Bradshaw, Corey J.A., Ulm, Sean, Williams, Alan N., Bird, Michael I., Roberts, Richard G., Jacobs, Zenobia, Laviano, Fiona, Weyrich, Laura S., Friedrich, Tobias, Norman, Kasih, and Saltré, Frédérik (2019) ***Minimum founding populations for the first peopling of Sahul.*** **Nature Ecology & Evolution, 3 pp. 1057-1063.**

https://doi.org/10.1038/s41559%2D019%2D0902%2D6

TITLE: Minimum founding populations of the first people to colonise 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 Laviano[1], Laura S. Weyrich[8,2], Tobias Friedrich[9], Kasih Norman[7,2], and Frédérik Saltré[1,2]

[1]Global Ecology, College of Science and Engineering, Flinders University, GPO Box 2100, South Australia 5001, Australia
[2]ARC Centre of Excellence for Australian Biodiversity and Heritage. EpicAustralia.org.au
[3]College of Arts, Society and Education, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia
[4]Climate Change Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, NSW 2052, Australia
[5]Extent Heritage Pty Ltd, 3/73 Union Street, Pyrmont, New South Wales 2009, Australia
[6]College of Science and Engineering, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia
[7]Centre for Archaeological Science, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia
[8]Australian Centre for Ancient DNA, University of Adelaide, Adelaide, South Australia 5005, Australia
[9]International Pacific Research Center, School of Ocean and Earth Science and Technology, University of Hawaii, Honolulu, Hawai'i, 96822, USA

ORCID ID

Corey J. A. Bradshaw:	0000-0002-5328-7741
Sean Ulm:	0000-0001-6653-9963
Alan N. Williams:	0000-0003-4133-4229
Michael I. Bird:	0000-0003-1801-8703
Richard G. Roberts:	0000-0002-0128-4119
Zenobia Jacobs:	0000-0001-5424-5837
Laura S. Weyrich:	0000-0001-5243-4634
Tobias Friedrich:	0000-0001-7324-4100
Frédérik Saltré:	0000-0002-5040-3911

[*]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 colonisation, founding population size, extinction, demography, Aboriginal settlement

Abstract

The timing, context, and nature of the first people to enter Sahul is still poorly understood owing to a fragmented archaeological record. But quantifying the plausible demographic context of this founding population is essential to determine how and why colonisation 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 resilience and minimum sizes required to avoid extinction. A census founding population of between 1300 and 1550 total individuals was necessary to maintain a quasi-extinction threshold $\lesssim 0.1$. This minimum founding population could have arrived at a single point in time, or through multiple voyages ≥ 130 people over $\gtrsim 700$ years. This result shows that substantial population amalgamation in Sunda and Wallacea in Marine Isotope Stages 3–4 provided the conditions for successful, large-scale, and likely planned colonisation of Sahul.

Main

An understanding of the demographic circumstances and ecological repercussions of the arrival of the first people to Sahul (mainland Australia, Tasmania, and New Guinea joined at times of lower sea level) in the Late Pleistocene remains elusive[1-3]. Some have previously proposed that colonisation arose from only small family groups consisting of < 150 people[4-7], while more recent human behavioural-ecology models suggest that several hundred people would have been required for long-term survival[7]. These estimates are largely speculative, but genomic research and radiocarbon-inferred demographic modelling support the larger values, and imply that population sizes of 1000 to 3000 people were more probable[8-10]. Quantifying the plausible demography of the first humans (i.e., the rate of population changes relative to regional carrying capacity, and the duration of time populations could have persisted at low density following initial colonisation) is essential to ascertain to what extent increasing human populations could have altered their environments. Quantifying demographic transitions could also potentially help to interpret the likelihood of discovering archaeological evidence, given the persistence of small human populations over extended windows of time so long ago[6].

The oldest archaeological evidence claimed in Australia is 65.0 ± 5.7 ka (95% confidence interval) for Madjedbebe rockshelter in Arnhem Land[11,12], and an increasing number of early sites have been reported dating to around or before 47 ka[13-21]. For our purposes here, we therefore take the broad interval of 65–50 ka as the likely arrival window of people into Sahul. Arrival most likely occurred somewhere in the northern regions of Sahul, closest to the islands of Wallacea in the Timor Sea, Arafura Sea, and across Torres Strait and Carpentarian Plain during times of lower sea levels[22-26]. However, given that only a few archaeological sites from the north have revealed cultural remains within the putative arrival window and that ancient DNA is poorly preserved in this region of the world, it is difficult to estimate when and where enough people first arrived in Australia to produce one of the longest standing, successful human populations in the world outside of Africa — a population that went on to adapt successfully and populate the entire continent over the following several thousand years[10,27,28]. Recent studies have modelled plausible routes and therefore the potential geographic locations that would have supported a successful migration to Australia[22-26,29], but the numbers and diversity of humans that first arrived on the continent remain largely unknown[10,27,28]. Fundamentally then, the size and migration patterns of founding populations (i.e., whether it was accidental by a small band of hunter-gatherers, or something larger-scale and more complex) directly contributes to our understanding of modern human societies at this time, and how the colonisation of Sahul fits into this broader story.

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

Results

Deterministic matrix properties

The base matrix **M** using the Siler hazard model[30] to estimate the survival vector (Fig. S1) produced a dominant eigenvalue $\lambda = 1.0037$, which equates to an instantaneous rate of population change (r) = 0.0037. Applying different underlying parameters for the Siler hazard model for 'average forager-horticulturist' and 'Northern Territory Aborigines'[31] increased the base matrix's dominant eigenvalue ($\lambda = 1.0085$ and 1.0201, respectively). However, given the assumed hunter-gatherer mode of subsistence during the time of initial colonisation of Sahul, and the rapid rate of increase from the Aboriginal data (collected 1958–1960) that likely underreported infant deaths[31], we decided to remain with the lowest λ for the 'average hunter-gatherer' scenario in all subsequent simulations. This model gives a ratio of the number of female offspring in year t+1 to the number born in the previous year (R_0) of 1.11, and a mean generation time (G) of 27.7 years, which agrees well with the ~ 29-year generation length estimated from genealogy-based studies of hunter-gatherers[32]. Life expectancy (e_x) according to this model increases from around 31 to a maximum 42 years between the ages of 1 and 5 years old, after which point it declines linearly with age (Fig. S1). Thus, a 20-year-old has $e_x = 35$ (additional) years of expected life, and a 40-year-old has $e_x = 24$ additional years of expected life (Fig. S1).

