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REVIEW

# Investigating the palaeoenvironmental context of Late Pleistocene human dispersals into Southeast Asia: a review of stable isotope applications

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## Abstract

We review palaeoenvironmental applications of stable isotope analysis to Late Pleistocene archaeological sites across Southeast Asia (SEA), a region critical to understanding the evolution of *Homo sapiens* and other co-existing Late Pleistocene (124–11.7 ka) hominins. Stable isotope techniques applied to archaeological deposits offer the potential to develop robust palaeoenvironmental reconstructions, to contextualise the occupational and non-occupational history of a site. By evaluating the published research in this field, we show that sediments, guano, tooth enamel, speleothem and biomolecular material such as leaf waxes have great potential to provide site-specific palaeoenvironmental records and local and catchment-scale landscape context to hominin dispersal in the region. However, stable isotope techniques used in these contexts are in their infancy in SEA, and the diagenetic controls associated with hot and humid environments that typify the region are not yet fully understood. Additionally, availability of sources of stable isotopes varies between sites. Nonetheless, even the limited research currently available shows that stable isotope analyses can aid in developing a better understanding of the role of the environment on the nature and timing of dispersals of our species eastwards into SEA and beyond.

**Keywords** Stable isotopes · Southeast Asia · Late Pleistocene · Palaeoenvironments · Hominins

## Introduction

Recent years have seen a resurgence of archaeological interest in the Late Pleistocene (marine isotope stages 5–2, ~ 124–11.7 ka) dispersal of *Homo sapiens* into Southeast Asia (SEA) (Bae et al. 2017; Boivin et al. 2013; Groucutt et al. 2015; Morley, 2017). The tropical setting of this emerging human evolutionary narrative—an understudied climatic zone—has incentivised archaeological scientists to apply state-of-the-art scientific techniques to human evolutionary studies in the region. These have taken a number of forms, including palaeogenetics (Meyer et al. 2012; Reich et al 2011; Slon et al. 2018), leaf wax biomarkers (Rabett et al. 2017), microstratigraphy (McAdams et al. 2020; Morley et al. 2017; Morley and Goldberg, 2017) and stable isotope analyses of guano (Bird et al. 2007, 2020; Wurster et al. 2010, 2017, 2019), molluscs (Hawkins et al. 2017; Milano et al. 2018), tooth enamel (Louys and Roberts, 2020; Roberts et al. 2020) and speleothems (Westaway et al. 2007). The results of these studies paint an increasingly intricate picture of Late Pleistocene *H. sapiens* demographics and habitats across SEA.

To better understand the nature and timing of the spread of hominins into SEA, and their capacity to adapt to potentially unfamiliar environmental niches (Roberts and Amano, 2019), the environmental dynamics of the site and local catchment need to be reconstructed. By generating local landscape and vegetation dynamics, evidence of human behavioural change can be contextualised against an environmental backdrop. At present, palaeoenvironmental

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records are often located at a considerable distance from the archaeological site in question, and the temporal resolution and time scales of archaeological records can differ from palaeoclimate archives, precluding a direct comparison between cultural and environmental records. To avoid questions over how representative a palaeoenvironmental record is for a given archaeological site (owing to geographic proximity and the spatial heterogeneity of vegetation) (Rabett et al. 2017), it is preferable that environmental data can be generated from the site itself, providing a direct link between environmental dynamics and cultural records (Morley, 2017). Whilst relying on palaeoenvironmental records from archaeological sites alone presents potential complications (e.g. over-representation of certain plant types as a result of human transport, as well as burning activities compromising biomarker preservation), combining local archaeological palaeoenvironmental (on-site) records with regional (off-site) records (Patalano et al. 2021) allows increased identification of local and regional environmental parameters.

The application of stable isotope analyses to sedimentary materials deposited within or associated with archaeological sites (e.g. inorganic carbonates, bone, teeth, guano, molluscs) provides a powerful tool with which to reconstruct the environmental conditions local to a specific site (Bird et al. 2020; Roberts et al. 2020). The application of such studies to archaeological sites in SEA is limited and piecemeal at present, although studies published to date have produced promising results (Bird et al. 2007; Rabett et al. 2011, 2017; Roberts et al. 2020; Westaway et al. 2007; Wurster et al. 2010, 2017, 2019). Here, we assess the application of stable isotope techniques to Late Pleistocene archaeological and fossil sites across SEA and the potential role of these studies in furthering our understanding of human evolution in this region. We particularly focus on the stable isotope analysis of bulk organic matter, leaf waxes, guano, faunal and hominin bone collagen and tooth enamel, speleothems and molluscs (Fig. 1) and how these data can be used to develop palaeoenvironmental reconstructions of environmental conditions existing in and around archaeological sites during periods of occupation and non-occupation.

## Late Pleistocene hominin demographics of Southeast Asia

The climate of SEA has been characterised by the East Asian Monsoon (EAM) system since the Late Cenozoic (25–22 million years ago) (Guo et al. 2008; Lu and Guo, 2014). The weather systems of the EAM drive the climate of SEA today and did so during the Late Pleistocene when *H. sapiens* first dispersed into the region. The EAM causes high seasonal rainfall and wind speed variability. Warm and wet conditions characterise the boreal summer monsoon (May–October), with cold and dry conditions prevailing during the boreal winter monsoon (November–April) (Herrmann et al. 2020; Wang et al. 2005).

The vegetation regimes that characterise SEA today are dipterocarp rainforests which cover an area of 2.1 million km$^2$ (Qian et al. 2019). During periods of lower sea levels (i.e. the Last Glacial Period, LGP), the exposure of the currently submerged continental shelf, Sundaland, is believed to have affected significant environmental and vegetational change throughout the region (Bird et al. 2005; Heaney, 1991). The southward migration of the Intertropical Convergence Zone (ITCZ) and EAM during glacial periods led to significantly reduced levels of precipitation across much of SEA, giving rise to the expansion of relatively open areas of grassland and shrub environments (Louys and Roberts, 2020) although localised refugial rainforest did exist (Rabett et al. 2017).

Our understanding of the hominin demographics of Pleistocene SEA has become markedly more nuanced over the past decade, with new details derived primarily though advances in palaeo and modern genomic studies that have demonstrated interbreeding events occurring between *H. sapiens* and other co-existing *hominin* groups including

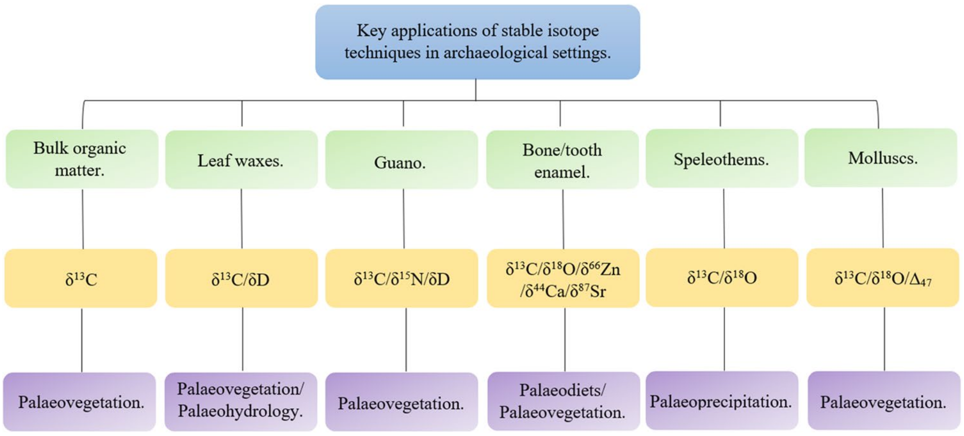

**Fig. 1** Flow diagram identifying the key applications of stable isotope techniques in archaeological settings, their sources and what proxy information can be reconstructed

Neanderthals and Denisovans (Green et al. 2010; Larena et al. 2021; Reich et al. 2011; Pickrell and Reich, 2014). This rapidly evolving field of research has shown that some of these interbreeding events occurred either within SEA or prior to dispersal of hominins into the area. There are a number of competing models that describe the timing and nature of dispersals of *H. sapiens* from mainland Southeast Asia (including Sunda), through island Southeast Asia (broadly Wallacea) and beyond into Australasia (Sahul) (Bae et al. 2017; Clarkson et al. 2017; O'Connell et al. 2018). Whilst several migratory pathways have been proposed for *H. sapiens* (Bird et al. 2019; Bradshaw et al. 2021; Kealy et al. 2016; Norman et al. 2018), a growing body of research demonstrates that they traversed climatically and environmentally diverse land and sea-scapes prior to arrival in Sahul (Bird et al. 2007; Westaway et al. 2017).

It is believed by some that *H. sapiens* did not arrive and settle into SEA until MIS 3 (55–50 ka) (e.g. O'Connell et al. 2018; Sun et al. 2021). However, there are several sites that contain fossil evidence that appears to predate this time window, suggesting an earlier presence in the region associated with a wave of dispersal out of Africa possibly as early as MIS 5 (126–74 ka) (Fig. 2) (e.g. Groucutt et al. 2015; Morley, 2017). In mainland Southeast Asia (MSEA), *H. sapiens* fossils have been recovered from the cave site Tam Pà Ling, Laos, with a partial cranium extending presence in the region to 44–63 ka (MIS 4) (Demeter et al. 2012, 2015, 2017). Farther south in island Southeast Asia (ISEA), two teeth attributed to *H. sapiens* recovered from sediments at Lida Ajer, Sumatra, date to 73–63 ka (Westaway et al. 2017).

The recent work at Madjedbebe rockshelter, northern Australia, dates the earliest arrival of *H. sapiens* to Sahul at ~ 65 ka (Clarkson et al. 2017). This indicates that further evidence of *H. sapiens* in MSEA in MIS 4 and potentially even earlier is likely to be uncovered in the future. There is only one certainty in this field at present, and this is that the human evolutionary narrative will become far more complex over the next decade and beyond.

## Using stable isotopes to better understand the Pleistocene archaeological record

One of the earliest applications of stable isotope analysis to an archaeological investigation was van der Merwe and Vogel (1978), who successfully measured the carbon isotope ratios ($\delta^{13}$C) in bone collagen of fossil human remains in North America, enabling inferences about palaeodiets. Since then, the number of stable isotope studies applied to archaeological questions has steadily increased. Within SEA these include, but are not limited to, analyses of fossil remains and tooth enamel of past humans and fauna for further insights into palaeodiet preferences and wider vegetation reconstructions (Bacon et al. 2018a, 2018b; Bocherens et al. 2017; Janssen et al. 2016; Krigbaum, 2005; Louys and Roberts, 2020; Pushkina et al. 2010; Roberts et al. 2020; Suraprasit et al. 2018, 2019), analysis of organic matter preserved in sediment, biomolecules derived from leaf wax and bat and bird guano to develop a qualitative/semi-quantitative understanding of vegetation dynamics in and around archaeological sites (Bird et al. 2007, 2020; Mentzer and Quade, 2013; Page and Marwick, 2016; Wurster et al. 2010, 2017, 2019; Rabett et al. 2017). In addition, the analysis of mollusc shells has been investigated to develop a proxy of palaeorainfall (Hawkins et al. 2017; Marwick and Gagan, 2011; Milano et al. 2018; Stephens et al. 2008).

