



Review

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What caused extinction of the Pleistocene megafauna of Sahul?

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During the Pleistocene, Australia and New Guinea supported a rich assemblage of large vertebrates. Why these animals disappeared has been debated for more than a century and remains controversial. Previous synthetic reviews of this problem have typically focused heavily on particular types of evidence, such as the dating of extinction and human arrival, and have frequently ignored uncertainties and biases that can lead to misinterpretation of this evidence. Here, we review diverse evidence bearing on this issue and conclude that, although many knowledge gaps remain, multiple independent lines of evidence point to direct human impact as the most likely cause of extinction.

1. Introduction

Alfred Russel Wallace (1876) identified the extinction of the ‘hugest, fiercest and strangest’ animals from most land environments as one of the most significant biological changes in recent Earth history [1]. The ‘marvellous fact’ of megafaunal extinction is now far better described than it was in Wallace’s lifetime, but its cause is controversial. The two most widely accepted agents of extinction are human impact and climate change, but whether one or the other was dominant and how their importance varied globally is unclear [2–6].

Sahul—mainland Australia, New Guinea and Tasmania, as connected by dry land through much of the Pleistocene [7,8]—is crucial to this debate. This is because people reached Sahul by an ocean crossing mid-way through the last glacial cycle [9–14]. Later continental migrations through Eurasia and into the Americas were governed by changing climates in the approach to the Pleistocene/Holocene transition. These controlled the extent of ice sheets, the availability of migration routes and the distribution of environments suitable for people. The same changes also drove shifts in habitat for megafaunal species, making it difficult to separate the human and climatic contributions to megafaunal extinction [3]. The decoupling of migration from these global shifts should allow a clearer test of the impacts of newly arrived humans on ecosystems in Sahul.

2. Hypotheses

Today, Sahul has no native terrestrial animal larger than about 40 kg, but for much of the Pleistocene it supported diverse large vertebrates up to almost three tonnes [6,15,16]. The overkill hypothesis proposes that human hunting drove these animals extinct. Conceivably, this resulted from selective killing of big animals [17,18]. It is also possible that non-selective hunting differentially removed large species because of their low population growth rates and consequent sensitivity to small increases in mortality [15,19,20]. The main alternative to overkill is the idea that the megafauna disappeared because of climate change. Several authors argue that over the last 450 ka (thousands of years) the climate of Sahul became more variable and arid. This is thought to have placed increasing environmental stress on large vertebrates, reducing their distribution and abundance and causing a staggered series of extinctions over several glacial cycles [6,21,22]. A third hypothesis envisages anthropogenic fire as a cause of extinction of at least some megafauna. Many of Australia's extinct megaherbivores appear to have been browsers, and so presumably benefitted from a high diversity of shrubs and small trees; perhaps burning removed or degraded habitat for these species [23,24]. Although these causal mechanisms can be evaluated independently, they might also have combined in various ways.

Several types of evidence can be used to test these hypotheses. Most obviously, evidence on the timing of extinction and human arrival is essential to show if the extinctions were synchronized and closely followed human arrival, rather than being spread over some long interval unrelated to human impact. Data on past climates are needed to test for trends that might have driven megafaunal decline. The pattern of change in population size preceding extinction is also crucial: if climate trends caused gradual attrition of megafauna, populations of large vertebrates should have been in long-term decline under the stress of worsening environmental conditions before finally disappearing; on the other hand, human impact ought to have precipitated abrupt decline to extinction of species that need not have been declining beforehand. Palaeoecological reconstructions can test whether extinctions were associated with specific environmental changes, particularly shifts in fire regime (possibly caused by people) or alterations of vegetation state that might have been caused by anthropogenic fire or climate change. Also relevant is archaeological evidence on interactions between humans and extinct megafauna.

Here, we synthesize current understanding of this problem. Our review has two main aims. First, we aim to encompass the broadest possible range of evidence. This is important because the use of multiple independent lines of evidence is the most promising avenue to resolve this problem, in Sahul and globally. Second, we address uncertainties and biases that are inevitable features of data on events from the distant past, and deal with these explicitly in interpreting evidence.