Minimum founding population size

The probability of quasi-extinction ($N < 50$ individuals or < 25 females) stabilised at around 0.1 over 100 generations for founding population sizes of 1300 to 1550 individuals (Fig. 2), or between 650 and 775 females assuming an equal sex ratio. There was quantitatively no difference between the two curves assuming different timing of initial colonisation, 65–55 ka or 60–50 ka (Fig. 2). The relationship between probability of quasi-extinction and founding population size takes into consideration all uncertainty associated with the hindcasted carrying capacity K (Fig. 1), start year, and error (process and sampling) in the Leslie matrix's demographic-rate elements (survival and fertility; Fig. S1, S2), but it assumes a single-year introduction event (i.e., all founding individuals arrive 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. 2b), 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. 3b). 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. 3b); 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) (Fig. S3). 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) (Fig. S3).

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 then, limited ancient DNA evidence, uncertainties associated with dating, taphonomic biases, and 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. Accordingly, 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 intervals[10] over a long period or 1300 at one time, are substantively larger than ethnographically observed

Aboriginal hunter-gatherers, except during larger ceremonial gatherings[33]. 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) — much denser 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, it implies modern human populations at that time were sufficiently socially integrated[34] to be able to achieve the construction and successful voyaging of multiple ocean-going vessels[26]. It further demonstrates cognitive ability and planning, and likely deliberate migration given the numbers of people involved[22,26].

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 time[35]. 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 (Fig. S3). Nonetheless, our adoption of 'average' hunter-gatherer demographic rates appears reasonable and probably does not over-estimate infant survival[31]. We also assumed carrying capacity was proportional to net primary productivity[36], 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 productivity[37]. 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. 2), 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 (Fig. S3). 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].

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 Zealand[38], as few as 70 individuals based on mitochondrial and Y-chomosome DNA for the colonisation of the New World from Asia[39], and 150 female Yakuts in north-eastern Siberia based on mitochondrial DNA[40]. 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 assessment[41], 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)[22]. This range is likely to be a conservative minimum boundary, as founding populations with limited female diversity (< 10 per haplogroup) have little chance of survival[42]. 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 population amalgamation 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 migrations[22-25,29] 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 model[30] 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:

$$l_x = e^{\left(\frac{-a_1}{b_1}\right)\left(1-e^{-b_1 x}\right)} e^{-a_2 x} e^{\left(\frac{a_3}{b_3}\right)\left(1-e^{b_3 x}\right)} \tag{1}$$

where a_1 = initial infant mortality (also described elsewhere as α_t), 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 Kaplan[31] (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 (Fig. S1) as:

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

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 groups[43], 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 years[44-46]. 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 society[48] (Fig. S2).

Age-structured (Leslie) matrix model

From these estimated demographic rates, we constructed a pre-breeding, 81 (i) × 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 step[49]. Thus, we used a longevity (ω) of 80 years based on cross-cultural examination of hunter-gatherer societies[31], 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 ($\mathbf{M}_{i,j}$) 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 reconstruction[50]. LOVECLIM is a three-dimensional Earth system model of intermediate complexity[51] (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). 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)[52,53] at a spatial resolution of 1° × 1°. 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 production[54]. 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 $|\rho| \geq 0.842$; Table S1), so we chose net primary production (kg C m^{-2} 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 humans[55-59]. To focus on the region of interest, we took all Sahul (Australia, New Guinea and Tasmania) 1° × 1° 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. 1a), 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)[60-63], when conditions were cooler than today and much (but not all[64-67]) of the continent was drier[68-75]. 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 interval[62], or at least a major spatial thinning of populations (perhaps as much as 60%) during this period[9]. From these demographic reconstructions, we set the baseline population size at the Last Glacial Maximum at 47,000 people continent-wide[76]. This figure is based on an estimated area of habitable land[76] for of Sahul 9.4 million km^2 and a population density[62] of 0.005 individuals km^{-2}, which is similar to historical estimates of population densities for Australian deserts[77]. We recognise that inferences of past population size are subject to many uncertainties[63,78-81] and note accordingly that our model results are not critically dependent on the above input values (see the global sensitivity analysis and Fig. S3).

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. 1b). 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. 1c). 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 vertebrates[35]:

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

where p_C = probability of catastrophe (set at 0.14)[35] and G = mean generation time calculated from the deterministic matrix **M**, which was 27.6 years[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 year[82]. 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 **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 σ_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 this[83], so our approach is conservative).

To estimate a realistic extinction risk, we must borrow from the ecological concept of minimum viable population size[84]. Here, there is a rising consensus that several thousand individuals are normally required to avoid inbreeding depression and maintain evolutionary potential[83], and thus avoid extinction[85]. 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 evidence[9]) have estimated minimum founder population sizes from 80 to several thousand effective individuals[9,39,86-90]. However, the relationship between N_e and N_c is complex and variable[41], depending in part on the timeframe over which the data are collected and measured[91]. 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. 2c,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[92,93]. We applied a Latin-hypercube-sampling protocol[93] 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[62,76]). 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 tree[94] emulator with the function *gbm.step*[95] 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 influence[93].

Data availability

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

References

1 Saltré, F. *et al.* Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nat. Comm.* **7**, 10511, doi:10.1038/ncomms10511 (2016).

