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Minimum founding populations for the first peopling of Sahul

Corey J. A Bradshaw
Flinders University

Sean Ulm
James Cook University (JCU), James Cook University, sean.ulm@jcu.edu.au

Alan Williams
University of New South Wales

Michael I. Bird
James Cook University (JCU), James Cook University, Michael.bird@jcu.edu.au

Richard G. Roberts
University of Wollongong, rgrob@uow.edu.au

See next page for additional authors

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Minimum founding populations for the first peopling of Sahul

Abstract

The timing, context and nature of the first people to enter Sahul is still poorly understood owing to a fragmented archaeological record. However, quantifying the plausible demographic context of this founding population is essential to determine how and why the initial peopling of Sahul occurred. We developed a stochastic, age-structured model using demographic rates from hunter-gatherer societies, and relative carrying capacity hindcasted with LOVECLIM's net primary productivity for northern Sahul. We projected these populations to determine the resilience and minimum sizes required to avoid extinction. A census founding population of between 1,300 and 1,550 individuals was necessary to maintain a quasi-extinction threshold of ≤ 0.1 . This minimum founding population could have arrived at a single point in time, or through multiple voyages of ≥ 130 people over ~ 700 -900 years. This result shows that substantial population amalgamation in Sunda and Wallacea in Marine Isotope Stages 3-4 provided the conditions for the successful, large-scale and probably planned peopling of Sahul.

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Authors

Corey J. A Bradshaw, Sean Ulm, Alan Williams, Michael I. Bird, Richard G. Roberts, Zenobia Jacobs, Fiona Laviano, Laura S. Weyrich, Tobias Friedrich, Kasih Norman, and Frrik Saltr

TITLE: Minimum founding populations for the first peopling of Sahul

SHORT TITLE: Founding populations of Sahul

Corey J. A. Bradshaw^{1,2,*}, Sean Ulm^{3,2}, Alan N. Williams^{4,5,2}, Michael I. Bird^{6,2}, Richard G. Roberts^{7,2}, Zenobia Jacobs^{7,2}, Fiona Laviano¹, Laura S. Weyrich^{8,2}, Tobias Friedrich⁹, Kasih Norman^{7,2}, and Frédérik Saltré^{1,2}

¹Global Ecology, College of Science and Engineering, Flinders University, GPO Box 2100, South Australia 5001, Australia

²ARC Centre of Excellence for Australian Biodiversity and Heritage. EpicAustralia.org.au

³College of Arts, Society and Education, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia

⁴Climate Change Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, NSW 2052, Australia

⁵Extent Heritage Pty Ltd, 3/73 Union Street, Pyrmont, New South Wales 2009, Australia

⁶College of Science and Engineering, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia

⁷Centre for Archaeological Science, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia

⁸Australian Centre for Ancient DNA, University of Adelaide, Adelaide, South Australia 5005, Australia

⁹International Pacific Research Center, School of Ocean and Earth Science and Technology, University of Hawaii, Honolulu, Hawai'i, 96822, USA

* corresponding author, Corey J. A. Bradshaw, College of Science and Engineering, Flinders University, GPO Box 2100, South Australia 5001, Australia. e-mail: corey.bradshaw@flinders.edu.au; tel: +61 8 8201 2090

Key words: Australia, Sahul, founding population size, extinction, demography, Aboriginal settlement

36 **Abstract**

37 The timing, context, and nature of the first people to enter Sahul is still poorly understood
38 owing to a fragmented archaeological record. But quantifying the plausible demographic
39 context of this founding population is essential to determine how and why colonisation of
40 Sahul occurred. We developed a stochastic, age-structured model using demographic rates
41 from hunter-gatherer societies and relative carrying capacity hindcasted with LOVECLIM's
42 net primary productivity for northern Sahul. We projected these populations to determine
43 resilience and minimum sizes required to avoid extinction. A census founding population of
44 between 1300 and 1550 total individuals was necessary to maintain a quasi-extinction
45 threshold $\lesssim 0.1$. This minimum founding population could have arrived at a single point in
46 time, or through multiple voyages ≥ 130 people over ≥ 700 years. This result shows that
47 substantial population amalgamation in Sunda and Wallacea in Marine Isotope Stages 3–4
48 provided the conditions for successful, large-scale, and likely planned, colonisation of Sahul.
49

