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Corey Bradshaw (✉ corey.bradshaw@flinders.edu.au)

Flinders University   https://orcid.org/0000-0002-5328-7741

Frederik Saltre

Flinders University   https://orcid.org/0000-0002-5040-3911

Stefani Crabtree

Utah State University   https://orcid.org/0000-0001-8585-8943

Christian Reepmeyer

Commission for Archaeology of Non-European Cultures

Theodora Moutsiou

University of Cyprus

Article

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Corey J. A. Bradshaw[1,2,*], Frédérik Saltré[1,2], Stefani A. Crabtree[3,4,2], Christian Reepmeyer[5,6,2], Theodora Moutsiou[7,6,†]

[1]Global Ecology | *Partuyarta Ngadluku Wardli Kuu*, College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia
[2]Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, Wollongong, New South Wales, Australia
[3]Department of Environment and Society, Utah State University, 5200 Old Main Hill, Logan, Utah, 84322, USA
[4]The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico, 87501, USA
[5]Commission for Archaeology of Non-European Cultures, German Archaeological Institute, Dürenstr. 35-37, 53173 Bonn, Germany
[6]College of Arts, Society and Education, James Cook University Cairns, Nguma-bada campus, GPO Box 6811 Cairns, Queensland 4870, Australia
[7]Archaeological Research Unit, University of Cyprus, 12 Gladstone Street, 1095 Nicosia, Cyprus

[*]Corresponding author: CJAB: corey.bradshaw@flinders.edu.au
[†]Contributed equally

ORCID
CJA **Bradshaw**: 0000-0002-5328-7741; SA Crabtree: 0000-0001-8585-8943; T **Moutsiou**: 0000-0001-6150-5107; C **Reepmeyer**: 0000-0002-3257-0898; F **Saltré**: 0000-0002-5040-3911

Abstract

The hypothesised main drivers of megafauna extinctions in the late Quaternary have wavered between over-exploitation by humans and environmental change, with recent investigations demonstrating more nuanced synergies between these drivers depending on taxon, spatial scale, and region. However, most studies still rely on comparing archaeologically based chronologies of timing of initial human arrival into naïve ecosystems and palaeontologically inferred dates of megafauna extinctions. Conclusions arising from comparing chronologies also depend on the reliability of dated evidence, dating uncertainties, and correcting for the low probability of preservation (Signor-Lipps effect). While some models have been developed to test the susceptibility of megafauna to theoretical offtake rates, none has explicitly linked human energetic needs, prey choice, and hunting efficiency to examine the plausibility of human-driven extinctions. Using the island of Cyprus in the terminal Pleistocene as an ideal test case because of its late human settlement (~ 14.2 ka–13.2 ka), small area (~ 11,000 km^2), and low megafauna diversity (2 species), we developed stochastic models of megafauna population dynamics, with offtake dictated by human energetic requirements, prey choice, and hunting-efficiency functions to test whether the human population at the end of the Pleistocene could have caused the extinction of dwarf hippopotamus (*Phanourios minor*) and dwarf elephants (*Palaeoloxodon cypriotes*). Our models reveal not only that the estimated human population sizes (N = 3,000–7,000) in Late

46 Pleistocene Cyprus could have easily driven both species to extinction within < 1,000 years,
47 the model predictions match the observed, Signor-Lipps-corrected chronological sequence of
48 megafauna extinctions inferred from the palaeontological record (*Phanourios* at ~ 12 ka–11.1
49 ka, followed by *Palaeoloxodon* at ~ 10.3 ka–9.1 ka).
50

Παλαιολιθικοί ανθρώπινοι πληθυσμοί στην Κύπρο και οι μηχανισμοί κυνηγιού της εγγενούς μεγαλοπανίδας εώς την εξαφάνιση

