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Least-cost pathway models indicate northern human dispersal from Sunda to Sahul

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ABSTRACT

Archaeological records from Australia provide the earliest, indirect evidence for maritime crossings by early modern humans, as the islands to the north-west of the continent (Wallacea) have never been connected to the mainland. Suggested in 1977 by Joseph B. Birdsell, the two main routes from Sunda (mainland Southeast Asia) to Sahul (Australia-New Guinea), still in debate today, are a northern route through Sulawesi with a landing in New Guinea, or a southern route through Bali, Timor and thence landing in northern Australia. Here we construct least-cost pathway models of human dispersal from Sunda to Sahul at 65 ka and 70 ka by extending previous out-of-Africa least-cost models through the digitization of these routes. We recover overwhelming support for a northern route into Sahul, with a landing location on present-day Misool Island. Minimal support is also recovered for the southern route at 70 ka, with a possible crossing to Sahul from eastern Timor. Review of archaeological records on the Wallacean islands crossed by our northern route indicate a dearth of archaeological research in this region. Meanwhile, the comparatively better studied southern islands still lack any archaeological dates comparable to those known for initial occupation in Sunda and Sahul. Based on our model results we suggest Misool Island as the initial landing site for early modern humans on Sahul and recommend a future focus on archaeological fieldwork in the northern Wallacean islands.

1. Introduction

The oldest dates for human occupation on the Australia-New Guinea continent (Sahul) represent the earliest, indirect evidence for sea faring by early modern humans anywhere in the world, as the islands directly to the north and west of Sahul (Wallacea) were never connected to the mainland, requiring multiple successful water crossings east from mainland Southeast Asia (Sunda). Birdsell (1957) was the first of a series of works exploring the movement of early modern humans from Sunda to, and throughout, Sahul. Many of his ideas concerning population dynamics were further explored by Birdsell (1977) in relation to the island geography of Wallacea (the biogeographic region between continental Sunda and Sahul), and it is this publication that has received the greatest attention in the field of Australasian archaeology. In particular, the two main routes he identified from Sunda to Sahul (Birdsell, 1977: routes 1 and 2; Fig. 1) remain the main pathways examined by archaeologists today. Only two other routes through Wallacea have been proposed (Sondaar, 1989; Morwood and Van Oosterzee, 2007), and they share Sahul landing locations with those already suggested by Birdsell's routes 1 and 2 (Kealy et al., 2016:Fig. 2). While Birdsell's route 1 through the north of Wallacea has generally been preferred based on shorter crossing distances between islands (Birdsell, 1977; Irwin, 1992; Allen and O'Connell, 2008; O'Connell and Allen, 2012), the southern route 2 has been considered more favorable based on the greater antiquity of archaeological sites in that region (e.g., O'Connor, 2007; Clarkson et al., 2017). However, there remains debate as to the most likely of these, as no modern human occupation sites in Wallacea have yet been discovered that predate the earliest occupation sites known in Sahul (Kealy et al., 2016; Wood et al., 2016; Clarkson et al., 2017; Hawkins et al., 2017). While the earliest date currently proposed for Sahul is ca. 65 ka based on dating of Madjedbebe, Northern Territory, Australia (Clarkson et al., 2017), this date has not been universally accepted by the archaeological community (O'Connell et al., 2018). However, even if we consider a more conservative

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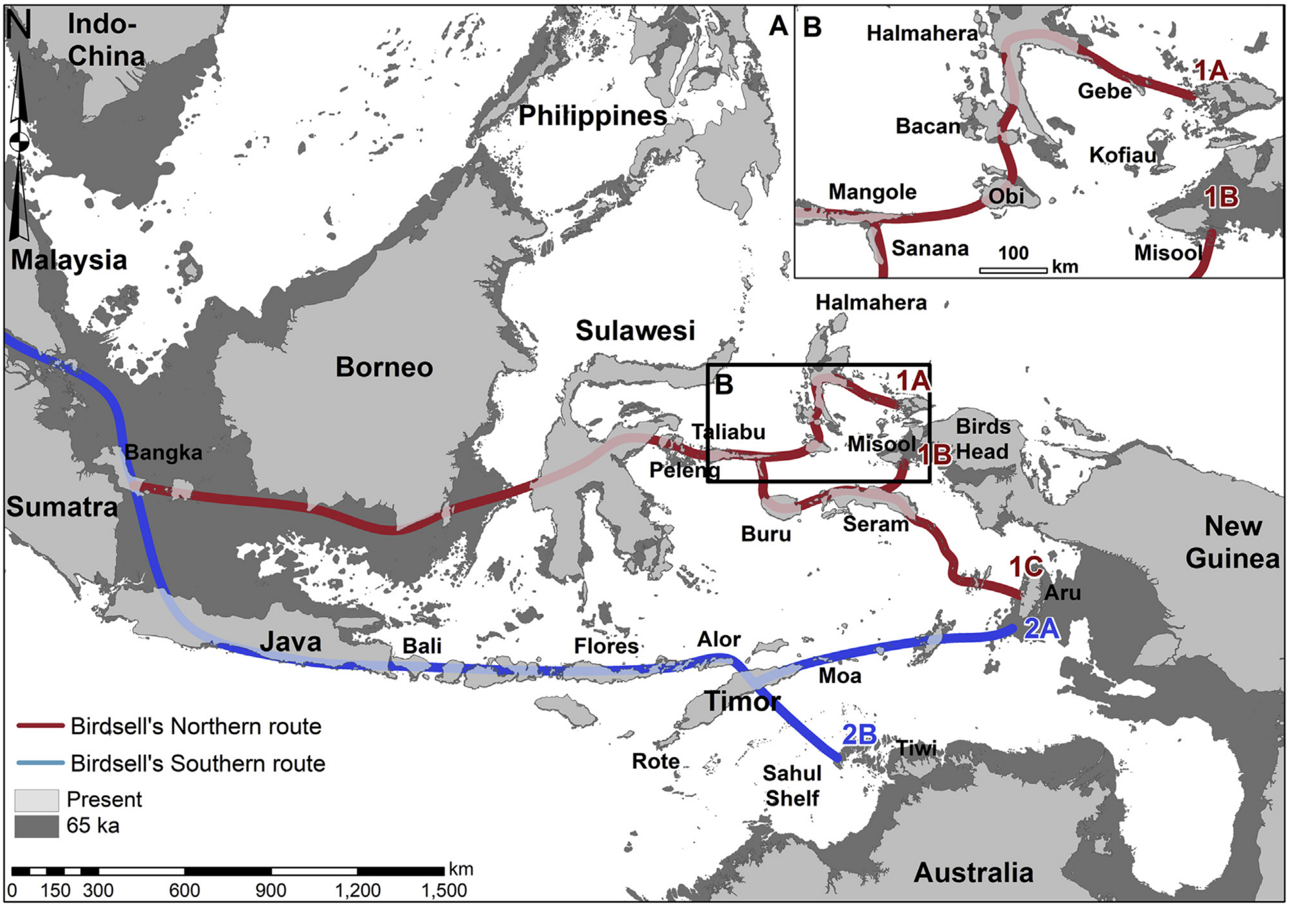

Figure 1. Map of island Southeast Asia showing Birdsell's (1977) routes from Sunda to Sahul, route 1 is drawn in red with the three alternatives (1A, 1B, and 1C) indicated, and route 2 is drawn in blue with the two alternatives (2A and 2B) also indicated. The extent of the continental shelves at 65 ka (accounting for uplift: see Fig. 2) is indicated by dark gray shading. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

estimate of a ca. 50–55 ka for colonization of Sahul, as proposed by O'Connell et al. (2018), significant chronological gaps still remain between the Sahul and Wallacean records (Kealy et al., 2016; Hawkins et al., 2017).

