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Hominin Dispersal and Settlement East of Huxley's Line

The Role of Sea Level Changes, Island Size, and Subsistence Behavior

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The thousands of islands east of Huxley's Line have never formed a single land mass or been connected to Sunda or Sahul. The earliest records of hominins in this area are stone tools recovered from Pleistocene deposits on Flores and Sulawesi. Subsistence by these hominins as well as the later subsistence patterns exhibited by *Homo floresiensis* suggest that exploitation of marine resources was, at best, rare and opportunistic. Likewise, the fragmentary hominin remains recovered from Late Pleistocene deposits from Callao Cave in the Philippines exploited large game at the expense of marine resources. In contrast, the earliest zooarchaeological records of modern humans are dominated by marine fish and shellfish and include the earliest evidence of pelagic fishing using shell tools, implying complex fish-capture technology. Pleistocene lithic assemblages on these islands are unspecialized, indicating reduction of predominantly locally available stone to produce flakes and irregularly retouched pieces. By the terminal Pleistocene, records of human subsistence on very small islands indicate almost total reliance on marine foods for protein. We propose that strong links exist between subsistence strategies and dispersal throughout Wallacea, with subsistence strategies available to pre-*sapiens* hominins in the region being a major limiting factor in their dispersal.

The movement of hominins through island Southeast Asia and into Australia is the last leg of several migration events that began in Africa thousands of years before. Debate over the route(s) taken by these hominins is ongoing, with various hypotheses supporting an inland or coastal route (Erlandson and Braje 2015; Groucutt et al. 2015; Reyes-Centeno et al. 2014 and other papers in this volume). Regardless of route choice, however, once hominins arrived at Huxley's Line (see fig. 1), earlier Pleistocene hominins would have had to undertake sea journeys to reach Sulawesi and Flores, and late Pleistocene *Homo sapiens* would have had to undertake even longer sea crossings to arrive on Sahul.

Dispersals by the earliest hominins in the region are likely to have been incidental and possibly enabled by natural rafts carried by oceanic currents and perhaps tsunamis (Dennell et al. 2014). Irrespective of dispersal mechanism, successful colonization of an island requires that subsistence needs are met, although this aspect does not appear to have been given as much consideration in the migration of pre-*sapiens* east of Huxley's Line as in the migration of *H. sapiens*. For example, Allen and O'Connell (2003, 2008) and O'Connell and Allen (2007, 2012) applied the tenets of optimal foraging to predict the pattern of human dispersal to Australia, arguing that the movement of humans through Wallacea was driven by a negative change in resource availability, which was driven, in turn, by fluctuations in sea level that encouraged relocation to more optimal areas (i.e., new islands). However, hypotheses such as these have yet to be convincingly tested due to limited archaeological records in the region (Anderson 2017; Kealy, Louys, and O'Connor 2016).

Sea level changes also affect island size and intervisibility between islands. The lower sea levels produced during glacials are generally thought to have been optimal for migration in the Wallacean archipelago, because the shorter distances between

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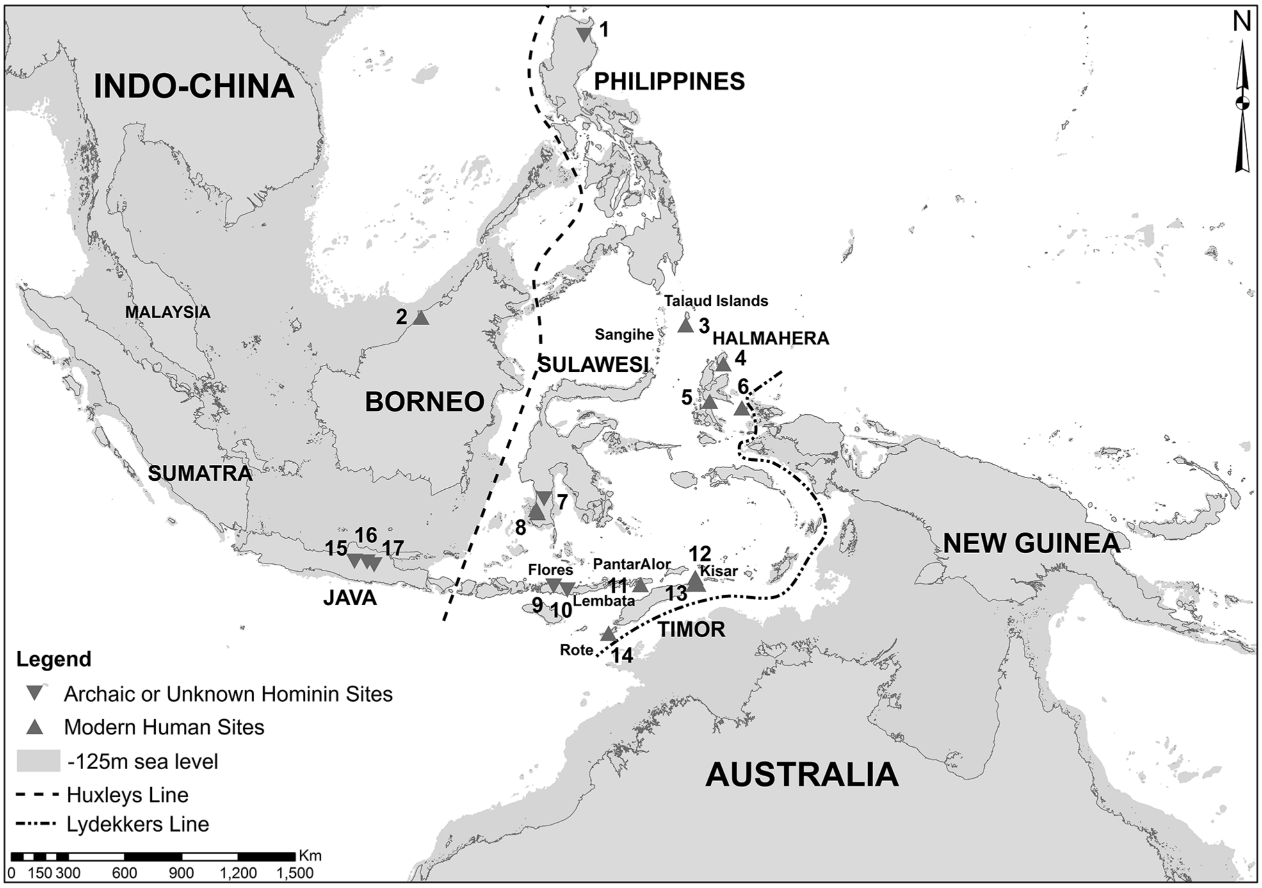

Figure 1. Map of island Southeast Asia showing sites mentioned in text. Downward-pointing triangles indicate sites associated with archaic or "unknown" hominin localities, and upward-pointing triangles indicate sites associated with modern humans. A color version of this figure is available online.

islands would presumably have made sea crossings easier (Birdsell 1977; Kealy, Louys, and O'Connor 2016, 2017). However, some researchers (Chappell 1993; O'Connell, Allen, and Hawkes 2010; O'Connor and Chappell 2003) have argued that rising sea levels after 55 ka might have encouraged and even facilitated colonization. The small number of Pleistocene archaeological sites in the region makes it hard to test competing migration hypotheses as they relate to timing and sea level changes (Anderson 2017; Kealy, Louys, and O'Connor 2016).

Although Pleistocene archaeological records are rare in Wallacea, the situation is beginning to improve, with new sites recorded and sequences analyzed in the past few years (O'Connor 2007; O'Connor et al. 2010; Pawlik et al. 2015; Robles et al. 2015; Samper Carro et al. 2016; Szabó, Brumm, and Bellwood 2007). In particular, the zooarchaeological records produced on several Wallacean islands allow for the examination of some of the factors that may have been influential in facilitating dispersals in the region. Here, we review these records, paying particular attention to the environmental limitations of small oceanic islands for successful colonization. We examine the probable subsistence behavior and distribution of the first hominins in the region and contrast these with *H. sapiens* in the later Pleistocene in the context of sea level changes and island size during the likely periods of movement.

Bathymetry and Sea Level Changes at the Regional Scale

The Pleistocene saw enormous changes in the spatial environment of the Wallacean Archipelago (Kealy, Louys, and O'Connor 2017). Driven largely by dramatic changes in climate, with secondary tectonic influences, the islands of Wallacea have experienced a combination of emerging and subsiding phenomena, enlargements and shrinkages, and joining and separation that have affected the dynamics of this area. Such changes had a major impact on the island ecosystems as well as the most parsimonious pathways for human movement between islands (Kealy, Louys, and O'Connor 2016).