53 Οι κύριες υποθέσεις που έχουν διατυπωθεί αναφορικά με τους πρωταρχικούς παράγοντες
54 εξαφάνισης της μεγαλοπανίδας στο τέλος του Τεταρτογενούς αφορούν είτε στην
55 υπερεκμετάλλευση από τον άνθρωπο ή στην περιβαλλοντική αλλαγή. Πρόσφατες έρευνες
56 καταδεικνύουν ελαφρώς διαφοροποιημένες συνέργειες μεταξύ αυτών των παραγόντων
57 ανάλογα με την ταξινομική βαθμίδα, την χωρική κλίμακα και την περιοχή. Ωστόσο, οι
58 περισσότερες μελέτες εξακολουθούν να βασίζονται στη σύγκριση χρονολογιών της αρχικής
59 ανθρώπινης άφιξης σε παρθένα οικοσυστήματα σύμφωνα με αρχαιολογικά δεδομένα και
60 παλαιοντολογικά συναγόμενες ημερομηνίες εξαφανίσεων της μεγαλοπανίδας. Τα
61 συμπεράσματα που προκύπτουν από τη σύγκριση χρονολογιών εξαρτώνται επιπλέον από την
62 αξιοπιστία των χρονολογημένων στοιχείων, τις αβεβαιότητες χρονολόγησης και τη διόρθωση
63 για την χαμηλή πιθανότητα διατήρησης (φαινόμενο *Signor-Lipps*). Παρόλο που διάφορα
64 μοντέλα έχουν αναπτυχθεί για να διερευνήσουν την ευαισθησία της μεγαλοπανίδας σε
65 θεωρητικά ποσοστά απόληψης, κανένα δεν έχει συνδέσει ρητά τις ανθρώπινες ενεργειακές
66 ανάγκες, την επιλογή θηραμάτων και την αποτελεσματικότητα του κυνηγιού για να εξετάσει
67 την αξιοπιστία των εξαφανίσεων ως ανθρωπογενές φαινόμενο. Το νησί της Κύπρου στο
68 τέλος του Πλειστόκαινου αποτελεί ιδανική περίπτωση διερεύνησης του φαινομένου της
69 εξαφάνισης της εγγενούς μεγαλοπανίδας λόγω της ύστερης ανθρώπινης εγκατάστασης (~
70 14,200 χ.α.σ.–13,200 χ.α.σ.), της μικρής έκτασης του νησιού (~ 11,000 χμ²) και της χαμηλής
71 ποικιλότητας της μεγαλοπανίδας (2 είδη). Για το σκοπό αυτό, αναπτύξαμε στοχαστικά
72 μοντέλα της δυναμικής του πληθυσμού της μεγαλοπανίδας, με απόληψη που υπαγορεύεται
73 από τις ανθρώπινες ενεργειακές απαιτήσεις, την επιλογή θηράματος και τις λειτουργίες
74 απόδοσης κυνηγιού ώστε να εξετάσουμε εάν ο ανθρώπινος πληθυσμός στο τέλος του
75 Πλειστόκαινου θα μπορούσε να είχε προκαλέσει την εξαφάνιση του νάνου ιπποπόταμου
76 (*Phanourios minor*) και των νάνων ελεφάντων (*Palaeoloxodon cypriotes*). Τα μοντέλα μας
77 αποκαλύπτουν ότι τα εκτιμώμενα μεγέθη ανθρώπινου πληθυσμού (N = 3,000–7,000) στην
78 Κύπρο του Ύστερου Πλειστόκαινου θα μπορούσαν εύκολα να οδηγήσουν και τα δύο είδη σε
79 εξαφάνιση εντός < 1,000 ετών. Επιπλέον, οι προβλέψεις των μοντέλων μας ταιριάζουν με
80 την παρατηρούμενη, διορθωμένη με *Signor-Lipps,* χρονική ακολουθία των εξαφανίσεων της
81 μεγαλοπανίδας όπως προκύπτει από το παλαιοντολογικό αρχείο (*Phanourios* σε ~ 12,000–
82 11,100 χ.α.σ. και *Palaeoloxodon* σε ~ 10,300–9,100 χ.α.σ.).
83

84 *Key words*: carrying capacity, cohort models, dwarf elephant, dwarf hippopotamus, human
85 expansion, hunter-gatherers, mammals, Mediterranean, offtake, pre-agropastoralist
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Introduction

Explanations for the global extinction of hundreds of large terrestrial species during the late Quaternary[1] have matured from relying on simple binary drivers, to a more nuanced demonstration of synergistic mechanisms varying across taxa and regions[2-9]. However, temporal variation in species composition inferred from the zooarchaeological record is still often attributed either to (*i*) changing environmental conditions altering natural abundances, (*ii*) humans depleting populations through subsistence offtake, or (*iii*) a combination of the two[10-13]. Yet, the relative contribution of these two mechanisms and/or their combination to the loss of megafauna during the Late Pleistocene and early Holocene are still largely examined based on inferred chronologies of relative human appearance and megafauna extinctions[5,8,14]. When the estimated window of human appearance to naïve ecosystems estimated from archaeological evidence precedes (but not by too much) palaeontologically inferred extinction dates, the conclusion tends to invoke human endeavour as the primary cause of the extinction[15,16]. On the other hand, when the palaeontological record suggests an extinction event occurred well before inferred human arrival, the assumed mechanism underlying the extinction tends to be environmental change. Here, proxy data indicating large climatological fluctuations[17] or via species distributions derived from climate niche models[13] in the period immediately before inferred extinction tend to be the basis for conclusions that environmental change drove regional extinctions of large terrestrial species.

Despite recent analytical advances in such (spatio-) temporal analyses[8,18], the quality and robustness of the underlying date estimates are still central to the appearance-extinction chronology, and therefore, the conclusions regarding the proximal drivers of extinction. Acknowledging that robust time series of a species' decline to extinction and the clear, unambiguous dates of initial human arrival are extremely rare, even high-quality data can still only hypothesise the mechanisms underlying the overarching causes[19]. In other words, how were particular populations of humans able to drive specific species to extinction, and how did an environment change express as a loss of fitness and the eventual demise of an entire species? While the literature is rife with supposition, there are in fact few quantitative or modelled examples of plausible ecological mechanisms driving extinction, whether the main determinants were human over-exploitation, environmental change, or a combination of both. Exceptions include mechanistic models of varying complexity that have been developed to discern the dynamics of megafauna extinctions[19-24]; however, none of these models has explicitly included the energetic needs of palaeolithic hunter-gatherers, hunting efficiency, and prey selection, and converted these parameters into equivalent animal offtake rates by humans. The main reasons for this gap likely arise from the complexity of hunter-gatherer foraging systems[25], a lack of relevant data, and uncertainties regarding human patterns of expansion and settlement[26].