2 Johnson, C. N. *et al.* What caused extinction of the Pleistocene megafauna of Sahul? *Proc. R. Soc. Lond. B* **283**, 52399, doi:10.1098/rspb.2015.2399 (2016).

3 O'Connell, J. F. *et al.* When did *Homo sapiens* first reach Southeast Asia and Sahul? *Proc. Natl. Acad. Sci. USA* **115**, 8482-8490, doi:10.1073/pnas.1808385115 (2018).

4 Birdsell, J. B. Some population problems involving Pleistocene man. *Cold Spring Harbor Symp. Quant. Biol.* **22**, 47-69 (1957).

5 McArthur, N. Computer simulations of small populations. *Aust. Archaeol.* **4**, 53-57, doi:jstor.org/stable/40286251 (1976).

6 Allen, J. & O'Connell, J. F. in *Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes, Terra Australis* Vol. 29 (eds G. Clark, F. Leach, & S. O'Connor) 31-46 (ANU E Press, 2008).

7 O'Connell, J. F. & Allen, J. The Restaurant at the End of the Universe: modelling the colonisation of Sahul. *Aust. Archaeol.* **74**, 5-17, doi:10.1080/03122417.2012.11681932 (2012).

8 Rasmussen, M. *et al.* An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* **334**, 94-98 (2011).

9 Williams, A. N. A new population curve for prehistoric Australia. *Proc. R. Soc. Lond. B* **280**, 20130486 (2013).

10 Malaspinas, A.-S. *et al.* A genomic history of Aboriginal Australia. *Nature* **538**, 207-214, doi:10.1038/nature18299 (2016).

11 Clarkson, C. *et al.* Human occupation of northern Australia by 65,000 years ago. *Nature* **547**, 306-310, doi:10.1038/nature22968 (2017).

12 Clarkson, C. *et al.* Reply to comments on Clarkson et al. (2017) 'Human occupation of northern Australia by 65,000 years ago'. *Aust. Archaeol.* **84**, 84-89, doi:10.1080/03122417.2018.1462884 (2018).

13 Roberts, R. G. *et al.* The human colonisation of Australia: optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. *Quat. Sci. Rev.* **13**, 575-583, doi:10.1016/0277-3791(94)90080-9 (1994).

14 Turney, C. S. M. *et al.* Early human occupation at Devil's Lair, southwestern Australia 50,000 years ago. *Quat. Res.* **55**, 3-13, doi:10.1006/qres.2000.2195 (2001).

15 Bowler, J. M. *et al.* New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature* **421**, 837-840, doi:10.1038/nature01383 (2003).

16 Wood, R. *et al.* Towards an accurate and precise chronology for the colonization of Australia: the example of Riwi, Kimberley, Western Australia. *PLoS One* **11**, e0160123, doi:10.1371/journal.pone.0160123 (2016).

17 Hamm, G. *et al.* Cultural innovation and megafauna interaction in the early settlement of arid Australia. *Nature* **539**, 280-283, doi:10.1038/nature20125 (2016).

18 Veth, P. *et al.* Early human occupation of a maritime desert, Barrow Island, North-West Australia. *Quat. Sci. Rev.* **168**, 19-29, doi:10.1016/j.quascirev.2017.05.002 (2017).

19 Delannoy, J.-J. *et al.* in *The Archaeology of Rock Art in Western Arnhem Land, Australia, Terra Australis* Vol. 47 (eds B. David, P.S.C. Taçon, J-J. Delannoy, & J-M. Geneste) 197-243 (ANU Press, 2017).

20 Maloney, T., O'Connor, S., Wood, R., Aplin, K. & Balme, J. Carpenters Gap 1: A 47,000 year old record of indigenous adaption and innovation. *Quat. Sci. Rev.* **191**, 204-228, doi:10.1016/j.quascirev.2018.05.016 (2018).

21 McDonald, J. *et al.* Karnatukul (Serpent's Glen): a new chronology for the oldest site in Australia's Western Desert. *PLoS One* **13**, e0202511, doi:10.1371/journal.pone.0202511 (2018).

22 Bird, M. I. *et al.* Palaeogeography and voyage modeling indicates early human colonization of Australia was likely from Timor-Roti. *Quat. Sci. Rev.* **191**, 431-439, doi:10.1016/j.quascirev.2018.04.027 (2018).

23 Norman, K. *et al.* An early colonisation pathway into northwest Australia 70-60,000 years ago. *Quat. Sci. Rev.* **180**, 229-239, doi:10.1016/j.quascirev.2017.11.023 (2018).

24 Kealy, S., Louys, J. & O'Connor, S. Reconstructing palaeogeography and inter-island visibility in the Wallacean Archipelago during the likely period of Sahul colonization, 65–45 000 years ago. *Archaeol. Prospect.* **24**, 259-272, doi:10.1002/arp.1570 (2017).

25 Kealy, S., Louys, J. & O'Connor, S. Islands under the sea: a review of early modern human dispersal routes and migration hypotheses through Wallacea. *J. Isl. Coast. Archaeol.* **11**, 364-384, doi:10.1080/15564894.2015.1119218 (2016).

26 Bird, M. I. *et al.* Early human settlement of Sahul was not an accident. *Sci. Rep.* (2019).

27 Nagle, N. *et al.* Aboriginal Australian mitochondrial genome variation – an increased understanding of population antiquity and diversity. *Sci. Rep.* **7**, 43041, doi:10.1038/srep43041 (2017).

28 Tobler, R. *et al.* Aboriginal mitogenomes reveal 50,000 years of regionalism in Australia. *Nature* **544**, 180-184, doi:10.1038/nature21416 (2017).

29 Kealy, S., Louys, J. & O'Connor, S. Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. *J. Hum. Evol.* **125**, 59-70, doi:10.1016/j.jhevol.2018.10.003 (2018).