Although initial applications of stable isotope ratios to archaeological settings in SEA have proven fruitful, there are still large knowledge gaps. In particular, a cross-site, uniform application of each of these methods to Pleistocene archaeological sites across MSEA, ISEA and down to Sahul has not yet been achieved; thus, there remains no robust and uninterrupted palaeoenvironmental reconstruction through MIS 5–2. Such a record is necessary to establish the true impact of local environmental parameters on early *H. sapiens* migration through the area during MIS 5, as well as addressing the existence and extent of a hypothesised savanna corridor (Bird et al. 2005; Wurster et al. 2019).

### Bulk organic $\delta^{13}$C analyses from archaeological sites

Whilst initial $\delta^{13}$C studies largely focused on marine and aquatic sourced sediments, DeNiro and Hastorf (1985) expanded studies of $\delta^{13}$C ratios to bulk organic matter from demineralised terrestrial sediments of archaeological sites in Peru, dating from 400 to 4,000 years ago. The ecological studies of Bender (1968, 1971) provided the founding principles for initial applications of $\delta^{13}$C to archaeological sediments. These studies found that $\delta^{13}$C values in modern plants and recent sediment vary as a function of the $\delta^{13}$C value of atmospheric $CO_2$ and the isotopic fractionation occurring during photosynthesis (a sequence of chemical reactions converting inorganic carbon into organic molecules) and that the degree of fractionation differed in plants that utilise different photosynthetic pathways.

Plants which utilise the $C_3$ photosynthetic pathway (Calvin-Benson) have $\delta^{13}$C values between − 32 and − 20‰, whereas $C_4$ (Hatch-Slack) photosynthesising plants fall within a higher range of − 17 to − 9‰, compared to average $\delta^{13}$C values of modern $CO_2$ at − 8‰ (O'Leary, 1988). These distinctive stable isotope values are the result of variations in the physiologies of $C_3$ and $C_4$ plants resulting in the differential fractionation of $^{12}$C and $^{13}$C by these two photosynthetic pathways (Tipple and Pagani, 2007). $C_3$ photosynthesis represents the primitive pathway utilised by plants, originating at a time when Earth's atmosphere consisted of much higher

**Fig. 2** Map of South China to Sahul arc with locations of key Pleistocene archaeological and palaeoenvironmental sites regularly referred to within this review

$CO_2$ and lower $O_2$ levels (Bekker et al. 2004). $C_4$ photosynthesis evolved in response to lower $CO_2$ levels and changing climatic conditions beginning in the Oligocene (34 to 23 million years ago) and originated independently in at least 60 different lineages (Sage, 2016).

During $C_3$ photosynthesis, $CO_2$ fixation via the ribulose biphosphate carboxylase/oxygenase (Rubisco) significantly discriminates against $^{13}C$, leading to highly depleted $\delta^{13}C$ values (Ehleringer et al. 1997). $C_4$ plants, on the other hand, isolate Rubisco from the site of $CO_2$ uptake through their distinctive anatomy (known as 'Kranz Anatomy'), that is comprised of a ring of mesophyll cells that surround bundle sheath cells (Ehleringer and Monson, 1993). Atmospheric $CO_2$ diffuses into the intercellular spaces, is initially fixed in the outer mesophyll cells by the enzyme phosphoenolpyruvate carboxylase (PEP-C) and is transformed into $C_4$ acids (Ehleringer and Monson, 1993). The rate-limiting step in $C_4$ photosynthesis is diffusion, and as a result, Rubisco cannot significantly fractionate carbon isotopes, leading $C_4$ plants to have less negative $\delta^{13}C$ values than $C_3$ plants (O'Leary, 1988). Due to the greater efficiency of PEP-C at fixing $CO_2$, the $CO_2$ surrounding Rubisco in $C_4$ plants is at significantly higher concentration than in $C_3$ plants (Ehleringer and Monson, 1993). Therefore, Rubisco reactions in

$C_4$ plants occur in a high $CO_2$:$O_2$ setting, essentially eliminating any photorespiration (fixation of oxygen and loss of $CO_2$) (Ehleringer, 2005). Due to their ability to more efficiently assimilate carbon, in the process of losing less water to transpiration, $C_4$ photosynthesis has flourished in environments where they can outcompete $C_3$ plants, such as in arid or saline settings, in regions dominated by warm-season rainfall and at times where atmospheric $pCO_2$ levels were comparatively low (Tipple and Pagani, 2007).

Plants that use the $C_3$ photosynthetic pathway include nearly all trees, most shrubs as well as all temperate grasses. In contrast, plants that use $C_4$ photosynthesis include tropical and subtropical grasses and arid-adapted shrubs (Sage, 2016). The relationship between $\delta^{13}C$ in plants and sediments enables a first-order vegetation reconstruction from archaeological sediments (Kingston et al. 1994; Roberts et al. 2013).

$\delta^{13}C$ analyses of sediments have been conducted on archaeological excavations worldwide, dating back to the Pleistocene and earlier. In Africa, this includes the early studies of Cerling (1992), which demonstrated the preservation of $\delta^{13}C$ values in sediments and, along with Kingston et al. (1994), offered insights into the Neogene expansion of $C_4$ vegetation to Africa and the associated implications for early hominin species. Kingston et al. (1994) further determined hominin evolution in this period to have been impacted by climate, with their evolution having taken place across a mosaic environmental setting. More recent investigations by Roberts et al. (2013) and Garret et al. (2015) successfully expanded $\delta^{13}C$ investigations to the archaeological contexts in Lesotho, Southern Africa, and the Rusinga and Mfangano islands in the Lake Victoria Basin, Kenya, respectively. Researchers working at archaeological sites in North America have also utilised sediment isotope techniques to reconstruct local environments during site occupation (Huckleberry and Fadem, 2007).

One potential problem with $\delta^{13}C$ analysis of bulk organic material in sediment is the potential for $\delta^{13}C$ alteration as a result of microbial degradation (Wynn, 2007). To improve confidence, analysis of modern sediment samples collected from the same site can provide data to validate the interpretation. By measuring the organic carbon (OC) content of modern sediment, this allows for the determination of the extent of $^{13}C$ enrichment the sediment may have undergone as a result of Rayleigh distillation (observed patterns of kinetic fractionation of stable isotopes), which can lead to a ~ 6‰ $^{13}C$ enrichment, as well as identifying and excluding $^{13}C$-enriched products as a result of microbial degradation (Wynn, 2007). To further strengthen the palaeoenvironmental record, bulk organic $\delta^{13}C$ analysis of sediments can be coupled with an additional palaeoenvironmental technique.

To date, $\delta^{13}C$ analyses of archaeological sediments in SEA are scarce. However, a successful preliminary application has been undertaken in Madjedbebe rockshelter, northern Australia (Page and Marwick, 2016). This site provides the earliest evidence to date of *H. sapiens* presence in Australia and so is crucial to understanding the migration of *H. sapiens* from MSEA, through ISEA and into Sahul (Clarkson et al. 2017; Florin et al. 2020; Gaffney 2021). Page and Marwick (2016) applied $\delta^{13}C$ analysis to the sediments of Madjedbebe to assess if vegetation changes in the late Pleistocene through to the Holocene influenced adaptions to hunting and technological changes observed in the artefact record between 70 and 5 ka. The arrival of *H. sapiens* could not be correlated with major vegetation change, but for much of the Late Pleistocene and Early Holocene, $C_3$ vegetation dominated site surroundings with $\delta^{13}C$ values averaging − 25.3‰. A slight increase in $\delta^{13}C$ values to − 23.6‰ at 5 ka is suggested to represent a warmer growing season but without dramatically altered rainfall patterns, giving rise to small patches of $C_4$ vegetation in a $C_3$-dominated landscape, similar to that of today. This work highlights the preservation potential of $\delta^{13}C$ signals within tropical archaeological sediments and provides a foundational understanding of the climate context of *H. sapiens* first arrival in Australia.

## Leaf wax lipid isotopes from archaeological sites in SEA

Terrestrial plant biomarkers are valuable proxies within the sedimentary record, offering insights into present and past patterns of carbon cycling in the ecosystem, as well as changes in palaeovegetation and palaeoprecipitation on both a global and local scale (Diefendorf and Freimuth, 2017). Within terrestrial plants, long chain ($C_{21}$ to $C_{35}$) normal alkanes (*n*-alkanes) exist within the cuticle of the leaf. They contribute to a protective waxy layer that restricts water loss, protects against UV radiation damage and defends against fungal and bacterial pathogens (Eglinton and Hamilton, 1967; Riederer and Markstaedter, 1996).

Long-chain *n*-alkanes are widely utilised in palaeoenvironmental investigations due to their high preservation potential (Diefendorf et al. 2011). Typically, terrestrial higher plants produce a homologous series of *n*-alkane chain lengths (e.g. from $C_{27}$ to $C_{35}$) with an odd-over-even chain length predominance (Eglinton et al. 1962). Owing to their straight chain hydrocarbon structure, they can remain stable in many depositional settings (marine, lacustrine and terrestrial), surviving within the fossil record, largely unaltered by microbial and diagenetic processes for many millions of years (Diefendorf et al. 2011; Smith et al. 2007). However, it is important to acknowledge that their preservation is not guaranteed. Nie et al. (2014) have observed that *n*-alkanes can be subject to degradation by microbial action in the sediment matrix. Potential alterations of *n*-alkanes have also been recorded during deposition into the sediment and in storage ahead of analyses (Brittingham et al. 2017; Grimalt et al. 1988; Li et al. 2018; Nguyen et al. 2017; Shilling, 2019).

Over the last two decades, research has focused on constraining the variables that influence plant biomarkers and their isotopic composition to maximise their utility as palaeoenvironmental proxies (Diefendorf and Freimuth, 2017; Sachse et al. 2012). Whilst plants produce a range of *n*-alkanes of varying lengths, they often have a preferential production of one or two chain lengths (Eglinton and Hamilton, 1967). The *n*-alkane average chain length (ACL) is determined as the amount-weighted average chain length a plant produces. The ACL was originally proposed as a proxy for particular plant functional types, with $C_{27}$ and $C_{29}$ believed to be preferentially sourced from woody plants, and the longer chain lengths of $C_{31}$–$C_{35}$ sourced from graminoids (grasses) (Meyers and Ishiwatari, 1993; Poynter and Eglinton, 1990). However, investigations of modern plants indicate the ACL to be highly variable among different plant groups, with no difference between grasses and woody vegetation on a global scale (Bush and McInerney, 2013). However, in certain regions, such as Africa (Vogts et al. 2009) and Australia (Andrae et al. 2020; Howard et al. 2018), grasses do appear to demonstrate preferential production of longer chain lengths ($C_{31}$–$C_{35}$), with woody vegetation predominantly producing shorter chain lengths ($C_{27}$ to $C_{29}$). Therefore, the ACL of *n*-alkanes has been applied as a vegetation indicator in certain regions. Further studies of plants growing along climatic gradients suggest that both climatic and genetic factors appear to exert a degree of influence over the *n*-alkane ACL production (Andrae et al. 2019; Bush and McInerney, 2013, 2015; Diefendorf et al. 2011, 2015; Hoffman et al. 2013).