Recent intervisibility studies and agent-based models of paleo-Wallacea provide support for the northern route into Sahul (Kealy et al., 2017 and Norman et al., 2018, respectively). Kealy et al. (2017) defined two different forms of intervisibility: relative intervisibility to indicate regions at sea where land is visible, and an estimate for absolute intervisibility to indicate shore-to-shore visibility. In contrast, Norman et al. (2018) identified the key vantage points on islands throughout the region and used these to measure visibility. While Norman et al. (2018) showed that the paleoislands of the Sahul shelf were visible at 65 ka from Timor's mountain tops, both visibility studies by Kealy et al. (2017) and Norman et al. (2018) supported the presence of relative intervisibility (Kealy et al., 2017), but the absence of absolute shore-to-shore intervisibility, between Timor and Sahul at this time. Norman et al. (2018) suggested that early mountaineers on Timor could have identified the direction of islands invisible from the shore, establishing voyage direction prior to departure. However, unless one assumes advanced navigational abilities, known directionality prior to departure is only slightly advantageous unless it can also be combined with relative intervisibility, as this allows voyagers to maintain a visual reference at all times (under assumed optimal conditions; see Kealy et al., 2017). Regardless, a greater connectivity between islands along the northern route favors greater intervisibility (Kealy et al., 2017) and thus a higher probability of a northern landing location (Kealy et al., 2017; Norman et al., 2018).

In contrast, drift voyage models support the southern route (Bird et al., 2018). Bird et al. (2018) attempted to find a middle ground between the visibility measures of Kealy et al. (2017) and Norman et al. (2018) by limiting their vantage points to locations within 10 km of the coast (Bird et al., 2018). However, they focused their model only on the southern crossing between Timor and Australia and did not extend their study to include the rest of Wallacea. The focus on a southern route was based on paleoenvironmental reconstructions, suggesting the past existence of a savanna corridor (see Bird et al., 2005) would have facilitated the successful movement of early modern humans through the region in that direction.

Here, we use geographic information systems (GIS) software and the most inclusive bathymetric data for Wallacea to digitally recreate Birdsell's (1977) route model and investigate the most likely route used by early modern humans to colonize Sahul. To achieve this, we extend the least-cost model of Field and Lahr (2005) for human dispersal out of Africa, east from its stopping point on the coast of Sunda. By combining the cost variables of Field and Lahr (2005) with novel values based on the variables developed by Birdsell (1977), we aim to produce a 'seascape cost surface' which represents travel difficulty for early modern humans throughout the Wallacean Archipelago. The results of our models provide a visual summary of the effect these variables would have had on early human population movements, as well as

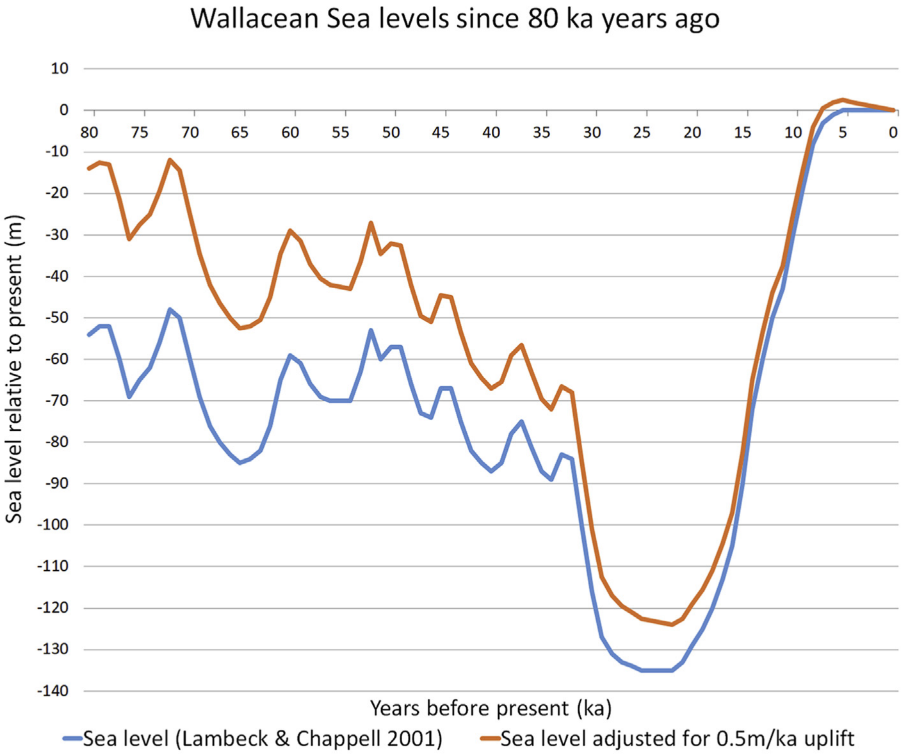

Figure 2. Sea level curves for the last 80 ka; showing the Lambeck and Chappell (2001) Huon Peninsula relative sea level curve (blue) alongside the adjusted sea level curve (orange) to account for an average Wallacean uplift rate of 0.5 m/ka (Kealy et al., 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

recommending key locations both on Sahul and in Wallacea for future archaeological survey and excavation.

1.1. Archaeological sampling in Wallacea

Archaeological sampling throughout the Wallacean region has been comparatively limited, especially when one considers that the majority of islands throughout the archipelago are completely lacking in archaeological data (Kealy et al., 2016). Additionally, sampling is not just limited at the regional level but also at the island and site levels as well. With the exception of islands such as Timor and Sulawesi, most Wallacean islands that have been investigated archaeologically have only one or two excavated sites recorded (e.g., Ono et al., 2009; Samper Carro et al., 2016; O'Connor et al., 2018a). Furthermore, the vast majority of excavations in Wallacea have thus far been limited to just one or two 1 × 1 m test pit excavations (e.g., O'Connor, 2007; O'Connor et al., 2010; Samper Carro et al., 2016; Hawkins et al., 2017; O'Connor et al., 2018a), which, based on the complex nature of cave depositional histories, are unlikely to recover the entire occupation record for any site in question (O'Connor et al., 2010, 2017a). Only lateral sampling and a composite stratigraphy across the entire site will provide a holistic understanding of site use (O'Connor et al., 2010, 2017a). Furthermore, Wallacea (and the humid tropics more generally) are notorious for their poor preservation of biological material (Louys et al., 2017; O'Connor et al., 2017a). Such preservation issues likely explain why certain sites, such as Liang Sarru in the Talauds (Supplementary Online Material [SOM] Fig. S1), lack a vertebrate archaeological record (Tanudirjo, 2001; Ono et al., 2009). Excavation methods, however, have also affected data recovery. For example, excavations at Tron Bon Lei, Alor, used 1.5 mm mesh sieves and the consequent zooarchaeological analysis (of ca. 40,000 bones) revealed the majority of fish vertebrae recovered were less than 3 mm in width (Samper Carro et al., 2016). In contrast, the smallest mesh used in the Liang Sarru excavation was 3 mm (Ono et al., 2009). The restricted nature of the current archaeological record for Wallacea, in particular the limiting factors surrounding small and limited sample sizes of excavated sites, is fundamentally important when considering the (very few) early dates from the region (Morley, 2017). The current archaeological record of Wallacea is thus almost certainly woefully incomplete at a site level, if not at an island or regional level, and comparisons between model outcomes and dates are considered with this in mind.