30 Siler, W. A competing-risk model for animal mortality. *Ecology* **60**, 750-757, doi:10.2307/1936612 (1979).

31 Gurven, M. & Kaplan, H. Longevity among hunter-gatherers: a cross-cultural examination. *Pop. Dev. Rev.* **33**, 321-365, doi:10.1111/j.1728-4457.2007.00171.x (2007).

32 Fenner, J. N. Cross-cultural estimation of the human generation interval for use in genetics-based population divergence studies. *Am. J. Phys. Anthropol.* **128**, 415-423, doi:10.1002/ajpa.20188 (2005).

33 Gould, R. A. Puntutjarpa Rockshelter and the Australian desert culture. *Anthropol. Pap. Am. Mus. Nat. Hist.* **54**, 1-187 (1977).

34 Durkheim, É. *The Division of Labour in Society (with an introduction by Lewis A. Coser); translated by W.D. Halls*. (Macmillan, 1984).

35 Reed, D. H., O'Grady, J. J., Ballou, J. D. & Frankham, R. The frequency and severity of catastrophic die-offs in vertebrates. *Anim. Conserv.* **6**, 109-114, doi:10.1017/S1367943003147 (2003).

36 Tallavaara, M., Eronen, J. T. & Luoto, M. Productivity, biodiversity, and pathogens influence the global hunter-gatherer population density. *Proc. Natl. Acad. Sci. USA* **115**, 1232-1237, doi:10.1073/pnas.1715638115 (2018).

37 Finlayson, C. *et al.* The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quat. Sci. Rev.* **30**, 1525-1532, doi:10.1016/j.quascirev.2011.01.010 (2011).

38 Whyte, A. L. H., Marshall, S. J. & Chambers, G. K. Human evolution in Polynesia. *Hum. Biol.* **77**, 157-177, doi:10.1353/hub.2005.0045 (2005).

39 Hey, J. On the number of New World founders: a population henetic portrait of the peopling of the Americas. *PLoS Biol.* **3**, e193, doi:10.1371/journal.pbio.0030193 (2005).

40 Zlojutro, M. *et al.* Coalescent simulations of Yakut mtDNA variation suggest small founding population. *Am. J. Phys. Anthropol.* **139**, 474-482, doi:10.1002/ajpa.21003 (2009).

41 Frankham, R. Effective population size/adult population size ratios in wildlife: a review. *Genet. Res.* **66**, 95-107, doi:10.1017/S0016672300034455 (1995).

42 Moore, J. H. Evaluating five models of human colonization. *Am. Anthropol.* **103**, 395-408 (2001).

43 Walker, R. *et al.* Growth rates and life histories in twenty-two small-scale societies. *Am. J. Hum. Biol.* **18**, 295-311, doi:10.1002/ajhb.20510 (2006).

44 Hawkes, K., Smith, K. R. & Robson, S. L. Mortality and fertility rates in humans and chimpanzees: how within-species variation complicates cross-species comparisons. *Am. J. Hum. Biol.* **21**, 578-586, doi:10.1002/ajhb.20890 (2009).

45 Hawkes, K. & Coxworth, J. E. Grandmothers and the evolution of human longevity: a review of findings and future directions. *Evol. Anthropol.* **22**, 294-302, doi:10.1002/evan.21382 (2013).

46 Blurton Jones, N. G., Hawkes, K. & O'Connell, J. F. Antiquity of postreproductive life: are there modern impacts on hunter-gatherer postreproductive life spans? *Am. J. Hum. Biol.* **14**, 184-205, doi:10.1002/ajhb.10038 (2002).

47 Bradshaw, C. J. A. & Brook, B. W. Human population reduction is not a quick fix for environmental problems. *Proc. Natl. Acad. Sci. USA* **111**, 16610-16615, doi:10.1073/pnas.1410465111 (2014).

48 Bentley, G. R. Hunter-gatherer energetics and fertility: a reassessment of the !Kung San. *Hum. Ecol.* **13**, 79-109, doi:10.1007/BF01531090 (1985).

49 Caswell, H. *Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edn*. (Sinauer Associates, Inc., 2001).

50 Goosse, H. *et al.* Description of the Earth system model of intermediate complexity LOVECLIM version 1.2. *Geosci. Mod. Dev.* **3**, 603-633 (2010).

51 Claussen, M. *et al.* Earth system models of intermediate complexity: closing the gap in the spectrum of climate system models. *Clim. Dyn.* **18**, 579-586, doi:10.1007/s00382-001-0200-1 (2002).

52 Lorenz, D. J., Nieto-Lugilde, D., Blois, J. L., Fitzpatrick, M. C. & Williams, J. W. Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100 AD. *Sci. Dat.* **3**, 160048, doi:10.1038/sdata.2016.48 (2016).

53 Wilby, R. L. & Wigley, T. M. L. Downscaling general circulation model output: a review of methods and limitations. *Prog. Phys. Geogr. Earth Environ.* **21**, 530-548, doi:10.1177/030913339702100403 (1997).

54 Timmermann, A. & Friedrich, T. Late Pleistocene climate drivers of early human migration. *Nature* **538**, 92-95, doi:10.1038/nature19365 (2016).

55 Coe, M. J., Cumming, D. H. & Phillipson, J. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**, 341-354, doi:10.1007/BF00345312 (1976).

56 Krausmann, F. *et al.* Long-term trajectories of the human appropriation of net primary production: lessons from six national case studies. *Ecol. Econ.* **77**, 129-138, doi:10.1016/j.ecolecon.2012.02.019 (2012).

57 Whittaker, R. H. & Likens, G. E. Primary production: the biosphere and man. *Hum. Ecol.* **1**, 357-369, doi:10.1007/BF01536732 (1973).

58 Phillipson, J. Rainfall, primary production and 'carrying capacity' of Tsavo National Park (East), Kenya. *Afr. J. Ecol.* **13**, 171-201, doi:10.1111/j.1365-2028.1975.tb00134.x (1975).