Given that climatic factors (i.e. temperature, precipitation, humidity and aridity) and/or genetics influence the ACL, ideally palaeoclimatic studies of ACL would be conducted on a single plant species. However, identifying plant *n*-alkanes to species level in the fossil record is frequently impossible, so Diefendorf and Freimuth (2017) instead proposed *n*-alkane reference studies be conducted on modern plant samples from study areas. ACL of *n*-alkanes can also distinguish between terrestrial origin ($C_{27}$–$C_{35}$) and algal/lacustrine environments ($C_{17}$-$C_{25}$) (Andrae et al. 2020; Diefendorf et al. 2011; Ficken et al. 2000). Submerged aquatic macrophytes produce shorter chain lengths with less negative $\delta^{13}C$ ratios than terrestrial vegetation, and thus compound-specific isotope analysis (CSIA) of the $\delta^{13}C$ ratios of individual chain lengths enables examination of the different sources of *n*-alkanes to sediments (Andrae et al. 2020). $\delta^{13}C$ ratios of sedimentary long-chain *n*-alkanes reflect the different relative abundance of terrestrial vegetation using the $C_3$ and $C_4$ photosynthetic pathways (Bi et al. 2005). Leaf wax *n*-alkanes are even more $^{13}C$-depeleted than the bulk tissues, with $\delta^{13}C$ values for $C_3$ plants ranging from − 31‰ to − 39‰ and for $C_4$ plants ranging between − 18 and − 25‰ (Collister et al. 1994; Liu and An, 2020; Rieley et al. 1991).

In the last two decades, advancements in analytical techniques have enabled the CSIA of the stable hydrogen isotope ($\delta D$) composition of *n*-alkanes (Burgoyne and Hayes, 1998). *n*-Alkane $\delta D$ signatures have now been established as a useful palaeohydrological proxy due to their ability to record variations in regional hydrological characteristics (Sachse et al. 2004, 2012; Niedermeyer et al. 2016; Tipple and Pagani, 2013). Specifically, leaf wax *n*-alkane $\delta D$ values reflect the isotopic composition of source water (e.g. precipitation) and subsequent isotopic enrichment by transpiration (evaporation through the stomata) which is related to aridity (Feakins and Sessions, 2010; Freimuth et al. 2017; Smith and Freeman, 2006). Leaf wax *n*-alkane $\delta D$ values can differ significantly depending on the plant type (e.g. dicots, monocots and gymnosperms) (Gao et al. 2014; Liu and An, 2018; McInerney et al. 2011; Sachse et al. 2012). These studies emphasise the necessity to take into account these variables and to investigate the $\delta D$ of modern plants in the surrounding study area.

The application of these palaeoenvironmental techniques to sediments in archaeological settings is expanding (Patalano et al. 2021), with $\delta^{13}C$ and $\delta D$ applications offering insights into the palaeovegetation and palaeohydrological conditions early humans encountered. To date, the $\delta^{13}C$ of leaf wax *n*-alkanes have been applied to reconstruct catchment area vegetation in and around archaeological sites in Europe (Connolly et al. 2019; Égüez and Makarewicz, 2018), and most notably Africa (Collins et al. 2017; Magill et al. 2013a, 2016) to name a few, to build a deeper understanding of the influence of the local environment on early hominin behaviours in archaeological sites. $\delta D$ has also been successfully employed as an indicator of palaeohydrological patterns of the local environments surrounding archaeological sites in Europe (Connolly et al. 2019), China (Patalano et al. 2015) and Africa (Collins et al. 2017; Magill et al. 2013b).

*n*-Alkane biomarkers have recently been applied to lacustrine sediments from Lake Towuti (Konecky et al. 2016; Russell et al. 2014) and Lake Matano, Sulawesi (Wicaksono et al. 2015) and marine sediments from Mandar Bay, Sulawesi (Wicaksono et al. 2017) as well as southern Sumatra (Windler et al. 2020) to better understand the palaeohydrology and palaeovegetation of the regions during the LGM. However, to date, site-specific studies using leaf wax isotope ratios and molecular distributions to reconstruct local habitats at archaeological sites in SEA are scarce. Rabett et al. (2017) demonstrated the possibility of successfully applying these approaches to SEA in the cave sites of Hang Boi, Hang Trông in the Tràng An massif, Northern Vietnam. Across both sites, Rabett et al. (2017) measured

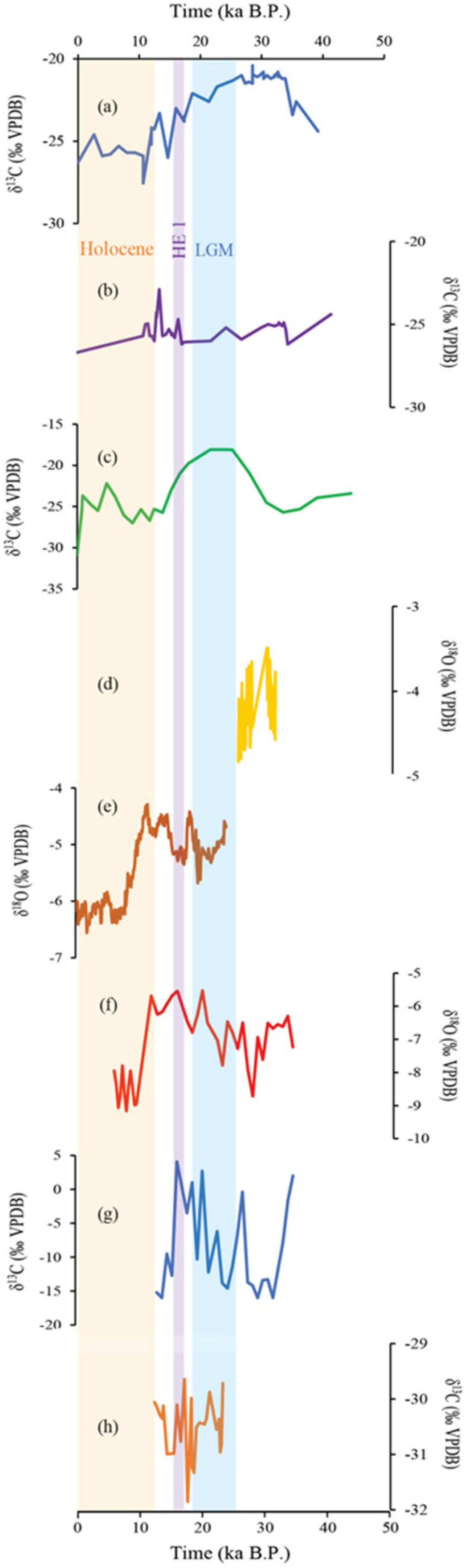

**Fig. 3** $\delta^{13}C$ profiles of four guano deposits from **(a)** Batu cave, peninsular Malaysia; **(b)** Niah Cave, Sarawak **(c)** and Gangub Cave, Palawan Island, Philippines; two $\delta^{18}O$ profiles of speleothems from Liang Luar Cave, Flores, by Lewis et al. (2011) **(d)** and Ayliffe et al. (2013) **(e)**; **(f)** $\delta^{18}O$ values from the freshwater bivalve *Margaritanopsis laosensis* from Tham Lod Rockshelter (TLR), in Marwick and Gagan (2011); **(g)** $\delta^{13}C$ values from *H. sapiens* and fauna tooth enamel from TLR in Suraprasit et al. (2021) and **(h)** $\delta^{13}C$ from leaf wax alkanes from Hang Trông, Vietnam, in Rabett et al. (2017). Data for **(a)**, **(b)** and **(c)** provided by C. M. Wurster

ACL and $\delta^{13}C$, finding that the $C_{31}$ *n*-alkane was the dominant chain length in the sediment, with $C_{29}$ and $C_{33}$ present in lesser quantities, and its $\delta^{13}C$ values largely fell within the ranges of – 30 and – 35‰ (Fig. 3h). Rabett et al. (2017) suggest that this indicates that $C_3$ vegetation remained largely persistent through the Last Glacial Maximum (LGM), similar to the vegetation landscape present today. This study only extends back to 29 ka, leaving a substantial research gap for the application of *n*-alkanes as a quantitative palaeovegetation proxy across all of SEA and expanding back to when early *H. sapiens* are now believed to have first arrived in MIS 5 (~ 124–70 ka) (Demeter et al. 2012, 2015,2017; Westaway et al. 2017).

The extraction of *n*-alkanes from sediment and the analysis of compound specific $\delta^{13}C$ and $\delta D$ has potential to be more broadly applied to SEA archaeological sites. Analysis of $\delta^{13}C$ and $\delta D$ will enable a greater understanding of how ecological and hydrological conditions may have influenced migration and settlement patterns. Conducting this across sites in MSEA, ISEA and Sahul will enable a robust reconstruction of how palaeovegetation and palaeoprecipitation varied across these sites, expanding current knowledge on how our species came to adapt and settle here. This proxy will prove valuable in testing the hypothesis that tropical vegetation, characterising much of the landscape today, was not always uniform across Sunda and Sahul, but rather gave way to a more diverse landscape in the Pleistocene (Wurster et al. 2019).

## Guano isotope records

The isotope geochemistry of bat and bird guano provides insights into the diet of those animals and hence the vegetation composition of past ecosystems (Cleary and Onac, 2020). In one of the earliest studies of guano at an archaeological site conducted in Carlsbad, New Mexico, Des Marais et al. (1980) posited that the $\delta^{13}C$ of the individual hydrocarbons of bat guano represent the exoskeleton remains of prey insects, and this in turn reflected the photosynthetic pathways used by local plants. Since the 1980s, $\delta^{13}C$ analysis of guano has been applied to Holocene and late Pleistocene sediments in Jackson's Bay Cave, Jamaica (McFarlane et al. 2002; Mizutani et al. 1992), the Grand Canyon, USA

(Wurster et al. 2007, 2008, 2009), Guadeloupe, Eastern Caribbean (Royer et al. 2015, 2017) and Gaura cu Muscă Cave, southwest Romania (Onac et al. 2015).

Much like the isotopic values of organic matter in sediment, the $\delta^{13}$C composition of guano is inferred to reflect vegetation in the vicinity of the site (Wurster et al. 2007). Whilst trophic discrimination has been demonstrated to vary between species, within the tissues of species and across diets (Brauns et al. 2018; Newsome et al. 2012), discrimination factors have not yet been determined for most insect species (Quinby et al. 2020). When this is the case, researchers often apply an arbitrary discrimination of 1‰ for $\delta^{13}$C (DeNiro and Epstein, 1978). Guano is directly deposited within the cave by birds and bats and is therefore less susceptible to post-depositional alteration than aeolian or water-transported sediments (Onac et al. 2014).