50 **Main**

51 An understanding of the demographic circumstances and ecological repercussions of the
52 arrival of the first people to Sahul (mainland Australia, Tasmania, and New Guinea joined at
53 times of lower sea level) in the Late Pleistocene remains elusive¹⁻³. Some have previously
54 proposed that colonisation arose from only small family groups consisting of < 150 people⁴⁻
55 ⁷, while more recent human behavioural-ecology models suggest that several hundred
56 people would have been required for long-term survival⁷. These estimates are largely
57 speculative, but genomic research and radiocarbon-inferred demographic modelling
58 support the larger values, and imply that population sizes of 1000 to 3000 people were
59 more probable⁸⁻¹⁰. Quantifying the plausible demography of the first humans (i.e., the rate
60 of population changes relative to regional carrying capacity, and the duration over which
61 populations could have persisted at low density following initial colonisation) is essential to
62 ascertain the extent to which increasing human populations could have altered their
63 environments. Quantifying demographic transitions can also potentially help to interpret
64 the likelihood of discovering archaeological evidence, given the persistence of small human
65 populations over extended windows of time so long ago⁶.

66 The oldest archaeological evidence claimed in Australia is 65.0 ± 5.7 ka (95% confidence
67 interval) for Madjedbebe rockshelter in Arnhem Land^{11,12}, and an increasing number of early
68 sites have been reported dating to around or before 47 ka¹³⁻²¹. We therefore take the broad
69 interval of 65–50 ka as the likely arrival window of people into Sahul. Arrival most likely
70 occurred somewhere in the northern regions of Sahul, closest to the islands of Wallacea in
71 the Timor Sea, Arafura Sea, and across Torres Strait and Carpentarian Plain during times of
72 lower sea levels²²⁻²⁷. However, given that only a few archaeological sites from the north
73 have revealed cultural remains within the putative arrival window and that ancient DNA is
74 poorly preserved in this region of the world, it is difficult to estimate when and where
75 enough people first arrived in Australia to produce one of the longest standing, successful
76 human populations in the world outside of Africa — a population that went on to adapt
77 successfully and populate the entire continent over the following several thousand
78 years^{10,28,29}. Recent studies have modelled plausible routes and therefore the potential
79 geographic locations that would have supported a successful migration to Australia²²⁻²⁷, but
80 the numbers and diversity of humans that first arrived on the continent remain largely
81 unknown^{10,28,29}. Fundamentally then, the size and migration patterns of founding
82 populations (i.e., whether arrival was accidental by a small band of hunter-gatherers, or
83 something larger-scale and more complex) directly contributes to our understanding of
84 modern human societies at this time, and how the peopling of Sahul fits into this broader
85 story.

86 To determine the likely range of these unknown demographic conditions, we develop a
87 stochastic, age-structured demographic model for ancient Australians to (i) estimate the
88 minimum size of a founding population that would be required to avoid a high risk of
89 extinction at the time of colonisation, and (ii) calculate the interval and frequency of smaller
90 introductions that would maintain a low probability of extinction over the initial arrival
91 window (65–50 ka). Our model is based on realistic estimates and assumptions of hunter-
92 gatherer demography, as well as a reconstruction of carrying capacity based on hindcasted
93 estimates of net primary production. We hypothesise that several thousand individuals
94 arriving over a defined period within several centuries were required to avoid extinction
95 within the first 100 human generations following initial colonisation.

96

97 **Results**

98 *Deterministic matrix properties*

99 The base matrix **M** using the Siler hazard model³⁰ to estimate the survival vector
100 (Supplementary figure 1) produced a dominant eigenvalue $\lambda = 1.0037$, which equates to an
101 instantaneous rate of population change (r) = 0.0037. Applying different underlying
102 parameters for the Siler hazard model for ‘average forager-horticulturist’ and ‘Northern
103 Territory Aborigines’³¹ increased the base matrix’s dominant eigenvalue ($\lambda = 1.0085$ and
104 1.0201, respectively). However, given the assumed hunter-gatherer mode of subsistence
105 during the time of initial colonisation of Sahul, and the rapid rate of increase from the
106 Aboriginal data (collected 1958–1960) that likely underreported infant deaths³¹, we
107 maintained the lowest λ for the ‘average hunter-gatherer’ scenario in all subsequent
108 simulations. This model gives a ratio of the number of female offspring in year $t+1$ to the
109 number born in the previous year (R_0) of 1.11, and a mean generation time (G) of 27.7
110 years, which agrees well with the ~ 29-year generation length estimated from genealogy-
111 based studies of hunter-gatherers³². Life expectancy (e_x) according to this model increases
112 from around 31 to a maximum 42 years between the ages of 1 and 5 years old, after which
113 point it declines linearly with age (Supplementary figure 1). Thus, a 20-year-old has $e_x = 35$
114 (additional) years of expected life, and a 40-year-old has $e_x = 24$ additional years of expected
115 life (Supplementary figure 1).