1.2. Dating archaeological remains in Wallacea

A number of controversies surrounding the dating of archeological sites in Wallacea and its neighboring regions exist. In addition to a very limited sample size for Wallacea (see Section 1.1 above), the earliest dates for early modern humans (SOM Fig. S1) in Sumatra (63–73 ka at Lida Ajer; Westaway et al., 2017), mainland Southeast Asia (48–70 ka at Tam Pa Ling, Laos; Shackelford et al., 2018), Australia (53–65 ka at Madjedbebe, Northern Territory; Clarkson et al., 2017), and possibly the Philippines (ca. 67 ka at Callao cave, Luzon; Mijares et al., 2010) were recovered by uranium-series or thermoluminescence/optically-stimulated luminescence (TL/OSL) methods, while in Wallacea the vast majority of dates for modern human occupation have been achieved by radiocarbon dating. As the most recent radiocarbon calibration curve only extends back to 50 ka (Reimer et al., 2013), and accurate dating and calibration of radiocarbon samples becomes increasingly difficult as one nears this point (Gillespie, 1998; Price et al., 2011), disparities between Wallacean dates and neighboring Sunda and Sahul dates could potentially reflect an artifact of different dating techniques. Additionally, the majority of Pleistocene dates from Wallacea are based on marine shell (Kealy et al., 2016:Table 1), which must be calibrated without a ΔR correction as a marine radiocarbon reservoir variable has yet to be calculated for the region. Alternatively, O'Connell et al. (2018) suggested that the older Sunda and Sahul dates listed above should be considered unreliable, the exclusion of which significantly narrows the gap between Wallacean and Sunda/Sahul dates. Regardless of whether we are simply missing dates, suffering the effects of dating artefacts, or working from incorrect dates, further excavations and dating efforts, using multiple techniques, will be required throughout Wallacea to resolve these hypotheses and confidently establish the timing of first human arrivals.

2. Materials and methods

2.1. Study area and period

This study focuses on the Wallacean Archipelago, the biogeographic region between the continental shelves of Sunda (mainland Southeast Asia) and Sahul (Australia and New Guinea), significant due to the islands' continued separation from either continent. We follow the definition of Kealy et al. (2016) for this region, which considers Wallace's Line to be the region's westerly boundary, excluding the Philippines. The oldest date for early modern humans in Wallacea is known from Laili Cave, Timor-Leste (SOM Fig. S1), with a date of 43.3–44.6 ka cal BP (D-AMS-007344; Hawkins et al., 2017). If we accept the oldest neighboring dates for modern human occupation on Sunda at 63–73 ka (Westaway et al., 2017) and Sahul for 65 ka (Clarkson et al., 2017), this suggests a colonization period between ca. 70–65 ka for Wallacea and Sahul. When compared to the adjusted sea level curve for Wallacea (Fig. 2), the two periods of 70 ka and 65 ka are revealed to represent the highest and lowest sea levels (respectively) for the entire period between 40 and 70 ka. Thus, even if we were to discount the Madjedbebe dates and use a more conservative estimate, such as 50 ka, for Sahul colonization (O'Connell et al., 2018), by studying the two time periods of 70 ka and 65 ka we are able to interpret patterns for variations in sea level between these two extremes. Based on this, we tested colonization and dispersal through Wallacea at 70 and 65 ka.

Table 1
Equations used in the development of the cost surfaces for Wallacea.

Output	Code	Formula
Uplift adjusted sea-level	UA	$UA = sl + (0.5 \times age)$ Where sl = sea-level, and age is in ka
Distance from rivers (km)	DR	Euclidean distance calculated in ArcGIS 10.5.1
River distance cost	RC	$RC = (TfExp(DR, 0.1, maxDR)) + \left(\frac{DR}{10}\right)$ TfExp base factor calculated automatically in ArcGIS based on upper and lower input values.
Slope (degrees)	S	Slope function in ArcGIS 10.5.1 calculated in degrees
Slope cost	SC	$SC = \frac{\tan S}{\tan 1^\circ}$
Land cost	LC	$LC = SC + RC$
Relative intervisibility (km)	RI	$RI = (3.57 \times \sqrt{0.5}) + (3.57 \times \sqrt{h_i})$ Where h_i = max island height (m)
Absolute intervisibility estimate (km)	AI	$AI = \frac{RI}{2}$
Visibility cost	VC	$VC = AI + RI + OI$ With the following cost values assigned: AI = 1, RI = 5, OI(no intervisibility) = 15
Distance at sea (km^{-1})	DS	Euclidean distance calculated in ArcGIS 10.5.1
Maritime cost	MC	$MC = VC + (DS \times MT)$ Where MT is the variable for marine technological levels = 1, 3 or 5
Total cost surface	TCS	$TCS = LC + MC$

2.2. Bathymetry of Wallacea

The General Bathymetric Chart of the Oceans 2014 (GEBCO14; Smith and Sandwell, 1997) 30-arc second dataset (available for download from http://www.gebco.net/) is the most accurate and detailed bathymetric chart of Wallacea currently available, and it is this chart that is used for all paleogeographic reconstructions produced as part of this study (see Section 2.3). Paleoislands were reconstructed by combining GEBCO14 bathymetric contours, the Lambeck and Chappell (2001) sea level curve and an averaged uplift rate for all of Wallacea (see Kealy et al., 2017 and O'Connor et al., 2017b for details on the latter). Figure 2 illustrates the relative sea level curve for the last 80 ka from the Huon Peninsula, following Lambeck and Chappell (2001), alongside the adjusted sea level curve, which accounts for an average of 0.5 m/ka uplift of Wallacea as per Kealy et al. (2017). We use the relative consensus curve drawn by Lambeck and Chappell (2001) and do not include their degrees of uncertainty in our calculations. For our period of interest (40–70 ka) the sea level curve is bound by degrees of uncertainty between ca. ±4 m and ±8 m (Lambeck and Chappell, 2001). Within the scope of the models produced here, this degree of uncertainty would have minimal impact on the final outcomes and is thus not incorporated into the model calculations (but see model sensitivity tests below).

The adjustment of past sea levels based on island uplift rates is important for reconstructions of past island extant and elevation (Kealy et al., 2017). While Bird et al. (2018) suggested that the effect of uplift on maximum elevation is balanced by the rate of denudation for Timor, this conclusion is, however, based on modern denudation rates (Milliman et al., 1999). These would have fluctuated significantly over the Pleistocene (Douglas, 1996). Furthermore, while some islands in the Wallacean region have been subject to uplift studies (e.g., Timor), the majority have not, making the use of an average uplift rate the only available option for incorporating an uplift variable (Kealy et al., 2017). Thus, until a better understanding of Pleistocene denudation rates, subsidence, and uplift for all the islands throughout Wallacea is available, we consider the inclusion of an average uplift rate to be an important variable in reconstructing paleogeography of the region (Kealy et al., 2017).

