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1-1-2016

What caused extinction of the pleistocene megafauna of sahul?

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Recommended Citation

Johnson, Chris N.; Alroy, John; Beeton, Nicholas; Bird, Michael I.; Brook, Barry W.; Cooper, Alan; Gillespie, Richard; Herrando-Pérez, Salvador; Jacobs, Zenobia; Miller, Gifford H.; Prideaux, Gavin J.; Roberts, Richard G.; Rodríguez-Reya, Marta; Saltré, Frédéric; Turney, Christian; and Bradshaw, Corey J. A, "What caused extinction of the pleistocene megafauna of sahul?" (2016). *Faculty of Science, Medicine and Health - Papers: part A*. 3645.
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What caused extinction of the pleistocene megafauna of sahu?

Abstract

2016 The Author(s) Published by the Royal Society. All rights reserved. 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.

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

Johnson, C. N., Alroy, J., Beeton, N. J., Bird, M. I., Brook, B. W., Cooper, A., Gillespie, R., Herrando-Pérez, S., Jacobs, Z., Miller, G. H., Prideaux, G. J., Roberts, R. G., Rodríguez-Reya, M., Saltréa, F., Turney, C. S. M. & Bradshaw, C. J. A. (2016). What caused extinction of the pleistocene megafauna of sahu?. *Proceedings of the Royal Society B: Biological Sciences*, 283 (1824), 20152399-1 - 20152399-8.

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1 What caused extinction of the Pleistocene megafauna of Sahul?

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

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54 **1. Introduction**

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

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

71 72 **2. Hypotheses**

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

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

103 Here, we synthesise current understanding of this problem. Our review has two main
104 Aims. First, we aim to encompass the broadest possible range of evidence. This is important

105 because the use of multiple independent lines of evidence is the most promising avenue to
106 resolve this problem, in Sahul and globally. Second, we address uncertainties and biases that are
107 inevitable features of data on events from the distant past, but deal with these explicitly in
108 interpreting evidence.

109

110 3. Human arrival

111 It is still uncertain when people first set foot on Sahul: it might have been around 50 ka, or as
112 much as 10 ka earlier [10, 25, 26]. However, it is generally accepted that people were
113 widespread over the continent by 45 ka or a few millennia earlier [13, 14, 27, 28]. There is as yet
114 no obvious geographic pattern in first-appearance dates to indicate the progress of a wave of
115 colonization across Sahul. This is not surprising, because dates older than 40 ka typically have
116 uncertainty ranges of several thousand years. If people dispersed over Sahul within a few
117 millennia, we would be unable to resolve that process. Also, we still have few dated sites from
118 the earliest phase of the prehistory of Sahul. Only 20 archaeological sites have been dated to 40
119 ka or older [14]; for comparison, the archaeological record in Australia consists of 1,748 dated
120 sites [29]. Most of the arid centre lacks evidence of human occupation until just after 40 ka [30],
121 but whether this truly indicates late settlement rather than poor preservation and limited
122 sampling is unclear. Occupation of Tasmania had to await the emergence of a land bridge at 43
123 ka [8].

124 This picture suggests that declines and extinctions of species due to human impact should
125 have been concentrated in the period 50-40 ka. Quantitative population models suggest that if
126 hunting was the primary driver of decline, demographic lags might have caused delays of several
127 hundred to several thousand years between first contact and extinction in any given region [20,
128 31]. Late occupation of some regions might plausibly have delayed continent-wide extinction
129 several thousand years more. Taking these factors into account, a concentration of extinctions
130 between about 50 and 35 ka might be attributable to the impact of human arrival. Later
131 extinctions are less likely to have been due to direct human impact, although they could
132 conceivably have resulted from the slow emergence of interactions between human and climate
133 impacts or other delayed effects of people on ecosystems [32]. Extinctions earlier than 60 ka can
134 be attributed to non-human factors.

135

136 4. Chronology of megafaunal extinction

137 There are two contending views on the timing of extinction. A series of recent studies restricted
138 to specimens and sites dated with high confidence suggest that the extinctions were
139 concentrated between 50 and 40 ka on mainland Australia [24, 26, 33-36], and slightly later in
140 Tasmania [37]. On the other hand, more extensive compilations of occurrences in the fossil
141 record, lacking controls on date quality, suggest staggered extinction through the period from
142 400 to about 20 ka [6].