To date, archaeological investigations in the Wallacean Archipelago have been patchy, with most research focused on the larger islands of Sulawesi, Flores, and Timor. Logically, the larger Wallacean islands would have presented more diverse and reliable habitats for sustaining genetically viable populations. In the past 100,000 years, sea levels in Wallacea have fluctuated below present-day heights, with drops of up to 135 m during the last glacial maximum (LGM; Lambeck and Chappell 2001). Studies in Timor and other islands also suggest the region has experienced a significant degree of tectonic uplift during this time, although neither the geographic extent nor the results of the research are consistent throughout Wallacea (Chappell and Veeh 1978; Cox 2009; Hantoro et al. 1994; Jouannic et al. 1988; Major et al. 2013; Nexer et al. 2015; Pirazzoli et al. 1993; Sumosusastro et al. 1989). A summary of these studies and the uplift rates recorded therein indicates a dearth of uplift research in regions such as the Halmahera Archipelago (Kealy, Louys, and O'Connor 2017, their table 1); in contrast, Timor-Leste has had numerous studies producing uplift rates that range from 0.1 to 0.6 m/kyr.

The consideration of an uplift variable in paleogeographic reconstructions is important for avoiding overestimations of island size and connectivity at times of lower sea levels. The lack of comprehensive uplift measurements throughout Wallacea means an accurate model of island uplift is currently unavailable; however, an average rate, calculated from islands with known uplift data, provides one alternative (Kealy, Louys, and O'Connor 2017). We acknowledge that this is an average calculated from data with significant variability; however, we consider a conservative estimate on past island extent preferable to ignoring uplift entirely. Thus, we adjusted the Lambeck and Chappell (2001) sea level curve to account for an average uplift rate of 0.5 m/kyr (Kealy, Louys, and O'Connor 2017) for the past 100,000 years (fig. 2). As the majority of the uplift rates are from Quaternary (and largely Holocene) limestone (Chappell and Veeh 1978; Cox 2009; Hantoro et al. 1994; Major et al. 2013; Sumosusastro et al. 1989), any minor changes in uplift rate over this time will also be averaged out across the 100-kyr sea level curve. When sea level fluctuations are adjusted for this uplift rate, the sea level trend remains the same; however, the relative drop in sea level as measured from the shoreline decreases over time (fig. 2). This is an important consideration for paleo-shoreline reconstructions, particularly those concerning the periods hypothesized for initial human colonization of Wallacea and Sahul (fig. 3). The reconstructions presented here are based on the most recent bathymetric chart of Wallacea (obtained from the General Bathymetric Chart of the Oceans data set, downloaded from http://www.gebco.net; Smith and Sandwell 1997) and the adjusted sea levels from figure 2. The reconstruction does not take sedimentation and erosion processes into account because of the unavailability of such data. Hindcasting these changes in sea level and uplift to the period of earliest hominin movements at ~1 Ma is not realistic. Nevertheless, while lowered sea levels created larger landmasses and allowed for some Wallacean islands to be connected, many of the volcanic islands in this region—for example, Pantar—were

Table 1. Archaeological sites pertaining to hominin dispersal and settlement east of Huxley's Line

Site	Published date[a]	Reference(s)
Callao Cave	66.7 ± 1 ka to Late Holocene	Mijares et al. 2010
Niah Cave	~50 ka (47,170–50,000 ka) to Late Holocene	Higham et al. 2016
Liang Sarru	35,034–33,864, 22,628–21,941 and Holocene	Ono, Soegondho, and Yoneda 2009
Daeo 2	16,767–15,889 to Late Holocene	Bellwood et al. 1998
Siti Nafisah	5,572–5,296 to Late Holocene	Bellwood et al. 1998
Golo Cave	36,350–35,001 to Late Holocene	Bellwood et al. 1998
Talepu	194–118 ka to after 103 ± 9 ka	van den Bergh et al. 2016*b*
Leang Timpuseng and Maros region	40.70 +0.87/–0.84 ka to Late Holocene	Aubert et al. 2014
Liang Bua	193 ± 33 ka (initial hominin occupation), 49.6 ± 0.5 ka (*Homo floresiensis* terminal date), 19.2 ka to Late Holocene (modern humans)	Sutikna et al. 2016; Westaway et al. 2007
Liang Bawah	238–181 ka to Late Holocene	Gagan et al. 2015
Mata Menge	810 ± 40 ka to 650 ± 20 ka	Brumm et al. 2016
Tangi Talo	No in situ artifacts; fauna dated to 900 ± 70 ka	Aziz et al. 2009; Morwood et al. 1998
Tron Bon Lei	21,000–20,560 to 3,195–3,010	O'Connor et al., forthcoming *b*; Samper Carro, Louys, and O'Connor 2017
Here Sorot Entapa	15,338–15,091 to Late Holocene	New data, this article
Jerimalai	43,002–41,313 to Late Holocene	O'Connor 2007
Lene Hara	42,454 ± 450 to Late Holocene	O'Connor, Allen, and Hawkes 2010
Matja Kuru 2	36,307–35,031 to Late Holocene	O'Connor, Robertson, and Aplin 2014
Lua Meko	28,603–27,676 to Late Holocene	Mahirta 2009
Sangiran Dome	1.66 ± 0.04 Ma to Middle Pleistocene	Bouteaux et al. 2007; Sémah, Saleki, and Falguéres 2000
Ngebung	800 ka	Bouteaux and Moigne 2010
Trinil	540 ± 100 ka to 430 ± 50 ka	Joordens et al. 2015
Kedung Brubus	700–800 ka	Storm 2012; van den Bergh et al. 1996

[a] Ages are the published calibrated ^{14}C, electron spin resonance, and U-series dates.

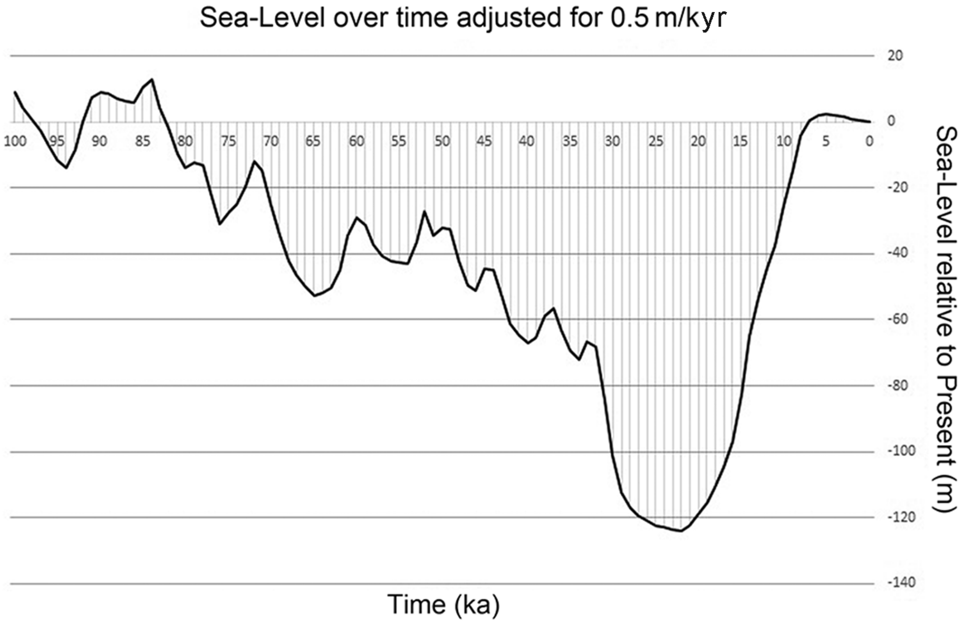

Figure 2. Sea level for the past 100 kyr (Lambeck and Chappell 2001) adjusted for 0.5 m/kyr uplift as calculated in Kealy, Louys, and O'Connor (2017, their table 1).

smaller than today, because they have been undergoing active formation since that time.

Subsistence and Dispersal of Early Hominins in Asia

When hominins began to introduce large amounts of animal protein into their diets through access and processing of carcasses is not known; however, by at least 2 Ma, hominins (likely *Homo erectus*) were practicing persistent carnivory in East Africa (Ferraro et al. 2013; Lemorini et al. 2014; Parkinson 2013; Plummer 2004), and in the Early Pleistocene, primary access of fleshed carcasses by hominins is recorded at several sites (Domínguez-Rodrigo, Bunn, and Yravedra 2014; Organista et al. 2016). Organista et al. (2016:620–621) suggest that the hominin group responsible for the dense concentration of megafauna at Bell Korongo, Olduvai Gorge, exhibited "a degree of cooperative behaviour that required a capacity for strategy, organization, communication, and physical effort." Such traits were no doubt useful in the initial dispersal of hominins outside of Africa and into Asia, although, as many other mammalian families attest, such traits are not absolutely essential for widespread migrations between Asia and Africa (e.g., O'Regan et al. 2011).