The island of Cyprus in the eastern Mediterranean offers an ideal set of conditions to test whether recently arrived populations of pre-agropastoralist humans had the capacity to drive megafauna species to extinction. Cyprus is an insular environment with a maximum area at the approximate period of human arrival (~ 14.2 ka–13.2 ka)[27] of only ~ 11,000 km^2, making spatial heterogeneity in archaeological and palaeontological evidence less important for inferring regional trends compared to large regions such as Eurasia with considerably larger

3

132 gaps in spatial coverage of the available evidence[21], South America[5], or Sahul[8,16]. Most
133 importantly, there were only two megafauna species on the island when people first arrived
134 (although there were other, smaller terrestrial species recovered from zooarchaeological
135 records — a genet *Genetta plesictoides*, a murid *Mus* sp., a shrew *Crocidura suaveolens*
136 *praecypria*, and a megachiropteran)[28], making models of prey choice more tractable to
137 construct compared to those situated in more biodiverse environments. Neither is there any
138 evidence that Cyprus had predators large enough to kill either species[29,30] prior to humans
139 arriving. In addition, the patterns of initial human arrival and spread in Cyprus have recently
140 been established with considerable certainty[27].

141   The two 'large' (> 100 kg body weight) species present on Cyprus when people first
142 arrived were the dwarf hippopotamus *Phanourios minor* and the dwarf elephant
143 *Palaeoloxodon cypriotes*[31]. *Phanourios* was the smallest dwarf hippopotamus in the
144 Mediterranean region[30] and weighed ~ 130 kg at adulthood[32]. It was adapted to a largely
145 terrestrial, browsing lifestyle given its lower orbits and nostrils[33,34], loss of the 4th molar,
146 brachydont molars, and a shortened and narrow muzzle[34-36] when compared to semi-aquatic
147 forms. *Palaeoloxodon cypriotes* probably derived from the straight-tusked elephant *P.*
148 *antiquus* that inhabited Europe and Western Asia during the Middle and Late Pleistocene[37]. It
149 weighed only about 530 kg and was therefore < 10% of the size of its mainland ancestor[32].

150   The arrival of an efficient, novel predator (humans) was therefore potentially catastrophic
151 to these predator-näive populations. Despite strong evidence that large accumulations of
152 *Phanourios* and *Palaeoloxodon* bones are anthropogenic in origin[31,33,38], and global evidence
153 that the likelihood of extinction is highest in the most extreme island dwarfs and giants[39],
154 many contend that humans played no part in their extinction[29,40-42].

155   In this paper, we hypothesise that pre-agropastoralist human populations in Cyprus were
156 capable of driving these megafauna species to extinction. To test this hypothesis, we first (*i*)
157 re-examined the extinction chronology for *Phanourios* and *Palaeoloxodon*, accounting for
158 both dating uncertainty and the Signor-Lipps effect — the low probability of archaeological
159 or palaeontological evidence being preserved or discovered, such that first and last dates in a
160 time series almost never indicate the true dates of initial appearance or extinction,
161 respectively[43,44]. Our new Signor-Lipps-corrected windows of extinction for both species
162 now also account for dating uncertainty. (*ii*) Next, we developed stochastic, cohort-based
163 models of the population dynamics for both *Phanourios* and *Palaeoloxodon* to estimate the
164 offtake rates necessary to drive equilibrium populations of these two species to extinction in a
165 Cyprus-equivalent area. Finally, (*iii*) we expanded the demographic models to include both
166 hunting functions and the energetic requirements of pre-agropastoralist human populations to
167 express offtake in terms of 'meat equivalents' for human consumption. This approach allowed
168 us to estimate the size of the palaeo-Cypriot human population required to drive both species
169 to extinction, as well as the most ecologically realistic chronologies of any ensuing extinction
170 events. We show not only that the estimated human population sizes in Late Pleistocene
171 Cyprus could have easily driven both species to extinction, the predictions match the
172 observed chronological sequence of extinctions inferred from the palaeontological record.

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Methods

Inferring windows of extinction from the palaeontological record

To estimate a Signor-Lipps-corrected window of extinction for both *Phanourios minor* and *Palaeoloxodon cypriotes*, we sourced available radiocarbon-dated time series[41,45]. We applied a quality-rating protocol[46] to the radiocarbon dates using a customised R function[47]. The quality-rating algorithm uses information such as the type of material dated, quality pre-assessment, pretreatment, and association to calculate a quality rating from A* (highest quality), A (high-quality), B (possibly reliable), and C (unreliable)[46]. We obtained as much of this information as possible from the source papers, and then ran the quality-rating algorithm in R. None of the dates for either species achieved a quality rating > B, so we removed all C-rated dates from the series and applied the Signor-Lipps correction to estimate a possible (although only possibly reliable) window of extinction, as we explain below.

Using the uncalibrated, quality-rated radiocarbon dates described above, we applied the calibration-resampled inverse-weighted McInerny method (CRIWM)[48] that first calibrates the radiocarbon dates to calendar years before present based on a user-defined curve (we used the IntCal20 calibration curve[49]), and then resamples the intervals in the time series to provide a 95% confidence interval for the estimated extinction date.