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

154 The second problem is sparse sampling in the fossil record. Many megafaunal taxa from
155 Sahul are represented by few specimens, of which even fewer have reliable dates. The date of

156 extinction of a species is inferred from absence of fossils, but when we have only few dates this
157 inference is highly uncertain. This uncertainty can create the appearance of staggered extinction
158 even if all species disappeared at the same time [39]. To draw statistically robust inferences on
159 the pattern of extinction of assemblages of species, we need quantitative approaches that infer
160 probability intervals for extinction from the incomplete presence data furnished by the fossil
161 record [40-42].

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

168

169 5. Climate trends and variability

170 The Quaternary record of terrestrial climate change in Sahul is sparse, so climate trends are
171 mainly inferred from ice cores in Antarctica and syntheses of marine sequences, which indicate
172 broad trends in temperature. Unusually warm interglacials and cool glacials are irregularly
173 distributed through almost the entire 800 ka of the EPICA Dome C ice-core from Antarctica [43].
174 Several syntheses have suggested a cooling trend over the last million years, with variable
175 expression of the Mid-Brunhes event at ~ 430 ka, but this is not universally recognised [44-46].
176 Records of sea-surface temperatures near Sahul in the Coral Sea [47, 48] do not show cooling
177 over the last million years, nor increased variability across the Mid- Brunhes event or thereafter
178 [46]. There is no clear trend through the last million years in the rate of change in oxygen-
179 isotope composition in the global benthic oxygen-isotope record (the LR04 stack) [49].

180 Some authors have suggested [6] that the EPICA Dome C ice core reveals increasing
181 variability in temperature proxies over the last 450 ka. We tested for this at millennial time
182 scales by calculating the mean deviation (sum of absolute differences from the mean divided by
183 the number of measurements) in δD (deuterium; this is a proxy for temperature, in which more
184 negative values indicate lower temperatures) from 450 ka to the present in this core. A challenge
185 for this analysis is that the time resolution of the core increases towards the present. For
186 example, the mean interval between successive temperature estimates for the last 12.2 ka is 12.2
187 years, increasing to 418.6 years from 500 to 550 ka. Fluctuations on short time-scales are
188 therefore more likely to be visible in recent parts of the record. To control for this uneven
189 sampling we resampled 1000 times (with a random uniform start date from within the first
190 interval) increasing temporal window lengths from 3 ka to 12 ka across the series to 450 ka. For
191 each resampled interval width, we calculated the mean deviation and tested for a linear trend of
192 increasing mean deviation toward the present. We used the range of evidence ratios (*ER*) to
193 compare the slope model (trend in increasing mean deviation toward the present) to the
194 intercept-only (null) model with no trend. An $ER \gg 1$ would support a linear change over the
195 null 'no trend' model, and thus the claim that variability increased. The linear trend model was
196 rarely favoured, the slope of the trend being near zero (supporting the null model) for most
197 sampling intervals (Fig. 2a). To visualise the absence of trend, we resampled at an interval of 3
198 ka (to ensure at least 5 temperature values were available to calculate mean deviations) over
199 1000 iterations, splitting the 450 ka-to-present series into four periods (24-156 ka, 156-271 ka,
200 271-342 ka and 342-437 ka - Fig. 2b), and calculated the temperature mean deviations for each
201 interval and iteration. The temperature record actually became less variable from 450 to 156 ka;
202 variability then increased, but only slightly, from 156 to 24 ka (Fig. 2c).

203 Much of the discussion of environmental stress on megafaunal populations has focussed
204 on moisture availability rather than temperature [50]. The last few glacial-interglacial cycles
205 (excluding the current interglacial) have been characterised by wetter conditions during
206 interglacial stages and comparatively arid conditions during glacials [51-55]. However, available

207 moisture records not support the existence of a strong trend to increasing aridity over the last
208 few glacial cycles.