59 Cao, M., Ma, S. & Han, C. Potential productivity and human carrying capacity of an agro-ecosystem: an analysis of food production potential of China. *Agric. Sys.* **47**, 387-414, doi:10.1016/0308-521X(95)92106-G (1995).

60 Williams, M. *et al.* Glacial and deglacial climatic patterns in Australia and surrounding regions from 35 000 to 10 000 years ago reconstructed from terrestrial and near-shore proxy data. *Quat. Sci. Rev.* **28**, 2398-2419, doi:10.1016/j.quascirev.2009.04.020 (2009).

61 Petherick, L. M., Moss, P. T. & McGowan, H. A. Climatic and environmental variability during the termination of the Last Glacial Stage in coastal eastern Australia: a review. *Aust. J. Earth Sci.* **58**, 563-577, doi:10.1080/08120099.2011.566281 (2011).

62 Williams, A. N., Ulm, S., Cook, A. R., Langley, M. C. & Collard, M. Human refugia in Australia during the Last Glacial Maximum and Terminal Pleistocene: a geospatial analysis of the 25–12 ka Australian archaeological record. *J. Archaeol. Sci.* **40**, 4612-4625, doi:10.1016/j.jas.2013.06.015 (2013).

63 Williams, A. N. *et al.* A continental narrative: human settlement patterns and Australian climate change over the last 35,000 years. *Quat. Sci. Rev.* **123**, 91-112, doi:10.1016/j.quascirev.2015.06.018 (2015).

64 Ellerton, D., Shulmeister, J., Woodward, C. & Moss, P. Last Glacial Maximum and Last Glacial–Interglacial Transition pollen record from northern NSW, Australia: evidence for a humid late Last Glacial Maximum and dry deglaciation in parts of eastern Australia. *J. Quat. Sci.* **32**, 717-728, doi:10.1002/jqs.2960 (2017).

65 Hesse, P. P. *et al.* Dramatic reduction in size of the lowland Macquarie River in response to Late Quaternary climate-driven hydrologic change. *Quat. Res.* **90**, 360-379, doi:10.1017/qua.2018.48 (2018).

66 Shulmeister, J., Kemp, J., Fitzsimmons, K. E. & Gontz, A. Constant wind regimes during the Last Glacial Maximum and early Holocene: evidence from Little Llangothlin Lagoon, New England Tablelands, eastern Australia. *Clim. Past* **12**, 1435-1444, doi:10.5194/cp-12-1435-2016 (2016).

67 Mueller, D. *et al.* Revisiting an arid LGM using fluvial archives: a luminescence chronology for palaeochannels of the Murrumbidgee River, south-eastern Australia. *J. Quat. Sci.* **33**, 777-793, doi:10.1002/jqs.3059 (2018).

68 Hope, G. *et al.* History of vegetation and habitat change in the Austral-Asian region. *Quat. Int.* **118-119**, 103-126, doi:10.1016/S1040-6182(03)00133-2 (2004).

69 Johnson, B. J. *et al.* 65,000 years of vegetation change in central Australia and the Australian summer monsoon. *Science* **284**, 1150-1152 (1999).

70 Fitzsimmons, K. E. *et al.* Late Quaternary palaeoenvironmental change in the Australian drylands. *Quat. Sci. Rev.* **74**, 78-96, doi:10.1016/j.quascirev.2012.09.007 (2013).

71 Barrows, T. T., Stone, J. O. & Fifield, L. K. Exposure ages for Pleistocene periglacial deposits in Australia. *Quat. Sci. Rev.* **23**, 697-708, doi:10.1016/j.quascirev.2003.10.011 (2004).

72 Barrows, T. T., Stone, J. O., Fifield, L. K. & Cresswell, R. G. The timing of the Last Glacial Maximum in Australia. *Quat. Sci. Rev.* **21**, 159-173, doi:10.1016/S0277-3791(01)00109-3 (2002).

73 Barrows, T. T., Stone, J. O., Fifield, L. K. & Cresswell, R. G. Late Pleistocene glaciation of the Kosciuszko Massif, Snowy Mountains, Australia. *Quat. Res.* **55**, 179-189, doi:10.1006/qres.2001.2216 (2001).

74 Reeves, J. M. *et al.* Climate variability over the last 35,000 years recorded in marine and terrestrial archives in the Australian region: an OZ-INTIMATE compilation. *Quat. Sci. Rev.* **74**, 21-34, doi:10.1016/j.quascirev.2013.01.001 (2013).

75 Petherick, L. *et al.* Climatic records over the past 30 ka from temperate Australia – a synthesis from the Oz-INTIMATE workgroup. *Quat. Sci. Rev.* **74**, 58-77, doi:10.1016/j.quascirev.2012.12.012 (2013).

76 Gautney, J. R. & Holliday, T. W. New estimations of habitable land area and human population size at the Last Glacial Maximum. *J. Archaeol. Sci.* **58**, 103-112, doi:10.1016/j.jas.2015.03.028 (2015).

77 Smith, M. *The Archaeology of Australia's Deserts*. (Cambridge University Press, 2013).

78 Attenbrow, V. & Hiscock, P. Dates and demography: are radiometric dates a robust proxy for long-term prehistoric demographic change? *Archaeol. Oceania* **50**, 30-36, doi:10.1002/arco.5052 (2015).

79 Hiscock, P. & Attenbrow, V. Dates and demography? The need for caution in using radiometric dates as a robust proxy for prehistoric population change. *Archaeol. Oceania* **51**, 218-219, doi:10.1002/arco.5096 (2016).

80 Smith, M. The use of summed-probability plots of radiocarbon data in archaeology. *Archaeol. Oceania* **51**, 214-215, doi:10.1002/arco.5094 (2016).

81 Williams, A. N. & Ulm, S. Radiometric dates are a robust proxy for long-term demographic change: a comment on Attenbrow and Hiscock (2015). *Archaeol. Oceania* **51**, 216-217, doi:10.1002/arco.5095 (2016).