2.3. Paleogeographic reconstructions of Wallacea

We examined the paleogeography of Wallacea at 70 ka and 65 ka for our reconstructions. We used the bathometric data from GEBCO14 (Smith and Sandwell, 1997) to reconstruct island extant based on past sea-levels and an average island uplift rate of 0.5 m/ka (see 2.2.; Fig. 2). The GEBCO14 bathometric data was then adjusted for the change in sea level to reconstruct island topography. As the uplift rate has a significant impact on the adjusted sea level (Fig. 2), and thus the reconstruction and all subsequent measures of island connectivity, additional model sensitivity tests were conducted to determine the effects of variability in this averaged rate by reproducing the reconstructions and models for a number of alternative sea level values (see SOM Figs. S2–S4).

The 70 ka and 65 ka paleogeographic reconstructions were used to determine past intervisibility (as in Kealy et al., 2017) as well as paleoriver systems. The formulas used to measure absolute and relative intervisibility are expressed in Table 1. In order to detect the paleorivers from our reconstructed topography, we first hydrologically conditioned our Digital Elevation Model (DEM) using the

Optimized Pit Removal tool V1.5.1 (Soille, 2004; Jackson, 2013) to clearly establish flow direction and remove small errors from the data. The paleorivers were determined using the Hydrology toolset in ArcGIS 10.5.1 (ESRI, 2017), based on our reconstructed and conditioned topography. A standard drainage threshold of 100 cells was applied to the flow accumulation model to delineate paleostreams and paleorivers (Jackson, 2013; ESRI, 2017). See SOM Figures S5 and S6 for the resulting paleohydrological maps.

An important consideration regarding the reconstructions of Wallacea are the addition and/or significant enlargement of islands that emerge throughout the region as a result of lowered sea levels (Kealy et al., 2016). As Kealy et al. (2016) demonstrated, over 100 additional islands emerge throughout Wallacea if sea levels are lowered by 45 m. For our 70 ka and 65 ka reconstructions we recovered an additional ca. 300 emergent islands greater than 5 km^2 (see SOM Figs. S7 and S8). This has a significant impact on island connectivity, and thus the directions early modern humans potentially moved throughout the region (Kealy et al., 2016).

2.4. Extending the least-cost model from land out to sea

The least-cost pathway model for early modern human dispersal out of Africa by Field and Lahr (2005) focused on slope and waterway variables to calculate the most likely routes from Africa to Sahul. Their simulation did not, however, allow for the possibility of sea crossings, forcing them to pause their model when it reached Sunda's east coast. Field and Lahr superimposed Birdsell's (1977) routes onto their least-cost model to bring it to the Sahul coast, where they were able to restart their analysis. Here, we developed cost values for water crossings in order to allow a continuation of the least-cost path into and through the Wallacean archipelago.

Three separate variables were combined to produce a cost surface for sea travel in Wallacea at 70 and 65 ka. The first variable was distance from the coast in km^{-1} (Table 1), based on the assumption that voyage difficulty increases, and success rate decreases, the further one travels away from land. The second variable was intervisibility, with three separate categories for this variable: absolute intervisibility (an estimate only; see Kealy et al., 2017), relative intervisibility, and no intervisibility, following the calculations of Kealy et al. (2017). The assumptions of intervisibility are that sea travel to an island that is visible from the shore of another is likely to be both more successful and also more attractive to prehistoric travelers. While slightly less attractive and likely to incorporate greater risks than absolute intervisibility zones, sea travel through regions of relative intervisibility are significantly more likely than areas where intervisibility is entirely absent. Thus, the values of 1, 5, and 15 were assigned to areas of absolute intervisibility, relative intervisibility, and no intervisibility, respectively (Table 1). The latter was selected following Field and Lahr (2005), who assigned the cost value of 15 to ‘sand seas’ or desert areas to define a region where crossings are unfavorable but that “does allow for crossing of short stretches”. A sea crossing shares certain similarities with desert crossings, particularly in the lack of available fresh water and the necessity of particular equipment (and thus technology) to ensure a successful journey.

Thus, in our sea crossing cost surface, the distance and intervisibility values were combined resulting in a minimum cost value of 1.1 for sea travel directly along the coast, while regions distant from the coast and lacking intervisibility significantly exceeded a value of 15. This cost surface assumes the easiest sea travel, suggesting notable levels of maritime technology (Balme, 2013) and/or the presence of particularly favorable conditions such as currents and the Austral monsoon (Chappell, 2000; Bird et al., 2018). To examine the effect of even greater difficulty of sea crossings for early modern humans, we constructed two additional sea cost surfaces whereby the distance from the coast variable was multiplied by 3 and by 5, respectively (Table 1), before the addition of the intervisibility values, following on from Field and Lahr's (2005) ‘sand seas’ value whereby the regions of relative intervisibility would obtain total cost values of <15 for the ‘easiest’ sea crossings, ~15 for more difficult travel and >15 for the most difficult scenario. The calculations were based on the assumption that decreases in maritime abilities and/or the availability of favorable climatic conditions would result in increasing difficulties in sea journeys the further one travels away from the coast. Thus, in summary we produced cost surfaces for highly favorable, moderately favorable, and unfavorable (low) maritime travel.

Adjusting the values related to distance from the coast rather than increasing the overall seascape cost by a particular margin, assumes that some degree of the use of coast-hugging water craft was available to early Wallacean occupants. This assumption is well supported by archaeological evidence from the region (i.e., O'Connor et al., 2011), various hypotheses regarding early human dispersal from Sunda to Sahul (Birdsell, 1957, 1977; Clark, 1991; Bulbeck, 2007; Balme, 2013), and genetic studies which support theories of relatively large groups comprising the Sahul founder population (Tobler et al., 2017; Bird et al., 2018).

2.5. Digitizing Birdsell's routes by least-cost pathway analysis in ArcGIS

When Birdsell (1977) drew his likely routes from Sunda to Sahul, he employed three key variables to determine their direction: 1) distance between islands; 2) island height; and 3) island width. Here these variables are replicated digitally, and additional variables based on the least-cost path analysis of Field and Lahr (2005) are also incorporated into the model.

In all three seascape cost surfaces, the minimal value is greater than the minimal values of travel by land, encouraging the model to favor land travel and minimize sea travel where possible. In this way the immediate effect of distance between islands (Birdsell's first variable) is incorporated into our model as it is run spatially in GIS. In addition, we have incorporated values for distance from the coast into our seascape cost surface, further building on this key variable. Birdsell's (1977) second variable of island height was a proxy for island visibility. Here we use the intervisibility variables originally developed by Kealy et al. (2017) based on our reconstructed island heights (see Section 2.2 above). Birdsell's (1977) third variable, island width, is not assigned explicit values in our model, however by developing our analysis in GIS we are able to incorporate the effect of island width as this directly affects the exact distances between islands as well as the extent of the intervisibility buffers.