116

117 *Minimum founding population size*

118 The probability of quasi-extinction ($N < 50$ individuals or < 25 females) stabilised at around
119 0.1 over 100 generations for founding population sizes of 1300 to 1550 individuals (Fig. 1),
120 or between 650 and 775 females assuming an equal sex ratio. There was quantitatively no
121 difference between the two curves assuming different timing of initial colonisation, 65–55
122 ka or 60–50 ka (Fig. 1). The relationship between probability of quasi-extinction and
123 founding population size takes into consideration all uncertainty associated with the
124 hindcasted carrying capacity K (Fig. 2), start year, and error (process and sampling) in the
125 Leslie matrix’s demographic-rate elements (survival and fertility; Supplementary figures 1
126 and 2), but it assumes a single-year introduction event (i.e., all founding individuals arrive
127 during the same year).

Taking this range (650–775 founding females) and dividing it by 10, such that one-tenth of this minimum arrive at incrementing intervals from 10 to 200 years, the probability of extinction rises approximately linearly with increasing interval length (Fig. 1b), but remains near 0.1 for up to about 70-year intervals (i.e., 65–75 founding females arriving every 70 years over seven centuries) (Fig. 1b). Assuming a non-regular (random) arrival frequency and a Gaussian-resampled arriving population size, the rate of increase in Pr(quasi-extinction) was also linear, but less than the rate based on a regular arrival frequency (Fig. 1b); for the latter, however, the probability remained ~ 0.1 up to approximately 70- to 90-year arrival intervals on average.

Global sensitivity analysis

The boosted-regression tree emulator for the twelve-dimension, Latin hypercube-sampled parameter space indicated that the dominant (negative) influence on the probability of quasi-extinction was variation in age-independent mortality (b_1 in the Siler hazard model) (Supplementary figure 3). Total fertility (F) had the next-highest relative (negative) influence, followed by the (positive) influence of infant mortality rate (a_1), and the (positive) influence of the rate of mortality decline (a_2), with all other parameters considered having relatively weak or no detectable influence on the Pr(quasi-extinction) (Supplementary figure 3).

Discussion

Discerning the plausible demographic conditions of human arrival to Australia is problematic because of the deep age of the event(s), the differential preservation of archaeological material since that time, limited ancient DNA evidence, uncertainties associated with dating, taphonomic biases, as well as the incomplete temporal and spatial coverage of samples. However, stochastic demographic models built from realistic human demographic rates, hindcasts of indicative regional carrying capacity, and relevant archaeological and genetic data to guide inference, return ecologically credible conditions. Future archaeological and palaeo-ecological data could also potentially exclude ecologically unrealistic hypotheses. Using the best data available (while acknowledging that having more is desirable), our models estimate that as few as ~ 650 females (representing ~ 1300 individuals total) arriving

in small groups (~ 130 each) over as much as 700–900 years would be sufficient to avoid a high probability of extinction during the likely environmental conditions that dominated northern Sahul between 65 and 50 ka.

These numbers of people, whether ~ 130 arriving at semi-regular intervals¹⁰ over a long period or 1300 at one time, are substantively larger than ethnographically observed Aboriginal hunter-gatherers, except during larger ceremonial gatherings³³. It therefore suggests that large populations were likely present in Wallacea during Marine Isotope Stages 3 (29–57 ka) and possibly 4 (57–71 ka) — at much greater densities than their counterparts in Australia for much of the last 50 ka — or that smaller hunter-gatherer groups banded together to make one or more migrations to Sahul. In either case, our results imply that modern human populations at that time were sufficiently socially integrated³⁴ to be able to achieve the construction and successful voyaging of multiple ocean-going vessels²⁷. It further demonstrates cognitive ability and planning, and likely deliberate migration given the numbers of people involved^{25,27}.

Unlike the mostly genetics-based estimates of founding *effective* population size (N_e) that cannot easily discern an associated *census* population size (N_c), our estimates provide a N_c that does not necessarily imply random breeding among all individuals alive. This is because we indirectly accounted for potential inbreeding depression that could arise from non-random breeding by including a catastrophic mortality function that scales with generation time³⁵. This added stochasticity thus more closely aligns with the ecological reality of a population constrained not only by environmental variability, but also by demographic and genetic stochasticity. Furthermore, genetics-based estimates of N_e cannot typically identify fine-scale details of multiple arrival events over the period of several human generations. Thus, our resampling approach also provides the unique minimum interval over which successive human arrivals could have occurred. This does not necessarily imply that arrivals of small groups of humans occurred over the 700- to 900-year (i.e., 25- to 32-generation) window we estimated; rather, it merely indicates that extinction probability remained low within this window. This does not therefore preclude the occurrence of larger and more frequent introduction pulses over longer timeframes.