3. Human arrival

It is still uncertain when people first set foot on Sahul: it might have been around 50 ka, or as much as 10 ka earlier [10,25,26]. However, it is generally accepted that people were widespread over the continent by 45 ka or a few millennia earlier [13,14,27,28]. There is as yet no obvious geographical pattern in first-appearance dates to indicate the progress of a wave of colonization across Sahul. This is not surprising, because

dates older than 40 ka typically have uncertainty ranges of several thousand years. If people dispersed over Sahul within a few millennia, we would be unable to resolve that process. In addition, we still have few dated sites from the earliest phase of the prehistory of Sahul. Only 20 archaeological sites have been dated to 40 ka or older [14]; for comparison, the archaeological record in Australia consists of 1748 dated sites [29]. Most of the arid centre lacks evidence of human occupation until just after 40 ka [30], but whether this truly indicates late settlement rather than poor preservation and limited sampling is unclear. Occupation of Tasmania had to await the emergence of a land bridge at 43 ka [8].

This picture suggests that declines and extinctions of species owing to human impact should have been concentrated in the period 50–40 ka. Quantitative population models suggest that if hunting was the primary driver of decline, demographic lags might have caused delays of several hundred to several thousand years between first contact and extinction in any given region [20,31]. Late occupation of some regions might plausibly have delayed continent-wide extinction several thousand years more. Taking these factors into account, a concentration of extinctions between about 50 and 35 ka might be attributable to the impact of human arrival. Later extinctions are less likely to have been owing to direct human impact, although they could conceivably have resulted from the slow emergence of interactions between human and climate impacts or other delayed effects of people on ecosystems [32]. Extinctions earlier than 60 ka can be attributed to non-human factors.

4. Chronology of megafaunal extinction

There are two contending views on the timing of extinction. A series of recent studies restricted to specimens and sites dated with high confidence suggest that the extinctions were concentrated between 50 and 40 ka on mainland Australia [24,26,33–36], and slightly later in Tasmania [37]. On the other hand, more extensive compilations of occurrences in the fossil record, lacking controls on date quality, suggest staggered extinction through the period from 400 to about 20 ka [6].

Two methodological problems affect these inferences. First, dates on fossil remains are subjected to many technical limitations and potential biases. Therefore, it is necessary to screen date-lists for reliability. Because in Sahul, the period of potential human–megafauna overlap is close to or beyond the limit of ^{14}C dating, a wide range of techniques in addition to ^{14}C has been applied to the problem, making it difficult to standardize the reliability of age determinations. In response, we developed a set of criteria for assessing reliability of age determinations across the full range of methods applied to Quaternary palaeontology and archaeology, and used these to assess reliability of all published age estimates on Sahul's extinct megafauna [38]. Figure 1 illustrates the impact of screening of dates using the example of *Diprotodon* sp., the largest marsupial. There are approximately 100 ages on *Diprotodon* from more than 1 Myr to 2 ka. After filtering for reliability, only 23 reliable dates remained, none younger than 44 ka.

The second problem is sparse sampling in the fossil record. Many megafaunal taxa from Sahul are represented by few specimens, of which even fewer have reliable dates. The date of extinction of a species is inferred from the absence of fossils, but when we have few dates this inference is highly uncertain. This uncertainty can create the appearance of

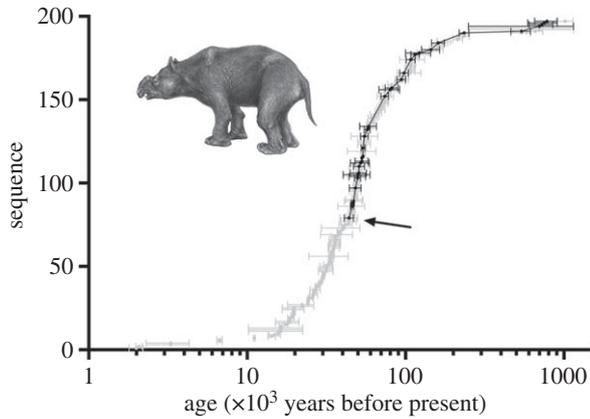


Figure 1. Time-series of dated specimens of *Diprotodon* sp., arranged in sequence from youngest to oldest, with ± 1 s.d. High-reliability dates [38] are black and low-quality dates grey; youngest reliable date is arrowed. *Diprotodon* sketch by Peter Murray.

staggered extinction even if all species disappeared at the same time [39]. To draw statistically robust inferences on the pattern of extinction of assemblages of species, we need quantitative approaches that infer probability intervals for extinction from the incomplete presence data furnished by the fossil record [40–42].