In Asia, subsistence behavior of Early to Middle Pleistocene hominins is poorly known, due in large part to a dearth of zooarchaeological evidence (Dennell 2015). Whether this dearth represents a genuine lack of evidence or reflects the much smaller volume of zooarchaeological studies in the region is unknown, but certainly taphonomic studies of faunal remains associated with hominins in the region are rare. Boaz et al. (2004) has suggested that Chinese *H. erectus* scavenged remains from a hyena den in Locality 1 of Zhoukoudian. A more recent taphonomic analysis of cervid remains from layer 3 of Zhoukoudian found no evidence of anthropogenic modifications (Zhang et al. 2015). Likewise, visual examination of a subset of faunal remains from Gongwangling found no evidence of cut marks on bones (Louys et al. 2009). Hominins likely had a role in the accumulation of large-bodied mammal remains in Panxian Dadong; however, whether this was primarily from scavenging or from hunting activities remains unresolved (Schepartz, Stoutamire, and Bekken 2005; Schepartz et al. 2003). Findings from Ubeidiya tentatively suggest some evidence for butchery and hunting of medium-size game (Gaudzinski 2004).

In Java, Storm (2012) has suggested that *H. erectus* occupied a largely carnivorous niche on the basis of the number of identified specimens and minimum number of individuals from Dubois legacy collections (specifically, Kedung Brubus and Trinil; see table 1). Storm (2012) was understandably cautious in his conclusions; a visual examination of these collections by one of the authors (J. Louys) in 2006 revealed no marks that could be unambiguously attributed to Pleistocene hominins. Likewise, Bouteaux et al. (2007) found no evidence of anthropogenic modifications on remains from several Sangiran Dome localities (Tanjung, Sendang Busik, Ngrejeng Plupuh, Grogol Plupuh, and Bukuran; table 1). The lack of obvious marks on these bones does not necessarily mean that Early and Middle Pleistocene hominins did not have access to or consume large and medium-size game. They may instead be a result of processing with tools made of materials other than stone that leave less obvious signatures on the bone, such as bamboo (West and

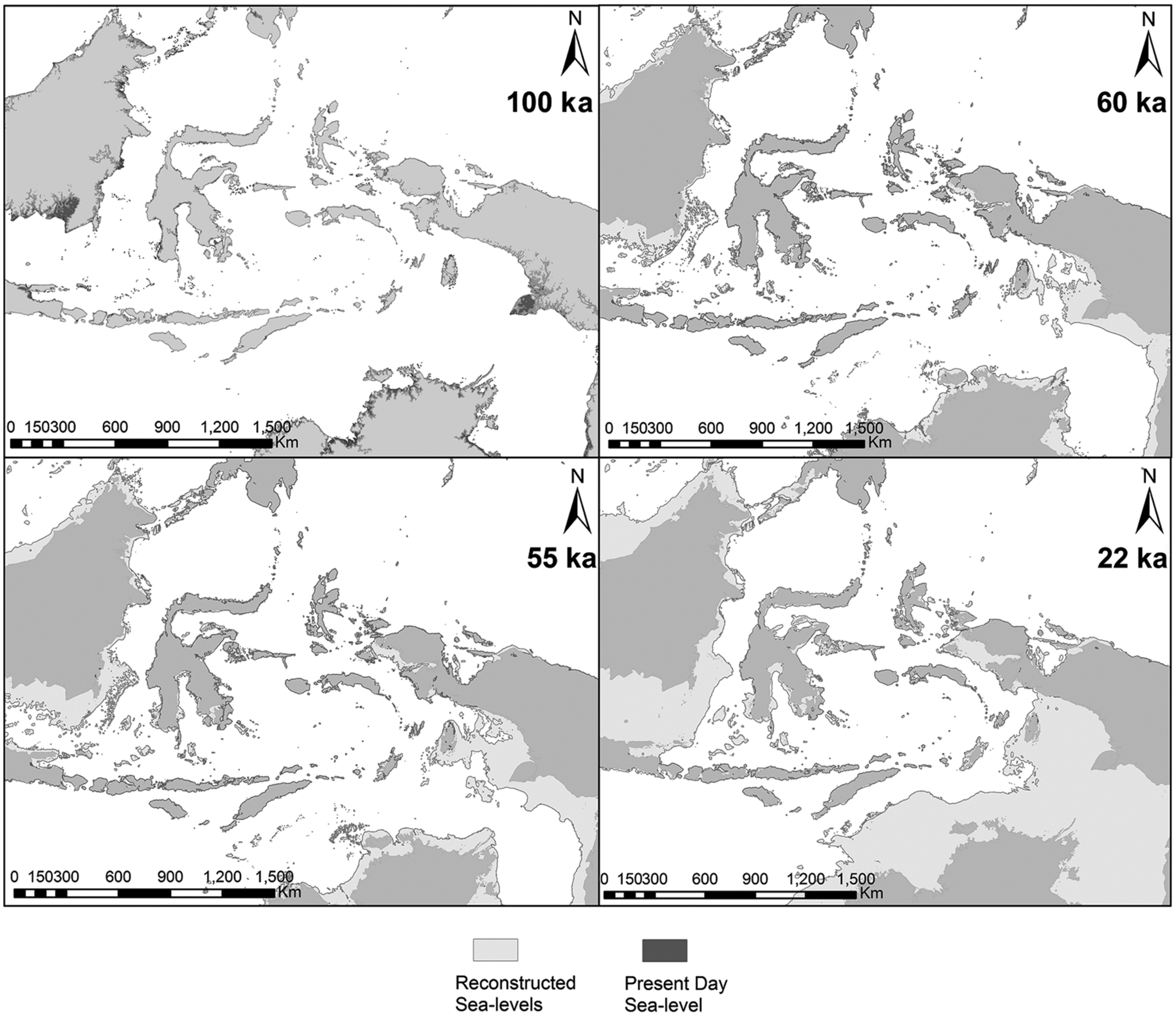

Figure 3. Palaeo-shoreline reconstructions for Wallacea and neighbors for 100 ka, 60 ka, 55 ka, and 22 ka. Modeled using the General Bathymetric Chart of the Oceans 30 arc-second bathometry chart (Smith and Sandwell 1997). Sea levels are based on the adjusted curve in figure 2. A color version of this figure is available online.

Louys 2007) or shells (Choi and Driwantoro 2007), as well as the depositional setting of the assemblages in question, minimizing the potential for hominin actions on faunal remains. For example, Zhoukoudian is primarily interpreted as a hyena den, and the aforementioned Sangiran Dome deposits represent natural fluvial accumulations (Bouteaux et al. 2007), neither of which might attract hominin attention.

Although rare, direct evidence of processing of animal carcasses by Asian *H. erectus* does exist. Choi and Driwantoro (2007) report likely shell tool cut marks on bovid (*Bos* species) remains from Bukuran and Sangiran, and Bouteaux and Moigne (2010) reported cut marks and percussion damage on long bones belonging to *Axis* species and *Duboisia* species recovered from Ngebung 2 (table 1). Despite limited direct evidence, the use and processing of large and medium-size game by Pleistocene Asian hominins is inferred by most researchers through extension of the realized niche that *H. erectus* occupied in Africa (e.g., Bouteaux et al. 2007; Dennell 2014; Larick and Ciochon 2015). This represents a reasonable inference.

Evidence of the use of marine resources for subsistence by *H. erectus*, however, is even more circumstantial. Freshwater shellfish were known to *H. erectus* populations, and the shells were used as tools and perhaps even for decorative art (Choi and Driwantoro 2007; Joordens et al. 2015). Evidence of coastal, lacustrine, swamp forest, lagoon, and marshy environments present during the deposition of the Trinil HK assemblage demonstrates that aquatic resources were present at the same time as *H. erectus* in Middle Pleistocene Java (Joordens et al. 2009). Likewise, the presence of crocodile and fish remains in Ngebung is suggestive of exploitation of aquatic resources

(Moigne et al. 2004). However, direct evidence of the exploitation of marine resources by Early and Middle Pleistocene hominins has yet to be shown. No doubt Pleistocene hominins were opportunistic omnivores and would not have refrained from using any resources available to them. Nevertheless, on the basis of the environmental contexts in which they have been recovered, it is probable that pre-*sapiens* hominin populations were constrained to environments where fresh water, animals, and plants were plentiful (Dennell 2014), and it appears that aquatic resources constituted only a minor element of protein intake.

