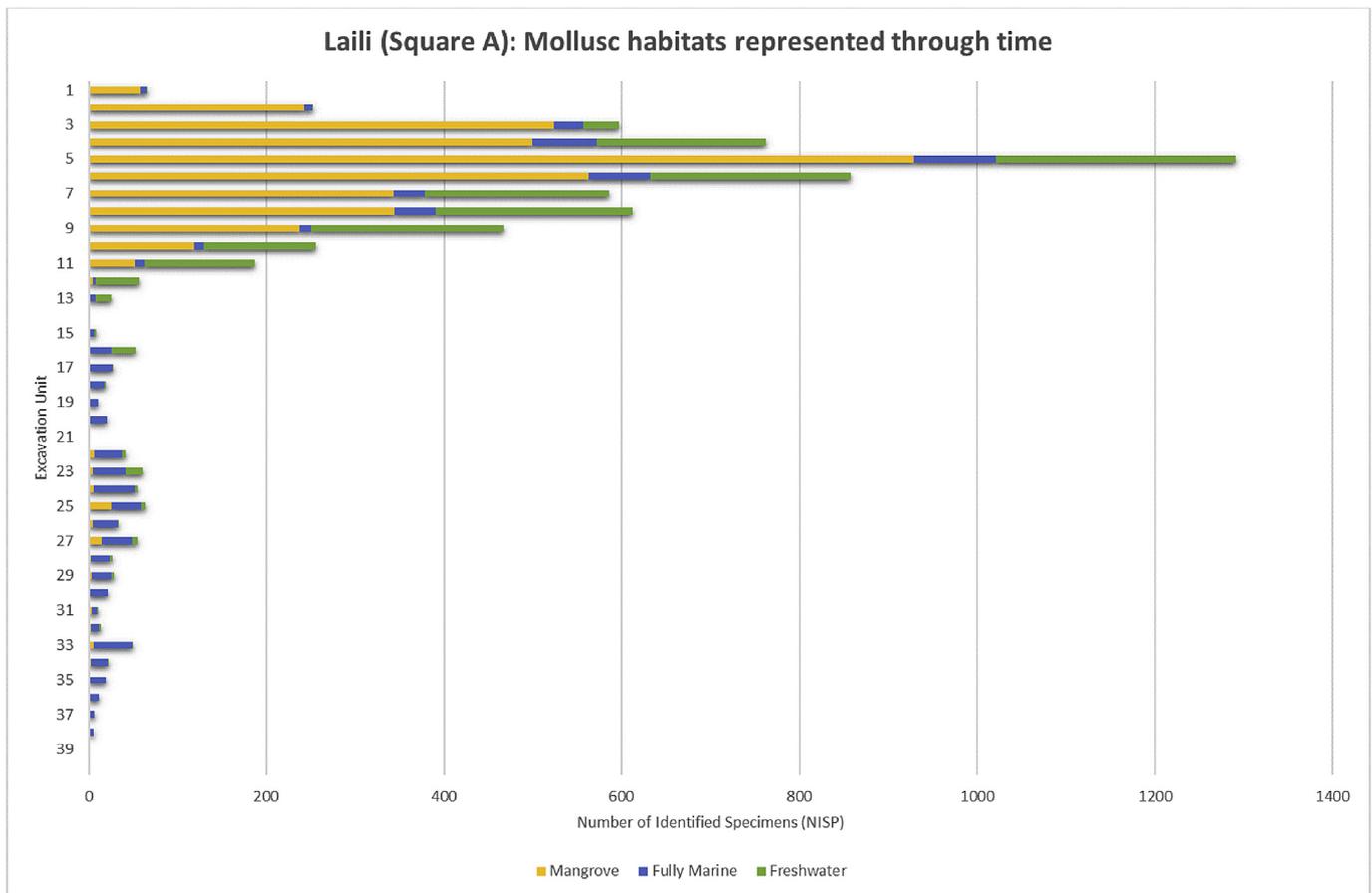


Fig. 10. Laili Cave mollusc NISP by habitat and spit.

we noted the presence of the species *Cardisoma carnifex* and the genus Gecarcoidea. In lesser quantities, Grapsidae (9% of NISP) was also represented and more specifically *Grapsus* sp. *Cardisoma carnifex* is found in mangroves, while Grapsidae live in brackish water and coastal areas.