Demographic parameter estimation

To build age-structured population models for the two extinct species, we applied allometric, phylogenetic, and measured relationships to predict plausible component demographic rates. We used the estimated adult body mass of 132 kg for *Phanourios minor* and 531 kg for *Palaeoloxodon cypriotes*[32]. For each species, we calculated the maximum rate of instantaneous population growth (r_m) using the following equation for mammals[50]:

$$r_\mathrm{m} = 10^{0.6914 - 0.2622\log_{10}M} \qquad [\text{eq } 1]$$

where M = mass (g). We then calculated theoretical equilibrium population densities (D, km^{-2}) based on the following:

$$D = 10^{4.196 - 0.740\log_{10}M}/2 \qquad [\text{eq } 2]$$

for mammalian herbivores[51] (M = body mass in g), where dividing by 2 predicts for females only (i.e., assumed 1:1 sex ratio). We estimated the maximum age (ω) of each species according to:

$$\omega = 10^{0.89 + 0.13\log_{10}M} \qquad [\text{eq } 3]$$

for non-volant birds and mammals[52] (M in g). We estimated fecundity (F; mean number of female neonates produced per year and per breeding female) for mammals[53] as:

$$F = e^{2.719 - 0.211\log M}/2 \qquad [\text{eq } 4]$$

dividing by 2 for daughters only (M in g). To estimate the age at first breeding (α), we used the following relationship for mammals[54]:

$$\alpha = e^{-1.34 + 2.14\log M} \qquad [\text{eq } 5]$$

218   We fit a logistic power function to estimate age-specific fertilities (m_x) from F and α of the
219   general form:

$$m_x = \frac{a}{1+\left(\frac{x}{b}\right)^c} \qquad \text{[eq 6]}$$

221

222   where x = age in years, and a, b, c are constants estimated for each species, to a vector
223   composed of (α-1) values at $0F$, $\frac{\alpha}{2}$ values at $0.75F$, and for the remaining ages up to ω, the full
224   value of F. This produced a continuous increase in m_x up to maximum rather than a less-
225   realistic stepped series.

226   To estimate realistic survival schedules, we first used the allometric prediction of adult
227   survival (s_{ad}) as:

$$S_{ad} = e^{-e^{-0.5-0.25\log M}} \qquad \text{[eq 7]}$$

229

230   for mammals[55], where M = body mass (g). For *Phanourios*, we obtained age-specific
231   mortality rates[42] (q_x) from which we calculated age-specific survival ($S_x = 1 - q_x$). For
232   *Palaeoloxodon*, we applied the Siler hazard model[56] to estimate the age- (x-) specific
233   proportion of surviving individuals (l_x); this combines survival schedules for immature,
234   mature, and senescent individuals within the population:

$$l_x = e^{\left(\frac{-a_1}{b_1}\right)\left(1-e^{-b_1 x}\right)} e^{-a_2 x} e^{\left(\frac{a_3}{b_3}\right)\left(1-e^{b_3 x}\right)} \qquad \text{[eq 8]}$$

236

237   where a_1 = initial immature mortality, b_1 = rate of mortality decline in immatures, a_2 = the
238   age-independent mortality due to environmental variation, a_3 = initial adult mortality, and b_3
239   = the rate of mortality increase (senescence). From l_x, age-specific survival can be estimated
240   as:

$$S_x = 1 - \frac{(l_x - l_{x+1})}{l_x} \qquad \text{[eq 9]}$$

242

243   We estimated the component parameters starting with $1 - S_{ad}$ for a_1 and a_2, adjusting the
244   other parameters in turn to produce a dominant eigenvalue (λ_1) from the transition matrix
245   containing S_x such that $\log_e \lambda_1 \approx r_m$.

246

Leslie matrix projections
248   From the estimated demographic rates for each species, we constructed a pre-breeding, $\omega+1$
249   (i) × $\omega+1$ (j) element (representing ages from 0 to ω years old), Leslie transition matrix (**M**)
250   for females only (males are demographically irrelevant assuming equal sex ratios). Fertilities
251   (m_x) occupied the first row of the matrix, survival probabilities (S_x) occupied the sub-
252   diagonal, and we set the final diagonal transition probability (**M**$_{i,j}$) to S_ω. Multiplying **M** by a
253   population vector **n** estimates total population size at each forecasted time step (Caswell
254   2001). Here, we used $\mathbf{n}_0 = AD\mathbf{Mw}$, where **w** = the right eigenvector of **M** (stable stage
255   distribution), and A = the surface area of Cyprus at 14 ka (approximate period of arrival of
256   humans) applied in the stochastic extinction scenario ($A = 11,194$ km^2)[27].

257   To avoid an exponentially increasing population without limit generated by a transition
258   matrix optimised to produce values as close to r_m as possible, we applied a theoretical

259 compensatory density-feedback function. This procedure ensures that the long-term
260 population dynamics were approximately stable by creating a second logistic function of the
261 same form as m_x to calculate a modifier (S_{mod}) of the S_x vector according to total population
262 size ($\Sigma\mathbf{n}$):

$$S_{mod} = \frac{a}{1+\left(\frac{\Sigma n}{b}\right)^c} \qquad \text{[eq 10]}$$

265 We adjusted the a, b, and c constants for each species in turn so that a stochastic projection of
266 the population remained stable on average for 40 generations ($40G$), where:

$$G = \frac{\log\left(\left(v^T M\right)_1\right)}{\lambda_1} \qquad \text{[eq 11]}$$