A recent study addresses both problems. Saltré *et al.* [26] compiled all available dates on Australia's Pleistocene megafauna and screened them for reliability [38], then derived statistically robust estimates of extinction timing for the 14 genera with sufficient reliable dates for analysis. They concluded that these genera went extinct between approximately 61 and 35 ka, with a peak in extinction probability at 42.1 ka. The picture remains incomplete because we cannot infer extinction chronologies for many poorly dated taxa, representing as many as 15 [6] genera.

5. Climate trends and variability

The Quaternary record of terrestrial climate change in Sahul is sparse, so climate trends are mainly inferred from ice cores in Antarctica and syntheses of marine sequences, which indicate broad trends in temperature. Unusually warm interglacials and cool glacials are irregularly distributed through almost the entire 800 ka of the EPICA Dome C ice-core from Antarctica [43]. Several syntheses have suggested a cooling trend over the last million years, with variable expression of the Mid-Brunhes event at approximately 430 ka, but this is not universally recognized [44–46]. Records of sea-surface temperatures near Sahul in the Coral Sea [47,48] do not show cooling over the last million years, nor increased variability across the Mid-Brunhes event or thereafter [46]. There is no clear trend through the last million years in the rate of change in oxygen-isotope composition in the global benthic oxygen-isotope record (the LR04 stack) [49].

Some authors have suggested [6] that the EPICA Dome C ice core reveals increasing variability in temperature proxies over the last 450 ka. We tested for this at millennial time scales by calculating the mean deviation (sum of absolute differences from the mean divided by the number of measurements) in δD (deuterium; this is a proxy for temperature, in which more negative values indicate lower temperatures) from 450 ka to the present in this core. A challenge for this analysis is that the time resolution of the core increases towards the present. For

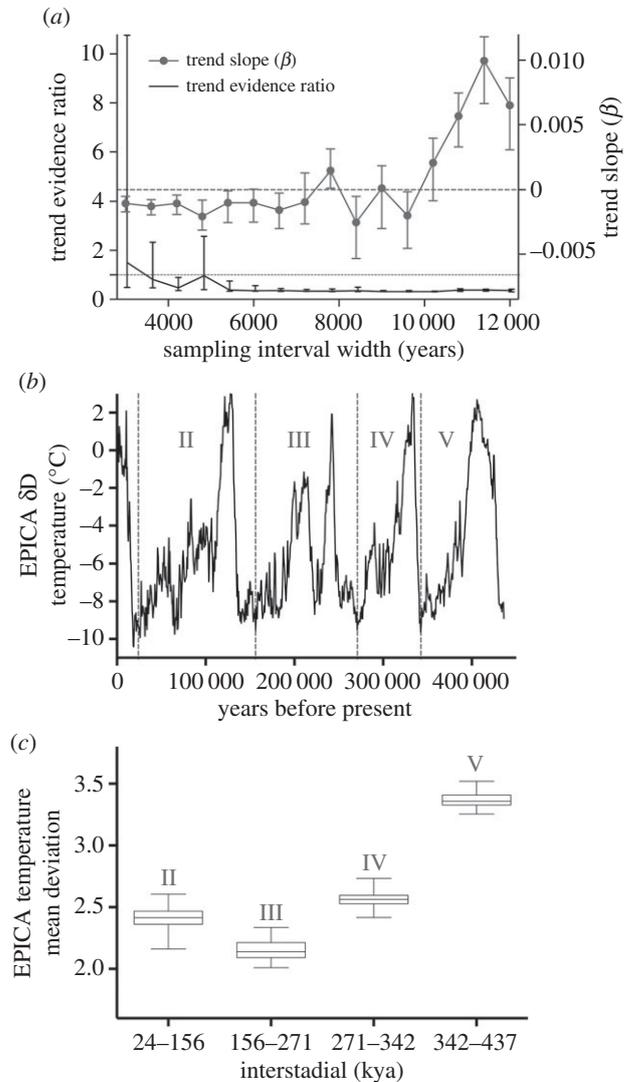


Figure 2. Trends in variability of temperature in the EPICA Dome C core over the last 450 000 years. (a) ER for linear trend in mean deviation in EPICA δD (δ deuterium = a proxy for temperature: more negative values indicate lower temperatures) from 450 to 24 ka ($ER \gg 1$ indicates evidence for linear trend) across sampling intervals of increasing width; also shown is the mean trend slope (β) per sampling interval width; (b) example EPICA temperature series resampled at a constant window of 600 years from present back to 450 ka; and (c) average and 95 percentile mean deviation of temperature within the four interstadials since 450 ka.