209 There is little evidence for exceptional climate change around the time of human arrival.
210 During MIS (Marine Isotope Stage) 3 (57 to 29 ka) dust flux into the Tasman Sea from south-
211 eastern Australia, and into the Indian Ocean from north-western Australia, remained
212 approximately constant [52], and there was no substantial variation in summer rainfall and dry
213 season length over the Arafura Sea [56] or in discharge from the Murrumbidgee River in south-
214 eastern Australia [57]. Australian palaeo-lake levels were high in early MIS 3, generally
215 decreasing after 48-42ka over a period of 10-15ka [50, 54, 55]. Millennial-scale Asian monsoon
216 variability, which is probably coupled with Australian monsoon variability, is similar in
217 amplitude throughout the interval 60-30 ka [58-60]. While grass pollen is anomalously high off
218 northwest Australia during the last interglacial [61, 62], this was evidently not part of a longer
219 trend to increased aridity in northern Australia. Water levels in the Lake Eyre and Lake Frome
220 mega-lakes, in the southeast of the arid zone, fell between 50 and 40 ka, after which those lakes
221 filled only intermittently [50]. Possibly, this drying provides an explanation for the extinction of
222 the giant bird *Genyornis newtoni* in that region [50], although it is unknown if these changes
223 were exceptional or typical of a pattern that recurred through successive glacial cycles.

224

225 **6. Trends in megafaunal abundance**

226 Trends in abundance of species cannot easily be inferred from the fossil record, because the
227 abundance of fossils varies for many reasons unrelated to abundance in the source populations,
228 such as age-dependent preservation bias [63, 64] or stochastic variation in conditions affecting
229 the likelihood of preservation. Three datasets attempt to overcome these problems in different
230 ways.

231 First, cave deposits from subterranean galleries with openings to the surface that act as
232 passive pitfall traps should accumulate remains at rates roughly proportional to population
233 abundance. If conditions for preservation are excellent there may be little loss of fossil material
234 over the period of accumulation. Two such cases from southern Australia, spanning periods of
235 500 to 150 ka, revealed long-term stability in the mammalian assemblage, despite climate-
236 related variation in the relative abundance of small and large species. Large species declined
237 relative to smaller ones during dry periods, probably due to local range contractions, but
238 rebounded subsequently [65, 66].

239 Second, comparison of the frequencies through time of remains of species that are subject
240 to similar preservation biases may reveal shifts in their relative abundance [64]. *Genyornis*
241 *newtoni* was a flightless, ground-nesting bird with a distribution overlapping the emu *Dromaius*
242 *novaehollandiae*, another flightless ground-nester. Eggshells of both birds are abundant in the
243 same sedimentary contexts and so are subject to the same processes of deposition and
244 preservation, and are dateable by the same methods [24, 67]. If abundances of fossil eggshells of
245 both species are affected by the same biases, the ratio of their abundances should be free of bias.
246 Changes in that ratio through time depict trends in the abundance of a species that went
247 extinct—*Genyornis*—relative to a species that survived (emu). Figure 3 collates the relative
248 abundance of *Genyornis* and emu eggshells through time, and shows that *Genyornis* tended to
249 decline relative to the emu from the last interglacial to about 70ka, then increased from about 65
250 to 50 ka, before crashing to extinction just after 50 ka.

251 Third, spores of fungi (*Sporormiella* spp. and others) that sporulate on the dung of large
252 herbivores indicate the presence of those animals in past environments [68, 69]. The spores are
253 abundant and so provide a continuous measure of activity of large herbivores that can be
254 quantified as spore-influx rates or indexed relative to pollen counts. A dung-fungus record from
255 north-eastern Australia showed no trend from 130 ka until a steep decline at about 41 ka [70].
256 This decline cannot be explained by climate, which was evidently stable at the time [71].
257 Analysis of potential deposition biases suggest that the drop in dung fungi was a genuine

258 indicator of an abrupt decline of the biomass of large herbivores [68].

259 Studies of ancient DNA in other regions have revealed long-term trends in population size
260 [3], and local extinctions [72-74]. Unfortunately, we have little genetic information on Sahul's
261 extinct megafauna because of poor DNA preservation in this region. Recent advances in
262 molecular techniques have resulted in the first complete mitochondrial genome sequences of
263 extinct marsupial megafauna [75]. These methods hold promise for phylogenetic and
264 demographic studies, but population genetic analyses are currently out of reach.