82 Bradshaw, C. J. A. *et al.* More analytical bite in estimating targets for shark harvest. *Mar. Ecol. Prog. Ser.* **488**, 221-232, doi:10.3354/meps10375 (2013).

83 Frankham, R., Bradshaw, C. J. A. & Brook, B. W. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biol. Conserv.* **170**, 56-63, doi:10.1016/j.biocon.2013.12.036 (2014).

84 Traill, L. W., Bradshaw, C. J. A. & Brook, B. W. Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biol. Conserv.* **139**, 159-166, doi:10.1016/j.biocon.2007.06.011 (2007).

85 Traill, L. W., Brook, B. W., Frankham, R. & Bradshaw, C. J. A. Pragmatic population viability targets in a rapidly changing world. *Biol. Conserv.* **143**, 28-34, doi:10.1016/j.biocon.2009.09.001 (2010).

86 Harpending, H. C. *et al.* Genetic traces of ancient demography. *Proc. Natl. Acad. Sci. USA* **95**, 1961-1967, doi:10.1073/pnas.95.4.1961 (1998).

87 Murray-McIntosh, R. P., Scrimshaw, B. J., Hatfield, P. J. & Penny, D. Testing migration patterns and estimating founding population size in Polynesia by using human mtDNA sequences. *Proc. Natl. Acad. Sci. USA* **95**, 9047-9052, doi:10.1073/pnas.95.15.9047 (1998).

88 Tenesa, A. *et al.* Recent human effective population size estimated from linkage disequilibrium. *Genome Res.* **17**, 520-526, doi:10.1101/gr.6023607 (2007).

89 Liu, H., Prugnolle, F., Manica, A. & Balloux, F. A geographically explicit genetic model of worldwide human-settlement history. *Am. J. Hum. Gen.* **79**, 230-237, doi:10.1086/505436 (2006).

90 Zollner, P. A. & Lima, S. L. Search strategies for landscape-level interpatch movements. *Ecology* **80**, 1019-1030 (1999).

91 Eller, E., Hawks, J. & Relethford, J. H. Local extinction and recolonization, species effective population size, and modern human origins. *Hum. Biol.* **81**, 805-824, doi:10.3378/027.081.0623 (2009).

92 Wainwright, H. M., Finsterle, S., Jung, Y., Zhou, Q. & Birkholzer, J. T. Making sense of global sensitivity analyses. *Comput. Geosci.* **65**, 84-94, doi:10.1016/j.cageo.2013.06.006 (2014).

93 Prowse, T. A. A. *et al.* An efficient protocol for the global sensitivity analysis of stochastic ecological models. *Ecosphere* **7**, e01238, doi:10.1002/ecs2.1238 (2016).

94 Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802-813, doi:10.1111/j.1365-2656.2008.01390.x (2008).

95 Hijmans, R. J., Phillips, S., Leathwick, J. & Elith, J. dismo: Species Distribution Modeling. R package version 1.1-4. CRAN.R-project.org/package=dismo. (2017).

Acknowledgements

This study was supported by the Australian Research Council through a Centre of Excellence grant (CE170100015) to R.G.R., S.U., M.I.B., Z.J., C.J.A.B., and L.S.W., fellowships to S.U. (FT120100656), M.I.B. (FL140100044), R.G.R. (FL130100116), Z.J. (FT150100138), and L.S.W. (FT180100407), and an Australian Government Research Training Program Award to K.N.

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 (kg C m^{-2} $year^{-1}$) hindcasted by the LOVECLIM[50] Earth system model[51], showing an example for Sahul at 60,000 years ago (ka). The outlined box at the top of panel **a** indicates the 1° × 1° 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 Pr(quasi-extinction) ≈ 0.1, which we applied in the simulations shown in panel **b** (symbolised by the downward-pointing arrow from panels **a** to **b**). (**b**) Pr(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**.