Field and Lahr (2005) used five different variables in their least-cost pathway analysis: 1) slope; 2) major rivers; 3) riparian areas; 4) sand seas; and 5) sea. Here we replicate Field and Lahr's (2005) slope variable using the same formula to calculate energy cost values (Table 1), based on our reconstructed topography (see Section 2.2 above). While Field and Lahr (2005) modeled major rivers as impermeable to crossings by early modern humans, in this model we have ignored this variable for two reasons. Firstly, the lack of any known rivers in the Wallacean region of a magnitude significant enough to affect human movement (unlike, for example, the Ganges River in India; Field and Lahr, 2005). Secondly, unlike Field and Lahr (2005), we do not assume that early modern humans were incapable of water crossings (particularly by the time they reached Wallacea), thus negating their ‘major river’ barrier variable. We did, however, incorporate Field and Lahr's (2005) third variable of a preference for travel in riparian zones. Unlike Field and Lahr (2005), who only considered a riparian buffer zone of 1 km of rivers for this variable, we extrapolated this out into distance (km) from rivers for the entire region. We then converted these distance values into an exponential series before adding back the original distance values divided by ten (Table 1). This was done not only to account for the exponentially increasing difficulty of travel as one moves away from a source of fresh water, but also to mitigate the 'walk on water' effect, whereby the cost surface indiscriminately forces travel along river systems due to excessively low cost values (Surface-Evans, 2012). Field and Lahr's (2005) fourth variable was excluded from this analysis due to the absence of deserts in the region. The fifth variable was included but extensively modified in order to allow for the possibility of sea crossings (see Section 2.3 above).

Our final cost surface for Wallacea thus incorporated the following 5 travel variables for the periods 70 ka and 65 ka: slope energy cost, exponential distance from rivers cost, level of intervisibility at sea cost, distance out to sea cost, and the three options of ease of maritime travel (Table 1). Potential start points were placed at 200 km intervals along the east coast of the Sunda continental paleoextent. The Cost Distance, Cost Back-Link and Cost Path tools in the ArcGIS 10.5.1 (ESRI, 2017) Spatial Analyst Toolbox were then used to model a 'path of least resistance' across our cost surfaces between the point intervals on the Sunda paleocoast (source) to the Sahul paleocoastline (destination).

3. Results

3.1. 65 ka

The period of lowest adjusted sea level (52.5 m below present) and greatest extent of intervisibility in Wallacea within the envelope of likely human colonization was 65 ka (Kealy et al., 2017). Thus, the paleogeographic reconstruction of the region draws the Sunda coastline down the east coast of an expanded Borneo, south to Java and encompassing Bali before curving back to the west. Our least-cost model for this time period favors a single, central launch point just to the east of the present day Balabalagan archipelago and west of the West Sulawesi province capital Mamuju. The three least-cost analyses produced very similar paths which all terminate at present day Misool Island, at the time the most north westerly extent of the Sahul coast (Fig. 3). The most notable difference between the paths was the more northerly route through Obi and Kofiau Islands selected by the highly favorable maritime travel model (H; see Fig. 3), compared to the moderate (M) and low (L) favorable models that suggest a route through Buru and Seram Islands. While both the high and moderate models suggest a similar landing point at the very eastern tip of the continent, the low maritime favorability model predicts a slightly more westerly landing point. The only other variation in routes is after the eastern departure from Sulawesi; the paths taken through the Peleng Islands into the Sula Island group (Taliabu, Mangole, and Sanana Islands) are slightly different depending on the model. Once again, the most northerly path is drawn by the high maritime favorability model while the moderate and low models share the slightly more southern option with minor differences. At 65 ka our least-cost model does not provide any options for the southern route suggested by Birdsell (1977). Even forcing the model to start at the eastern tip of Bali or modeling a path from Lida Ajer in Sumatra to Madjedbebe in the Northern Territory, Australia, still results in the same pathways through Wallacea as those shown in Figure 3 (see also SOM Fig. S9).

3.2. 70 ka

At 70 ka, sea levels are significantly higher (adjusted sea level: −25 m) in Wallacea than they are at 65 ka, pushing the Sunda coastline back to Sumatra in the south and a slightly extended modern-day mainland Southeast Asia coastline (Vietnam). The results of the 70 ka models are significantly different from those for 65 ka, suggesting a secondary path as a possible, although less likely route through Wallacea (Fig. 4). After launching from modern day Bangka Island and traveling through the extended southern coast of Borneo, the most likely path to Sahul suggested by all three 70 ka models is essentially the same as that drawn for the 65 ka models. The alternative pathway suggested by the model, however, launches from the southern tip of expanded Sumatra (modern Lampung Province), travels through Java and the Nusa Tenggara archipelago before crossing from Alor Island into Timor near the present Timor-Leste town of Liquiçá. This secondary path then follows Timor's northern coastline east, crossing to the conjoined islands of Leti, Moa, and Lakor, onto Jagatutur and then south to the expanded Sahul coast at the modern Tiwi islands.

4. Discussion

Numerous studies (e.g., Birdsell, 1977; Clark, 1991; Chappell, 1993; Oppenheimer, 2009; O'Connell et al., 2010; Balme, 2013; Kealy et al., 2016; O'Connor et al., 2017b) have cited the effects of changing sea-levels on the colonization of Sahul; however, until now there has been no detailed and updated review of Birdsell's (1977) study. Additionally, while some studies (Butlin, 1993; Morwood and Van Oosterzee, 2007; Coller, 2009; Davies and Bickler, 2015; Kealy et al., 2016; Bird et al., 2018; Norman et al., 2018) have reconstructed various islands in Wallacea at differing periods of sea-level fall using bathometric data, only a very few (Langley et al., 2016; Hawkins et al., 2017; Kealy et al., 2017; O'Connor et al., 2017b, 2018a) have incorporated island uplift rates into their reconstructions.

The GEBCO14 30 arc-second dataset (Smith and Sandwell, 1997), used in most recent paleoreconstructions for Wallacea (Kealy et al., 2016; Reepmeyer et al., 2016; Clarkson et al., 2017; Hawkins et al., 2017; O'Connor et al., 2017b, 2017c; 2018a) as well as previous studies of intervisibility (Kealy et al., 2017) and dispersal pathways (Norman et al., 2018), is of a low resolution (ca. 950 m^2 pixels) that can misrepresent minimum and maximum elevations, particularly for small islands or narrow channels (Department of Hydrography, Netherlands, 1902; Bird et al., 2018). Bird et al. (2018) suggested this poor resolution leads to underestimations of maximum elevation on the small islands reconstructed for paleogeographic models, with a consequent underestimation of intervisibility for areas such as the Sahul Banks between Timor and Australia during the period of likely human colonization. When compared directly with specific sounding measurements taken by early Dutch explorers in the smaller channels of the Wallacean archipelago (Department of Hydrography, Netherlands, 1902), it is also evident that the GEBCO14 dataset can result in overestimations of reconstructed island connectivity. Unfortunately, while good, high resolution bathymetric data is available for the region between Timor and Australia (see Bird et al., 2018), such data is not yet available in a digital format for the rest of Wallacea and its neighboring regions. Thus, until better resolution datasets are made available, studies which analyze the Wallacean Archipelago in its entirety must depend on the GEBCO14 database (i.e., Kealy et al., 2017; Norman et al., 2018) as we do here.

The digitization of Birdsell's 1977 Sunda to Sahul route model into a GIS least-cost pathway analysis has resulted in overwhelming support for a northern route for both 65 ka and 70 ka.

