An early colonisation pathway into northwest Australia 70-60,000 years ago

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ABSTRACT

Colonisation of Sahul 70-60 thousand years ago (kya) represents the first great maritime migration undertaken by anatomically modern humans in one of the final phases of the Out of Africa dispersal. Visual connectivity network analyses, agent-based simulations and ocean current modelling reveal that modern humans could follow numerous northern and southern migration pathways into Sahul. Our results support a southern route out of Africa through South Asia with entry into ISEA through the Banda Arc, culminating in an early colonisation of Sahul on the northwest shelf. Our results show multiple colonisation events through other entry points were also probable, and raise interesting possibilities for complex regional migration and population histories.

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1. Introduction

The colonisation of Sahul — the combined Pleistocene landmass of Australia and New Guinea — at 65 ± 5 kya (Clarkson et al., 2017) by anatomically modern humans (AMHs) involved the maritime navigation of the Wallacean archipelago and greater Island Southeast Asia (ISEA). ISEA is a key region for potential interactions between AMHs and *Homo floresiensis* (Sutikna et al., 2016), hybridizations with the Denisovans (Mallick et al., 2016; Reich et al., 2011), and possibly an additional unknown hominin (Mallick et al., 2016; Mondal, 2016). While AMHs, *Homo floresiensis*, *Homo erectus*, and potentially the Denisovans colonised ISEA (Brumm et al., 2016; Mondal, 2016; Rasmussen et al., 2011; Reich et al., 2011; Swisher et al., 1994; Westaway et al., 2017), only AMHs made the final migration to people Sahul (Clarkson et al., 2017). Genetics have continued to highlight the great age depth of the maritime colonisation of Australia, and its genetic isolation since that event (Malaspinas et al., 2016; Nagle et al., 2016, 2017; Tobler et al., 2017).

A series of hypothetical migration pathways have been previously identified through northern and southern Wallacea to Sahul during times of low sea level (Birdsell et al., 1977) (Fig. 1B). While archaeologists have long made a case for a crossing from Timor to Sahul (O'Connor, 2007; Butlin, 1993), the southern pathways have been largely dismissed on the grounds of very large final crossing distances and lack of island-to-island visual connectivity. This suggested the northern route through the Bird's Head of New Guinea was the most likely colonisation gateway (Birdsell et al., 1977; Irwin, 1992; O'Connell and Allen, 2012). However,

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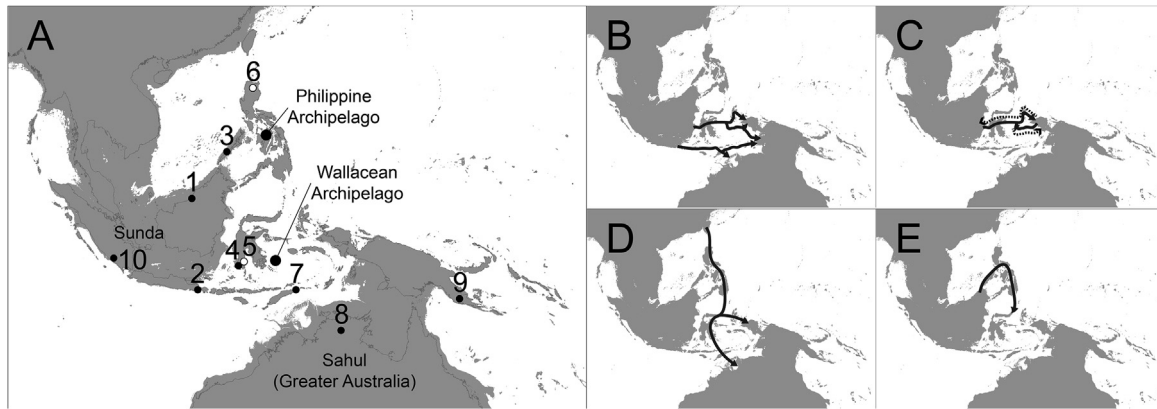E-mail address: kasih.norman@uqconnect.edu.au (K. Norman).

Fig. 1. Oldest archaeological sites in ISEA and Sahul and previous migration pathway models. Open circles represent unknown hominin species, closed circles AMHs. **(A)** Archaeological site locations: 1. Niah Cave c. 45 kya; 2. Wajak c. 45 kya; 3. Tabon Cave c. 47 kya; 4. Maros-Pangkep c. 40 kya; 5. Talepu c. 100–200 kya (unknown hominin species); 6. Callao Cave c. 67 kya (unknown hominin species); 7. Laili 44.6 kya; 8. Northern Australia 65 kya; 9. Kosipe 49 kya. 10. Lida Ajer 73-63 kya. Modern coastline indicated. **(B)** Birdsell et al.'s (1977) northern and southern migration routes, based on shortest inter-island crossing distances. **(C)** Irwin's (1992) intervisible pathways – dashed lines indicate pathways not intervisible if travelling in the opposite direction. **(D)** Sondaar's (1989) pathways based on species distributions. **(E)** Morwood and Van Oosterzee's (2009) colonisation model based on biogeographic factors.