Figure 1

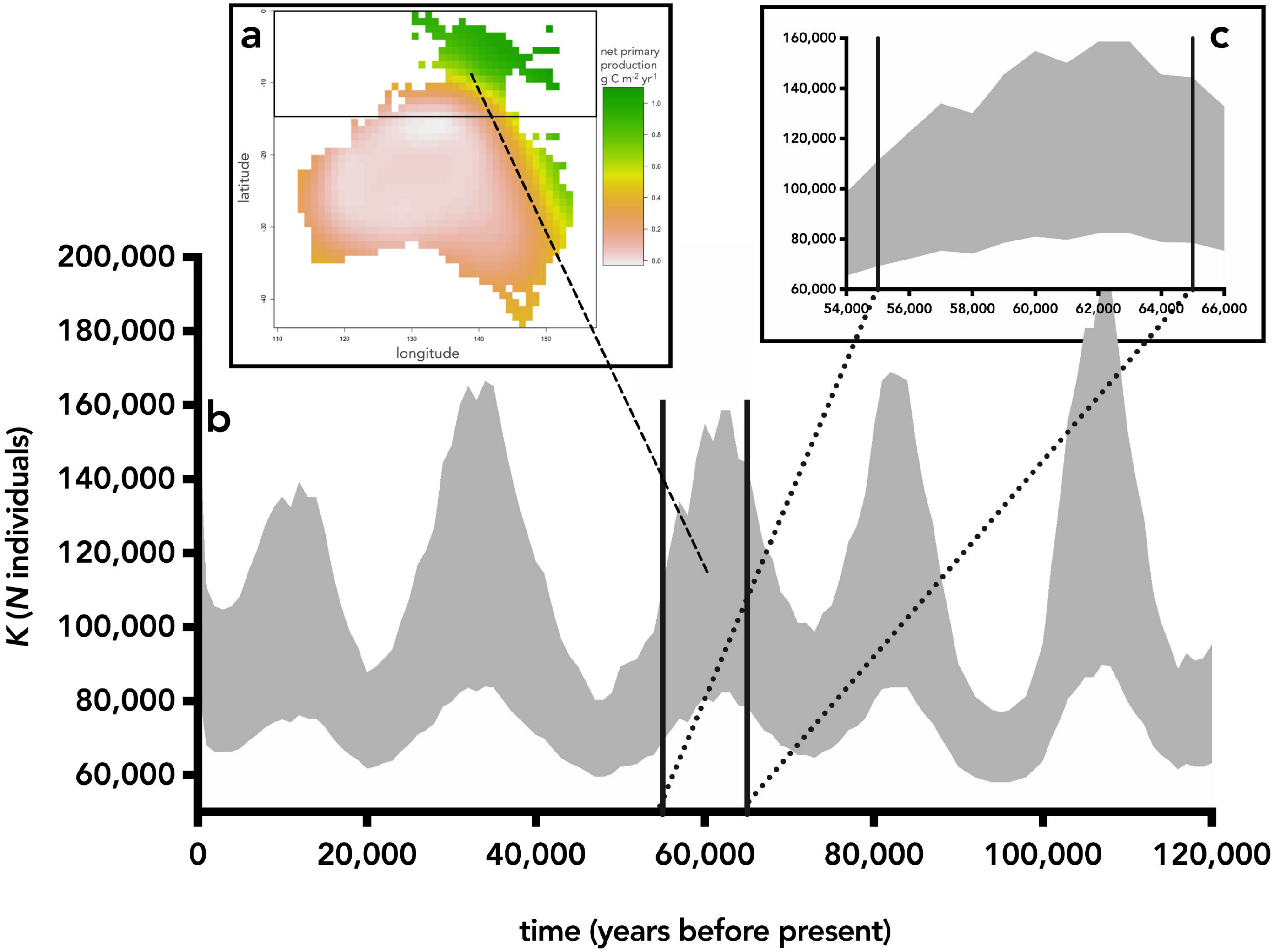
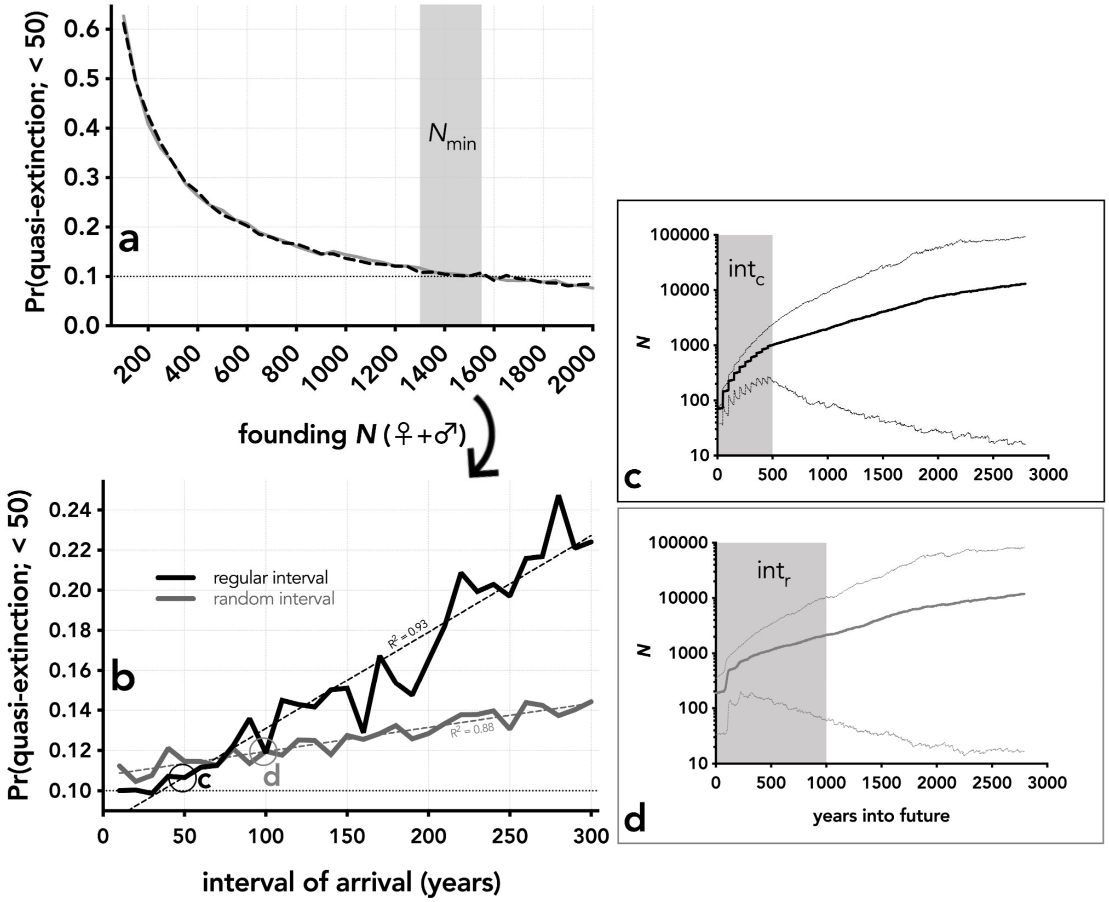

a
net primary
production
g C m-2 yr-1
1.0
0.8
0.6
0.4
0.2
0.0
latitude
0
-10
-20
-30
-40
110
120
130
140
150
longitude
b
200,000
180,000
160,000
140,000
120,000
100,000
80,000
60,000
K (N individuals)
0
20,000
40,000
60,000
80,000
100,000
120,000
time (years before present)
c
160,000
140,000
120,000
100,000
80,000
60,000
54,000
56,000
58,000
60,000
62,000
64,000
66,000

Figure 2


Pr(quasi-extinction; < 50)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
N_{min}
a
200
400
600
800
1000
1200
1400
1600
1800
2000
founding N (♀+♂)
Pr(quasi-extinction; < 50)
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
regular interval
random interval
$R^2 = 0.93$
$R^2 = 0.88$
b
c
d
0
50
100
150
200
250
300
interval of arrival (years)
100000
10000
1000
100
10
N
int_c
0
500
1000
1500
2000
2500
3000
c
100000
10000
1000
100
10
N
int_r
0
500
1000
1500
2000
2500
3000
years into future
d

Supporting Information

Table S1. Correlation matrix (Spearman's ρ) of the five potential indices of human carrying capacity hindcasted from the LOVECLIM[50] Earth system model[51] 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

Figure S1. Age-specific survival (S_x) calculated using the five-parameter Siler hazard model[30] 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).