269 and $(\mathbf{v}^T\mathbf{M})_1$ = the dominant eigenvalue of the reproductive matrix $\mathbf{R}$ derived from $\mathbf{M}$, and $\mathbf{v}$ =
270 the left eigenvector[57] of $\mathbf{M}$. Although arbitrary, we chose a $40G$ projection time as a
271 convention of population viability analysis to standardise across different life histories[58,59].
272   The projections were stochastic in that we β-resampled the S_x vector assuming a 5%
273 standard deviation of each S_x and Gaussian-resampled the m_x vector at each yearly time step
274 to $40G$. We also added a catastrophic die-off function to account for the probability of
275 catastrophic mortality events (C) scaling to generation length among vertebrates[60]:

$$C = \frac{p_c}{G} \qquad \text{[eq 12]}$$

278 where p_C = probability of catastrophe (set at 0.14). Once invoked at probability C, we
279 applied a β-resampled proportion centred on 0.5 to the β-resampled S_x vector to induce a $\sim$
280 50% mortality event for that year[19], as we assumed that a catastrophic event is defined as "…
281 any 1 yr peak-to-trough decline in estimated numbers of 50% or greater"[60]. Finally, for each
282 species we rejected the first G years of the projection as a burn-in to allow the initial
283 (deterministic) stable stage distribution to stabilise to the stochastic expression of stability
284 under compensatory density feedback[19]. We ran 10,000 stochastic iterations of each model
285 starting with allometrically predicted stable population size divided into age classes
286 according to the stable stage distribution. We projected all runs to $40G$ for both species
287 (removing the first G values as burn-in).

288
289 **Offtake simulation**
290 To determine relative susceptibility to offtake, first we progressively removed individuals
291 from the $\mathbf{n}$ population vector, with age-relative offtake following the stable stage distribution
292 of the target species. We then progressively increased the offtake and calculated the
293 proportion of 10,000 stochastic model runs where the final population size fell below a quasi-
294 extinction (E_Q) of 50 female individuals (100 total individuals total assuming 1:1 sex ratios).
295 This threshold is based on the updated minimum size below which a population cannot avoid
296 inbreeding depression[61]. This basic scenario does not link offtake to human dietary
297 requirements or hunting capacity, nor does it translate offtake to resident human population
298 sizes — it only establishes a relationship between gross offtake rates (individuals removed
299 per projection interval) and the probability of quasi-extinction.

300

7

Animal growth rates

For *Phanourios*, we sourced several parameters to estimate female and male Von Bertalanffy growth functions of the form:

$$M_x = M_{\max} - (M_{\max} - M_0)e^{-kx} \qquad \text{[eq 13]}$$

where M_0 = mass at birth (kg), $M_{\max}$ = maximum adult body mass (kg), k = growth rate constant, and x = age in years. We used 3 ages per sex (birth, age at sexual maturity, longevity) and corresponding mass estimates to fit the Von Bertalanffy equations using the *nls* function in R. We estimated sex-specific age at sexual maturity for females following equation 5, and adjusted for males by multiplying α_{female} by the ratio of mean age at sexual maturity for male (6–13 years) and female (7–15 years) extant pygmy hippopotamus (*Choerpsis liberiensis*)[62]. For the corresponding masses, we calculated a ratio of maximum adult weight for *Phanourios* (132 kg) to the extant pygmy hippopotamus (*Choerpsis liberiensis*; 179–273 kg)[62], and then used this ratio to correct size at birth for female (4.5 kg) and male (6.2 kg) *C. liberiensis*[63], and estimated size at sexual maturity based on the observation that female *H. amphibius* reach sexual maturity at 0.78 of maximum weight[64], and males at 0.65, as well as the maximum female and male weights estimated for *C. liberiensis* (179 kg and 273 kg, respectively[62]). The fitted *Phanourios* female and male Von Bertalanffy growth equations (Appendix I, Fig. S1) estimated median $k = 0.3722$ and 0.2972, respectively

For *Palaeoloxodon*, we first calculated the mean adult male and female masses for African savanna elephants (*Loxodonta africana*)[65], and proportioned the ratio across the mean mass for both sexes to estimate equivalent female and male maximum masses for *Palaeoloxodon*. We then substituted these masses into the sex-specific growth equations estimated for Asian elephants[66] of the form:

$$M_x = M_{max}\left(1 - e^{-k(x+a)}\right)^3 \qquad \text{[eq 14]}$$

where $k = 0.092$ (females) or 0.149 (males), $a = 6.15$ (females) or 3.16 (males), and x = age in years (Appendix I, Fig. S1).

Edible meat

To estimate the amount (mass) of edible meat ('meat weight') that can be obtained from a carcass of a large herbivore, we obtained data on the edible proportions (η) of several species of large ungulate[67]. There were multiple total weights of the edible portion available for the following species: barren-ground caribou (*Rangifer tarandus groenlandicus*), woodland caribou (*R. tarandus caribou*), moose (*Alces alces*), and muskox (*Ovibos moschatus*). We then divided these weights by the mean total mass (both sexes) of each species obtained from the following sources: *R. tarandus groenlandicus*[68,69], *R. tarandus caribou*[69], *A. alces*[70], and *O. moschatus*[71]. While no edible-meat data on similar-sized elephants or hippopotamus exist, the values we obtained for other species of similar size are indicative of the approximate edible meat proportions of *Phaniouros* and *Palaeoloxodon* (we also test the relative importance of variation in this parameter in the global sensitivity analysis provided in Supplementary Information Appendix II). We then bootstrapped (10,000 iterations) the mean

and standard deviation of these proportions combining all species to provide a global mean
proportion $\eta = 0.314 \pm 0.095$ that we used in the stochastic hunting scenarios described
below.