#### 4. Discussion

The quantified data by chronostratigraphic period at Laili shows some clear long-term trends in site use, palaeoecology, and foraging behaviour. The 11 stratigraphic units of the Laili sequence were grouped into three broad phases corresponding with changing climatic conditions and markedly different sea level stands: an early human settlement phase (spits 40–27), a LGM phase (spits 26–16), and a post-LGM phase, including the Terminal Pleistocene to Holocene transition (spits 15–3). These fluctuations had a significant impact on the size and shape of islands throughout the region (e.g., Kealy et al., 2015; 2017), thereby changing landscapes in terms of distances and elevation to coastal foraging zones. These varying conditions are likely to have influenced the proximity and distribution of local faunal communities and thus human foraging behaviour. We argue below that such changes may be reflected in the local palaeoenvironmental records as well as fauna recovered from the site.

##### 4.1. Palaeoecological reconstruction

The coastline adjacent to Laili varied considerably during the Pleistocene. In the early human settlement phase the average sea

level was 63 m lower than it is today. During the LGM sea levels dropped to about 130 m lower compared to modern levels, then steadily increased again into the Holocene. The steepness of the northern Timor-Leste offshore profile means that distance from the cave to the sea did not change dramatically, c. 4.3 km today to 5 km during the height of the LGM at c. 18 ka. However, the elevation of the cave during initial settlement (c. 44.6 ka), and even more so during the LGM, was considerably greater than today, bringing the site closer to the montane forest zone during periods that were also cooler and drier. For people using Laili during the LGM distances between the cave and the coast increased, the coastline became steeper and less easy to access, and the distance between the shoreline and the edge of the continental shelf (and thus the pelagic zone) decreased.

The oxygen isotope records were surprisingly uninformative with regards to palaeoenvironmental trends in the region. Specifically, given that temperature was relatively stable in the tropics during the late Pleistocene and that  $\delta^{18}\text{O}$  in shell is approximately four times as sensitive to  $\delta^{18}\text{O}$  changes in the water as to temperature changes (Böhm et al., 2000), we expected a pattern of decreasing  $\delta^{18}\text{O}$  from the LGM to the terminal Pleistocene. However, little pattern emerged from the data, with the increase in  $\delta^{18}\text{O}$  observed through time only just on the threshold of significance and with a large amount of variability within and among spits. It is likely that microenvironmental processes (perhaps local rainfall or slopewash patterns) were more important to  $\delta^{18}\text{O}$  in these shells than trends in the overall environment. On the other hand, carbon isotope data do show convincing change over time; however, while statistically significant, the magnitude of change recorded is not

large (averaging 1.3‰). Unfortunately, unlike oxygen, the processes involved in carbon uptake are highly variable:  $\delta^{13}\text{C}$  in shell depends on chiton behaviour, oceanic carbon upwelling, and carbon detritus or slope-wash. As there are no obvious reasons chiton behaviour would change over the small evolutionary timescales represented at Laili, the first of these appears unlikely to apply to our data. While it has been demonstrated that oceanic carbon upwelling can change over time (e.g., Franke et al., 2008; Ingram, 1998), given the steep offshore drop-offs in the area it is likely that, proximal to Laili, oceanic upwelling would not have changed much. The magnitude of change is unlikely to reflect a major onshore vegetation replacement of C4 plants by C3 plants; but it may represent a mostly C3 environment which develops a slightly more closed canopy through time, thereby decreasing  $\delta^{13}\text{C}$  ratios in the slope-wash. The decrease in  $\delta^{13}\text{C}$  ratios might also be related to the slight increase in  $\delta^{18}\text{O}$ , with increased hydrological flow in the river allowing transportation of detrital matter from further upstream, thus sampling a greater diversity of environments. Overall, the palaeoenvironmental signal, while difficult to interpret, hints at a degree of vegetation stasis but hydrological variability in the face of changing sea levels.