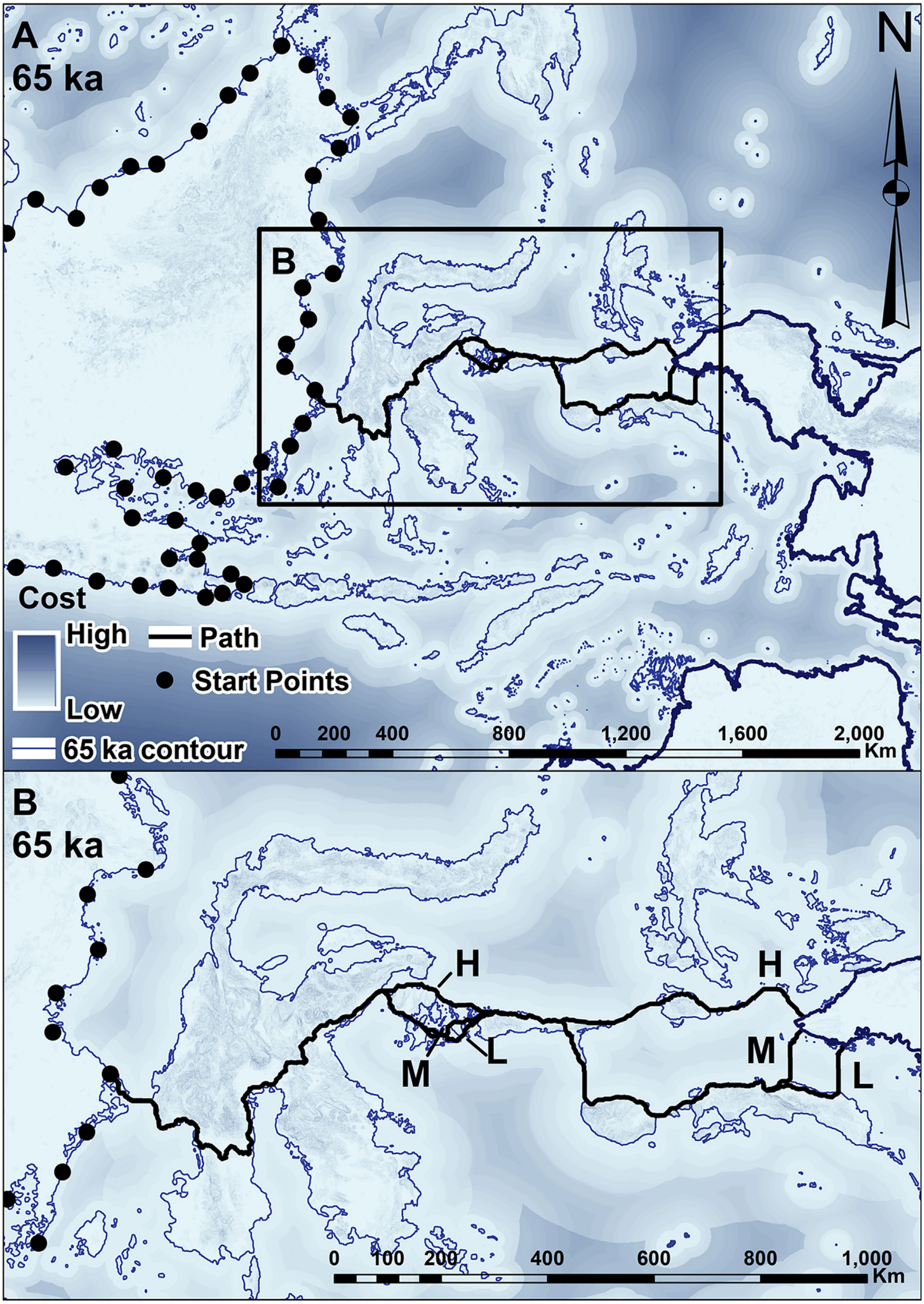

Figure 3. Least-cost pathways between Sunda and Sahul at 65 ka. Black lines indicate paths: H = high maritime favorability; M = moderate; L = low. Black dots indicate possible launch points from Sunda, dark blue line indicates the landing edge of Sahul. Blue lines indicate reconstructed island extent at 65 ka. Background shading represents the high favorability cost surface with darker shades indicating higher cost. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