Of course, our model predictions do rely on several unmeasurable parameters, not least of which are the types of survival and fertility schedules experienced by the first humans to colonise Sahul over 50–65 millennia ago. Indeed, our global sensitivity analysis

demonstrated that our results are most sensitive to variation in the underlying patterns of initial and environmentally stochastic survival probabilities estimated with the Siler hazard model, as well as total fertility (Supplementary figure 3). Nonetheless, our adoption of ‘average’ hunter-gatherer demographic rates appears reasonable and probably does not over-estimate infant survival³¹. We also assumed carrying capacity was proportional to net primary productivity³⁶, although it is also plausible that ancient humans struck a compromise between high productivity and ease of passage and/or visibility to hunt prey by tending toward ecotones of mid-range productivity³⁷. Had the ecological conditions at the time of colonisation favoured higher vital rates, then the true population size might have been larger than our estimates suggest; however, we are concerned here solely with estimating *minimum* viable population size derived from conservative, yet realistic, demographic parameters.

More importantly, assessments of relative carrying capacity appeared to have only weak effects on our model predictions, particularly given the near-identical form of the quasi-extinction/founding population size curve for the introduction windows of 65–55 ka and 60–50 ka (Fig. 1), as well as the low influence of the density-feedback survival modifier (S_{mod}) and nadir population density (D_{min}) identified in the global sensitivity analysis (Supplementary figure 3). Thus, the specific choice of carrying capacity (expressed in total humans permitted to occupy the landscape) and the arrival window *per se* have little bearing on our conclusions. This outcome holds even if carrying capacities were, in fact, higher than we assumed because of potentially higher prey availability at initial colonisation relative to later periods when many megafauna species were no longer present^{1,2} (although regional extirpation times of megafauna are still highly uncertain, especially for northern Australia).

Further, our estimate of ~ 1300 minimum founding individuals arriving within 25 to 32 generations agrees well with genetics-based estimates of total effective population size. For example, there are N_e estimates of populations as small as 170–230 Maori women based on mitochondrial DNA for the colonisation of New Zealand³⁸, as few as 70 individuals based on mitochondrial and Y-chromosome DNA for the colonisation of the New World from Asia³⁹, and 150 female Yakuts in north-eastern Siberia based on mitochondrial DNA⁴⁰. While the true $N_e:N_c$ for each of these populations is unknown, if we assume an average of ~ 0.10 based on a multi-species assessment⁴¹, the previously cited values of N_e would equate to an

N_c of 700–4600 individuals; the resemblance to our demographically based estimates is therefore striking. Previous studies of Aboriginal Australian DNA posited that at least 36–50 founding females were required to establish known Australian mitochondrial diversity (estimated from 4–5 founding females for each of the 9–10 haplogroups)²⁵. This range is likely to be a conservative minimum boundary, as founding populations with limited female diversity (< 10 per haplogroup) have little chance of survival⁴². Again assuming a $N_e:N_c = 0.1$ gives an N_c ranging from 720 to 1000, our results are not at odds with this argument, although our model conservatively suggests that the minimum number of females per haplogroup would likely have been higher. However, such estimates assume that known Australian haplogroups today represent the total mitochondrial diversity present during colonisation and this assumption is likely to be inaccurate.

In summary, our demographic models quantifying the ecologically plausible demographic context of the first humans to colonise Australia now allow for exploration of other questions regarding human adaptations and technological developments during this period, which could have assisted in the successful colonisation of Sahul. Possibly driven in part by the amalgamation of people in Sunda and Wallacea at this time, more research describing the antecedent conditions in those regions would assist greatly in describing the source population(s) and possibly reveal the impetus for subsequent directed migrations²²⁻²⁷ to Sahul.

Methods

Demographic rates

Our first requirement was to estimate realistic demographic rates (survival, fertility, longevity) for ancient Australians to parameterise an age-structured model. For survival, we used the five-parameter Siler hazard model³⁰ to estimate the age- (x) specific proportion of surviving individuals (l_x), which incorporates survival schedules for three stages: immature, mature, and senescent individuals within the population:

$$l_x = e^{\left(\frac{-a_1}{b_1}\right)(1-e^{-b_1x})} e^{-a_2x} e^{\left(\frac{a_3}{b_3}\right)(1-e^{-b_3x})} \quad (1)$$

where a_1 = initial infant mortality (also described elsewhere as α_i), b_1 = rate of mortality decline in immatures, a_2 = the age-independent mortality due to environmental influence, a_3 = initial adult mortality, and b_3 = the rate of mortality increase (senescence). We used the