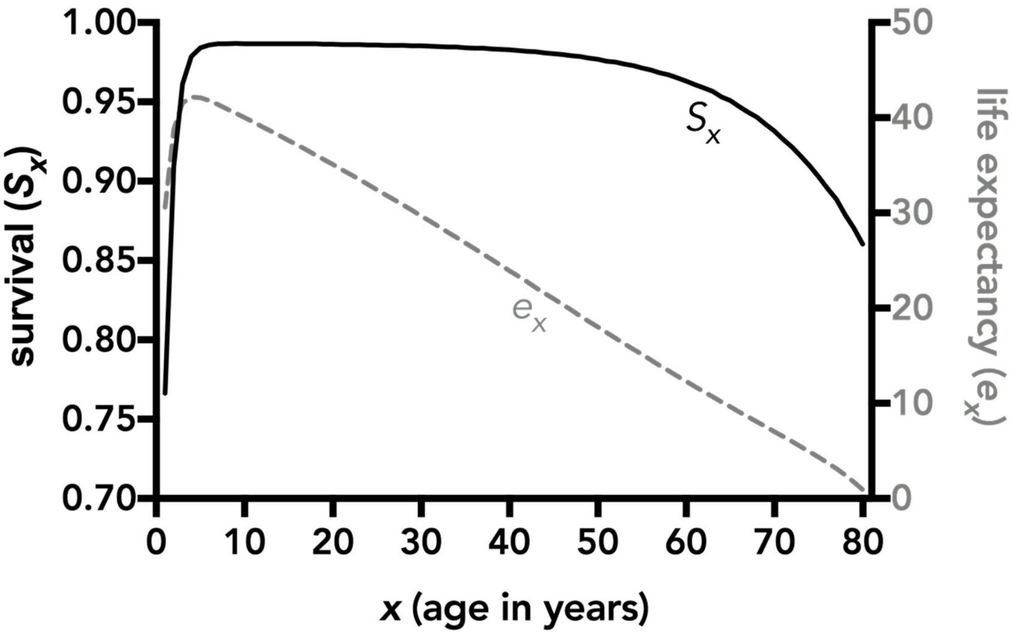


Figure S2. Age-specific fertility (m_x) based on age at primiparity (first reproduction) estimates for 22 hunter-gatherer groups[43], taking the average and 95% confidence interval of these for women as an indicator of the onset of reproduction in such societies. These give a mean age of 19 years old 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*[47]. For total fertility (F), we used the value of 4.69 births (i.e., 2.35 daughters) for the !Kung hunter-gatherer society[48].

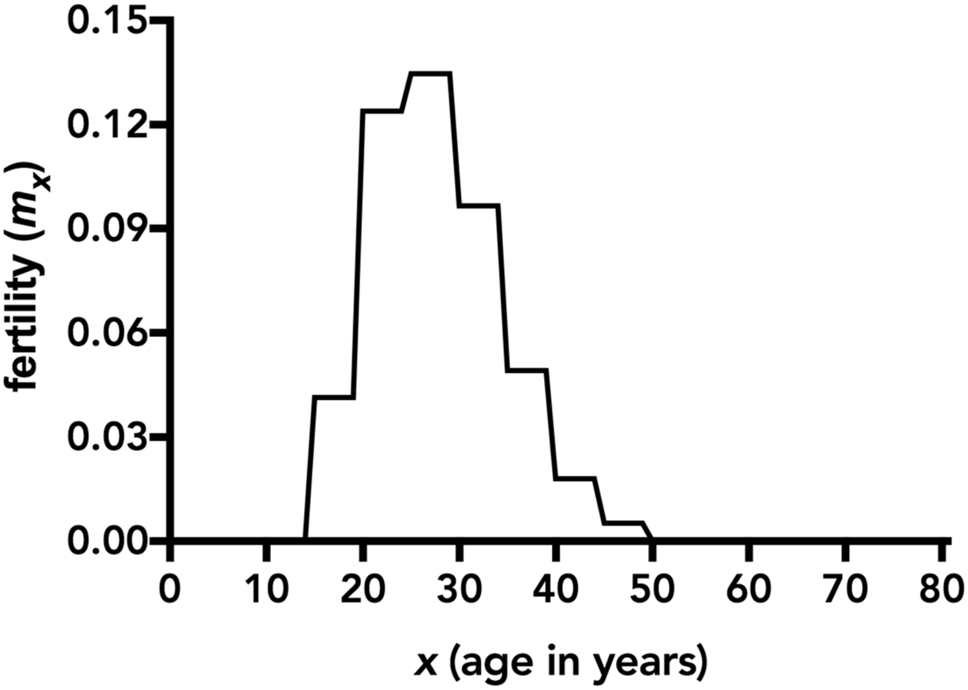


Figure S3. Global sensitivity analysis results. Shown are relative inference scores from a boosted-regression tree[94] of the relative importance of varied model parameters on the probability of quasi-extinction. See main text for parameter descriptions and ranges tested. The most influential parameters (five top-ranked) are also given with the direction of their influence on the probability of quasi-extinction: **(-)** = negative; **(+)** = positive.