In SEA, Bird et al. (2007) analysed $\delta^{13}$C from ancient guano deposits filling Makangit Cave, Palawan, Philippines, extending from the present into the LGM (> 30,000 years BP). Bird et al. (2007) suggested that local environmental conditions across ISEA during this period were potentially complex, with $\delta^{13}$C values reaching as high as – 13.5‰ during the LGM, suggesting a more open landscape dominated by $C_4$ grasses. The presence of $C_4$ vegetation would have contrasted with a largely uniform landscape of $C_3$ rainforest during the Late Pleistocene.

Wurster et al. (2010, 2019) extended guano isotope studies further into SEA and to ~ 40 ka (Fig. 3), in parallel with archaeological assessment of early modern human settlement patterns. Using $\delta^{13}$C of guano from peninsular Malaysia (Batu Cave), Palawan Island, Philippines (Makangit and Gangub Caves) as well as northern and southern Borneo (Niah Cave in Sarawak and Saleh Cave, East Kalimantan), they found that whilst rainforest persisted in northern Borneo during the LGM, Malaysia, Palawan and southern Borneo all experienced significant rainforest contraction.

Collectively, the guano isotope records developed by Bird et al. (2007) and Wurster et al. (2010, 2019) serve as evidence for the significant contraction of rainforest vegetation in ISEA during the LGM, as a result of increased exposure of significant landmasses due to lower sea levels in this period. They argue that this gave rise to a savannah corridor. As shown in Fig. 3a and c, Batu Cave and Gaungub Cave guano $\delta^{13}$C values rise to a high of – 21.7‰ and – 18‰, respectively, during the LGM, indicating the increasing presence of $C_4$ vegetation as a result of drier environmental conditions. This savannah corridor is hypothesised to have run north from peninsular Malaysia across to southern Borneo, indicating a strong but inconsistent sensitivity of vegetation across SEA to climate change during glacial/interglacial timeframes. The presence of a savannah corridor during the Last Glacial Period (LGP) would have provided a route for migration of *H. sapiens* into SEA and Australia, whilst also resulting in a biodiversity divide in faunal and flora species (Wurster et al. 2019).

Despite the evidence from guano records, the existence and extent of a savannah corridor remain hotly debated. Multiple studies present evidence for its presence (Bird et al. 2005; Heaney, 1991; Louys and Meijaard, 2010; Louys and Roberts, 2020; Wurster et al. 2019), whilst others maintain a rainforest-dominated landscape persisted in SEA during the LGM (Cannon et al. 2009; Chabangborn et al. 2014; Raes et al. 2014; Sun et al. 2000). Guano from Niah Cave in Borneo contains $\delta^{13}$C values lower than – 25‰ throughout the LGM (Fig. 3b) indicating little to no rainforest retraction. Similarly, in the $\delta^{18}$O speleothem records from Liang Luar, Flores (Fig. 3e and f), Ayliffe et al. (2013) recorded a decline in $\delta^{18}$O values during the LGM, falling from – 4.61‰ at 23.9 ka to values consistently below – 5‰ to ~ 19 ka, representing the persistence of wetter conditions, providing a suitable environment for forested vegetation to persist. The current data available from ISEA arguably indicates the vegetation landscape was complex, with local and regional variation.

Ultimately, analysis of guano is one of the more developed stable isotope analyses applied to archaeological sites in SEA. However, at present it remains largely confined to ISEA, providing data across this geographic area and back to at least 35 ka. Method development work exploring the interpretation of $\delta^{15}$N ratios in a tropical context should also be pursued.

## Isotope ratios from bone collagen and tooth enamel

The dictum 'you are what you eat' holds true to the extent that the stable carbon isotopes of tissues such as bone collagen and tooth enamel can be used to quantify past dietary habits (e.g. Joannes-Boyau et al. 2019; Krigbaum, 2005; Louys et al. 2007; van der Merwe and Vogel, 1978; Vogel and van der Merwe, 1977). Stable isotope analysis of individual amino acids isolated from bone collagen can be used to determine not only the proportion of marine versus terrestrial protein from ancient hominin diet, but also if there was a $C_3$ or $C_4$ vegetation preference (Ambrose and Norr, 1993; Howland et al. 2003). Moreover, where limitations arise from preservation issues with bone collagen, analysis of $\delta^{13}$C, $\delta^{15}$N, $\delta^{18}$O and more recently $\delta^{66}$Zn from human and faunal tooth enamel can be used to infer the diets of early *H. sapiens* and the wider surrounding environments (Lee-Thorp, 2008; Lee-Thorp et al. 1989; Roberts et al. 2020; Sponheimer et al. 2013; White et al. 2009).

There are isotopic differences between and within faunal (i.e. vertebrates and herbivores) and human tooth enamel, owing to different fractionation processes and discrimination factors occurring due to different digestive physiologies (Cerling and Harris, 1999; Cerling et al. 1999; Lee-Thorp et al. 1989; Passey et al. 2005). However, $\delta^{13}C$ values derived from both fauna and humans can represent palaeodiets and the wider local palaeoenvironment (Janssen et al. 2016; Roberts et al. 2015, 2017, 2020), as $\delta^{13}C$ values still reflect the photosynthetic pathway of the vegetation at the base of the food web, albeit markedly enriched compared to the $\delta^{13}C$ values of the plant source. This results from the secondary carbon isotope fractionation occurring during utilisation by consumers (DeNiro and Epstein, 1978; Lee-Thorp et al. 1989). Within bone collagen, this secondary fractionation leads to a $\delta^{13}C$ enrichment of 5‰ (Lee-Thorp and van der Merwe, 1987) and 13‰ in tooth enamel (Lee-Thorp et al. 1989).

Where fauna are primary consumers, $\delta^{13}C$ values of − 10‰ and lower in tooth enamel are indicative of a $C_3$ closed canopy ecosystem, and those of − 2‰ and higher represent a $C_4$ diet, indicating an open grassland landscape. Values falling between − 10 and − 2‰ signify a mixed diet of $C_3$ and $C_4$ vegetation (Cerling et al. 1997; MacFadden et al. 1999).

$\delta^{13}C$ values derived from human tooth enamel are − 14‰ and lower when representing a $C_3$ forest diet and surroundings, between − 11 and − 4‰ indicating a more open $C_3$ vegetation landscape with potential inclusions of $C_4$ vegetation, and for a purely $C_4$ ecosystem fall around − 2‰ and higher (Cerling and Harris, 1999; Cerling et al. 1997), mirroring those of faunal results. Humans consuming a marine diet have $\delta^{13}C$ values around − 4‰ (Levin et al. 2008; Roberts et al. 2017, 2020).

### Faunal stable isotope studies

Fossilised tooth enamel of vertebrate fauna has become an important source of $\delta^{13}C$ and $\delta^{18}O$ data for understanding palaeodiets and the wider palaeoenvironments of SEA (Bacon et al. 2018a, 2018b; Bocherens et al. 2017; Janssen et al. 2016; Louys and Roberts, 2020; Pushkina et al. 2010; Suraprasit et al. 2018, 2019, 2021). $\delta^{18}O$ values in bioapatite of teeth are largely determined by the water that the animals consume, either directly or as a constituent of their food (Bocherens et al. 1996; Sponheimer and Lee-Thorp, 1999). The $\delta^{18}O$ of the meteoric water is sensitive to climate and hydrology, principally condensation temperature, humidity, evaporation and the partitioning of waters between the atmosphere, land surface and biological tissue (Dansgaard, 1964). As temperatures in SEA are not subject to extreme annual fluctuations, temperature has a weak influence on the $\delta^{18}O$ values in precipitation (Gat, 1996). Therefore, $\delta^{18}O$ values of precipitation in SEA are predominantly influenced by the amount of precipitation, the source of the precipitation, potential evapotranspiration from the moisture source and altitude (Araguás-Araguás et al. 1998), with $\delta^{18}O$ values becoming more depleted with increased precipitation and/or evaporation decreases and vice versa (Dansgaard, 1964).

In environments where surface evaporation is minimal, water in the roots and stems of plants hold similar $\delta^{18}O$ to meteoric water; however, as $^{16}O$ is more readily evapotranspired than $^{18}O$, there is $^{18}O$ enrichment of the remaining leaf water (Dongmann et al. 1974; Gonfiantini et al. 1965; Epstein et al. 1977). Therefore, $\delta^{18}O$ from tooth enamel can be a proxy for the animal's diet (i.e. open or closed vegetation) or the climatic or hydrological conditions of its habitat (Lee-Thorp et al. 1989; Sponheimer and Lee-Thorp, 1999). Bryant and Froelich (1995) advised that where possible, tooth enamel from larger sized fauna should be used for $\delta^{18}O$ analysis. This is because $\delta^{18}O$ fractionation between the water ingested, the body water and the enamel phosphate reduces with increasing body size (Bryant and Froelich, 1995). Variation of body size and associated effects on fractionation means that, although generally $^{18}O$ enrichment occurs in parallel with $^{13}C$ enrichment (Helliker and Ehleringer, 2002), it is not a given that $C_4$ grazers will have an enriched $\delta^{18}O$ values when compared with $C_3$ consumers.

Pushkina et al.'s (2010) study from Tham Wiman Nakin (TWN) (Snake Cave) marked the first dietary and environmental reconstruction via stable isotope analysis of mammalian tooth enamel in MSEA, dating to the late Middle Pleistocene. Analysing tooth enamel bioapatite from cervids, bovids, suids, carnivores, rhinoceros, wild pig, porcupine and orangutan, Pushkina et al. (2010) found $\delta^{13}C$ values ranging between − 29.2 and − 11.2‰, with an average of − 19.2‰. They determined this to represent the presence of a mixed $C_3$ and $C_4$ habitat. Notably, bovids and cervids showed a predominantly $C_4$ diet, with carnivores reflecting a consumption of a mixture of $C_3$ (suids) and $C_4$ (bovids and cervids) reliant prey. In contrast, Pushkina et al. (2010) found that much like modern rhinoceroses and orangutans, those from the Middle Pleistocene also consumed a predominantly $C_3$ diet. By analysing the bioapatite and hair of modern samples of the surviving species, Pushkina et al. (2010) observed a significant shift to a $C_3$ dominant diet across all species, with the presence of $C_4$ vegetation declining from over 70% in the Middle Pleistocene to 13% in modern samples. They determined this to result from a move to foraging within forested habitats and the loss of open areas of $C_4$ landscapes. This work demonstrates that the landscapes surrounding TWN were much more diverse in the Middle Pleistocene than today, with areas of both closed-canopy forests ($C_3$) and open grasslands ($C_4$). Pushkina et al. (2010) also highlighted the need for future researchers to consider the impact of early modern humans on the local ecosystems and associated diets.