East of Huxley's Line, Early Pleistocene hominins are restricted to the islands of Flores. There, the Early Pleistocene vertebrate fauna population was clearly impoverished (Dennell et al. 2014; Meijer et al. 2010), particularly in comparison with the faunal records of similar periods on Java and China. Only a dwarf stegodon (*Stegodon sondaari*), the Komodo dragon (*Varanus komodoensis*), and a giant tortoise (*Geochelone* species) are known from the site of Tangi Talo (Brumm et al. 2010; Meijer et al. 2010), dated to approximately 0.9 Ma (Aziz et al. 2009; Morwood et al. 1998). After the deposition of Tangi Talo, a turnover was recorded at Mata Menge and similarly aged sites, and a new, larger species of stegodon (*Stegodon florensis*), a rat (*Hooijeromys nusatenggara*), the Komodo dragon, and a tool-making hominin are recorded (Brumm et al. 2010, 2016; Meijer et al. 2010; van den Bergh et al. 2016*a*; see table 1). The habitat at Mata Menge has been reconstructed as one composed of open, savannah-like grasslands with a wetland component (Brumm et al. 2016). The specific identity of the small-bodied hominin responsible for the stone tools on Mata Menge is not known (van den Bergh et al. 2016*a*); however, recent analyses have suggested *H. erectus* was the likely ancestor of this hominin (as well as the later *Homo floresiensis*; Kaifu et al. 2015; van den Bergh et al. 2016*a*; van Heteren 2012; van Heteren and de Vos 2007; van Heteren and Sankhyan 2009), and its dispersal from Java in the Early Pleistocene is not contradicted by paleobiogeographical data (Dennell et al. 2014). In addition to the terrestrial fauna and associated archaeology, crocodiles, ducks, swans, and abundant freshwater mollusc species were recovered from Mata Menge (Brumm et al. 2016; van den Bergh et al. 2009*a*). Whether these were natural or anthropogenic is not known, although the age profile of the stegodon assemblage is consistent with a natural mass death event (Brumm et al. 2016). This age profile contrasts with both the later Liang Bua and the Middle Pleistocene Panxian Dadong stegodon assemblages, which are dominated by young individuals and thought to have been, at least in part, accumulated by hominins (table 1; Brumm et al. 2016; Schepartz, Stoutamire, and Bekken 2005).

A much more nuanced and detailed record of faunal-hominin associations is present in the *H. floresiensis*–bearing Liang Bua deposits. There, a long sequence of faunal and archaeological records are dated to earlier than ca. 50 ka (Sutikna et al. 2016), suggesting that the dominant animal resources used by *H. floresiensis* were potentially stegodons, Komodo dragons, monitor lizards, and a variety of birds and rats (van den Bergh et al. 2009*b*). Most significantly, although small amounts of terrestrial gastropods were recovered in the excavations, molluscs and other aquatic fauna are completely absent from deposits dating to earlier than 11 ka; deposits from 11 ka and after are accepted to have been accumulated by *Homo sapiens*, which suggests that such resources played no part in the subsistence strategies of *H. floresiensis* (Szabó and Amesbury 2011). This is consistent with the (admittedly sparse) evidence of subsistence strategies of hominins across Asia. Overall, these records suggest that *H. floresiensis* and its ancestor, probably *H. erectus*, made no use of aquatic resources on Flores and required access to large- and medium-bodied vertebrate remains for survival.

Sulawesi has often been cited as the origin of *H. floresiensis* populations (e.g., Morwood and Oosterzee 2007), and recent lithic finds from Talepu in the Walanae Valley on this island are consistent with early hominin colonization of Wallacea (van den Bergh et al. 2016*a*; table 1). Although the stone tools from Talepu in Sulawesi cannot be tied to any particular hominin species, van den Bergh et al. (2016*b*) make a case that they could have been made by archaic *Homo*. As on Flores, the fauna recovered in association with the tools are medium- to large-bodied terrestrial species, namely buffalo, stegodon, and a large extinct endemic pig (*Bubalus*, *Stegodon*, and *Celebochoerus*), and could thus have been used by hominins for subsistence. In addition to these species, Sulawesi also hosts seven extant species of macaque, the Sulawesi babirusa (*Babyrousa celebensis*), the Sulawesi warty pig (*Sus celebensis*), and two species of anoa (*Bubalus depressicornis* and *Bubalus quarlesi*) that would have potentially been available to early hominin scavengers or hunters, although these species have thus far not been recovered from Early to Middle Pleistocene archaeological excavations.

In the Philippines, a hominin fossil from Callao Cave in Luzon has not yet been identified to species. It was referred to *Homo* species (Mijares et al. 2010) and favorably compared with small-bodied *Homo* species, such as *Homo habilis* and *H. floresiensis* (Larick and Ciochon 2015), although provisionally attributed to *H. sapiens* by Mijares et al. (2010). It has a minimum age of around 50 kyr (Grün et al. 2014) and is found in association with several large taxa: the native brown deer (*Cervus mariannus*), the Philippine warty pig (*Sus philippensis*), and an extinct bovid (Piper and Mijares 2007). The brown deer dominates the assemblage, with more than 90% of the identifiable bone fragments assigned to cervid. Interestingly, although no stone tools have been recovered from this level at Callao Cave, cut marks are present on deer remains, implying the use of perishable tools by this hominin (Mijares et al. 2010). Only miniscule aquatic remains have been recovered from the cave (Piper and Mijares 2007), which suggests that these did not constitute a part of subsistence behavior at this site (see table 1).

With so few Early to Middle Pleistocene hominin sites east of Huxley's Line, it is difficult to be confident about the realized niche of pre-*sapiens* hominins on Wallacean islands. The African record gives every reason to expect that *H. erectus* was a resourceful and opportunistic species, making use of whatever resources were on hand. This is reflected, albeit less clearly, in the Asian record. Regardless, however, it would appear that this species had a reliance on sources of large- or medium-bodied carcasses to survive, and we argue that these requirements help explain the restricted distribution of hominins in Wallacea. *Homo floresiensis* and the new records from Sulawesi (van den Bergh et al. 2016*b*) demonstrate that water crossings were not a barrier to hominin dispersals, even if such dispersals were unintentional and subject to prevailing oceanic conditions (Dennell et al. 2014). However, successful colonization of islands requires not only travel but that the subsistence requirements of the colonizing species are met. We argue that, for early hominins, this would have required access to adequate terrestrial faunal resources and that complete or near-complete reliance on aquatic resources required technological and behavioral innovations that were beyond the reach of pre-*sapiens* hominins in Wallacea.

Zooarchaeological Records and Subsistence Strategies of *Homo sapiens* in Wallacea

There are few sites in Sunda that inform on the subsistence of *H. sapiens* at the time of first modern human maritime dispersal. Niah Cave in Sarawak, with a record spanning at least 50,000 years (Higham et al. 2016), perhaps gives us the clearest picture of the eclectic and flexible nature of modern human economic activities in Sunda before their arrival in Wallacea. At the time of the earliest recorded occupation, Niah was about 30 km from the Pleistocene coastline, and the people living there pursued diverse subsistence strategies, exploiting resources from the forests surrounding the caves and a range of freshwater environments. Pig seems to have been a major prey (*Sus barbatus*), but a wide range of species were exploited, including langurs, macaques, porcupines, monitors and smaller lizards, snakes, birds, and bats as well as molluscs and fish (Piper and Rabett 2017). Niah continued to be used during the LGM when lowered temperatures and a downward migration of the montane forest are indicated by the presence of the lesser gymnure (*Hylomys suillus*) and the ferret badger (*Helictis orientalis*), species that are today restricted to the highlands of Mount Kinabalu (Cranbrook 2000). As sea level rose after the LGM and coastal estuaries began to establish, there is evidence for an increasing focus on estuarine resources. The Niah fish assemblage includes large individuals from freshwater streams and estuaries, which indicates the use of nets or spears in their capture (Barker et al. 2007). Niah is also unique in preserving evidence of Pleistocene plant exploitation and includes fragments of fruits, nuts, and parenchyma (Barton, Paz, and Carlos 2017; Paz 2005), showing that "rainforest tuberous plants such as aroids, taro, yam, and sago palm" (Barker 2005:97; Barton 2005) were collected. Interestingly, many of the tubers required multistage processing to render them safely edible, demonstrating that early modern humans west of Huxley's Line possessed an advanced knowledge of plants, at least some of which would be familiar east of Huxley's Line.