265

266 7. Palaeoecological reconstructions

267 Prideaux *et al.* [76] reconstructed the ecology of *Procoptodon goliath*, a large kangaroo that once
268 occurred through semi-arid southern and eastern Australia [77]. Dental morphology and
269 microwear showed that *P. goliath* had a tough browse diet, and stable isotopes confirmed that a
270 major component was C4 chenopods (saltbush, Chenopodiaceae). Chenopod shrublands remain
271 widespread through the southern semi-arid and arid zones. Because chenopods are poorly
272 flammable, it seems unlikely that anthropogenic fire had a large impact on *P. goliath*'s habitat, but
273 the species could have been highly exposed to hunters in its shrubland habitat.

274 At the Lynch's Crater site, Rule *et al.* [70] used counts of spores of dung fungi, pollen
275 grains and charcoal particles to reconstruct environmental changes associated with megafaunal
276 extinction. Before the decline of dung fungi at 41 ka, the vegetation around the site was a
277 mixture of angiosperm and gymnosperm rainforests and dry sclerophyll forest with little or no
278 fire. Decline of dung fungi was closely followed by a sharp increase in the influx of charcoal and a
279 more gradual change in vegetation composition leading to replacement of the original mixed
280 forest by uniform sclerophyll forest of higher density. Possibly, increased fire was caused by a
281 build-up of fine fuel following the relaxation of herbivory, while vegetation changes resulted
282 from some combination of release from herbivore pressure and impacts of fire. A parallel study
283 at a cool alpine site in south-eastern Australia [78] also revealed a steep and unprecedented
284 drop in dung fungi in the middle of the last glacial cycle, but this was not accompanied by any
285 change in fire activity or vegetation, which remained a grass/shrub steppe.

286 Stable isotope analysis of eggshells showed that extinction of *Genyornis* coincided with a
287 sustained change in diet of sympatric emu, from mixed feeding on C3 and C4 plants to
288 predominantly C3 plants [24]. The change was unprecedented in a record reaching back to 140
289 ka and cannot be attributed to climate, but its cause remains unclear. Possibly, an altered fire
290 regime induced a shift in the composition of vegetation, but there are no suitable charcoal
291 records to verify this. Alternatively the change in emu diet could reflect vegetation change
292 resulting from megaherbivore extinction. This also cannot be tested owing to the lack of pollen
293 records for the arid zone. A marine core with a source area overlapping part of the same region
294 shows a transient increase in biomass burning from 43 to 40 ka [79] and an excursion to C3-
295 dominated vegetation; a low-resolution terrestrial record to the southwest, in the same climate
296 zone, reveals no such increase in charcoal [80].

297 A synthesis of charcoal records from the Australasian region found some indication of
298 increased charcoal input between 50 and 40 ka but the deviation during that period was small
299 compared to variation before 50 and after 40 ka [81]. Some sites do show charcoal peaks around
300 the time of human arrival and megafaunal extinction, but others do not. Some caution in the
301 interpretation of charcoal records is warranted, because human and natural fire regimes might
302 differ in their ecological effects while producing similar influxes of charcoal, especially when
303 these are averaged over long intervals. Also, many charcoal records have only loose
304 chronological control through the crucial period between 50 and 35 ka, so sharp changes could
305 be obscured by imprecision when different records are combined. Bearing these reservations in
306 mind, it is unlikely that human firing of Sahul landscapes produced continent-wide impacts,
307 although some environments may have sensitive to changes in the frequency and timing of
308 ignition with human colonization.

309

310 8. Human-megafauna interaction

311 Archaeological evidence of hunting is rare and questionable for most species of Sahul's
312 megafauna [15]. The one clear exception is the giant bird *Genyornis* [82]. Some eggshells of
313 *Genyornis* show distinct charring patterns indicating they were heated over campfires, but only
314 from 54 to 47 ka, during the interval when *Genyornis* declined to extinction. Similar charring
315 patterns first appear on emu eggshells at the same time, and continue thereafter. Simultaneous
316 onset of charring at widespread locations provides a signal of the early arrival and rapid spread
317 of human populations through the arid regions of southern Australia. It also shows that these
318 early populations exerted hunting pressure that could have contributed to the extinction of
319 *Genyornis*.