The fauna has perhaps proven more informative as to what palaeoenvironments were like during the Pleistocene. They indicate a heterogeneous landscape including marine, mangrove, riverine, grassland, and forested habitats were present in the vicinity of the cave. Both the invertebrate and fish remains at Laili represent riverine environments as well as marine and estuary. The birds are all represented by extant taxa (Trainor et al., 2007, 2008) and indicate a local environment dominated by grasslands and woodland habitats, with a minor forest and wetlands component. Six insectivorous bat taxa, and at least one fruit bat taxa (out of twenty-two native species of bat present on Timor today; Goodwin, 1979), also suggests various degrees of forest cover in the surrounding region. For instance, *Rhinolophus* and possibly *Hipposideros* species are indicative of some closed canopy forests within foraging distance from Laili, vespertilionids and some *Hipposideros* species indicate semi-closed canopies, while *Taphozous* and *Chaerephon* species prefer open spaces above forested canopies at distances from the roost site (McKenzie et al., 1995; Stimpson, 2012). Finally, previous studies have revealed that a once relatively diverse murid rodent fauna existed on Timor (Aplin and Helgen, 2010; Glover, 1986). This study extends the knowledge of large murid diversity back to at least 44 ka, and suggests the presence of forested habitats.

The lack of significant changes in murid presence through the Laili sequence suggests that Pleistocene human activities had little impact on Timor's murids either as a result of hunting pressure or habitat clearance. Today all these murid taxa except one, *Rattus timorensis*, is extinct, probably due to severe forest clearance in the late Holocene (Aplin and Helgen, 2010). Today Timor hosts several recently introduced commensal rat species, particularly *Rattus rattus* and *Rattus exulans*, species that thrive in disturbed habitats. No commensal rat species were recovered from Laili, suggesting their introduction by people occurred sometime during the Holocene.

#### 4.2. Site use and technological innovation

The relative stasis in local habitats perhaps explains why the stone technology at Laili, like that described from most other pre-Neolithic assemblages in Wallacea, is characterised by minimal technological diversity, and a low frequency of retouched artefacts. Technological activity at Laili appears to have been singularly focused on the procurement and reduction of stone. Compared to other Pleistocene sites in Sunda, Wallacea or Sahul (Brumm and

Moore, 2012; Glover, 1986; Marwick et al., 2016), however, stone artefact numbers at Laili are significantly higher (per unit volume of sediment excavated). This is likely due to the ready availability of high quality chert, reducing the need to conserve raw material or prolong artefact use life. Simple sharp flakes could be utilised as is, or retouched opportunistically as the need arose. We have shown some artefacts were made following a similar reduction sequence to the Levallois-like cores and truncated faceted flakes found at Jerimalai (Marwick et al., 2016) as well as Mata Menge in Flores (Brumm et al., 2006: 626, Fig. 3; Marwick et al., 2016). Given the identification of this unique reduction sequence on both Timor and Flores (according to Marwick et al., 2016), it seems plausible that technological innovations which emphasised efficient use of raw material to produce abundant suitable sharp flakes as tools would benefit the colonizers of novel environments. Site use, as reflected in stone artefact discard, dramatically increased towards the close of the LGM and terminal Pleistocene, likely indicating population increase and/or an increase in settlement intensity at Laili, coinciding with sea level rise and hydrological output.

#### 4.3. Human Pleistocene foraging adaptations

The Laili data supports previous research which suggested that the prehistoric terrestrial fauna of Timor was already impoverished upon early human arrival (Louys et al., 2016; O'Connor and Aplin, 2007; O'Connor et al., 2011), especially when compared to Java (Morwood et al., 2008), the Aru Islands (O'Connor and Aplin, 2007) and New Guinea (Field et al., 2008; Mountain, 1993). It also contrasts markedly with hypothesised archaic hominin subsistence on Flores (van den Bergh et al., 2009) or on the largest Wallacean island of Sulawesi where a range of extinct proboscideans, and extant endemic pigs, monkeys, and bovids dominate Pleistocene deposits (van den Bergh et al., 2016). While fossils of pygmy stegodons, a giant tortoise and a large komodo dragon-like lizard have been found in Timor (Hooijer, 1969), their overlap with human settlement is considered unlikely (Louys et al., 2016; O'Connor and Aplin, 2007). These extinct fauna have never been found in any of the archaeological caves or shelters thus far excavated in Timor and it is thought that they likely became extinct prior to the arrival of modern humans on this island (Louys et al., 2016). Fauna associated with the oldest dates recovered from Laili do not contradict this hypothesis.