Sulawesi, the largest of the Wallacean islands, was first occupied by modern humans by at least ∼40 ka (Aubert et al. 2014). The earliest archaeological records on this island thought to be definitely attributable to *H. sapiens* are in South Sulawesi in the limestone karst near the modern city of Maros (table 1). Simons and Bulbeck (2004) show that, in the earliest period of modern human occupation, hunting focused on the endemic suids *Sus celebensis* and *Babyrusa* but included *Anoa* species as well as an extensive range of medium-size to small mammals (Simons and Bulbeck 2004). Interestingly, the South Sulawesi sites have no evidence for maritime resources use, but this may be due to transport distance, because at the time of earliest settlement, the Pleistocene shore would have been approximately 60–80 km away.

The Talaud-Sangihe Archipelago, lying between Mindanao and North Sulawesi, is of particular interest because it comprises 77 tiny and remote islands with little in the way of terrestrial faunal resources. Despite intensive coastal survey of a number of islands in this group, the only Pleistocene-aged site discovered in the Talauds to date is Liang Sarru shelter on Salibabu, which today is only ∼100 km^2. Liang Sarru has evidence of episodic use in the Pleistocene between ∼35 and 32 ka and again between 22 and 17 ka, after which it appears to have remained unoccupied until the Holocene (table 1; Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001). There is currently no archaeological evidence that the Talaud group acted as a stepping stone for colonization from the Philippines to Sulawesi, because the Liang Sarru sequence postdates initial modern human settlement in Sulawesi (Aubert 2014; Ono, Soegondho, and Yoneda 2009), and commensal rodent genetics suggest colonization of Talaud by agriculturalists from the south (Louys et al., forthcoming). While fossils of *Stegodon* are known from the Sangihe group, and bats, rats, birds, and marine vertebrates occur in the extant fauna, the Pleistocene occupation levels of Liang Sarru consist entirely of marine shellfish and a few urchin remains. The complete lack of Pleistocene vertebrate fossils from the Talaud Islands is puzzling. Poor preservation is unlikely to be the explanation, because marine shells are abundant and would have assisted the preservation of bone if it was deposited. While the lack of vertebrate fauna may be an effect of small sample size, exploration and excavation has been more intensive here than in many islands of the other Wallacean groups. It seems possible that the initial phase of settlement of the Sangihe-Talaud Islands comprised fleeting opportunistic visits by small, highly mobile groups of mariners coming to exploit seasonal island resources. Alternatively, perhaps the Liang Sarru sequence records an early "Robinson Crusoe" settlement that was ultimately unsuccessful (Leppard 2015; Leppard and Runnels 2017), and thereafter the islands remained unoccupied until about 22 ka when, due to the lowered sea levels of the LGM, individual islands of the Talaud group were connected to form a single mega-island incorporating the current islands of Karakelong, Salibabu, Kabaruan, and Sara. The Talaud mega-island reached between 1654.4 km^2 (calculated with average Wallacan uplift of

0.5 m/kyr) and 1693.9 km^2 (excluding uplift; fig. 4). Occupation of Liang Sarru during this phase appears to have been intensive but again short lived, lasting only until the end of the LGM ~17 ka. The subsistence record during this phase is also solely shellfish, but stone artefacts are significantly more abundant, perhaps indicating a larger population or more regular use of the cave. Except in terms of total numbers, the stone artefact assemblage has been characterized as changing little through time. The earliest and LGM assemblages include low numbers of retouched flakes, some of which are classified as concave and convex scrapers with steep working edges suitable for wood working (Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001:239–247).

Golo Cave on Gebe Island in northern Maluku has parallels with Liang Sarru. Golo was occupied by ~36 ka (table 1; Bellwood et al. 1998). At this time, Gebe Island was merged with neighbouring Yu, Fau, and Uta islands, forming a single landmass of between 644.30 km^2 (using average 0.5 m/kyr uplift) and 724.09 km^2 (excluding uplift; fig. 5). Golo contains no subsistence evidence in the Pleistocene levels aside from marine shellfish (Bellwood et al. 1998:239). These comprise predominantly upper intertidal species dominated by a variety of limpets and small gastropods (*Nerita* species and *Thais* species) as well as barnacles (arthropods), some oysters, and carnivorous gastropods from Muricidae, which Szabó and Amesbury (2011:12) believe indicate foraging at local oyster beds. The Pleistocene horizons at Golo Cave contain few stone artefacts. The lithic assemblage includes a mere 51 stone artefacts made on a variety of metavolcanic rocks and comprises flake shatter, simple unretouched flakes, undiagnostic fragments, three cores, and a hammerstone. No retouched pieces were identified. However, flaked *Turbo marmoratus* opercula occur, and flakes of this dense shell may have substituted for flaked stone (Szabó, Brumm, and Bellwood 2007).

At ~8 ka, Golo sees the first appearance of vertebrate fauna: bones of a now extinct *Dorcopsis* wallaby (Bellwood et al. 1998: 251–253; Flannery et al. 1998), a cuscus (*Phalanger alexandrae*) that still occurs on the island today (Flannery and Boeadi 1995), and a small quantity of reptile, bird, and fish bone (Bellwood et al. 1998). Because there are "no good taphonomic reasons" (Szabó and Amesbury 2011:12) for the absence of bone below the 8-ka level, the wallaby and phalanger have been argued to be human introductions to Gebe in the Holocene. However, the cuscus is apparently endemic to Gebe, and the absence of any bone whatsoever in the Pleistocene levels makes it difficult to test whether the wallaby is indeed a translocation (P. Piper, personal communication, February 2015). If preservation were not an issue, it would be expected that some bones of endemic species would occur in the Pleistocene deposit, and perhaps changes in site function provide a better explanation for the absence of bone in the Pleistocene layers at Golo. The terminal Pleistocene horizon, just below the first appearance of vertebrate fauna, is said to contain circular and semicircular coral stone arrangements containing volcanic pebbles, the latter transported to the cave from the southern part of the island, which suggests a ritual use of the cave at this time (Bellwood et al. 1998:252). Golo also contains large numbers of coral cooking stones, and the marine shell is reportedly heavily burnt (Bellwood et al. 1998:252). It is possible that this area of the site had a specialized function for cooking vegetable foods. This could perhaps be resolved by micromorphological work on the sed-

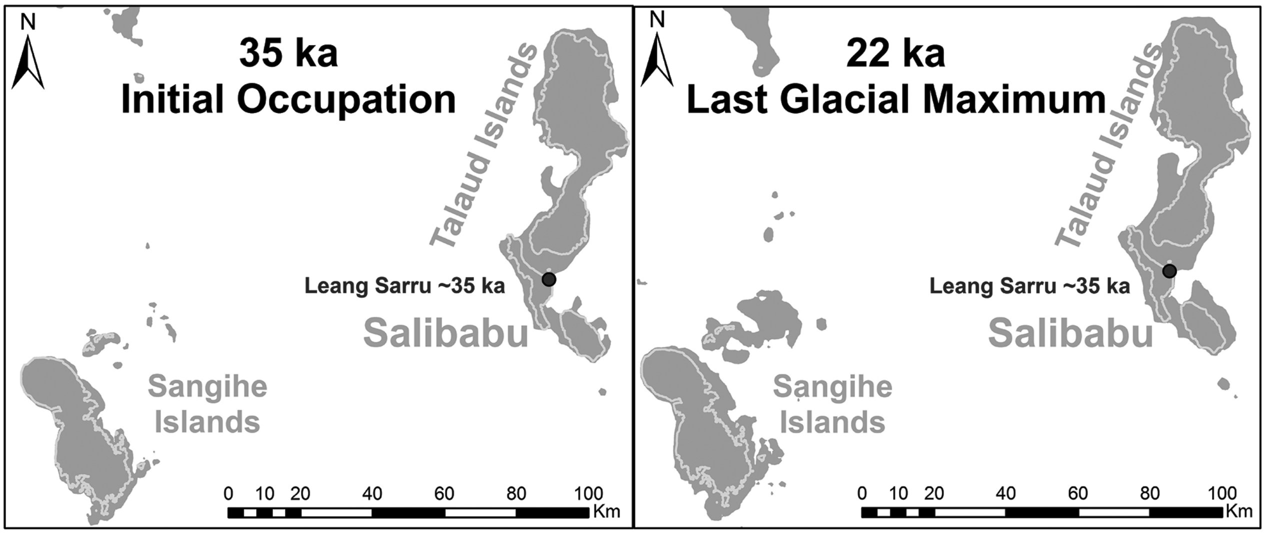

Figure 4. Reconstructions of the Talaud and Sangihe island archipelagos at the time of the first known occupation (~35 ka at Leang Sarru) and during the peak of the last glacial maximum (~22 ka). Reconstructed using the uplift-adjusted sea level curve from figure 2 and the General Bathymetric Chart of the Oceans bathometry chart (Smith and Sandwell 1997). A color version of this figure is available online.