example, the mean interval between successive temperature estimates for the last 12.2 ka is 12.2 years, increasing to 418.6 years from 500 to 550 ka. Fluctuations on short time-scales are therefore more likely to be visible in recent parts of the record. To control for this uneven sampling, we resampled 1000 times (with a random uniform start date from within the first interval) increasing temporal window lengths from 3 ka to 12 ka across the series to 450 ka. For each resampled interval width, we calculated the mean deviation and tested for a linear trend of increasing mean deviation towards the present. We used the range of evidence ratios (ER) to compare the slope model (trend in increasing mean deviation towards the present) to the intercept-only (null) model with no trend. An $ER \gg 1$ would support a linear change over the null 'no trend' model, and thus the claim that variability increased. The linear trend model was rarely favoured, the slope of the trend being near zero (supporting the null model) for most sampling intervals (figure 2a). To visualize the absence of trend, we resampled at

an interval of 3 ka (to ensure at least five temperature values were available to calculate mean deviations) over 1000 iterations, splitting the 450 ka-to-present series into four periods (24–156 ka, 156–271 ka, 271–342 ka and 342–437 ka; figure 2*b*), and calculated the temperature mean deviations for each interval and iteration. The temperature record actually became less variable from 450 to 156 ka; variability then increased, but only slightly, from 156 to 24 ka (figure 2*c*).

Much of the discussion of environmental stress on megafaunal populations has focused on moisture availability rather than temperature [50]. The last few glacial–interglacial cycles (excluding the current interglacial) have been characterized by wetter conditions during interglacial stages and comparatively arid conditions during glacials [11,51–54]. However, available moisture records do not support the existence of a strong trend to increasing aridity over the last few glacial cycles.

There is little evidence for exceptional climate change around the time of human arrival. During Marine Isotope Stage (MIS) 3 (57–29 ka), dust flux into the Tasman Sea from south-eastern Australia, and into the Indian Ocean from north-western Australia, remained approximately constant [52], and there was no substantial variation in summer rainfall and dry season length over the Arafura Sea [55], or in discharge from the Murrumbidgee River in south-eastern Australia [56]. Australian palaeo-lake levels were high in early MIS 3, generally decreasing after 48–42 ka over a period of 10–15 ka [11,50,54]. Millennial-scale Asian monsoon variability, which is probably coupled with Australian monsoon variability, is similar in amplitude throughout the interval 60–30 ka [57–59]. While grass pollen is anomalously high off northwest Australia during the last interglacial [60,61], this was evidently not part of a longer trend to increased aridity in northern Australia. Water levels in the Lake Eyre and Lake Frome megafakes, in the southeast of the arid zone, fell between 50 and 40 ka, after which those lakes filled only intermittently [50]. Possibly, this drying provides an explanation for the extinction of the giant bird *Genyornis newtoni* in that region [50], although it is unknown if these changes were exceptional or typical of a pattern that recurred through successive glacial cycles.

6. Trends in megafaunal abundance

Trends in abundance of species cannot easily be inferred from the fossil record, because the abundance of fossils varies for many reasons unrelated to abundance in the source populations, such as age-dependent preservation bias [62,63] or stochastic variation in conditions affecting the likelihood of preservation. Three datasets attempt to overcome these problems in different ways.

First, cave deposits from subterranean galleries with openings to the surface that act as passive pitfall traps should accumulate remains at rates roughly proportional to population abundance. If conditions for preservation are excellent there may be little loss of fossil material over the period of accumulation. Two such cases from southern Australia, spanning periods of 500–150 ka, revealed long-term stability in the mammalian assemblage, despite climate-related variation in the relative abundance of small and large species. Large species declined relative to smaller ones during dry periods, probably owing to local range contractions, but rebounded subsequently [64,65].