320 Otherwise, does the lack of evidence for hunting of other species mean that hunting must
321 have been negligible, as several authors have argued [6, 83, 84]? Surovell and Grund [85] argue
322 that for Sahul especially, archaeological evidence of hunting of species that went extinct soon
323 after human arrival ought to be rare even if that hunting was ecologically important. The main
324 reason is that, given the early date of human arrival, the period of interaction between humans
325 and extinct megafauna is only a small proportion of the total archaeological record of Sahul.
326 Further, the quantity of evidence should be limited by the fact that hunting rates would have
327 been highest early in the interaction when hunted populations were abundant but human
328 populations were still small and of low archaeological visibility, and the effects of time-
329 dependent loss of evidence would increase the rarity of signs of human-megafauna interaction.
330 The predicted rarity of this evidence means that a very large archaeological and palaeontological
331 sample would be needed to detect it, and it would be dangerous to use the failure to detect such
332 evidence in a small sample to conclude that no such interaction occurred. Given these
333 considerations, it is not surprising that the strongest evidence for hunting comes from *Genyornis*,
334 whose remains are outstandingly abundant (1,327 eggshell collections[82]).

335

336 9. Conclusions

337 Evidence on causes of megafaunal extinction in Sahul is still patchy: we have less information on
338 the changing climate of Sahul through the Middle and Late Pleistocene than for other parts of the
339 world; many species that went extinct during this period are poorly dated; we have few
340 archaeological sites attesting to the timing and pattern of early human occupation; and we lack
341 detailed ecological information for most extinct megafauna. As a result, we still lack a detailed
342 picture of the processes leading to megafaunal extinction in Sahul. Nonetheless, the weight of the
343 evidence that we do have points clearly to direct human impact as the main cause of extinction.
344 Although it is likely that there was a general cooling trend over Sahul through much of the
345 Pleistocene, the evidence that megafaunal extinction was related to an increased rate of drying
346 and amplified climate variability is weak at best. There were periods of aridity in the last glacial
347 cycle, but they appear not to have been exceptional in comparison with previous cycles. There is
348 no rigorously tested evidence for a staggered series of extinctions, either within the last glacial
349 cycle or over several glacial cycles. Instead, high-quality dates indicate synchronous extinction
350 within a few thousand years of human arrival. Where it is possible to interpret dynamics of
351 megafaunal populations, populations appear to have crashed to extinction shortly after human
352 occupation of Sahul rather than declining gradually over long periods beforehand. For species
353 with well-described habitat preferences, it is clear that the animals disappeared despite their
354 habitat remaining widespread. Reconstruction of the environmental context of extinction
355 suggests that extinction preceded vegetation change, and that increased fire (where it occurred)
356 was a consequence rather than a cause of decline of large herbivores.

357 Extinction of megafauna in Sahul presaged comparable losses on other continents and
358 large islands over the last 50,000 years. Because the arrival of people in Sahul in the middle of
359 the last glacial cycle was the first time in Earth history that modern humans reached a large

360 landmass not already occupied by other hominids, Sahul provides an exceptionally valuable case
361 for our understanding of the impacts of early humans on naïve ecosystems. The evidence
362 summarized here for a dominant role of direct human impact is therefore globally significant.
363 Several recent analyses of global databases agree in finding a dominant role for humans in most
364 of the world [2, 5, 86]. The evidence from Sahul in these analyses is less clear, probably because
365 the data on Sahul's megafauna were relatively sparse and of variable quality. The more
366 comprehensive approach to data sources in this review is therefore valuable in clarifying
367 evidence on the relative contributions of humans and climate to megafaunal extinction in Sahul,
368 and strengthening support for a consistently large global impact of early humans on the diversity
369 of large vertebrates.

370

371 **Authors' contributions.** All authors contributed to planning and drafting of the manuscript; CNJ
372 led the writing; CJAB conducted the analysis of climate variability; NJB conducted the analysis of
373 *Genyornis* and emu abundance; MRR and CJAB analysed the *Diprotodon* date list; All authors gave
374 final approval for publication.

375

376 **Competing interests.** We have no competing interests.

377

378 **Acknowledgments.** The Australian Research Council provided funding for this work through
379 research fellowships to CNJ, JA, MIB, AC, RGR, CSMT and CJAB.