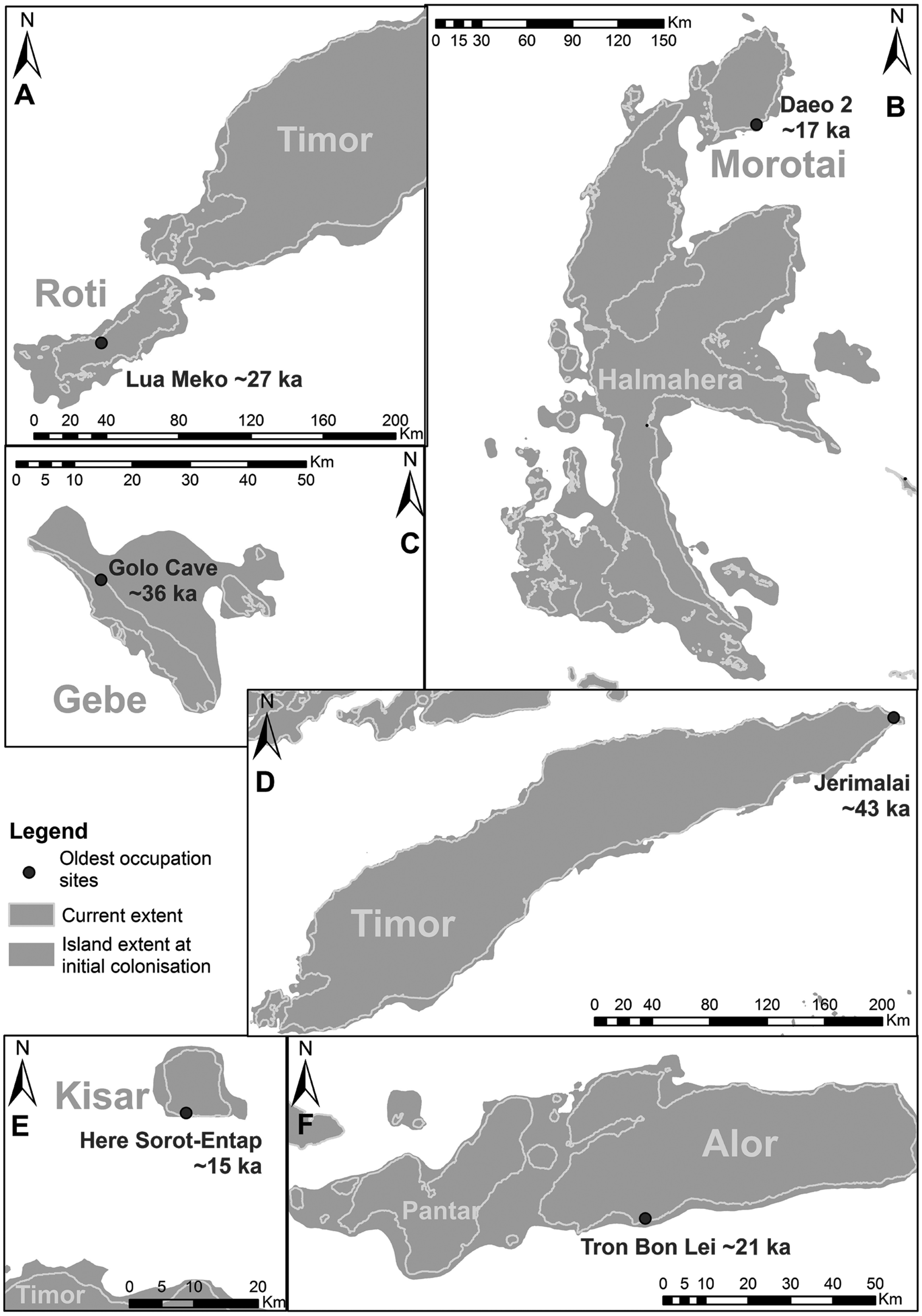

Figure 5. Reconstructions of island size at the time of first known occupation for Roti (*A*), Morotai (*B*), Gebe (*C*), Timor (*D*), Kisar (*E*), and Alor (*F*) islands. Reconstructed using the uplift-adjusted sea level curve from figure 2 and the General Bathymetric Chart of the Oceans bathometry chart (Smith and Sandwell 1997). A color version of this figure is available online.

iments. Siti Nafisah Cave in Halmahera also has *Dorcopis*, along with an unknown bandicoot species, in layers dating to the mid-Holocene, but by the Late Holocene, both had become extinct (table 1; Bellwood et al. 1998:253).

Daeo 2 Cave in Morotai to the north in Halmahera was first occupied ~17 ka (table 1; Bellwood et al. 1998) and, at this time, was connected to Halmahera, Bacan, and other smaller surrounding islands (fig. 5). This combined land area would have been approximately 39,422 km^2 (using an average 0.5 m/kyr uplift) to 40,161 km^2 (without uplift). Interestingly, despite relatively good faunal preservation down to the Pleistocene units, Daeo 2 has no evidence of the extinct *Dorcopsis* or bandicoots found in Gebe and Halmahera, but it does have a cuscus, murids (including one large species), and quantities of fish bone, the latter being most abundant in the Holocene units (Bellwood et al. 1998:246). Bellwood et al. conclude that, because Morotai is visible from and close to Halmahera, and these marsupials are absent, it would seem that initial colonization was followed by a long period of relative isolation (Bellwood et al. 1998:246–247). The absence of *Dorcopsis* and bandicoot on Morotai at the time when Morotai and Halmahera were joined suggests that the marsupials were translocated to Halmahera, but they must have been introduced after the two islands were separated, perhaps in the mid-Holocene. Simple unretouched flakes made on locally available beach pebbles occur at Daeo 2, but the authors are not specific about technology or distribution within the site.

Timor, the largest island on the southern dispersal route (as defined by Birdsell 1977), has produced some of the earliest dates for modern human use of the Wallacean Archipelago. Jerimalai Shelter and Lena Hara Cave have sequences dating back to ~42 ka (see table 1; O'Connor 2007; O'Connor, Allen, and Hawkes 2010). These sites are formed in uplifted coralline terraces and are within a kilometer of today's coastline. Due to the steep bathymetric drop off in this region, the sites would always have been proximal to the coast. Rocky shore shellfish, fish, and marine turtle dominate the earliest Pleistocene levels of both sites. The Pleistocene levels of Jerimalai contain a large quantity of fish bone, and pelagic species form a significant component of the assemblage (O'Connor, Ono, and Clarkson 2011). In contrast, Matja Kuru 2 of comparable antiquity (O'Connor, Robertson, and Aplin 2014), but located about 6 km from the coast today, has a Pleistocene assemblage dominated by giant rats; reptiles, such as pythons, lizards, and freshwater turtle; and some bat and small murid that may not be of anthropogenic origin. Marine shell was recovered in the Pleistocene and Holocene levels, but quantities are small in comparison with Lene Hara and Jerimalai, and marine fish and sea turtle are poorly represented, no doubt due to the greater transport distance from the coastline to this site. The Timor lithic assemblages evidence the predominant use of good-quality chert to produce flakes from a range of cores that include multiplatform, single-platform, bidirectional, bipolar, and radial cores. At Jerimalai, the only assemblage yet studied in detail, retouched pieces occur in low numbers, and overall the assemblage shows remarkable conservatism over time (Marwick et al. 2016). Small numbers of very tiny obsidian flakes from an as-yet-unknown source—but one thought likely to be external to Timor—were also identified in deposits dating predominantly to after ~14 ka (Reepmeyer, O'Connor, and Brockwell 2011). The Timor-Leste sites also contain a range of shell items, including fish hooks by at least ~16 ka (O'Connor, Ono, and Clarkson 2011) and decorative items that begin to be made immediately after first occupation; like the lithics, these change little through time (Langley and O'Connor 2016; Langley, O'Connor, and Piotto 2016).