Taxonomic representation at Laili is characterised by changing foci of local faunal resources. While no direct evidence of faunal consumption at Laili was observed, nevertheless the use of fauna by people can be reasonably inferred. These inferences are based on the most likely sources of faunal remains in the cave: namely humans or owls (with small bats likely troglaphiles). While regionally, microfauna including small birds and small murids show direct evidence (digestion marks) of owl predation, faunal remains of a body size larger than regularly taken by owls, and lacking owl digestion marks, are likely to have been human prey species (Hawkins et al., 2017; Hawkins et al., in press). At Tron Bon Lei on Alor in eastern Indonesia these included marine fishes, giant rats, large fruit bats, and marine turtles (Hawkins et al., 2017). At Laili the medium-sized birds (imperial pigeon, duck), large fruit bats and turtles (marine and freshwater) are likely to result from the subsistence activities of Pleistocene hunter gatherers.

Small freshwater fish remains have been identified as barn owl prey in some North American archaeological sites adjacent to lakes (Broughton et al., 2006) and Buffy fish-owls (*Ketupa ketupu*) native to the region have been observed to prey on small crabs and freshwater fish (BirdLife International, 2016), so the possibility that avian predation accounts for the presence of these fauna cannot be ruled out. However, we note that fish-owls rarely roost in caves and

rock-shelters, preferring trees and have yet to be recorded on Timor (Trainor et al., 2008), no digestion patterns were found on any of the fish bones from Laili, and no evidence for fish predation has been observed for a modern owl roost deposit in the nearby island of Alor (Hawkins et al., 2017). The two species of owls present on Timor today (barn owl, southern boobook) have not been known to hunt fish and crabs (Trainor et al., 2008). We therefore consider avian predation of these fauna unlikely. Fish remains, however, make only a modest contribution to the Laili faunal assemblage, and only two families could be positively identified (parrotfishes and freshwater eel). Species in the parrotfish family are common nearshore herbivorous fish in tropical reef systems throughout the Indo-Pacific region (Randall, 1998). This indicates that some reef platform was present near the north coast of Laili despite the steep coastline. There are just three freshwater eel species found in Timor waters today (Fishbase, 2016), which spend most of their time in freshwater streams and rivers, moving to sea to breed and spawn, while the young spend their time at sea or in river mouths (Jacoby et al., 2014). Prehistoric hunter-gatherers are likely to have caught these with traps, nets, or spears, although eels could also take a baited hook (Ono, 2010).

With regards to bats, these are still hunted in the region today using projectiles, sticks or nets (Glover, 1986), and during excavation at Laili Cave young boys were observed hunting insectivorous bats and small fruit bats with sling shots. Most Timorese fruit bat species roost in trees, preferably in lowland to highland forests, although two species, the cave nectar bat and the western naked-backed fruit bat, are both equally adept at roosting in forest and cave environments (Goodwin, 1979). Since large fruit bat specimen identifications are not precise enough given the skeletal material available, these may also represent troglodiles.

Molluscs and the larger crustaceans were also almost certainly gathered and consumed by humans at Laili. Mollusc gathering appears to have been a significant foraging activity during the Pleistocene, representing mobile foraging between three general zones, marine, estuarine and freshwater. Harvesting of mangrove and terrestrial mollusc resources intensified during the post-LGM compared to earlier periods. This is likely tied to the changes in site use and sea level; mangrove and freshwater species would have been most accessible during the post-LGM period, as warmer wetter conditions expanded riverine habitats and rising sea levels reduced the steep decline to the coastline creating estuarine swamps, and improved foraging opportunities. Such a strategy is flagged as important to early modern humans at other sites in the region, where brackish-water mollusc foraging appears more dominant during periods of sea level rise (Szabó and Amesbury, 2011). Significantly, *Terebralia* is the dominant genus in the Holocene breccia, the only remains of the early to late Holocene deposit, and well-developed mangrove swamps are found today near the junction of the coast and the Laleia River c. 4.3 km northeast of the cave. The decline of freshwater species between spits 17 and 20 correlates with the height of the LGM between about 18,000 and 21,000 years ago, and likely reflects the sharp drop in precipitation associated with this phase. This would have resulted in decreased water flow in the Laleia River and loss or diminishment of freshwater habitats. *Stenomelania* sp. reappears from spit 22 to the base of the site where it makes a small contribution to the molluscan diet. Crustaceans were mostly represented by terrestrial specimens, with some marine specimens present. These were probably collected by trap and bait but could also have been hand caught (Guinot, 1966).