average ‘hunter-gatherer’ parameter estimates from Gurven and Kaplan³¹ (based on modern populations and compared to palaeo-demography) to construct l_x ($a_1 = 0.422$, $b_1 = 1.131$, $a_2 = 0.013$, $a_3 = 0.000147$, $b_3 = 0.086$), and then calculated the age-specific survival (S_x) for life tables (Supplementary figure 1) as:

$$S_x = 1 - \frac{(l_x - l_{x+1})}{l_x} \quad (2)$$

From the l_x vector, we also calculated the age-specific life expectancy (e_x) as:

$$e_x = \sum_{i=1}^n \left(\frac{(l_x + l_{x+1})}{2} \right)_i$$

For fertility, we first estimated a fertility schedule based on age at primiparity estimates for 22 modern hunter-gatherer groups⁴³, taking the average and 95% confidence interval of these for women as an indicator of the onset of reproduction in such societies. These give a mean age of 19 years old for primiparity among women (95% confidence interval: 16–24). Further evidence on reproductive senescence and menopause in hunter-gatherer women suggests that hunter-gatherer societies include many women beyond their fertile years⁴⁴⁻⁴⁶. Thus, the onset of reproduction and the implied fertility decline compares well with the global average fertility schedule of modern *Homo sapiens*⁴⁷. For total fertility (F), we used the value of 4.69 births (i.e., 2.35 daughters) for the !Kung hunter-gatherer society⁴⁸ (Supplementary figure 2).

Age-structured (Leslie) matrix model

From these estimated demographic rates, we constructed a pre-breeding, 81 (i) $\times$ 81 (j) element (representing ages from 0 to 80 years old), Leslie projection matrix (**M**) for females only (males are demographically irrelevant in this context assuming equal sex ratios), multiplying a population vector **n** to estimate total population size at each forecast time step⁴⁹. Thus, we used a longevity (ω) of 80 years based on cross-cultural examination of hunter-gatherer societies³¹, which is itself founded on the modal adult death of about 70 years. Fertilities (m_x) occupied the first row of the matrix, survival probabilities (S_x) occupied the sub-diagonal, and we set the final diagonal transition probability (**M** _{i,j}) to zero. We projected the **Mn** combinations for each iteration of the simulation (see below) to obtain yearly total population size.

Carrying capacity

In the absence of measured compensatory density-feedback mechanisms for ancient humans, we used a hypothetical reduction in the survival vector by constructing a theoretical carrying capacity (K) built from a hindcasted estimate of net primary production based on the LOVECLIM climate reconstruction⁵⁰. LOVECLIM is a three-dimensional Earth system model of intermediate complexity⁵¹ (i.e., its spatial resolution is coarser than that of state-of-the-art general circulation models, and its representation of physical processes is simpler) that has been validated extensively for the last few glacial cycles and for many regions of the world⁵²⁻⁵⁵. LOVECLIM includes representations of the atmosphere, ocean and sea ice, land surface (including vegetation), ice sheets, icebergs and the carbon cycle, and produces climates over the past 120 ka in 1000-year snapshots downscaled (using a bilinear interpolation)^{56,57} at a spatial resolution of $1^\circ \times 1^\circ$. For each grid cell and each 1000-year snapshot, we extracted mean annual temperature, mean annual precipitation, freshwater availability (i.e., evapotranspiration – precipitation), bottom (soil) moisture, desert fraction, and net primary production⁵⁸. The candidate K output variables (freshwater availability, bottom moisture, desert fraction, and net primary production) for northern Australia (see below) were highly correlated (Spearman's $|\rho| \geq 0.842$; Supplementary table 1), so we chose net primary production ($\text{kg C m}^{-2} \text{ year}^{-1}$) as the comprehensive indicator of relative carrying capacity through time. Indeed, regional carrying capacity is correlated with net primary production for many species, including humans⁵⁹⁻⁶³. To focus on the region of interest, we took all Sahul (Australia, New Guinea and Tasmania) $1^\circ \times 1^\circ$ grid cells from the equator (0°) to 14° south latitude to represent 'northern' Sahul (including New Guinea, most of the Top End of the Northern Territory and Cape York Peninsula) (Fig. 2a), and calculated the 25% and 75% percentiles for net primary production across this region; from within this quartile range, we stochastically sampled annual net primary production per projection iteration (see below).