Louys et al. (2007) hypothesised that the extinctions of several taxa from SEA during the Pleistocene resulted from a combined impact of eustatic sea level change, climatic variations and human activity. These include but are not limited to proboscideans (*Stegodon* and *Palaeoloxodon*), orangutan (*Pongo*), hyenas (*Crocuta crocuta* and *Crocuta ultima*) and the giant Asian ape (*Gigantopithecus*) (taxonomic names have been updated in accordance with Suraprasit et al. (2016)). Janssen et al. (2016) took this further, localising their study to Java and Sumatra to assess the impact of glacial/interglacial changes on species dispersal and vegetation patterns. Utilising analysis of both $\delta^{13}C$ and $\delta^{18}O$ from enamel of bovids, cervids and suids, they found that individual sites are strongly dominated by either $C_3$ browsers or $C_4$ grazers, with little to no mixing. Herbivores from Padong Highlands (Sumatra) and Hoekgrot Cave (Java) indicated a $C_3$ vegetation signal, whereas herbivores from *Homo erectus* bearing sites Trinil and Sangiran, Java, displayed an almost exclusively $C_4$ diet (Janssen et al. 2016). However, this lack of mixing may be due to the limited number of mammalian groups studied; bovids, cervids and suids have specific feeding strategies and habitat preferences, which are not necessarily reflective of the entire range of local environments. Moreover, Lee-Thorp and van der Merwe (1987) demonstrated the necessity of conducting pre-treatment procedures (detailed by Lee-Thorp and van der Merwe (1987), revised in Lee-Thorp et al. (1997) for smaller samples) on sample material prior to isotopic analysis in order to remove contaminants. Janssen et al. (2016) only conducted pre-treatment procedures on 40 of their 101 samples, meaning that data from the untreated samples need to be interpreted with caution. Nonetheless, Janssen et al. (2016) does demonstrate the complexity of the environments of SEA in the Middle/Late Pleistocene.

Puspaningrum et al. (2020) sought to reconstruct the palaeovegetation of Java, extending their study into the Early Pleistocene (before 1.5 million years) through to the present day by analysing the $\delta^{13}C$ and $\delta^{18}O$ from proboscidean tooth enamel. They conducted their study on six proboscidean taxa: *Stegoloxodon indonesicus*, *Sinomastodon bumiajuensis*, pygmy *Stegodon* sp., *Stegodon trigonocephalus*, *Elephas hysudrindicus* and *Elephas maximus*, each of which are well documented for Java. Depleted $\delta^{13}C$ values ranging between − 14.1 and − 12.8‰ for the earliest proboscidean taxa are recorded on Java, and *St. indonesicus* indicated that the island was likely characterised by a closed canopy rainforest ($C_3$ vegetation) in the earliest Pleistocene. However, *Si. bumiajuensis*, pygmy *Stegodon* sp. and *St. trigonocephalus* recovered from Citalang, Kaliglagah, Mengger, Pucangan and Sangiran Formation showed a larger range of $\delta^{13}C$ values (− 14.1 to − 0.9‰). Puspaningrum et al. (2020) suggested this is evidence for herbivore foraging in both closed canopy forests and open grasslands. Middle Pleistocene $\delta^{13}C$ values from *St. trigonocephalus* and *E. hysudrindicus* were between − 5.9 and − 1.4‰, representing a shift to a predominantly $C_4$ diet with some $C_3$ vegetation, representative of a predominantly open vegetation landscape. $\delta^{13}C$ values show depletion towards the late Middle Pleistocene, and by the Late Pleistocene-Holocene, $\delta^{13}C$ values of − 15.1‰ to − 8.7‰ are consistent with a predominantly $C_3$ vegetation (closed canopy), with some $C_4$ vegetation also present. Puspaningrum et al. (2020) concluded that the causes of extinction of $C_3$ and $C_4$ consumers *Stegodon trigonocephalus* and *Elephas hysudrindicus* were unlikely to be the result of major vegetation shifts as a result of climate change and more likely to be due to an inability to compete with new taxa or human activity.

Louys and Roberts (2020) explored the different ecological tolerances of megafauna and hominins and the environmental drivers of their extinctions in SEA through $\delta^{13}C$ and $\delta^{18}O$ analyses of tooth enamel from a dataset of 269 modern and historical mammalian taxa. They concluded that savannah expanded in the Early-Middle Pleistocene, leading to the expansion of grazing mammal species and the reduction of browser species, but then retreated in the Late Pleistocene to completely vanish in the Holocene epoch. This gave rise to the expansion of closed-canopy rainforest environments. Louys and Roberts (2020) found this significant change in vegetation landscape to be correlated with the loss of grazing taxa *Elephas hysudrindicus* and *Stegodon trigonocephalus* and the elephant species becoming restricted to forested environments. $C_3$ vegetation expansion also served as a major extinction event for open environment-adapted hyenas (Louys and Roberts, 2020).

Both Puspaningrum et al. (2020) and Louys and Roberts (2020) show that $\delta^{13}C$ and $\delta^{18}O$ stable isotopic analyses of tooth enamel can reconstruct past environments in SEA as far back as the Early Pleistocene, even if the two papers do not fully agree on the causes of extinction.

### Hominin bone collagen and tooth enamel

Krigbaum (2005) applied stable $\delta^{13}C$ isotope analysis to bone collagen of Late Pleistocene hominin remains from Niah Cave, Borneo, and noted that researchers have previously been deterred from such studies in SEA due to the current ubiquity of $C_3$ vegetation. Wurster et al. (2010, 2019) determined that northern Borneo remained $C_3$ vegetation dominated during the LGM, whilst southern Borneo experienced a $C_4$ vegetation expansion. However, analysing the $\delta^{13}C$ variation within $C_3$ plants can help to decipher which vegetation sources within the rainforest canopy hominins may have utilised. In this microhabitat, plants grown in more open spaces are enriched in $^{13}C$, reflected by more positive $\delta^{13}C$ values (− 27‰). Conversely, those under extensive canopy cover yield considerably more negative $\delta^{13}C$ readings of − 30 to − 35‰ (Buchmann et al. 1997; van der Merwe and Medina, 1989, 1991).

Ideally, these isotopic variations should be reflected, albeit enriched by trophic fractionation, in the $\delta^{13}C$ values of bone collagen. Unfortunately, Krigbaum's results failed to return conclusive results of early hominin subsistence strategies, largely due to the post-mortem diagenesis and degradation that bone is subjected to in the tropics (Lee-Thorp, 2002; Schoeninger et al. 1989). As with fauna, tooth enamel provides a more resistant alternative media for isotopic analyses, already proven successful in the studies of African hominins (Lee-Thorp et al. 2010; Levin et al. 2015; White et al. 2009).

Addressing the lack of case studies applied to the adaption of our own species to rainforest environments, Krigbaum (2003, 2005) and Roberts et al. (2015) applied isotope analysis to tooth enamel of *H. sapiens* remains associated with early modern human occupation of the tropical rainforests of Sri Lanka. Until recently, it was assumed that modern human occupation of rainforests only occurred in the Holocene (Bailey et al. 1989). Following stable $\delta^{13}C$ and $\delta^{18}O$ isotope analysis on hominin teeth from the sites of Fa Hein-lena, Balangoda Kuragala and Bellan-bandi Palassa, coupled with the calibrated radiocarbon ($^{14}C$) dates from the sites, the timing of modern human exploitation of rainforest resources has now been extended back to the Late Pleistocene, at least 20,000 years ago (Roberts et al. 2015).

Within the rainforest environments of SEA, Janssen et al. (2016) also conducted $\delta^{13}C$ and $\delta^{18}O$ analyses on seven *Homo erectus* bones from Sangiran and Trinil. Although they found the bone material to be structurally well preserved, the $\delta^{13}C$ and $\delta^{18}O$ signatures were subject to significant diagenetic overprint, with the $\delta^{13}C$ and $\delta^{18}O$ values being systematically lower than the mammalian tooth enamel $\delta^{13}C$ and $\delta^{18}O$ signatures by an average of 6.9‰ and 2.3‰. Moreover, as pre-treatment of the *H. erectus* bone failed to remove the diagenetic overprint, Janssen et al. (2016) were unable to confidently reconstruct the $\delta^{13}C$ and $\delta^{18}O$ signatures of the *H. erectus* bones. Whilst Janssen et al. (2016) highlighted this study provided the isotopic framework to enable isotopic analyses on *H. erectus* enamel, they did not attempt these analyses within this study.

Roberts et al. (2020) determined that the earliest human foragers within Wallacea now dates to 42,000 years. They further provided evidence that these early foragers in Wallacea (specifically the islands of Timor and Alor) relied on both marine and rainforest resources and were more adaptable than previously considered. Marine producers have a higher $\delta^{13}C$ value (− 14 to − 4‰) than all terrestrial $C_3$ plants. Whilst these values share an overlap with the $\delta^{13}C$ isotopic values representing a mixed $C_3/C_4$ diet (− 10 to − 2‰), marine producers can be distinguished from terrestrial through the analysis of the nitrogen system ($\delta^{15}N$). In marine environments, there are a greater number of trophic levels compared to terrestrial environments, leading to more trophic enrichment of the isotope ratios. Therefore, higher $\delta^{15}N$ values in the collagen signify the food sources to be of marine origin, with lower $\delta^{15}N$ values indicating a terrestrial vegetation source (Kusaka et al. 2015).

Most recently, Suraprasit et al. (2021) conducted $\delta^{13}C$ and $\delta^{18}O$ analysis on both *H. sapiens* and faunal tooth enamel (a mix of omnivore, carnivore and herbivore species) from Tham Lod Rockshelter (TLR), located in the highland Pang Mapha, northwestern Thailand. Suraprasit et al. (2021) sought not only to reconstruct the palaeovegetation context for hunter-gatherer societies towards the end of the Late Pleistocene (34–12 ka) in highland MSEA, but also to investigate the potential northern limit of the LGM savannah corridor. $\delta^{13}C$ results from both *H. sapiens* and faunal tooth enamel returned a median of − 4.3‰ and a range of − 16.0‰ to + 4.7‰ (Fig. 3g). The $\delta^{13}C$ values for *H. sapiens* specifically fell within the ranges of − 14‰ and − 9.4‰. Suraprasit et al. (2021) determined these results to represent *H. sapiens* consuming mixed vegetation, with a higher quantity of $C_3$ plants, indicating that tropical forests and grasslands were more widespread and connected in MSEA during the LGM than previously considered. Suraprasit et al. (2021) suggest that these results alongside the work of Bourgon et al. (2020) on Tam Hay Marklot, northeast Laos, serve as evidence to extend the latitudinal limit of the savannah corridor farther north. Further research into the arguably still understudied highlands of MSEA is clearly needed.

Ultimately, stable isotope analysis conducted on both fauna and hominin tooth enamel has proven successful in expanding understanding of the palaeodiets of these species, allowing for a reconstruction surrounding palaeovegetation of archaeological sites of both mainland and island SEA. Research in this area is far from complete. Whilst stable isotope studies on bone collagen have proved unsuccessful in the tropical climate, there remains significant potential to apply isotope studies of faunal and hominin tooth enamel at archaeological sites where these fossils are found. This will enable the further development of a quantitative argument for the existence of a dynamic vegetation landscape across SEA and ISEA during the Pleistocene and how this influenced the migrations and settlements of early *H. sapiens*. Recent advances in the application of $\delta^{66}Zn$ to faunal tooth enamel and its success in determining trophic levels at Tam Hay Marklot, northeast Laos (Bourgon et al. 2020), also suggest opportunities for expanding the range of stable isotope proxies routinely applied in the region.