Hunter-gatherer diet

We first obtained estimates of the daily energy intake for hunter-gatherers[72] for both adult
females ($\xi_f = 1877 \pm 364$ kCal day^{-1} = 7853 ± 1523 kJ day^{-1}) and adult males ($\xi_m = 2649 \pm$
395 kCal day^{-1} = 11083 ± 1653 kJ day^{-1}). Assuming the proportion of meat in the diet of
hunter-gatherers[73] (ζ) was 0.65, we translated meat into energy equivalents based on the mean
value for African elephants (*L. africana*) of 130 kCal (μ) 100 g^{-1} meat[74,75]. With these values,
we can estimate the total amount of meat consumed by an average adult female (342.6 kg)
and male (483.4 kg) per year. Compared to the highest per-capita meat-consuming countries
today (e.g., USA: 101.9 kg person^{-1} yr^{-1}; Israel: 90 kg person^{-1} yr^{-1}; Australia: 89.6 kg person^{-1} yr^{-1}; data for 2019)[76], the estimated values for palaeo-hunter-gatherers are just over 4 times
higher.

   To create a function of annual meat requirements for each human age class from 0 to
longevity, we obtained data on age-specific protein requirements for people[77] (50 kg adult: 40
g protein day^{-1}, 14–18 year olds: 37 g day^{-1}, 9–13 year olds: 24 g day^{-1}, 4–8 year olds: 13.5 g
day^{-1}, 1–3 year olds: 9.2 g day^{-1}) that we first transformed to proportions of the adult
requirement (I_p) to which we fitted a logistic power function of the form:

$$I_p = a\frac{b}{(a-b)e^{-cx}+b} \qquad \text{[eq 15]}$$

to estimate age- (year-) specific proportions and correct for the age class consuming meat (a
= 1.1381, b = 0.1393, c = 0.1983, and x = age in years) (Appendix I, Fig. S2).

Prey choice

Different species provide different returns to human hunters based on components such as
capture probability, animal body size, edible portion, and handling costs (e.g., pursuit time,
butchering time, preparation time, etc.)[75]. We therefore applied the equations of Yaworsky et
al.[13] using the adult mass estimates of both species to estimate the mean and standard
deviation of post-encounter return rate (π; cal hour^{-1}) (defined as the energy provided divided
by handling costs[13]:

$$\pi_s = 60\frac{e_s(1-p_s)}{c_s+(1-p_s)h_s} \qquad \text{[eq 16]}$$

where e = energetic payoff (cal), p = probability of acquisition failure, c = pre-acquisition
handling time (min), h = post-acquisition handling time (min), s subscript indicates value for
species s, and the multiplier 60 converts to energy hour^{-1}. Using the coefficients and their
standard errors used to estimate the parameters in equation 16, we developed a resampling
approach where we produced 100,000 samples of $\pi_{Phanourios}$ and $\pi_{Palaeoloxodon}$, and then
calculated the number of times where $\pi_{Phanourios} > \pi_{Palaeoloxodon}$. The higher average relative
return rate of *Phanourios* compared to *Palaeoloxodon* results from the increased handling
costs of larger species due to higher probabilities of failed pursuit[13]. This sum divided by the

386   total number of iterations (100,000) gives the relative probability of targeting *Phanourios*
387   over *Palaeoloxodon* ($\psi = 0.773$). Therefore, we assumed that ψ represented the relative
388   likelihood of selecting *Phanourios versus Palaeoloxodon* that we resampled stochastically
389   (see below) following a β distribution with mean $= \psi$ and an arbitrary standard deviation $= \sigma_\psi$
390   $= p\psi(\psi) = 0.05\psi$ (but see global sensitivity analysis in Supplementary Informaiton Appendix
391   II regarding the choice of pψ = 0.05).

Hunting simulation

394   We developed a stochastic simulation similar to the offtake simulation described above, but
395   instead of sequentially reducing the **n** vectors for each species separately, we incremented the
396   number of humans on the island of Cyprus and converted this number into megafauna meat
397   equivalents to sustain the human population. This approach not only required translating
398   animals culled into protein energy required by humans of different ages and sex, we also
399   incorporated a prey-selection function (described in the previous section) as well as a density-
400   feedback on the meat portion of the human diet fulfilled by megafauna sources.

401   Assuming that 0.65 of the age-specific human energy requirements were provided by meat
402   (ζ) on average[73] (but see global sensitivity analysis in Supplementary Information Appendix
403   II regarding this value), we developed an arbitrary feedback function whereby the proportion
404   of 'other' meat sources (e.g., marine fish and shellfish, small terrestrial animals, etc.)[77]
405   increased from 0.33 at the time of initial human arrival (assuming the populations of
406   *Phanourios* and *Palaeoloxodon* were at their maximum equilibrium sizes), approaching 1.0
407   sigmoidally as the megafauna populations approached extinction. This function accounts for
408   decreasing prey encounter rates by human hunters as the prey populations dwindle, such that
409   0.67 of the meat requirements are provided by megafauna sources at maximum megafauna
410   densities, and approach zero as those populations approach extinction.