The archaeological assemblage from an area on the southern coast of Alor Island, Tron Bon Lei, provides insights about human subsistence strategies north of Timor. Settlement as recorded by the deposit in this shelter first occurred at ~21 ka (table 1; Hawkins et al. 2017), at a time when sea levels were low and Alor Island was merged with neighboring Pantar, Pura, Marisa, Rusa, Ternate, and Treweng islands, forming a single island of between 3,862 km^2 (estimated with an average 0.5 m/kyr uplift; fig. 2) and 3,910 km^2 (without uplift).

In one Tron Bon Lei shelter that is within a few hundred meters of the current coastline, a 1 × 1-m test pit yielded abundant marine shellfish and fish bone accumulations dated from 21 to 3 ka, along with stone artefacts manufactured from basalt, obsidian, and chert, which suggests a human population almost solely dependent on marine resources before the Neolithic (Hawkins et al. 2017; Samper Carro, Louys, and O'Connor 2017; Samper Carro et al. 2016). The faunal assemblage from the Late Pleistocene–early Holocene occupation levels contained over 40,000 fish bones, with differences observed in the quantity of remains, taxonomic representation, and prey size between the Late Pleistocene and early Holocene layers. The Pleistocene assemblages (dated from 21 ka to 10 ka) had a larger number of faunal remains compared with more recent accumulations, which suggests resource depression or alternatively a decrease in occupation intensity of the shelter during the early Holocene (S. C. Samper Carro, personal observation). This is surprising in view of the fact that coastal resources would have been more accessible in the Holocene after the rise in sea level and stabilization of near-shore coastal environments, and this contrasts with the abundance of Holocene-aged archaeological evidence documented in other Southeast Asia island environments more generally (e.g., Mahirta 2009:50, 61). The Tron Bon Lei Pleistocene assemblage contains a larger percentage of carnivorous fish families relative to herbivores as well as a larger number of remains from families of pelagic species. Prey size is larger in the Pleistocene levels, reflecting the larger quantity of pelagic fishes compared with reef environment fishes (O'Connor et al., forthcoming *b*; Samper Carro et al. 2016). This likely represents changes in fishing practices and/or technology, whereby hook and lure fishing during the Pleistocene declined in importance relative to other capture methods, such as netting. The fish assemblage from Alor has strong similarities with the assemblage composition at both Jerimalai and Lene Hara in Timor-Leste, except turtle bone is not common in the Alor deposits. In terms of nonvertebrate fauna, the

Tron Bon Lei pit B assemblage has a dense and well-preserved shell midden throughout the Pleistocene and early- to mid-Holocene levels. Interestingly, the Pleistocene levels are dominated by an arthropod: a large barnacle; there are kilograms of this barnacle in some of the Pleistocene excavation units. In terms of molluscs, rocky substrate marine species predominate and include limpets and false limpets (Fissurellidae; *Cellana* and *Patella* species), abalone (*Haliotis* species), Chitonidae, and Neritidae. *Turbo* species, *Tectus* species, *Soccostrea*, *Tridacna* species, *Hippopus* species, Thiaridae, Muricidae, and *Stombus* species are also represented, and there are very small contributions from freshwater taxa. Crabs and urchins were recovered from all excavation units in variable quantities (O'Connor, personal observation).

Analysis of the stone artefacts from this site is in progress, but like Jerimalai, the assemblage comprises cores, flakes, and low numbers of flake tools with no formal patterning. The obsidian artefacts have been identified as having distinct geochemical signatures indicating three separate source locations (Reepmeyer et al. 2016). One of the obsidians is a geochemical match for the high-silicate obsidian in the Timor-Leste sites and, interestingly, appears in Tron Bon Lei at about the same time, ~14 ka. While the source for this obsidian is not yet known, the small size of the artefacts made on it, the absence of artefacts with cortex, and the late appearance of this obsidian in the sequence combine to suggest that the source is not in Alor and instead suggest its maritime transport from elsewhere in the Sunda arc to Timor and Alor (Reepmeyer et al. 2016).

The tiny island of Kisar to the northeast of Timor is only approximately 10 km × 8.7 km with a total area of 81.15 km^2. It has a narrow coastal platform owing to its rapid rate of uplift and deep offshore profile. While it would have been slightly larger during periods of low sea level, it would never have been much larger than it is today. Our recent excavation at a shelter on the south coast, Here Sorot Entapa, demonstrates that the island was occupied by at least 15 ka. Based on a small testing in 2015 of two 1 × 1-m excavations (pits A and B), the site was first occupied at 13,176 ± 30 WK-43325 (15,091–15,338 cal BP; marine shell). The occupation horizon at 15 ka is directly underlain by sterile coralline sands that are dated to 45,840 ± 2,687 (WK-46537) on coral from a culturally sterile deposit. The coral date corresponds well with the estimated age for the uplift of the terrace in which the shelter is formed, demonstrating that it would have been available for habitation before 15 ka. The archaeological fauna in both test pits is overwhelmingly dominated by fish, shellfish, urchin, and crab. Aside from marine resources, these shelters contain only occasional bones of endemic small rodents, shrews, bats, small lizards, and snakes. Analysis of the lithics has not yet begun; however, as in the other Wallacean sites, the assemblage appears to be composed of cores, flakes, and low numbers of irregularly retouched flakes.

Roti Island immediately east of Timor was also occupied in the Pleistocene. Lua Meko Cave, near the north coast, has a lower nonbasal age of ~28 ka cal BP (24,420 ± 250 ANU-10908) associated with sparse stone artefacts and marine shell (table 1; Mahirta 2009:52). Roti was not connected to Timor at this time; however, the water crossing separating the two islands at this time would have been between 3.04 km (without uplift) and 3.52 km (with use of an average 0.5 m/kyr uplift). Vertebrate faunal remains occur in the older Pleistocene units of Lua Meko but are fragmentary, heavily encrusted in carbonate, and not identifiable to taxon, so discussing subsistence is challenging. Based on the internal structure, most of the bone fragments in this lower unit are probably marine turtle. Marine shell in the lower Pleistocene levels included species from the families Chitonidae, Turbinidae, and Cypraeidae, which can be collected on rocky substrate or intertidal areas of the reef. The Holocene units see the appearance of mangrove mudflat– and sandy substrate–associated shellfish as well as an overall increase in taxa from a broader range of habitats as sea levels rise and stabilize. Low numbers of stone artefacts occur in the earliest levels of Lua Meko and appear remarkably similar to those from Timor-Leste in that they evidence generalized reduction of chert to produce simple flakes but no specialized artefact forms (Mahirta 2009).

Discussion

On the basis of current data, it appears that *Homo erectus, Homo floresiensis*, and other non-*sapiens* hominins in the region made use of available terrestrial resources, particularly medium- to large-bodied fauna. No similar evidence of significant marine resource exploitation by these hominins exists. A scarcity of terrestrial faunal resources on the small islands east of Flores and Sulawesi, combined with an inability to develop and employ sophisticated fishing technologies, may have precluded successful dispersal by these hominins any farther east. Although unsuccessful dispersals to small islands (i.e., dispersals that did not produce a genetically viable population) are certainly possible or even likely, being unsuccessful, they would necessarily have been archaeologically short-lived, such that the chances of their discovery remain slim to nonexistent (e.g., Leppard and Runnells 2017).

Outside Flores, Luzon, and Sulawesi, conditions favorable for successful hominin colonization, based on island size and geological history, might have been present on the islands of Sumba and Timor. Sumba hosts at least one species of stegodon (*Stegodon sumbaensis*); however, its record is too poorly known, both archaeologically and palaeontologically, to speculate on further. Timor, on the other hand, has been explored extensively for archaeological deposits (e.g., Glover 1986; O'Connor 2007; O'Connor, Allen, and Hawkes 2010), and during the Pleistocene, it hosted two species of pygmy stegodons, a giant land turtle, and a Komodo dragon–sized lizard in the Late Pleistocene (Hooijer 1971). Although early claims were made for the association between stone tools and stegodon remains in Timor (e.g., Glover and Glover 1970; Maringer and Verhoeven 1975; Maringer and Verschuuren 1981), the idea that Pleistocene hominins other than *Homo sapiens* made it east of Flores is now discounted (Allen 1991; Jones and Spriggs 2002; O'Connor 2002). The subsistence constraints of pre-*sapiens* hominins may well explain this distribution. Certainly, direct movement of early hominins from Flores to Timor is possible; however, migration eastward through the islands of Lembata, Pantar, and Alor is more likely, because sea crossing distances are smaller (some of these islands were connected during glacial periods). Other than a giant (~2-kg) rat species, Alor Island hosts only small-bodied terrestrial endemics (Hawkins et al. 2017; Samper Carro et al. 2016). Lembata and Pantar have no Pleistocene prehistoric records, but Pantar's faunal history is likely to be similar to Alor's. Subsistence strategies of Pleistocene *H. sapiens* on the smaller Wallacean islands, such as Alor, appear to have required the exploitation of almost exclusively maritime resources (Samper Carro et al. 2016), strategies seemingly not employed by earlier hominins. The likely route to Timor would therefore have precluded hominins, which would explain their apparent absence from this large island.