To translate net primary production into a carrying capacity expressed in units of humans the landscape was capable of supporting, we used data derived from archaeological sites and the assumption of a putative population low (nadir) that occurred during and immediately after the Last Glacial Maximum (23–18 ka)⁶⁴⁻⁶⁷, when conditions were cooler than today and much (but not all⁶⁸⁻⁷¹) of the continent was drier⁷²⁻⁷⁹. Demographic reconstructions based on the spatial distribution of dated archaeological sites suggest that

up to 80% of Australia could have been abandoned or experienced reduced occupation at some point during this interval⁶⁶, or at least a major spatial thinning of populations (perhaps as much as 60%) during this period⁹. From these demographic reconstructions, we set the baseline population size at the Last Glacial Maximum at 47,000 people continent-wide⁸⁰. This figure is based on an estimated area of habitable land⁸⁰ for Sahul of 9.4 million km² and a population density⁶⁶ of 0.005 individuals km⁻², which is similar to historical estimates of population densities for Australian deserts⁸¹. We recognise that inferences of past population size are subject to many uncertainties^{67,82-85} and note accordingly that our model results are not critically dependent on the above input values (see the global sensitivity analysis and Supplementary figure 3).

From this putative population low at or around the Last Glacial Maximum, we back-tracked to the window of colonisation to estimate a relative carrying capacity for this period. We then scaled the relative net primary production curve by first adding the absolute minimum 25th percentile to each annual value, and then dividing by the maximum median value. To these scaled annual net primary production values, we multiplied by 47,000 people to provide an annual K in units of individual people (Fig. 2b). For the founding period of interest (65–50 ka), this translates into a minimum K of 69,230–111,329 individuals (25th–75th percentile limits) at 55 ka, and a maximum K of 82,297–158,645 individuals (25th–75th percentile limits) from 63 to 62 ka (Fig. 2c). We also reproduced the analysis with a starting window between 60 and 50 ka, assuming instead a later date of initial colonisation (see Results). It is important to understand that the precise timing of the putative population nadir is irrelevant from the perspective of the mathematical reconstruction of the K series, as long as a nadir occurred at some point after initial colonisation. Also, the specific K (carrying capacity) conditions at time of colonisation had little effect on our model outputs (see Results).

Compensatory density feedback

When the projected population exceeded the resampled net primary production K in person units that year, we multiplied the *beta*-resampled survival vector (see below) by a multiplier of 0.98 (S_{mod}) to impose a compensatory feedback mechanism. This is because the base $\mathbf{M}$ matrix had a low dominant eigenvalue (i.e., rate of population change; see Results), so this compensatory density-feedback mechanism amounts to a 2% drop in average survival each

time total abundance exceeded that time step's sampled K value. This acted to keep the projections from growing exponentially over the 100 human generations.

Catastrophic mortality events

We also included a catastrophic die-off function in the simulations to account for the probability of catastrophic mortality events (C) scaling to generation length among vertebrates³⁵:

$$C = \frac{p_c}{G}$$

where p_c = probability of catastrophe (set at 0.14)³⁵ and G = mean generation time (27.6 years) calculated from the deterministic matrix $\mathbf{M}$ ⁴⁹. Once invoked at probability C for any iteration of the model (see below), we halved the survival vector to induce a 50% mortality (d) event for that year⁸⁶. This is based on the definition of a catastrophe as "... any 1 yr peak-to-trough decline in estimated numbers of 50% or greater"³⁵.

Stochastic projections

We conservatively sampled the start date for each of 10,000 projection iterations using a stochastic uniform sampler between 65 and 50 ka (we aimed to use the full uncertainty of K during the approximate window of initial colonisation). We thus had a different, randomly selected start year for the 100 generations projected into the future (i.e., from 65 to 50 ka toward the present), based on the stochastically sampled $\mathbf{M}$ matrix elements. Here, we defined a function to estimate the shape parameters of a *beta* function, and then randomly *beta*-resampled each element of the survival vector for each year of the projection (assuming an arbitrary $\sigma_s = 5\%$ standard deviation on survival probability). For the fertility vector, we used a random Gaussian resampler for the total (female) fertility F described above, based also on an arbitrary 5% standard deviation.

Founding population size

We applied a starting population size from 50 to 1000 females in increments of 50, and calculated the probability of quasi-extinction as the number of iterations per founding population size, where at least one projected annual total population size fell below a quasi-extinction threshold (Q) of 50 individuals (i.e., 25 females, assuming equal sex ratios). This is

based on the minimum size below which a population cannot avoid inbreeding depression (although it could be twice as high as this⁸⁷, so our approach is conservative).

To estimate a realistic extinction risk, we must borrow from the ecological concept of minimum viable population size⁸⁸. Here, there is a rising consensus that several thousand individuals are normally required to avoid inbreeding depression, thereby maintaining evolutionary potential⁸⁷, and thus avoiding extinction⁸⁹. This is because non-random breeding generally equates to a lower effective population sizes (N_e) than census population sizes (N_c)⁴¹. In the case of founding *Homo* sp. populations, various population genetic approaches (in some instances combined with archaeological evidence⁹) have estimated minimum founder population sizes from 80 to several thousand effective individuals^{9,39,90-94}. However, the relationship between N_e and N_c is complex and variable⁴¹, depending in part on the timeframe over which the data are collected and measured⁹⁵. Even with a current lack of reliable estimates of N_e for the first people to arrive in Australia, the uncertainty associated with $N_e:N_c$ ratios means that another approach is required to estimate both the likely initial population size of founding humans arriving over 50 millennia ago and the period that these people likely arrived in Australia and became a genetically interacting and viable founding population.