411   Starting with an initial human population size of 1000 (i.e., 500 females) — a large-
412   enough predator population to elicit some extinctions during the iterative process), we
413   applied the age-specific energy requirements to the stochastic age structure generated by the
414   model at each time step. Next, we β-resampled the probability of successfully acquiring
415   *Phanourios* relative to *Palaeoloxodon*, and then calculated the number of individuals across
416   their age distribution required to fulfil this human meat requirement (i.e., using the female-
417   and male-specific growth curves for both species). We assumed that humans did not select
418   male or female prey preferentially (relative proportion female *versus* male prey taken $\varphi = 0.5$,
419   but see global sensitivity analysis in Supplementary Information Appendix II). We then
420   removed these meat equivalents in terms of individuals culled from the megafauna **n** vectors
421   at each time step, projecting those populations through to 80 generations (80G: to allow a
422   sufficiently large human population enough time to drive a megafauna population to
423   extinction) in each iteration. In cases when the *Phanourios* population declined enough to
424   where it could no longer supply sufficient meat as the prey with the highest energy return rate
425   (even after accounting for the change in 'other' meat categories described above), we
426   transferred that meat requirement to *Palaeoloxodon* by removing the equivalent number of
427   *Palaeoloxodon* individuals to account for the missing meat requirement.

428   We then incremented the number of humans on the island and recorded the probability of
429 quasi-extinction for each megafauna species, as well as the median time (years) required to
430 drive each population to extinction. For each human population size increment we tested, we
431 assumed that that human population remained stable during a 80 prey-generation projection
432 interval, so our extinction predictions are necessarily conservative. We ran all code on the
433 Flinders University High-Performance Computing facility *DeepThought*[78], and all code and
434 data required to repeat the analyses are available at
435 github.com/cjabradshaw/CyprusHippoElephant.
436
Results

Estimated extinction windows

439 After quality rating, there were 5 dates for *Phanourios* from the original 13 provided by
440 Zazzo et al.[41] that had a B rating, and 14 B-rated dates for *Palaeoloxodon* from the original
441 30 provided by Wigand and Simmons[45]. The resultant windows of extinction estimated using
442 the CRIWM unbiased algorithm on this B-rated dates were 11,995–11,092 calendar years
443 before present for *Phanourios*, and 10,347–9,073 calendar years before present for
444 *Palaeoloxodon.* Compared to the arrival window of 14,257–13,182 estimated for pre-
445 agropastoralist humans in Cyprus[27], the Signor-Lipps-corrected megafauna extinction
446 windows suggest that *Phanourios* went extinct 1,187–3,165 years after human arrival, and
447 *Palaeoloxodon* went extinct 2,835–5,184 after human arrival (Fig. 1), although with the
448 caveat that the extinction windows are not based on the highest-quality radiocarbon age
449 estimates.
450
451 **Figure 1**. Human arrival window (grey vertical bar; estimated[27] using the calibration-resampled inverse-
452 weighted McInerny method, CRIWM algorithm[48], and the CRIWM-estimated windows of extinction (red
453 vertical bars) for *Phanourios* and *Palaeoloxodon*. Also shown are the hindcasted temperature anomalies (ºC,
454 relative to the present) for Cyprus derived from the HadCM3[79] and TraCE21ka[80,81] global circulation models.
455 Also shown are major climatic periods: Last Glacial Maximum (LGM), Bølling-Allerød interstadial (B-O),
456 Younger Dryas (YD), and the early to mid-Holocene.