Thus, independent of seafaring abilities, we suggest that the distribution of modern humans in Wallacea was dictated by the flexibility of subsistence strategies, without which continuous and successful survival on small islands with depauperate faunas was not possible. The suggestion that the dispersal of pre-*sapiens* Asian hominins was limited by subsistence strategy is clearly one that requires additional testing, and future research in the area should aim to fill the dearth of detailed zooarchaeological studies of Early and Middle Pleistocene hominin assemblages. Furthermore, with so few islands in the region that boast any kind of Pleistocene archaeological record, further exploration and fieldwork in the region may dramatically alter this model. As aptly demonstrated with the announcement of the discovery of *H. floresiensis* over a decade ago, the potential for unexpected discoveries in the region should not be underestimated.

All records indicate that *H. sapiens* that moved through the islands east of Huxley's Line were able to do so as a result of ecological flexibility and innovation, which allowed them to successfully subsist on the most depauperate of islands through the exploitation of almost purely marine resources. Whether the direct ancestors of the first modern human colonizers of Wallacea were already exploiting such resources, or whether such innovations in subsistence behavior occurred as a result of the unique environments present in Wallacea, is not answered by the archaeological records west or east of Huxley's Line. Nevertheless, on the basis of current records from the region, it appears that extensive and systematic marine exploitation was the purview of only *H. sapiens* and that this shift in subsistence strategy occurred concurrent with first arrival on all island groups.

Detailed zooarchaeological examinations of Late Pleistocene archaeological assemblages consistently indicate that *H. sapiens* relied almost exclusively on marine resources on small islands and coastal sites. Away from the coast, modern humans on the larger Wallacean islands took advantage of a range of small and medium-size murids, reptiles, bats, and birds. As sea levels rose and fell over the past 50,000 years, the Wallacean islands changed size. In some cases, islands that are adjacent today were joined together, creating larger land masses that were perhaps better suited to sustaining permanent human populations. Conversely, when sea levels were high, these islands were separate, as they are today, and they may have been used in a more transient fashion with groups making their livelihood by moving between small island groups to take advantage of shifting or seasonal resources (Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001).

Most of the Wallacean sites lack skeletal remains in the earliest layers, and the stone artefact assemblages lack patterned, specialized, and curated tool production, such as retouched blades and backed artefact technologies that are typically associated with behaviorally modern humans in other regions of the world. However, the Pleistocene levels of Jerimalai, with its emphasis on pelagic fishing and shell artefact production, and the stone structures in Golo convincingly demonstrate modern humans to have been the occupants of these sites. It is likely that the development of specialized and curated technologies may have occurred in the face of specific or changing environmental conditions (Petraglia et al. 2009) and were simply not required in the islands of Wallacea, which did not experience major climatic oscillations during the human occupation timespan, and where maritime resources seem to have formed the mainstay of the diet before the Late Holocene ~3.5 ka (see also Szabó, Brumm, and Bellwood 2007). This hypothesis receives some support from the personal ornament repertoire made on marine shell in the Timor-Leste assemblages. These ornaments appear immediately after first settlement, perhaps indicating an early phase of experimentation and innovation following immediately on modern human entry into a new and unfamiliar environment. Once invented, however, these artefacts show remarkable conservatism over time in terms of form, raw material selection, manufacturing, and use wear (Langley and O'Connor 2016; Langley, O'Connor, and Piotto 2016).

Despite their maritime capabilities, there is no evidence for return voyaging after initial migration into Wallacea. Return voyaging might be seen in the human-assisted movement of animals or other resources, found to be absent in the islands after settlement, from the Asian mainland, from New Guinea, or from larger islands, such as Sulawesi. Human-assisted movement of faunal species would be one way of increasing available protein on the small islands with limited fauna. However, evidence that this strategy was pursued in the Pleistocene is scarce. The earliest-claimed translocation is from Laing Bawah, the cave adjoining Liang Bua in Flores, where a fragment of pig skull coated in carbonate was dated by U-Th to between 33 and 23 ka. Gagan et al. (2015:533) suggest that this indicates that *Sus* species "may have dispersed into Island Southeast Asia earlier than previously recognized." In the adjacent cave, Liang Bua, despite a well-stratified excavation spanning a period of ~20 ka, van den Berg report the presence of Sulawesi warty pig, *Sus celebensis*, at only 7 ka (van der Bergh et al. 2009*b*). All other introduced species at Liang Bua are associated with the Neolithic and the appearance of pottery. The potential translocation of *Sus* species in Flores at such an early date is very surprising in view of the fact that *Sus* species have not been reported elsewhere in the Wallacean islands until the Neolithic or more recently. There are no other records of Pleistocene faunal translocations into the Wallacean Archipelago.

Java is home to at least one species of endemic pig, *Sus verrucosus*, and Sulawesi hosts two endemic porcines (Corbet and Hill 1992). If the early occurrence for the pig in Flores is substantiated, it more likely represents an unusual (although by no means unique) colonization for a medium- to large-bodied placental east of Wallace's Line rather than a deliberate translocation by people. The *Dorcopsis* in Golo Cave on Gebe Island and at Siti Nafisah in Halmahera is likely to be a mid- to Late Holocene translocation, at least in Halmahera, in view of its absence in Daeo 2 Cave in Morotai (which was connected to Halmahera until the early Holocene). In Timor-Leste, the cuscus *Phalanger orientalis* was originally reported from ~9.5 ka on the basis of associated radiocarbon ages obtained on shellfish (O'Connor 2006). This specimen has now been directly dated to ~3 ka (O'Connor 2015). Our recent investigation of some of the smaller Wallacean islands has also found no evidence for species introductions until the Late Holocene. Alor and Kisar have no translocated fauna before the Neolithic (J. Louys, personal observation). If the introduction of exotic species stood to benefit human settlement anywhere, Kisar would seem to be a prime candidate. The evidence would suggest that modern humans did not need to take animal protein sources with them to successfully settle even the smallest islands east of Huxley's Line.

The earliest evidence for interisland transport of materials is the high-silicate obsidian artefacts found in the Timor-Leste coastal assemblages and in Tron Bon Lei in Alor after ~14 ka (Reepmeyer 2016). Although the source of this obsidian is currently unknown, it is likely to be on one of the volcanic islands of the Sunda arc to the east of Timor and Alor. The presence of this geochemically distinct obsidian demonstrates that regular interisland voyaging was occurring from this time, at least from the source island to Timor and Alor. In view of this, it is all the more surprising that no attempt was made to transport terrestrial fauna from the mainland or from the more faunally diverse islands in the archipelago.

Rather, it would seem that the maritime subsistence strategies honed in the Wallacean archipelago >40 ka were sufficient for the population sizes for tens of millennia after initial settlement. Resources such as plants must have been a mainstay of the diet, and a better understanding of their role should be a priority for future work. Perhaps most surprising of all is that, despite the unbalanced and depauperate terrestrial faunas on the islands of Wallacea, none of the Pleistocene faunal assemblages currently indicate that modern humans moving through the archipelago impacted ecosystems significantly as a result of clearance, firing, or direct predation. On the basis of current evidence, a human role in the extinction of stegodon on Timor has been argued as unlikely (Louys, O'Connor, and Price 2016). Of the four genera of giant rats on Timor, all of which are extinct today, all survived from the time of human arrival until a few thousand years ago (Louys, Aplin, and O'Connor 2015). Similarly, *Babyrusa* and the *Anoa* species in Sulawesi are today under threat of extinction but are found throughout Pleistocene archaeological sites and through to the Late Holocene in some sites in Southeast Sulawesi (O'Connor et al., forthcoming *a*). The *Dorcopsis* wallaby on Gebe and Halmahera and the Halmahera bandicoot are also Late Holocene extinctions, perhaps casualties of Neolithic land clearance (Bellwood et al. 1998). Although few Pleistocene sequences have been studied in depth, those currently available show no firm evidence of over hunting or extinctions. Contrasting the history of Pleistocene and Holocene extinctions on oceanic islands should be made a priority for future research.

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