However, this approach assumes an instantaneous arrival of the entire founding population in year 1, which is probably an unrealistic representation of the more likely sequence of multiple arrivals of smaller groups over the entire founding 'interval'. To estimate the frequency of smaller introduction events that maintained a low probability of extinction, we resampled 10,000 times the range of minimum viable population defined in the previous step (i.e., the minimum number of total founders maintaining a probability of quasi-extinction ~ 0.1). We first assumed that each introduction event represented one-tenth of the total founding population, but were spread out by an incrementing interval of decades. Thus, the first introduction frequency was every 10 years (i.e., one-tenth of the minimum viable founding population arriving every 10 years over one century), the second was every 20 years (one-tenth every 20 years over two centuries), and so on until a frequency of 300 years (i.e., one-tenth arriving every 300 years over 3000 years) (Fig. 1c,d). The resulting frequency-quasi-extinction probability relationship thus indicates at what frequency one-tenth of the minimum founding population is required to raise the probability of extinction beyond ~ 0.1 established in the first step.

But the reality of an even frequency of identical arriving population sizes is also unlikely, so we added complexity to our model (thus increasing realism) by randomly resampling 10,000 times both the number of introduction events and the frequency between events, such that the latter averaged an incrementing range of decades between events (as above). Here, we randomly resampled the initial introduction event as a random uniform number between 25 females (quasi-extinction threshold) and one-half of the minimum founding population established in the first step. We then randomly resampled the following introduction population sizes from the remaining number of individuals up to the minimum total founding population size, until we reached the cumulative minimum founding population size. We used a random Gaussian sampler of the same sequence as in the previous step, assuming a 10% standard deviation. Thus, the first frequency was an introduction interval resampled with a mean of 10 years and a standard deviation of 1 year, the second was resampled with a mean of 20 years and a standard deviation of 2 years, and so on up to a mean of 200 years between introductions (and the associated 20-year standard deviation).

Global sensitivity analysis

We designed a ‘global’ sensitivity analysis to provide robust sensitivity measures of the probability of quasi-extinction to variation in the underlying parameters of our stochastic model^{96,97}. We applied a Latin-hypercube-sampling protocol⁹⁷ of the parameter space assuming a founding population size of 700 females projected over 100 generations. We sampled 12 parameters from a uniform distribution as follows: (1–5) all five parameters used to calculate the Siler hazard model for age-specific survival: a_1 (varying from 0.3 to 0.5), b_1 (from 1.0 to 2.0), a_2 (from 0.010 to 0.015), a_3 (from 1.323×10^{-4} to 1.617×10^{-4}), and b_3 (from 0.060 to 0.095); (6) standard deviation of survival (σ_s) for stochastic resampling (from 0.025 to 0.100); (7) density-feedback survival modifier S_{mod} (from 0.95 to 0.99); (8) total fertility F (from 2.1105 to 2.5795); (9) quasi-extinction threshold Q (from 13 to 75 females); (10) probability of catastrophe p_c (from 0.1 to 0.2); (11) intensity of catastrophic die-offs d (from 0.25 and 0.75); and (12) nadir population density during/near the Last Glacial Maximum (from 0.0025 to 0.010 individuals km^{-2} ; i.e., from half to double the 0.005 value assumed in the model based on archaeological data^{66,80}). To sample using the Latin hypercube protocol, we ran the simulation for 100 iterations, with 1000 samples from the

parameter space. To test the effect of the parameter values on Pr(quasi-extinction), we used a boosted-regression tree⁹⁸ emulator with the function *gbm.step*⁹⁹ in the *dismo* R library, setting the error distribution family as Gaussian, the bag fraction to 0.75, the learning rate to 0.01, the tolerance to 0.0001, and the tree complexity to 2 (first-order interactions only). To assess the relative contribution of each sampled parameter to Pr(quasi-extinction), we present the boosted-regression tree metrics of relative influence⁹⁷.

Data availability

All data and R code are available for download at github.com/cjabradshaw/SahulHuman.

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Author contributions

C.J.A.B. and F.S. designed the research. C.J.A.B. did the analysis and sourced the data. C.J.A.B., F.S., S.U., A.N.W. and M.I.B. wrote the paper. All other co-authors contributed substantially to developing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at [xxxx.xxx/xxx ...](#)

Correspondence and requests for material should be addressed to C.J.A.B.