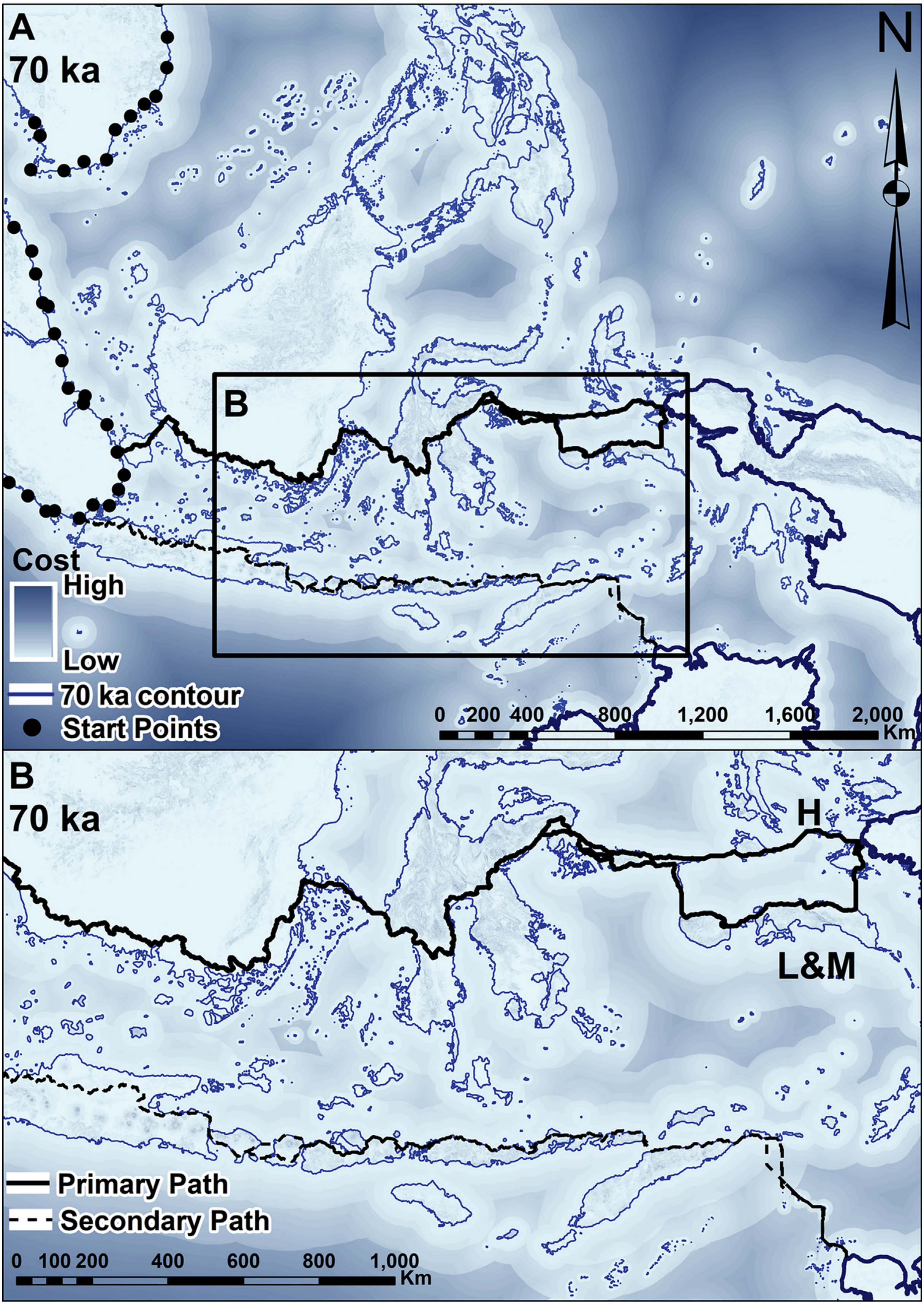

Figure 4. Least-cost pathways between Sunda and Sahul at 70 ka. Black lines indicate paths: H = high maritime favorability; M = moderate; L = low. The larger, solid line indicates the most likely paths; the thin/dotted line indicates the secondary, alternative path. Black dots indicate possible launch points from Sunda, dark blue line indicates the landing edge of Sahul. Blue lines indicate reconstructed island extent at 70 ka. Background shading represents the high favorability cost surface with darker shades indicating higher cost. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The combination of shorter crossing distances and continuous absolute intervisibility makes this route the most likely option in all modeled scenarios. This does not rule out the possibility that other routes were used by the early inhabitants of Wallacea to travel between islands and onto Sahul. Our model nevertheless suggests a northern route from Sulawesi, and through either Obi or Seram, with a landing point near the New Guinea Bird's Head (i.e., Misool) was the easiest based on the variables examined, and thus likely the earliest route taken through Wallacea and into Sahul. There is, however, a very limited archaeological record for these islands that could be used to test the model results. Sulawesi has been the focus of many archaeological excavations since the 1960s (O'Connor and Bulbeck, 2014; Brumm et al., 2017; Bulbeck et al., in press), and has received an increasing amount of attention recently with some of the oldest dates (ca. 40.7 ka) for early modern human occupation in Wallacea located just south of our modeled path (SOM Fig. S1; Aubert et al., 2014), but the archaeological record becomes increasingly sparse to the east.

Archaeological research is unknown for the Peleng islands, while in the Sula group just to the east, three sites have been excavated and produced radiocarbon dates for occupation on Sanana Island (Tanudirjo, 2001). The oldest of these, Fatiba Cave (SOM Fig. S1), records earliest occupation at 16.2–17.2 ka cal BP (14200 ± 150 ANU-10502; Tanudirjo, 2001), calibrated here using OxCal 4.3.2 (Ramsey, 2009) and the Marine 13 calibration curve (Reimer et al., 2013). The location of this date on Sanana Island does not provide any greater support for the low and moderate maritime favorability models due to both the lack of comparative research on the other islands in the Sula group, and the site's young age when compared to the oldest dates in the wider Wallacean and Sahul regions.

The only paleoecological research on the island of Obi was a paleoenvironmental reconstruction extending back to about 2.6 ka (Hope, 2015). No archaeological data is known from either Obi or Kofiau Island (islands traversed by the high maritime favorability models). For the Seram alternative (moderate and low favorability models), the situation is only slightly better. Buru, Ambon, Haruku, Saparua and Seram islands have all received some archaeological investigation (Röder, 1938; Ellen and Glover, 1974; Glover and Ellen, 1975; Bintarti et al., 1977; Spriggs and Miller, 1979; Stark and Latinis, 1996; Latinis and Stark, 2003, 2005; Lape et al., 2016); however, excavations and radiocarbon dates are limited, with the earliest calibrated dates for occupation of this island group no older than 7 ka (Latinis and Stark, 2005; Kealy et al., 2018).

For Misool Island, where all paths either terminate (for the 65 ka models) or pass through before reaching the New Guinea Bird's Head (for the 70 ka most likely models), extensive survey for rock art by multiple researchers has identified over 60 separate rock art localities (Chazine, 2011; Oktaviana, 2015; Oktaviana and Setiawan, 2016; Nasrudin, 2017). While not directly dated, these are considered older than 1 ka (Chazine, 2011), although how much older has yet to be determined. A recent cave excavation on Misool recovered samples for radiocarbon dating (Adhi Agus Oktaviana, pers. comm), which may elucidate its occupation history. On mainland Sahul the nearest archaeological sites with published radiocarbon dates are Kria and Toé Caves near the Ayamaru Lakes (SOM Fig. S1), Central-West Bird's Head, West Papua (Pasveer, 2004; Wright et al., 2013). Of these two sites, Toé Cave records the oldest occupation at 29.6–30.7 ka cal BP (25940 ± 180 OZG-063; Pasveer, 2004) calibrated here using OxCal 4.3 (Ramsey, 2009) and the IntCal13 calibration curve (Reimer et al., 2013).

When compared with Birdsell's (1977) northern route options (Fig. 1A–C), the moderate and low maritime favorability models match 1B, while the high favorability model follows the first half of Birdsell's (1977) 1A branch to Obi island, although instead of crossing to Halmahera our model suggests a crossing directly to the east through a few smaller emergent and enlarged islands including Kofiau Island before reaching Misool. Thus, neither Halmahera or Gebe Island are suggested in the most likely route to Sahul despite their archaeological records (Bellwood et al., 1998). However, as the oldest occupation dates for Halmahera and Gebe postdate the oldest dates in the region (Bellwood et al., 1998; Higham et al., 2009; Summerhayes et al., 2010; Clarkson et al., 2017; Westaway et al., 2017), these islands were possibly colonized as a result of later dispersals radiating out from the islands on the main route, or perhaps even by back colonization from the New Guinea Bird's Head following initial arrival on Sahul. Additional exploration and dating of archaeological sites in this region are required to further investigate these and other scenarios of early human colonization of the northern Maluku islands.

The oldest archaeological dates bracketing the northern route in Sunda and Sahul are known from Niah Cave, Borneo and Vilakuav, Papua New Guinea, respectively (SOM Fig. S1). Both these sites suggest human occupation through this region by at least 50 ka: 47–ca. 50 ka cal BP initial occupation at Niah (OxA-V-2057-31; the upper end at the limit of radiocarbon dating: Higham et al., 2009) and 43.1–49.1 ka cal BP initial occupation at Vilakuav (Wk 27072; Summerhayes et al., 2010). Thus, while our models strongly support a northern route from Sunda to Sahul, considering the few archaeological sites in the region and when compared with the significantly older dates along the southern route (Clarkson et al., 2017; Westaway et al., 2017), this path, unsurprisingly, receives little validation from the archaeological record. While the recent finds from Laili cave in Timor-Leste demonstrate that modern humans did breach the Wallace Line using a southern route by around 43.3–44.6 ka cal BP (Hawkins et al., 2017), the continued disparity between the Wallacean and Sahul dates (Clarkson et al., 2017) suggest that our current patterning for colonization of the region is suffering from both limited sampling of field sites, inadequate application of a variety of different dating methods at most of the sites excavated and uncertainties in the calibration curve at this age (O'Connor et al., 2010). Future intensive sampling and the application of alternative dating techniques throughout Wallacea will likely produce even older dates and possibly close up some of the gaps in the region.