## Stable isotopes in speleothems

Speleothems are precipitated cave carbonates formed by the degassing of $CO_2$ bearing water that enters the cave system via percolation through pores and cracks in the host limestone (White, 1976). Speleothems occur in a diversity of forms depending on cave morphology, but the most commonly used in stable isotope studies are flowstones and stalagmites, which have been used to infer palaeoenvironmental changes on both a global and local scales (Nguyen et al. 2020; Douglas et al. 2016; Hendy, 1971; McDermott, 2004).

Speleothems offer specific advantages as terrestrial proxy archives; they grow continuously for up to $10^5$ years, leaving undisturbed growth layers which do not lose resolution as they age and they exist on all continents, except Antarctica (Heidke et al. 2018). Speleothems are highly amenable to radio-isotope dating at a high resolution, particularly Uranium-series dating, and to a lesser extent, radiocarbon (Dorale et al. 2004; Hellstrom, 2006; Hellstrom and Pickering, 2015). Their terrestrial nature means that they can record local and regional climatic variations. As cave deposits, speleothems are also particularly well placed as climatic archives for sites of early human occupation. Speleothems are often associated with archaeological deposits and can therefore be used to infer the climatic conditions that may have prevailed at times of ancient hominin occupation and non-occupation.

### Stable oxygen isotope ratios ($\delta^{18}$O) of speleothems

Interpretation of speleothem $\delta^{18}$O as a climate proxy works on the basis that the $\delta^{18}$O held within the speleothems represents the $\delta^{18}$O of the surface precipitation at the time of deposition (Bar-Matthews et al. 2003; Braun et al. 2019; Westaway et al. 2007). Speleothems from significant hominin sites in Europe (Bischoff et al. 2003, 2007), sites contemporaneous with archaeological records in Israel (Vaks et al. 2007) and, to a lesser extent, Indonesia (Lewis et al. 2011 (Fig. 3d); Westaway et al. 2007) have been studied to better understand how environmental changes in these areas influenced early hominin movements and behaviours.

A question in interpreting $\delta^{18}$O isotope ratios from speleothems is whether they solely represent changes in meteoric $\delta^{18}$O. External factors such as temperature, pH of rainwater and transfer time from the surface all influence the $\delta^{18}$O signal preserved in the speleothem (Denniston and Luetscher, 2017; Guo and Zhou, 2019; McDermott, 2004). Karst processes such as kinetic isotope fractionation from the degassing of $CO_2$ during speleothem formation, prior calcite precipitation, karst hydrological processes and seasonal fluctuations in cave ventilation have also been identified as variables that can affect the $\delta^{18}$O signal (Partin et al. 2013 and references therein; Treble et al. 2022). To overcome this, contemporary studies of the modern cave system are used to better inform interpretation of palaeoenvironments. These assumptions can then be applied to palaeo samples from the same system (Tremaine et al. 2011). Alternative methods for identifying potential non-equilibrium fractionation processes include geochemical approaches, namely oxygen isotope analyses of samples along a transect perpendicular to the growth axis, a.k.a. the 'Hendy Test' (Hendy, 1971; Li et al. 2021) and examination of the magnesium to calcium (Mg/Ca) ratios (Ronay et al. 2019) to identify potential post-depositional recrystallisation.

Whilst controls of the isotopic composition of rainfall have site-specific complexities (size and height of the cave, location in the landscape, permeability of overhead limestone and distance from the sea), several studies use $\delta^{18}$O records to reconstruct variations in monsoon intensity (Cheng et al. 2012; Dennison et al. 2000; Johnson et al. 2006; Wang et al. 2001, 2008). A notable example of this is the reconstruction of the EAM through the last 224,000 years (Wang et al. 2008).

$\delta^{18}$O stable isotope analysis has been extensively applied to several caves in Mainland China, including Hulu and Sanbao Cave (Wang et al. 2001, 2008), Dongge Cave (Dykoski et al. 2005), Xiaobailong Cave (Cai et al. 2015) and Yangkou and Xinva Cave (Zhang et al. 2017), to better comprehend the climatic controls of the Asian Monsoon system on a global scale. Whilst these studies are essential to understanding both past and present behaviours of the monsoon, global climate can also be mediated by local scale factors (vegetation cover, sea levels and the resulting landmass exposure). Therefore, direct palaeoenvironmental evaluations of the local dynamics of key archaeological sites are essential. As a local palaeoenvironmental proxy, speleothems have not been explored to their maximum potential in SEA.

Speleothem data for SEA includes records from Flores, East Java and Borneo (Ayliffe et al. 2013 (Fig. 3e); Griffiths et al. 2009, 2016; Lewis et al. 2011; Partin et al. 2013; Westaway et al. 2007). Not all of these studies associate their palaeoenvironmental findings with the archaeological record of the site. Ayliffe et al. (2013) focused on the $^{230}$Thorium-dated stalagmite $\delta^{18}$O record from Liang Luar cave, west Flores. They assessed the millennial scale changes of the Australian-Indonesian monsoon system over the last 31,000 years as a larger scale palaeoclimate proxy. However, this site is within 2 km of Liang Bua Cave, Flores, where *Homo floresiensis* were initially believed to have been present from ~ 95 to 12.5 ka (Brown et al. 2004; Morley et al. 2017; Morwood et al. 2004; Sutikna et al. 2018), redated to ~ 100–60 ka by Sutikna et al. (2016). Evidence of *H. sapiens* (Sutikna et al. 2016) has also been found at the site. This makes the records a valuable local-scale palaeoprecipitation proxy to assess the implications of climate on the former species survival and extinction, and the arrival of the latter.

Westaway et al. (2007) analysed $\delta^{18}$O stable isotope records in a speleothem from Liang Luar and Liang Neki, (also within a 2-km radius of Liang Bua), Flores, to investigate if changing climate parameters were in part responsible for the extinction of *H. floresiensis*. This study returned inconclusive findings, allowing the possibility of a volcanic eruption at 12.5 ka and/or the arrival of *H. sapiens* as viable causes, based on the original dating. However, the redating by Sutikna et al. (2016) raises the question as to whether this hominin species was already previously extinct.

Westaway et al. (2007) show differences between Flores and Java speleothem records, with a shift towards higher $\delta^{18}O$ (indicating a prolonged dry period) occurring on Java at 38 ka, but significantly earlier on Flores at 43 ka. The onset of increased rainfall, interpreted as signifying the end of the LGM, also differs between sites, taking place on Java at 17–16.5 ka but with a delayed onset of 13 ka on Flores. Investigating archaeological sites in climatically marginal zones vulnerable to the migration of monsoonal systems, like Java and Flores, affords insights into the adaptability of early *H. sapiens* that inhabited these environments during the Late Pleistocene (Morley, 2017).

Speleothem $\delta^{18}O$ isotope records from Flores can be correlated with micromorphological thin sections from sediment samples from the site. Linking these records enables a greater insight into the depositional and diagenetic history of the cave during periods of human occupation and non-occupation (Morley et al. 2017). Where the speleothem $\delta^{18}O$ records provide a palaeoenvironmental proxy, the micromorphology can assist in discriminating human activities at the site, so utilising these together can better determine if there is a trend between these two factors.

## Stable carbon isotope ratios ($\delta^{13}C$) of speleothems

Changes in speleothem $\delta^{13}C$ has been suggested as a proxy for palaeovegetation patterns ($C_3$ versus $C_4$) (Bar-Matthews et al. 1999; Drysdale et al. 2006), with $\delta^{13}C$ values between − 14 and − 6‰ representing a $C_3$ vegetation, whereas elevated values of − 6 to + 2‰ signify a $C_4$ landscape (McDermott, 2004). However, additional factors can influence the $\delta^{13}C$ of speleothems. These include the atmospheric $pCO_2$ concentration (Schubert and Jahren, 2012), the water levels in the surrounding soil, levels of degassing of $CO_2$ from the epikarst, the carbonate content of the bedrock and the rooting depths of surrounding plant species (for a detailed review, see Wong and Breecker (2015) and references therein). The transfer of carbon within cave systems has been extensively explored (Carlson et al. 2019; Fohlmeister et al. 2020; McDermott, 2004; Wong and Breecker, 2015), and it is unlikely that a single process controls the $\delta^{13}C$ signal at all sites. As a result, $\delta^{13}C$ stable isotope data of speleothem as an independent palaeoclimatic proxy is less frequently discussed (Fohlmeister et al. 2020).

Separating the input from atmospheric, soil and microbial processes and vegetation type is a particular problem in using $\delta^{13}C$ records to interpret climate changes at a given site (Blyth et al. 2013a; Wong and Breecker, 2015). Partin et al. (2013) investigated $\delta^{13}C$ stable isotope data from Gunung Mulu and Gunung Buda National Parks, northern Borneo. Utilising Mg/Ca and Sr/Ca elemental analysis alongside $\delta^{13}C$, Partin et al. (2013) found no connection between the $\delta^{13}C$ of the bedrock and dripwater or speleothem $\delta^{13}C$. They concluded that the $\delta^{13}C$ stable isotope records resulted from changes in precipitation and/or vegetation dynamics above and surrounding the cave but were unable to isolate a single control on the signal. However, noting a $\delta^{13}C$ stable isotope decrease of 1–2‰ during the glacial-interglacial transition, Partin et al. (2013) argued that increased speleothem $\delta^{13}C$ during the LGM could be due to an increased presence of $C_4$ vegetation in accordance with the Heaney's (1991) 'savannah corridor' hypothesis.

Wong and Breecker (2015) argued that the decrease of 1–2‰ in the $\delta^{13}C$ is a result of deglacial warming, leading to a decrease in the $CaCO_3$-$CO_2$ carbon isotope fractionation in the karst system. Highlighting the need to analyse modern speleothem samples to refine palaeoclimatic data interpretation, they find atmospheric $CO_2$ and temperature explain $68 \pm 27\%$ of the degree of observed deglacial speleothem $\delta^{13}C$ declines. With this underlying knowledge, they recommend that the measurement of $\delta^{13}C$ from the speleothem $CaCO_3$ precipitated during periods of maximum and minimum cave ventilation be used to distinguish when different controls on the signal are at their maximum and minimum (Wong and Breecker, 2015). However, this is applicable only to speleothems in temperate climates that experience a sufficiently high seasonal contrast, having limited applicability in the tropical karst settings of SEA.

## Organic isotope proxies from speleothems

Over the past 20 years, there has been increasing focus on extracting molecular organic material from speleothems as another source of palaeoenvironmental information (Blyth et al. 2008, 2016). Potential proxies include biomarkers such as *n*-alkanes and lignin which relate to past vegetation (Blyth et al. 2007, 2010, 2011; Heidke et al. 2018; Xie et al. 2003) and microbial glycerol dialkyl glycerol tetraethers (GDGTs) whose composition and molecular structure are used to develop quantitative/semi-quantitative temperature reconstructions (Baker et al. 2019; Blyth and Schouten, 2013).