380

381

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644

645 LEGENDS TO FIGURES

646

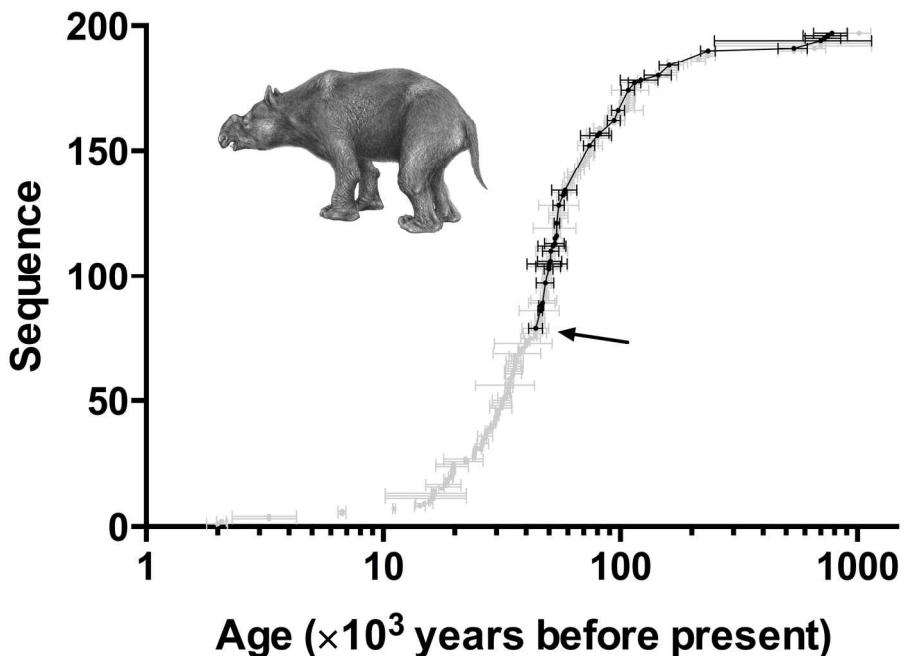
647 **Figure 1.** Time-series of dated specimens of *Diprotodon* sp, arranged in sequence from youngest
648 to oldest, with ± 1 standard deviation. High-reliability dates [38] are black and low-quality dates
649 grey; youngest reliable date is arrowed. *Diprotodon* sketch by Peter Murray.

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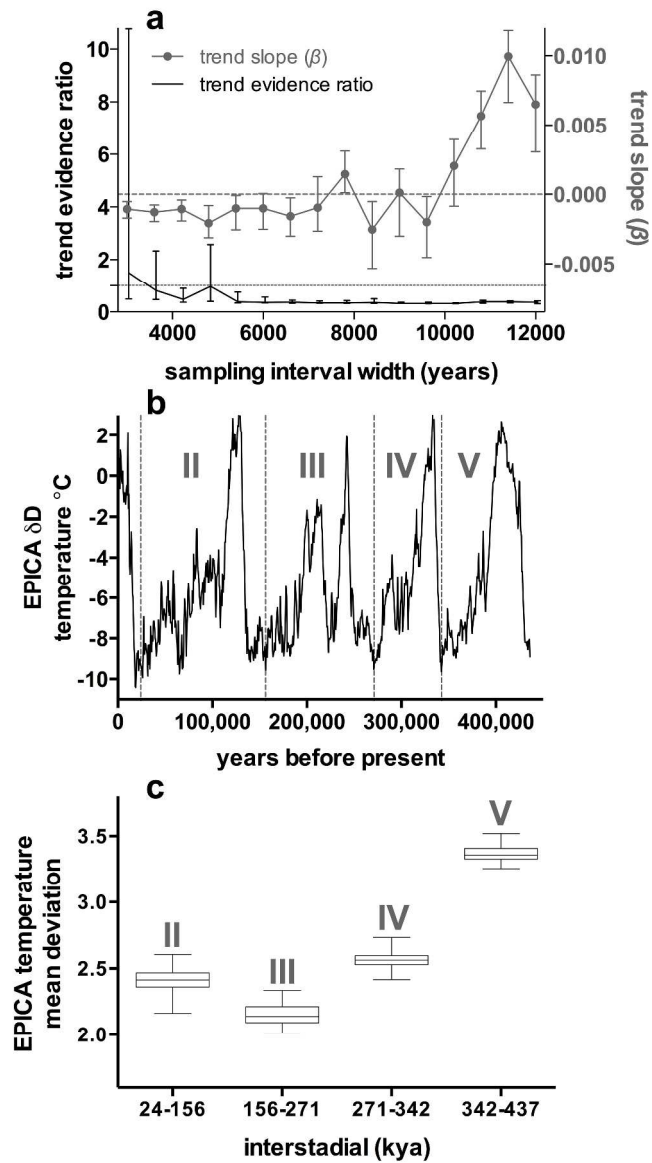
651 **Figure 2.** Trends in variability of temperature in the EPICA Dome C core over the last 450,000
652 years. **(a)** Evidence ratio for linear trend in mean deviation in EPICA δD (δ deuterium = a [proxy](#)
653 for temperature: more negative values indicate lower temperatures) from 450 to 24 ka ($ER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