Second, comparison of the frequencies through time of remains of species that are subject to similar preservation

biases may reveal shifts in their relative abundance [63]. *Genyornis newtoni* was a flightless, ground-nesting bird with a distribution overlapping the emu *Dromaius novaehollandiae*, another flightless ground-nester. Eggshells of both birds are abundant in the same sedimentary contexts and so are subject to the same processes of deposition and preservation, and are dateable by the same methods [24,66]. If abundances of fossil eggshells of both species are affected by the same biases, the ratio of their abundances should be free of bias. Changes in that ratio through time depict trends in the abundance of a species that went extinct—*Genyornis*—relative to a species that survived (emu). Figure 3 collates the relative abundance of *Genyornis* and emu eggshells through time, and shows that *Genyornis* tended to decline relative to the emu from the last interglacial to about 70 ka, then increased from about 65 to 50 ka, before crashing to extinction just after 50 ka.

Third, spores of fungi (*Sporormiella* spp. and others) that sporulate on the dung of large herbivores indicate the presence of those animals in past environments [67,68]. The spores are abundant and so provide a continuous measure of activity of large herbivores that can be quantified as spore-influx rates or indexed relative to pollen counts. A dung-fungus record from north-eastern Australia showed no trend from 130 ka until a steep decline at about 41 ka [69]. This decline cannot be explained by climate, which was evidently stable at the time [70]. Analysis of potential deposition biases suggest that the drop in dung fungi was a genuine indicator of an abrupt decline of the biomass of large herbivores [67].

Studies of ancient DNA in other regions have revealed long-term trends in population size [3], and local extinctions [71–73]. Unfortunately, we have little genetic information on Sahul's extinct megafauna because of poor DNA preservation in this region. Recent advances in molecular techniques have resulted in the first complete mitochondrial genome sequences of extinct marsupial megafauna [74]. These methods hold promise for phylogenetic and demographic studies, but population genetic analyses are currently out of reach.

7. Palaeoecological reconstructions

Prideaux *et al.* [75] reconstructed the ecology of *Procoptodon goliath*, a large kangaroo that once occurred through semi-arid southern and eastern Australia [76]. Dental morphology and microwear showed that *P. goliath* had a tough browse diet, and stable isotopes confirmed that a major component was C4 chenopods (saltbush, Chenopodiaceae). Chenopod shrublands remain widespread through the southern semi-arid and arid zones. Because chenopods are poorly flammable, it seems unlikely that anthropogenic fire had a large impact on *P. goliath*'s habitat, but the species could have been highly exposed to hunters in its shrubland habitat.

At the Lynch's Crater site, Rule *et al.* [69] used counts of spores of dung fungi, pollen grains and charcoal particles to reconstruct environmental changes associated with megafaunal extinction. Before the decline of dung fungi at 41 ka, the vegetation around the site was a mixture of angiosperm and gymnosperm rainforests and dry sclerophyll forest with little or no fire. Decline of dung fungi was closely followed by a sharp increase in the influx of charcoal and a more gradual change in vegetation composition leading to