To separate controls on the $\delta^{13}C$ signal in a stalagmite sample from Assynt, Scotland, Blyth et al. (2013a) combined stable isotope analysis of the calcite (representing the $CO_2$ dissolved in dripwater), with analysis of the non-purgeable organic carbon (NPOC) $\delta^{13}C$, via liquid chromatography-isotope ratio mass spectrometry (LC-IRMS) (Blyth et al. 2013b) and compound-specific isotope analysis (CSIA) from *n*-alkanes. By examining more than one carbon pool, Blyth et al. (2013a) identified an inverse correlation in the calcite $\delta^{13}C$ and NPOC $\delta^{13}C$. The calcite $\delta^{13}C$ was hypothesised to record dissolved $CO_2$ controlled by soil respiration. As microbes mostly selectively use and respire $^{12}$C, increased microbial activity should lead to a depletion in soil $CO_2$ $\delta^{13}$C and vice versa (Blyth et al. 2013a). Conversely, the NPOC $\delta^{13}$C responds positively to increased microbial activity, due to $^{13}$C enrichment of residual organic matter. The study suggested that when soil microbial activity becomes the dominant control in the isotope signal, this will be represented in an inverse relationship between the calcite $\delta^{13}$C and NPOC $\delta^{13}$C. This method potentially allows refinement of the controls on the $\delta^{13}$C signal in speleothems. However, vegetation change can and does occur in tandem with increased microbial activity. Therefore, combining $\delta^{13}$C speleothem data with additional proxy records to form a multi-proxy approach is imperative (Blyth et al. 2013a, 2016).

Measuring compound-specific $\delta^{13}$C in plant-derived molecules offers a way to separate the vegetation derived signal from other drivers. Blyth et al. (2013a) were able to extract enough long chain *n*-alkanes (plant wax derived hydrocarbons) from a speleothem in Lower Traligill Cave in Assynt, north-west Scotland, to obtain a $\delta^{13}$C signature of − 29.8 to − 34.4‰, which was reflective of the $C_3$ vegetated landscape around the test cave. However, the amount of compound obtained was not sufficient to constrain errors on the isotopic data, limiting its utility. The viability of this approach therefore depends on the compound abundance in each speleothem sample.

Currently, neither biomarker analysis nor isotopic analysis of organic matter preserved in speleothems has been successful in Pleistocene archaeological cave sites in MSEA or ISEA due to the low organic content of the samples (Blyth, pers. comm.). The methods required are destructive and often require a considerable sample size (Blyth et al. 2016). Nevertheless, the number of sites this approach has been tested on is limited, and so, if permission is granted during excavations, these methods could still be explored. Where successful, this has the potential to provide increased detail with regard to the palaeovegetation patterns and palaeoenvironments in and around caves during periods of early *H. sapiens* occupation.

## Stable isotopic analysis of bivalves and gastropods

Isotope analyses of mollusc shells have made a significant contribution to investigating past climates and environments since the early 1950s. Studies on both marine and terrestrial molluscs include North and South America (Yanes, 2015; Yanes et al. 2019), Europe (Holmes et al. 2020; Walliser et al. 2015; Wierzbowski, 2015), Africa (Alberti et al. 2019; Keleman et al. 2019; Prendergast et al. 2015) and China (Wang et al. 2019, 2020). At archaeological sites, studies of isotope ratios preserved in mollusc shells offer insights into past environments as well as the diets and behaviours of ancient peoples (Prendergast et al. 2015). In archaeological settings, molluscs of marine origin, terrestrial origin and freshwater origin can be present.

Within the tropical setting of SEA, mollusc $\delta^{18}$O ratios are used primarily as a proxy for precipitation variability, rather than temperature due the dominant effect of rainfall and evaporation on the $\delta^{18}$O of meteoric water in the low latitudes (see Dansgaard, 1964; Rozanski et al. 1993). There is a lack of seasonal temperature variation in the tropics, and so lower $\delta^{18}$O represents periods of lower $\delta^{18}$O of rainfall, which has been linked to a stronger Asian Monsoon (Marwick and Gagan, 2011). By contrast, higher $\delta^{18}$O values suggest a drier environment (weakening of the monsoon) (Rabett et al. 2011, 2017). $\delta^{13}$C can also be measured from mollusc shells, allowing inferences on mollusc diet and carbon cycling in either terrestrial or aquatic ecosystems (Goodfriend and Ellis, 2002; Goodfriend and Magaritz, 1987; Stott, 2002).

Unfortunately, molluscs found in archaeological settings are prone to recrystallisation as a result of diagenesis (dissolution and reprecipitation) after they have been deposited (Prendergast and Stevens, 2006). Subsequently, the isotopic signatures in affected shells represent in part the chemistry of the water when diagenesis took place, rather than a palaeoenvironmental signal (Prendergast and Stevens, 2006). However, bivalves and gastropods that have been subject to diagenetic alterations can now be identified and disregarded from palaeoenvironmental reconstructions through applications of high-resolution microscopy and X-ray diffraction (XRD).

Within SEA, stable isotope studies have been conducted on both aquatic and terrestrial molluscs. Stephens et al. (2008) applied $\delta^{18}$O and $\delta^{13}$C analysis to both modern and prehistoric samples of the estuarine bivalve *Geloina rosa* harvested from a mangrove by early modern humans at Niah Cave, Borneo. This study aimed to better understand the influence of seasonality on the subsistence strategies of early *H. sapiens.* The $\delta^{18}$O and $\delta^{13}$C values from two modern samples of *Geloina rosa* displayed a co-variation with $\delta^{18}$O values of − 6.7‰ and − 6.4‰ and $\delta^{13}$C values of − 9.9‰ and − 9.5‰, respectively. Stephens et al. (2008) attributed this common controlling factor to the heavy monsoon rains from November to March. In three prehistoric specimens of *Geloina rosa*, $\delta^{18}$O values of − 7.4‰, − 7.1‰ and − 6.9‰ were hypothesised to represent a period of moderate rainfall, leading Stephens et al. (2008) to conclude that these bivalves were collected from mangroves during periods of moderate runoff. However, there is a lack of co-variation between $\delta^{18}$O and $\delta^{13}$C isotope values of the prehistoric samples. Stephens et al. (2008) do not specify the $\delta^{13}$C data, going on to propose that metabolism of the mollusc rather than the molluscan diet was the dominant influence. These studies are only based on five bivalves in total (two modern and three prehistoric), which calls for future studies with larger sample sizes.

Marwick and Gagan (2011) highlighted the need for new and improved continuous records of palaeoenvironmental change spanning the Late Quaternary in SEA, to better understand the nature of early *H. sapiens* dispersal and settlement patterns across the region. Noting the consistency and abundance of the freshwater bivalve *Margaritanopsis laosensis* within Tham Lod and Ban Rai rockshelters, northwest Thailand, they conducted $\delta^{18}$O analysis on *M. laosensis* to develop a new palaeomonsoon proxy record extending to 35 ka BP, finding diagenetic processes to have not significantly altered their mineralogy. $\delta^{18}$O values correlated well with the $\delta^{18}$O records from Hulu and Dongge Caves, China, ranging from − 8.71 to − 6.03‰ between 33 and 20 ka and indicating a largely wet and unstable climate in northwest Thailand (Fig. 3f). After 20 ka through to the Early Holocene at 11.5 ka, the $\delta^{18}$O values from Tham Lod and Ban Rai increased to between − 7.23 and − 5.25‰, representing a shift towards drier conditions towards the end of the Pleistocene. Marwick and Gagan (2011) noted peak aridity to have occurred at 15.6 ka, with $\delta^{18}$O values increasing to − 5.4‰, occurring during Heinrich Event 1, indicating the ITCZ migrated south, resulting in cooler and drier conditions in SEA. A notable decrease in $\delta^{18}$O values to − 8.45‰ at 9.8 ka BP represent a significant increase in precipitation. In discussing the archaeological implications of these results, Marwick and Gagan (2011) drew upon archaeological evidence from Sai Yok in western central Thailand and Spirit Cave, northwest Thailand, highlighting that early *H. sapiens* experienced more complex environments than previously considered by van Heekeren and Knuth (1967) and Gorman (1972). Future investigation of how this palaeomonsoon record relates to the more local archaeological findings around Tham Lod and Ban Rai would add further value.

At Laili Cave, northern Timor-Leste, Hawkins et al. (2017) presented data on the potential adaptions of *H. sapiens* to the local Late Pleistocene ecosystem through stable isotopic analysis of $\delta^{18}$O and $\delta^{13}$C preserved within the aquatic chiton shell *Acanthopleura*. The cultural sequence of stone artefacts, serving as evidence for early *H. sapiens* presence at the site, dates to 44.6 ka, but there are limited palaeoenvironmental reconstructions during this period. Hawkins et al.'s (2017) attempt to refine the Late Pleistocene palaeoenvironmental setting ultimately proved inconclusive. Instead of a decrease in $\delta^{18}$O towards the end of the LGM, representing an increased rainfall pattern, the $\delta^{18}$O values from *Acanthopleura* instead decreased slightly with stratigraphic depth. This is attributed to microenvironmental processes such as local rainfall or slopewash patterns. It is presumed the latter refers to the deposition of molluscs from different time periods or the readjustment of previously deposited molluscs already in the stratigraphic sequence.

At Tam Pà Ling, Laos, Milano et al. (2018) applied stable isotope analysis to modern samples and a prehistoric sample of the terrestrial mollusc *Camaena massiei.* Understanding the palaeoenvironmental conditions of this site is imperative as the cave currently holds some of the earliest evidence for *H. sapiens* in mainland SEA (~ 70 ± 8 ka), supporting their presence in the region to as far back as MIS 4 (Demeter et al. 2012, 2015, 2017; Shackleford et al. 2018). Milano et al. (2018) aimed to validate the $\delta^{18}$O ratio obtained from the prehistoric *Camaena massiei* dated to between 62 and 78 ka, to improve the contextualisation of *H. sapiens* by reconstructing the environment at the time of their first known arrival.

Milano et al. (2018) concluded that the $\delta^{18}$O value of − 7.2‰ obtained from the *C. massiei* from 62 to 78 ka reflects a woodland ($C_3$ vegetation dominant) landscape prevailing during MIS 4. Whilst MIS 4 is known to have had a reduced summer monsoon intensity, which would have resulted in less rainfall, drier conditions and an increase in the presence of open grasslands ($C_4$ vegetation), this is not strongly seen in the *C. massiei* $\delta^{18}$O isotopic ratio. However, with only one *C. massiei* retrieved from the sediment sequence to represent 62–78 ka, interpretations of local conditions from this study alone must be taken with caution.