The Laili faunal record contrasts with other Pleistocene coastal settlements on Timor-Leste, which clearly had a more pronounced marine subsistence strategy judging by the focus on fish, sea turtle and marine shellfish (Glover, 1986; O'Connor and Aplin, 2007;

O'Connor et al., 2011). While Laili is currently only 4.3 km from the coast, fauna represented at the site have more in common with the inland sites Uai Bobo 2 (100 km inland c. 16,000 cal BP; Glover, 1986) and Matja Kuru 2 (10 km inland c. 35,000 cal BP; O'Connor et al., 2014; Veth et al., 2005). There, faunal assemblages have a larger terrestrial component containing an array of small to giant murids, small bats, and in the case of Matja Kuru 2 freshwater turtles (O'Connor and Aplin, 2007).

## 5. Conclusions

Data from Laili Cave indicates that Timor was first settled by at least 43,283–44,631 cal BP, earlier than the other early Pleistocene sites known in Wallacea (O'Connor et al., 2010; O'Connor et al., 2011), but it is still some way short of the earliest dated human occupation in northern Sahul c. 50–60 ka (Clarkson et al., 2015). It should be noted, however, that stone artefacts continued to the base of the excavation in spit 40 and so the earliest date at Laili, recovered from spit 35, does not necessarily represent the earliest occupation of the cave, or the island. It is also worth noting that all sites in Timor-Leste have thus far only been dated using the radiocarbon technique. The application of optically stimulated luminescence dating of sediments (the technique used to date the sites in Sahul which have produced the earliest ages), to the basal levels of the Timor sites may yet produce older ages.

The presence of high quality chert in the terraces and gravel beds of the Laleia River, coupled with the availability of freshwater, likely made the cave a focal point for habitation. Judging from the stone artefact record the earliest occupation at Laili cave was sporadic and non-intensive. Overall, however, artefact numbers were high but few artefacts show any evidence of retouch, and the technology changed little throughout the sequence, raising the question of what function the stone artefacts may have fulfilled. The lack of large fauna on the island would seem to exclude the need for stone tools for butchery or skin processing. Manufacture and maintenance of tools made of perishable materials seems likely, however, no adzing or scraping retouch is evident in the assemblage and only a few flakes show evidence of edge gloss that might be due to the repeated working of silica rich plant materials such as rattan. Perhaps the ready supply of chert led to profligate reduction and discard of unretouched sharp flakes which may have been used for a variety of tasks but did not sustain edge damage as they were not curated or reused.

The faunal remains suggest that a heterogeneous environment consisting of marine, mangrove, freshwater, grasslands, and forest habitats existed during the Pleistocene. The palaeoenvironmental reconstructions suggest vegetation was relatively stable while hydrological conditions varied. The earliest modern humans at Laili Cave inherited a local ecology lacking large terrestrial fauna. The diverse microfauna recovered from the Laili sequence likely represent both human and owl foraging during periods of site occupation and abandonment, although foraging for small land vertebrates was difficult to ascertain confidently. Nevertheless, the Pleistocene inhabitants at Laili Cave displayed flexibility in faunal procurement strategies, targeting vastly different resources depending on availability and seemingly without the requirements for complex stone artefact technology. Broad-spectrum foraging of terrestrial and coastal invertebrate and fish fauna in aquatic habitats is evident. Habitats exploited include marine rocky and sandy beaches, as well as rivers and mangrove swamps. These data also demonstrate significant hunter gatherer mobility between coastal and proximal riverine habitats since the earliest period of site use. The most dramatic changes in site use occurred during the terminal Pleistocene period, coinciding with the end of the peak LGM, steeper coastlines, and possible changes in hydrological conditions,

when stone artefact discard and the exploitation of fresh-water shellfish intensified relative to other occupation phases.

### Conflict of interest

None reported.

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### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2017.07.008>.

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