658

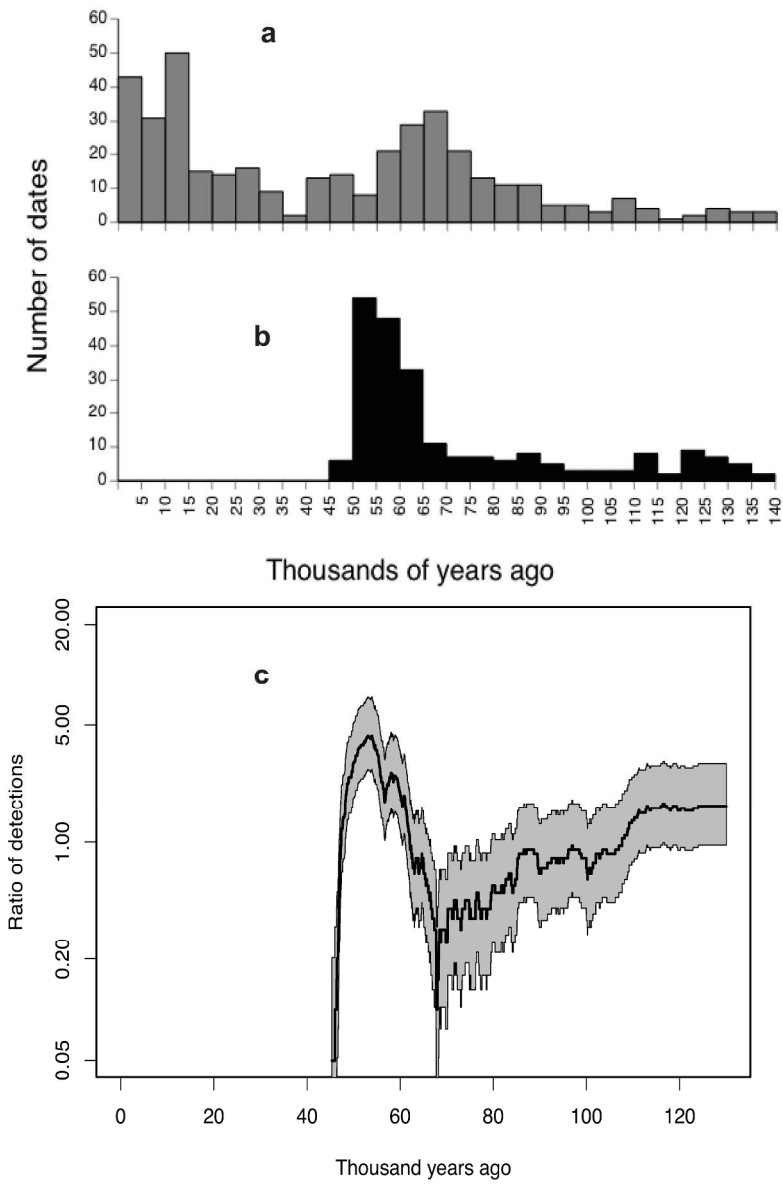
659 **Figure 3.** Relative abundance of eggshells of *Genyornis* and emu *Dromaius novaehollandiae*
660 through the last glacial cycle: **(a)** and **(b)** numbers of dated samples from *Genyornis* and emu
661 respectively, from [24]. **(c)** Ratio of frequencies of *Genyornis* to emu samples, with 95%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



167x124mm (300 x 300 DPI)



271x475mm (300 x 300 DPI)



207x312mm (300 x 300 DPI)