The clumped isotope composition of mollusc carbonate (quantified by $\Delta_{47}$ value) is a rapidly developing tool with the potential to serve as a quantitative palaeothermometer. To date, it has been applied to estimate the formation temperature of shell carbonate (Ghosh et al. 2006; Guo et al 2019; Zaarur et al. 2011, 2013), the growth temperatures of speleothem (Affeck et al. 2008) and the ground temperature during early diagenesis of fossil bone carbonate (Suarez and Passey, 2014). Clumped isotope thermometry is based on the ordering of the heavier isotopes $^{13}$C-$^{18}$O being dependent on external temperature of the surrounding environment at the time of formation (Eiler, 2007). Implementing the $\delta^{18}$O of terrestrial molluscs as a palaeotemperature proxy is difficult, as it often requires an independent analysis of the palaeowater composition of the shell (often determined by the $\delta^{18}$O of the local precipitation). To address this, Zaarur et al. (2011) conducted clumped isotopic analysis of modern land shells from a range of locations with differing environments conditions such as Negev, Israel, Davos, Switzerland and various locations from the USA, to assess the accuracy of the assumptions applied when determining $\delta^{18}$O of shells.

When comparing the $\Delta_{47}$ temperatures of mollusc shell to the local ambient temperatures, Zaarur et al. (2011) determined the shell calcification temperatures to be consistently higher than the local temperatures. Zaarur et al. (2011) reinforced the need to assess and understand not just the local environmental conditions molluscs habitat, but also the morphological characteristics of each shell species and their behavioural lifestyle adaptions as factors influencing the snail's body temperature (Heath, 1975; Dittbrenner et al. 2009). Zaarur et al. (2011) determined $\Delta_{47}$ values to represent the temperature during shell calcification. As a result, Zaarur et al. (2011) recommended applying $\Delta_{47}$ to terrestrial shell to each species analysed as a method to resolve the accuracy when extracting palaeoprecipitation isotopic signals from the shell $\delta^{18}$O composition.

## The bigger picture: the palaeoenvironments of Late Pleistocene SEA as indicated by stable isotopes

Through the application of stable isotope techniques discussed in this review as applied to archaeological sites across MSEA, ISEA and into Sahul, researchers have recreated a more nuanced environmental backdrop to frame the behaviours of early *H. sapiens* as they traversed into and through SEA in the Late Pleistocene. Whilst the environmental reconstruction of each archaeological site in SEA is far from complete, studies conducted to date highlight the fact that the environment and floral communities present across MSEA and ISEA were complex and far from uniform.

Within MSEA, palaeoenvironmental reconstructions using stable isotope techniques in the earlier part of the Late Pleistocene are rare. At Tam Pà Ling, Laos, Milano et al. (2018) conducted $\delta^{18}$O and $\delta^{13}$C analysis on a single prehistoric *Camaena massiei* dated to between 62 and 78 ka. Milano et al. (2018) argued that the $\delta^{18}$O value of − 7.2‰ indicated a period of weaker monsoon activity and potentially drier than expected conditions in early MIS 4 and $\delta^{13}$C values of − 8.6‰ show that $C_3$ vegetation persisted during this time. However, the fact that there is only one *C. massiei* to represent 16 ka of climate demonstrates that more palaeoenvironmental studies are needed to strengthen these results.

More data is available from MSEA for the period immediately around the LGM. Marwick and Gagan (2011) used $\delta^{18}$O analysis of the freshwater bivalve *Margaritanopsis laosensis* from archaeological rockshelters in Tham Lod and Ban Rai, northwest Thailand, showing that the area experienced a predominantly wet and unstable climate between 33 and 20 ka. By 20 ka, this transitioned to a drier environment that persisted through to the early Holocene (11.5 ka), likely leading to the expansion of $C_4$ vegetation ecosystems. Consistent with this at Tham Lod rockshelter, Suraprasit et al. (2021) found the $\delta^{13}$C values of both *H. sapiens* and faunal tooth enamel between 34 and 12 ka to lie within the ranges of − 16.0‰ and + 4.7‰. Although Suraprasit et al. (2021) did not observe a notable change in diet with time, they concluded the area of Tham Lod was likely more complex than it is today, characterised by a mosaic landscape, containing a mixture of grassland areas and forested vegetation. Suraprasit et al. (2021) suggested that the limit of the hypothesised LGM savannah corridor in SEA should therefore be extended northwards.

Elsewhere in MSEA, at the archaeological sites of Hang Boi and Hang Trông, Northern Vietnam, Rabett et al. (2017) conducted CSIA of $\delta^{13}$C from leaf wax *n*-alkanes and suggested that during MIS 2 (29–11.7 ka), the regional landscape was dominated by $C_3$ vegetation, largely persisting during the LGM. From these studies, we may conclude that, towards the end of the Late Pleistocene (35–11.7 ka), MSEA as a region most likely had a broadly $C_3$-dominated vegetation regime, but with persistent and significant areas of refugial $C_4$ vegetation on a local scale, especially during the LGM. Additional isotopic records from new proxies or sites would clearly be beneficial to clarify these scenarios.

Stable isotope-based palaeoenvironmental reconstructions from ISEA stretch as far back as the Early Pleistocene (~ 1.5 million years) with Puspaningrum et al.'s (2020) application of $\delta^{13}$C and $\delta^{18}$O analysis to Proboscidean tooth enamel. Whilst Puspaningrum and colleagues found the vegetation of several archaeological sites in Java to have been characterised by $C_3$ vegetation in the Early Pleistocene, in the Middle Pleistocene, $C_3$ vegetation gives way to a predominately $C_4$ landscape. However, towards the end of the Middle Pleistocene, $\delta^{13}$C values again deplete, giving rise to an ecosystem characterised by $C_3$ vegetation, with some $C_4$ inclusions by the Late Pleistocene-Holocene.

These findings broadly align with earlier research by Westaway et al. (2007) where $\delta^{18}$O data from speleothems in Gua Gebang cave, eastern Java, record a return to wetter conditions towards the later stages of the Late Pleistocene. However, whilst Westaway et al. (2007) observed an enrichment in $\delta^{18}$O values at 38 ka, indicating a prolonged dry period, Puspaningrum et al. (2020) does not observe this. These differences may be due to a difference in geographical location on the island of Java or due to proxy-specific issues. The studies of Bird et al. (2007) and Wurster et al. (2010, 2019) spanning several archaeological sites in Palawan, Philippines (Makangit and Gangub Caves), Malaysia (Batu Cave) and Borneo (Niah and Saleh Caves) are complimentary of one another and highlight the presence of significant savannah areas in the LGM, as well as sites where the $C_3$ vegetation persists. Collectively, these studies show that, as for MSEA, the vegetation landscape of ISEA in the Late Pleistocene (40–11.7 ka) is complex and locally varied. This complexity supports the case for a research focus on local detailed palaeoenvironmental reconstructions for each archaeological site.

## Conclusions and future research directions

Following their early application to archaeology by van der Merwe and Vogel (1978), stable isotope techniques have become a valuable, arguably essential asset in contextualising the environmental conditions of archaeological sites during varying periods of occupation. Applied to archaeological sites around the world, stable isotope research has advanced our understanding of past environments through the analysis of sediments (Huckleberry and Fadem, 2007), bat guano (Onac et al. 2015; Mizutani et al. 1992; Wurster et al. 2007, 2008, 2009), leaf wax CSIA (Collins et al. 2017; Magill et al. 2016; Rabett et al. 2017), speleothems (Bar-Matthews et al. 2000, 2003, Bar-Matthews and Ayalon, 2011; Drysdale et al. 2006; Vaks et al. 2007), molluscs (Leng and Lewis, 2016, and references therein; Pérez et al. 2020; Prendergast et al. 2015), as well as early human and faunal diets through the analysis of stable isotopes in bone and tooth enamel (Janssen et al. 2016; Lee-Thorp et al. 2010; Louys and Roberts, 2020; Sponheimer et al. 2013; White et al. 2009).

Whilst the most common approach to environment reconstruction in archaeological sites remains palynology, within the tropics, pollen preservation is often compromised, especially in upland cave sites where sediments are highly toxic (Rabett et al. 2017). Given the excellent preservation of materials amenable to stable isotope analysis, the incorporation of stable isotope techniques such as $\delta^{13}$C analysis on organic materials within archaeological sites is steadily increasing. Research papers published on human–environment interactions of the past have seen an exponential rise from as few as 10 per annum in the 1970s, to approximately 300 per annum since 2000 (Carleton and Collard, 2020). Of these, more than 77 per year interpret one or more proxy to reconstruct palaeoenvironments in and around archaeological sites. Carleton and Collard (2020) specifically noted the increasing application of dietary and environmental isotopes as the preferred proxy method. Developing interpretations of these early human interactions with the environment is not only essential for comprehending how our ancestors adapted to changing local climates, but also for present and future generations as we enter increasingly unprecedented times of anthropogenic driven climate change (IPCC 2021).

Applications of heavier and non-traditional isotope analysis such as zinc ($\delta^{66}$Zn), calcium ($\delta^{44}$Ca) and strontium ($\delta^{87}$Sr) in artefacts, bone and/or tooth enamel are also on the rise. Whilst these techniques are not new, having been applied within archaeological settings for over 20 years, $\delta^{87}$Sr and $\delta^{44}$Ca have yet to be expanded to archaeological sites in SEA. Applications of $\delta^{66}$Zn isotope ratios have recently been successfully applied to fauna tooth enamel in Tam Hay Marklot, Laos, proving they have the potential to be expanded to additional sites to further contextualise local environmental reconstructions as a trophic tracer of faunal dietary consumption (Bourgon et al. 2020).

In SEA, the application of isotope analysis varies across each Pleistocene archaeological site. Whilst applications and interpretations of $\delta^{13}$C ratios in guano and $\delta^{18}$O in speleothems are well developed, those derived from molluscs are more complex to interpret, especially with respect to $\delta^{13}$C. Meanwhile, analysis of stable isotopes in sediment organic matter and leaf waxes are still in their infancy in the region's archaeological sites. Expanding stable isotope analysis to all sites that contain the necessary source materials in Sunda, Wallacea and Sahul would enable the development of a more robust palaeoenvironmental proxy record, both for individual sites and SEA as a whole. The aim of sampling the local environment of archaeological sites in this region should not be to create a single coherent record of MIS 5 (as this is not likely obtainable) but to generate multiple palaeoenvironmental records of direct relevance to occupation and non-occupation periods at each site. This will provide a better understanding of the local conditions that influenced early modern humans to settle or leave certain sites. It will also increase understanding of how these factors varied across different locations of SEA at different times during MIS 5–2 (124–11.7 ka).

The purpose of this review is to address the current applications of stable isotope analysis in Pleistocene archaeological sites across SEA and assess how they can contribute to a more robust reconstruction of the environment when early *H. sapiens* arrived, settled and migrated through the landscape in the Late Pleistocene (124–11.7 ka). Existing stable isotope research shows that isotopic analyses of sediments, guano, speleothem, tooth enamel and leaf waxes offer considerable potential. When these techniques are combined with geoarchaeological techniques such as micromorphology, X-ray diffraction (XRD), X-ray fluorescence (XRF), scanning electron microscopy (SEM) and Fourier transform infrared (FTIR) to name but a few, we can address current knowledge gaps regarding the environmental conditions at each site and how these influenced *H. sapiens* migrations and behaviours during a crucial point in our species' history.

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