archaeological evidence unambiguously associated with AMH fossils is currently non-existent across the northern ISEA migration routes prior to ~47-45 kya (Barker et al., 2007; Detroit et al., 2004). In contrast, fossil evidence now places modern humans on the southern route on the island of Sumatra (part of the Pleistocene continent of Sunda) by 73-63 kya (Westaway et al., 2017), with occupation of northwest Sahul by 65 ± 5 kya (Clarkson et al., 2017).

Maritime passage through ISEA was likely facilitated by the shallow continental shelves of the Pleistocene continents of Sunda and Sahul emerging as sea levels fell during the last glacial period (Lambeck and Chappell, 2001). Substantially increased terrestrial land area resulted, with the Wallacean archipelago framed to either side by the expanded continental landmasses (Fig. 1). In addition, island-count and land area within the Wallacean and Philippine archipelagos increased extensively with glacial sea level fall, heightening island connectivity (Kealy et al., 2016; Robles et al., 2015). Between ~70 and 60 kya eustatic (global) Late Pleistocene ocean levels fell to depths second only to that of the Last Glacial Maximum (LGM). This process exhumed a large low region of northwest Sahul, forming either a broad arc of islands (Lambeck and Chappell, 2001) or a fully emergent continental shelf (Grant et al., 2012; Siddall et al., 2003; Waelbroeck et al., 2002) extending towards the Banda Arc island chain. Between ~60 and 48 kya rising sea levels once again drowned the northwest shelf, but after ~48 kya (with some variance across eustatic curves) sea levels again fell sufficiently to exhume the shelf until post-LGM sea level rise (Grant et al., 2012; Lambeck and Chappell, 2001; Siddall et al., 2003; Waelbroeck et al., 2002). Although oceanic area within ISEA was considerably diminished during the last glacial, the voyages undertaken along the proposed migration pathways incorporated numerous long water crossings, some considerably in excess of 65 km. Watercraft technology would therefore have been indispensable to this undertaking (Balme, 2013; Birdsell et al., 1977; Bulbeck, 2007; O'Connell and Allen, 2012). These factors, in addition to the requirement for a viable initial founding population size (Atkinson et al., 2007), strongly indicate purposeful maritime migration was instrumental in the peopling of Sahul. However, the results of analyses of Aboriginal Australian genetic diversity (mitochondrial DNA, Y-chromosomal DNA and autosomal DNA) are inconclusive as to the location of the initial landfall of Sahul's first migrants (Malaspinas et al., 2016; Nagle et al., 2017; Tobler et al.,

2017). Given the specific pathways, gateway regions, maritime technology and rate of migration all remain unknown, models become a valuable means of generating and testing hypotheses about the earliest modern human migrations through ISEA to Sahul.

We ran bi-directional macro-viewshed analyses across the full extent of ISEA to quantify Pleistocene continental coastline-to-island and island-to-island visual connectivity. From these analyses we generated a weighted bi-directional graph where edge (line) weights represent ISEA visual connectivity (see Methods). Optimal pathways through ISEA's visual connectivity network were then generated using network flow analysis from each of the identified jumping off points. The visual connectivity analysis results were then incorporated into the simulation environments of two agent-based models (ABMs). This allowed us to test the response to the connectivity network of agents operating under a range of different push-pull factors such as foraging strategies, carrying capacity and inter-population competition (Materials and methods). A transit probability function (see Materials and methods) guided agent decision-making processes around the choice of next island hop, acting as the controlling variable on directionality of movement. It is assumed within this model that Late Pleistocene hunter-gatherers, undertaking the first modern human maritime migration across a large and unknown geographic region, would prioritise and preferentially target visually identifiable landmasses and islands. Additional environment and agent parameters within the ABMs initiated agent movement and drove their rate of migration speed within the simulations. Due to the limited nature of the archaeological record within ISEA for the colonisation window, ABM parameters were grounded in ecological theory, which provided a predictive framework for the modelling of AMH hunter-gatherers' migratory movements through the region. Optimal foraging theory (OFT) (O'Connell and Allen, 2012; Winterhalder et al., 1992) drove agent migration in Model 1, while movement of agents in Model 2 was driven by agent population growth, island carrying capacity, and inter-agent population competition (see Materials and methods). Ocean current flow for ISEA was modelled using the CMCC eddy-permitting Global Ocean Physical Reanalysis (C-GLORS) with a 35-year hindcast (1980–2015). This allowed us to ascertain the level of difficulty for the final northern and southern water crossing points into Sahul.