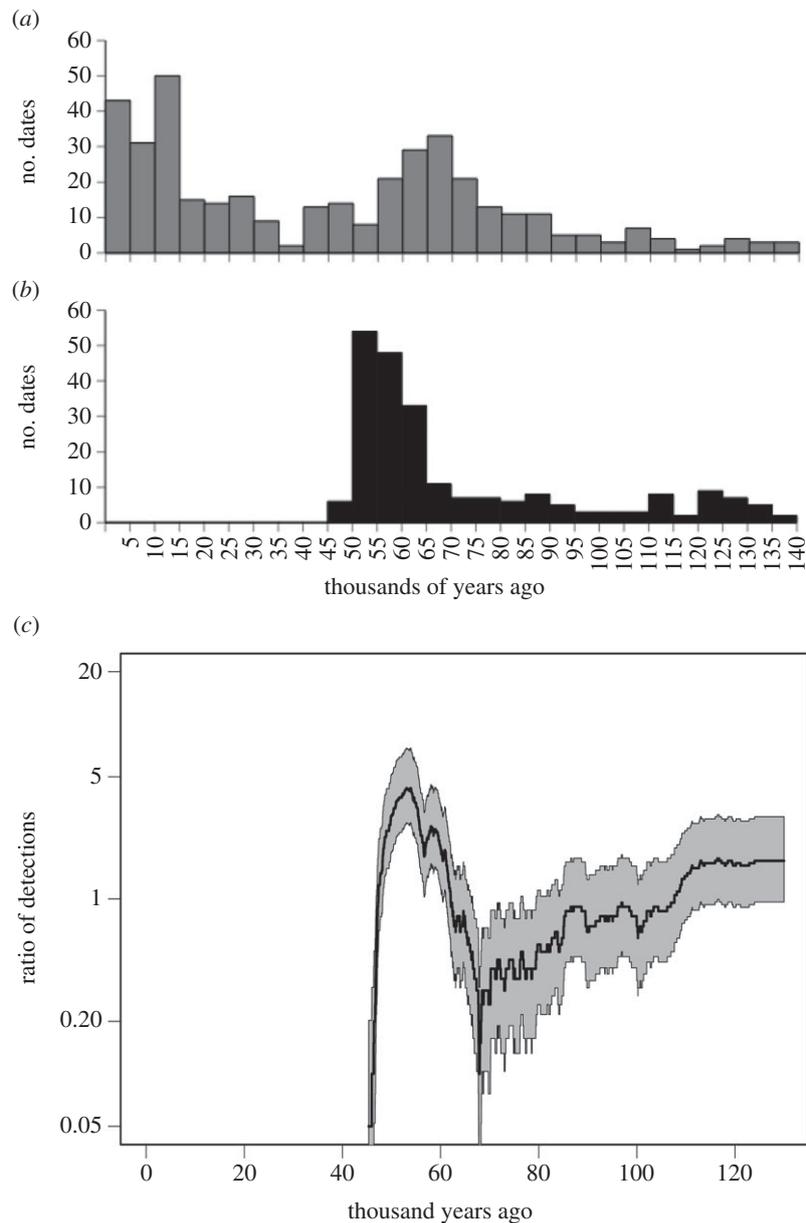


Figure 3. Relative abundance of eggshells of *Genyornis* and emu *Dromaius novaehollandiae* through the last glacial cycle: (a) and (b) numbers of dated samples from *Genyornis* and emu, respectively, from [24]. (c) Ratio of frequencies of *Genyornis* to emu samples, with 95% confidence intervals, calculated using a moving window (scaled to density of samples) to generate a smoothed curve.

replacement of the original mixed forest by uniform sclerophyll forest of higher density. Possibly, increased fire was caused by a build-up of fine fuel following the relaxation of herbivory, while vegetation changes resulted from some combination of release from herbivore pressure and impacts of fire. A parallel study at a cool alpine site in south-eastern Australia [77] also revealed a steep and unprecedented drop in dung fungi in the middle of the last glacial cycle, but this was not accompanied by any change in fire activity or vegetation, which remained a grass/shrub steppe.

Stable isotope analysis of eggshells showed that extinction of *Genyornis* coincided with a sustained change in diet of sympatric emus, from mixed feeding on C3 and C4 plants to predominantly C3 plants [24]. The change was unprecedented in a record reaching back to 140 ka and cannot be attributed to climate, but its cause remains unclear. Possibly, an altered fire regime induced a shift in the composition of vegetation, but there are no suitable charcoal records to verify this. Alternatively, the change in emu diet could reflect

vegetation change resulting from megaherbivore extinction. This also cannot be tested owing to the lack of pollen records for the arid zone. A marine core with a source area overlapping part of the same region shows a transient increase in biomass burning from 43 to 40 ka [78] and an excursion to C3-dominated vegetation; a low-resolution terrestrial record to the southwest, in the same climate zone, reveals no such increase in charcoal [79].

A synthesis of charcoal records from the Australasian region found some indication of increased charcoal input between 50 and 40 ka but the deviation during that period was small compared with variation before 50 and after 40 ka [80]. Some sites do show charcoal peaks around the time of human arrival and megafaunal extinction, but others do not. Some caution in the interpretation of charcoal records is warranted, because human and natural fire regimes might differ in their ecological effects while producing similar influxes of charcoal, especially when these are averaged over long intervals. In addition, many charcoal records have only loose

chronological control through the crucial period between 50 and 35 ka, so sharp changes could be obscured by imprecision when different records are combined. Bearing these reservations in mind, it is unlikely that human firing of Sahul landscapes produced continent-wide impacts, although some environments may have been sensitive to changes in the frequency and timing of ignition with human colonization.