Figure captions

Figure 1. Change in net primary production and indicative human carrying capacity. (a) Net primary production ($\text{kg C m}^{-2} \text{ year}^{-1}$) hindcasted by the LOVECLIM⁵⁰ Earth system model⁵¹, showing an example for Sahul at 60,000 years ago (ka). The outlined box at the top of panel **a** indicates the $1^\circ \times 1^\circ$ grid cells ($n = 166$) covering ‘northern’ Sahul (0° to 14° South latitude) used to derive relative human carrying capacity (K) used in subsequent analyses (see Methods). **(b)** Shaded area indicates the range between 25% and 75% percentiles of carrying capacity (K) from 120 ka to the present, expressed in terms of total human population size (N). **(c)** Same as in panel **b**, but focusing on the period of conservative initial colonisation, 65–55 ka.

Figure 2. Estimating quasi-extinction probability for Sahul colonisers. (a) Probability (Pr) of quasi-extinction (< 25 females or < 50 total individuals), expressed as function of the size of a one-off founding population (N) according to 10,000 runs of the stochastic demographic model. The dashed black line indicates the probability decay curve assuming the initial year of colonisation fell between 65 and 55 ka; the grey line is the curve derived from an initial colonisation window of 60–50 ka. The shaded $N_{\min}$ area indicates the range of minimum founding population sizes giving $\text{Pr}(\text{quasi-extinction}) \approx 0.1$, which we applied in the simulations shown in panel **b** (symbolised by the downward-pointing arrow from panels **a** to **b**). **(b)** $\text{Pr}(\text{quasi-extinction})$ as a function of an increasing interval between regularly spaced arrival events (10, 20, 30, ... 300 years), each comprising one-tenth of the total founding population of 650–775 females (black line = ‘regular interval’), or as a function of randomly sampled introduced-population sizes and randomly sampled intervals averaging 10, 20, 30, ... 300 years (grey line = ‘random interval’). Also shown are the least-squares linear-regression R^2 coefficients for both trajectories. The circles indicate example projections shown in panels **c** and **d**. **(c)** An example 50-year constant interval simulation occurring over 500 years (int_c). Upper and lower lines indicate the 95% confidence intervals of median (darker middle line) projected population size (N). **(d)** An example 100-year random interval simulation occurring over an average of 1000 years (int_r). Lines as described in panel **c**.

Supplementary Information

Minimum founding populations for the first peopling of Sahul

Corey J. A. Bradshaw, Sean Ulm, Alan N. Williams, Michael I. Bird, Richard G. Roberts, Zenobia Jacobs, Fiona Laviano, Laura S. Weyrich, Tobias Friedrich, Kasih Norman, and Frédérik Saltré

Supplementary table 1. Correlation matrix (Spearman's ρ) of the five potential indices of human carrying capacity hindcasted from the LOVECLIM¹ Earth system model² for the median of the 166 1° × 1° grid cells covering 'northern' Australia (10° to 18° latitude) from 120 ka to the present (in 1000-year slices).

	bottom moisture	water availability	mean annual temperature	mean annual precipitation	desert fraction
water availability	-0.853	1	-	-	-
mean annual temperature	-0.205	0.494	1	-	-
mean annual precipitation	0.940	-0.713	0.103	1	-
desert fraction	-0.903	0.931	0.436	-0.786	1
net primary production	0.982	-0.842	-0.188	0.934	-0.913

Supplementary figure 1. Age-specific survival (S_x) calculated using the five-parameter Siler hazard model³ for three stages: immature, mature, and senescent individuals within the population (solid black line), and the age-specific life expectancy (e_x) calculated from the same model (dashed grey line).

Supplementary figure 2. Age-specific fertility (m_x) based on age at primiparity (first reproduction) estimates for 22 hunter-gatherer groups⁴, taking the average and 95% confidence interval of these for women as an indicator of the onset of reproduction in such societies. These give a mean age of 19 years old for primiparity among women (95% confidence interval: 16–24). The onset of reproduction and the implied fertility decline compares well with the global average fertility schedule of modern *Homo sapiens*⁵. For total fertility (F), we used the value of 4.69 births (i.e., 2.35 daughters) for the !Kung hunter-gatherer society⁶.

Supplementary figure 3. Global sensitivity analysis results. Shown are relative inference scores from a boosted-regression tree⁷ of the relative importance of varied model parameters on the probability of quasi-extinction. See main text for parameter descriptions and ranges tested. The most influential parameters (five top-ranked) are also given with the direction of their influence on the probability of quasi-extinction: **(-)** = negative; **(+)** = positive.

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