While the 70 ka models do suggest a possible (although much less likely) southern route from Sunda to Sahul, it is interesting to note the absence of this possibility in the 65 ka model outcomes. Based on model sensitivity tests (see SOM Figs. S2–S4 and S9–S11) we hypothesize this is due to changes in sea level, which affect sea crossing distances. While low sea levels result in shorter crossing distances throughout Wallacea, the particularly short distances between the northern islands in the 65 ka models (when compared to the southern distances) pushes the model to overwhelmingly favor this route over any other. As sea levels rise and crossing distances increase, the disparity in distances between the north and south declines, opening the possibility for a secondary route to Sahul through the south (70 ka models). Our model sensitivity tests also demonstrate the transition point in sea levels where the secondary route becomes possible occurs between ca. 40–42 m below present (SOM Figs. S3–S4). Thus, when sea levels are at −40 m or higher (e.g., 70–69 ka, 61–57 ka, 53–49 ka; Fig. 2) the model suggests the southern route as a less favorable but possible pathway. However, when sea levels are below −42 m (e.g., 68–62 ka, 56–54 ka, 48–12 ka) the model only supports a northern route option. While the northern route is still the more parsimonious and likely path through Wallacea, this crossing distance effect suggests that periods of higher sea-level might have encouraged early modern humans to preferentially use the southern route into Sahul.

The alternative southern route proposed by the 70 ka models is essentially identical for all three maritime favorability options.

Following Birdsell's (1977) southern route 2B, the only variation suggested by our models is at the crossing from Timor to Australia. While Birdsell's (1977) 2B line is drawn at a direct south-east diagonal from central Timor to the expanded Australian coast, our models suggest the least-costly path on this alternative route to involve a crossing from the eastern tip of Timor to the conjoined islands of Leti, Moa and Lakor before taking a more directly southern path down to the Sahul coast. Minimal archaeological reconnaissance has been conducted on these three islands, and no sites with excavation potential have yet been identified, or excavations carried out (Sudarmika, 2001a,b; S.K. and S.O., pers. obs.). However, a launching point from the eastern tip of the island of Timor is supported by the islands' relatively extensive archaeological record. The oldest date for Timor (and Wallacea) is from Laili, a site ca. 125 km west of the eastern tip of the island (Hawkins et al., 2017). The initial occupation date for Laili is only 0.3 ka outside of the calibrated range of Timor's second oldest site, Jerimalai (O'Connor, 2007), which is located at the island's eastern end. In fact, the location and minimal age offset between these two early sites fits perfectly with our modeled colonizing path landing on the central north coast of Timor and moving east along the coast before the next launch from the island's most easterly point.

The results of our possible southern route contrast with Bird et al.'s (2018) drift voyage models, which favored a western departure point from Timor at the island of Roti, rather than the easterly option suggested here. The study by Bird et al. (2018), however, only focused on the crossing from Timor's southern margin to Australia and does not account for the extenuating effects of the initial landing point on Timor. Our model suggests a central-north landing, followed by eastward movement along the coast. While movement along the west coast is also likely, the central mountain range of Timor would have been a barrier to movement directly to the south. Thus, while Bird et al. (2018) proposed that Roti is the most favorable launch point, our least-cost model suggests launching from the east to have been a more likely initial exit based on Timor's topography and the landing location from Alor.

Bird et al.'s (2018) focus on a southern route was based on paleoenvironmental reconstructions that suggested a savanna corridor facilitated the successful movement of early modern humans through the region. Others (e.g., Birdsell, 1977; Anderson, 2018) have also pointed out paleoenvironmental restrictions to maritime dispersal, such as the distribution and availability of bamboo throughout the region that could affect local construction of sea-worthy vessels. While savanna ecosystems were likely attractive environments for early hominins in Sunda and by extension Wallacea (Louys and Turner, 2012), Bird et al.'s (2018) hypothesis that the lack of a savanna environment along the northern route had a negative impact on dispersal (by restricting pathways to coastlines or dense jungle) seems at odds with early records of rainforest use by modern humans (Baker, 2013; Roberts and Petraglia, 2015; Westaway et al., 2017). Furthermore, assuming early dispersers had some maritime capabilities (particularly necessary if voyaging to Sahul was purposeful as suggested by the drift models of Bird et al., 2018; and population genetics, see Tobler et al., 2017; Bird et al., 2018), then movement restricted to coastal regions seems unlikely to have acted as a deterrent to modern human dispersal. A maritime and coastally adapted subsistence culture is supported by the Wallacean archaeological record (e.g., Samper Carro et al., 2016, 2017; Hawkins et al., 2017; O'Connor et al., 2017c, 2018a) as well as early sites on either side of the archipelago (i.e., Niah: Baker, 2013; Barrow Island: Veth et al., 2017). Additionally, if one assumes a more coastally orientated dispersal out of Africa, as suggested by Bulbeck (2007) and largely supported by the results of Field and Lahr's (2005) least-cost pathway analysis, not only does this support the pre-existence of appropriate maritime technologies for the first crossing into Wallacea, but also suggests that the early occupants of Wallacea were comfortable in coastal environments and possibly may have favored these over savannas.

5. Conclusions

Our least-cost pathway models indicate that the most likely route taken by early modern humans in the colonization of Sahul from Sunda, ca. 65–70 ka, was a northern route through the Wallacean archipelago. Specifically, we recover strong support for Birdsell's (1977) route 1B and a modified 1A with landings on the modern island of Misool. While both 65 ka and 70 ka models strongly indicate the northern path as the most likely route, the 70 ka results are notable for the presence of a secondary, though much less likely option through the south that is made available through rising sea levels. Our models suggest that this would have also been the case for a later colonization scenario at ca. 50 ka.

The lack of Pleistocene dates from the islands along Birdsell's northern route has often been used to support a southern route from Sunda to Sahul. However, apart from Sulawesi, few of the northern islands crossed by our modeled path have been subject to concerted archaeological exploration for traces of early modern human occupations. Recent intensive exploratory fieldwork on the archaeology of the islands in Nusa Tenggara Timur and Maluku Barat Daya (i.e., the southern route) has resulted in a number of new sites with Pleistocene dates (Samper Carro et al., 2016, 2017; O'Connor et al., 2018a), as well as a significant expansion of the known rock art record (O'Connor et al., 2015, 2018b,c,d; Kealy et al., 2018), highlighting the importance of fieldwork in this region and the potential for similar findings on the islands in the north. In particular, the continued lack of sites along the southern route which predate initial occupation of Sahul supports the possibility that this route was not the one used for the initial colonization, but instead acted as a secondary pathway through the region following colonization of the islands of the northern route, perhaps facilitated by rises in sea levels after 65 ka.

Our least-cost models present the most likely route between Sunda and Sahul for early modern human dispersal, based on currently available data. Future refinements to this model will require the development of a more accurate bathymetry for Wallacea, a fine-scale paleocurrent model of Wallacea, more extensive uplift records throughout the region, and sediment core analyses to determine paleodenudation rates. Our models have nevertheless highlighted key regions in Wallacea for future archaeological fieldwork, specifically; the islands of Misool, Seram, Obi and the Peleng-Sula group. Strategic exploration of the archaeological records of these islands is imperative for further discussion and testing of the different modeled pathways presented here and elsewhere (i.e., Birdsell, 1977; Norman et al., 2018).

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Supplementary Online Material

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