8. Human – megafauna interaction

Archaeological evidence of hunting is rare and questionable for most species of Sahul's megafauna [15]. The one clear exception is the giant bird *Genyornis* [81]. Some eggshells of *Genyornis* show distinct charring patterns indicating they were heated over campfires, but only from 54 to 47 ka, during the interval when *Genyornis* declined to extinction. Similar charring patterns first appear on emu eggshells at the same time, and continue thereafter. Simultaneous onset of charring at widespread locations provides a signal of the early arrival and rapid spread of human populations through the arid regions of southern Australia. It also shows that these early populations exerted hunting pressure that could have contributed to the extinction of *Genyornis*.

Otherwise, does the lack of evidence for hunting of other species mean that hunting must have been negligible, as several authors have argued [6,82,83]? Surovell & Grund [84] argue that for Sahul especially, archaeological evidence of hunting of species that went extinct soon after human arrival ought to be rare even if that hunting was ecologically important. The main reason is that, given the early date of human arrival, the period of interaction between humans and extinct megafauna is only a small proportion of the total archaeological record of Sahul. Further, the quantity of evidence should be limited by the fact that hunting rates would have been highest early in the interaction when hunted populations were abundant but human populations were still small and of low archaeological visibility, and the effects of time-dependent loss of evidence would increase the rarity of signs of human–megafauna interaction. The predicted rarity of this evidence means that a very large archaeological and palaeontological sample would be needed to detect it, and it would be dangerous to use the failure to detect such evidence in a small sample to conclude that no such interaction occurred. Given these considerations, it is not surprising that the strongest evidence for hunting comes from *Genyornis*, whose remains are outstandingly abundant (1327 eggshell collections [81]).

9. Conclusion

Evidence on causes of megafaunal extinction in Sahul is still patchy: we have less information on the changing climate of Sahul through the Middle and Late Pleistocene than for other parts of the world; many species that went extinct during this period are poorly dated; we have few archaeological sites attesting to the timing and pattern of early human

occupation; and we lack detailed ecological information for most extinct megafauna. As a result, we still lack a detailed picture of the processes leading to megafaunal extinction in Sahul. Nonetheless, the weight of the evidence that we do have points clearly to direct human impact as the main cause of extinction. Although it is likely that there was a general cooling trend over Sahul through much of the Pleistocene, the evidence that megafaunal extinction was related to an increased rate of drying and amplified climate variability is weak at best. There were periods of aridity in the last glacial cycle, but they appear not to have been exceptional in comparison with previous cycles. There is no rigorously tested evidence for a staggered series of extinctions, either within the last glacial cycle or over several glacial cycles. Instead, high-quality dates indicate synchronous extinction within a few thousand years of human arrival. Where it is possible to interpret dynamics of megafaunal populations, populations appear to have crashed to extinction shortly after human occupation of Sahul rather than declining gradually over long periods beforehand. For species with well-described habitat preferences, it is clear that the animals disappeared despite their habitat remaining widespread. Reconstruction of the environmental context of extinction suggests that extinction preceded vegetation change, and that increased fire (where it occurred) was a consequence rather than a cause of decline of large herbivores.

Extinction of megafauna in Sahul presaged comparable losses on other continents and large islands over the last 50 000 years. Because the arrival of people in Sahul in the middle of the last glacial cycle was the first time in Earth history that modern humans reached a large landmass not already occupied by other hominids, Sahul provides an exceptionally valuable case for our understanding of the impacts of early humans on naive ecosystems. The evidence summarized here for a dominant role of direct human impact is therefore globally significant. Several recent analyses of megafaunal extinction using global databases agree in finding a dominant role for humans in most of the world [2,5,85]. The evidence from Sahul in these analyses is less clear, probably because the data on Sahul's megafauna were relatively sparse and of variable quality. The more comprehensive approach to data sources taken in this review is therefore valuable in clarifying evidence on the relative contributions of humans and climate to megafaunal extinction in Sahul, and strengthening support for a consistently large global impact of early humans on the diversity of large vertebrates.

Authors' contributions. All authors contributed to planning and drafting of the manuscript; C.N.J. led the writing; C.J.A.B. conducted the analysis of climate variability; N.J.B. conducted the analysis of *Genyornis* and emu abundance; M.R.R. and C.J.A.B. analysed the *Diprotodon* date list; all authors gave final approval for publication.

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