457
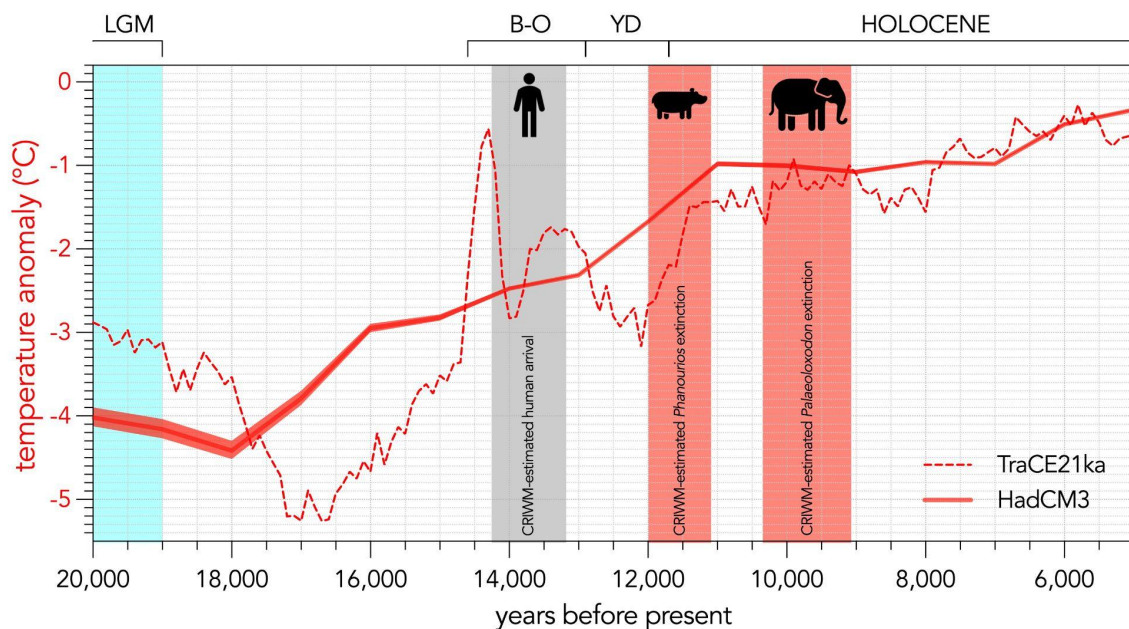
Demographic estimates

For *Phanourios* and *Palaeoloxodon*, respectively, the allometric equations predicted age at first breeding (α) = 4 and 5 years, maximum longevity (ω) = 36 and 43 years, equilibrium density = 1.28 and 0.46 individuals km^{-2} (corresponding to populations of 14,280 and 5,098 individuals assuming a land area[27] of Cyprus at 14 ka = 11,194 km^2), and maximum instantaneous rate of exponential increase (r_m) = 0.22 and 0.15. The deterministic matrix models provided generation lengths (G) of 11.4 and 14.2 years, respectively.

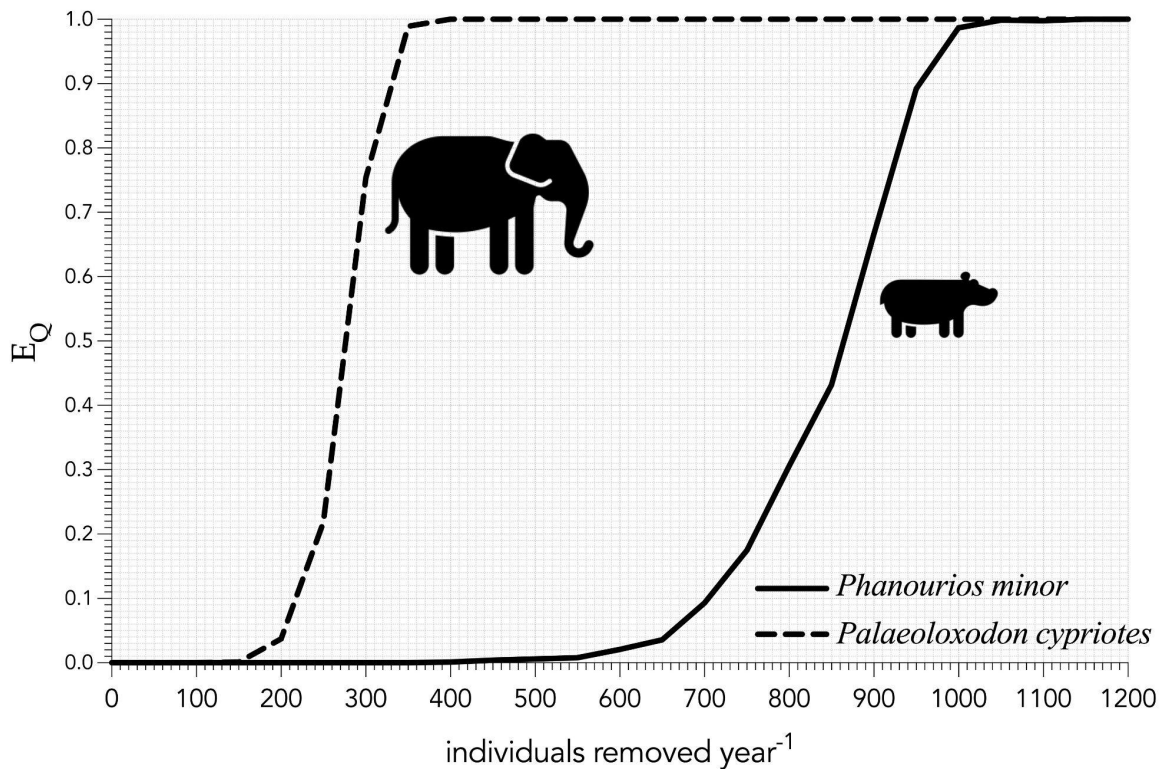## Offtake simulation

The offtake simulations demonstrated that *Palaeoloxodon* was more susceptible to extinction than *Phanourios* (Fig. 2), which is expected given the slower life history of the latter. Once the annual offtake of *Palaeoloxodon* began to exceed 200 individuals, the probability of quasi-extinction climbed precipitously, becoming close to 1.0 at an annual offtake of ~ 350 individuals (Fig. 2). The extinction probability of the smaller *Phanourios* only began to increase after an annual offtake of ~ 650 individuals, reaching near certainty at ~ 1000 animals annually (Fig. 2).

Figure 2. Probability of quasi-extinction (E_Q) of dwarf hippopotamus (*Phanourios minor*) and dwarf elephant (*Palaeoloxodon cypriotes*) as a function of the number of individuals removed per year (following the stable stage distribution).


Hunting simulation

However, these relative susceptibilities reverse when we consider the second set of simulations estimating offtake as a function of human dietary requirements and prey choice. Because of the higher relative return rate of *Palaeoloxodon*, as well as their ~ 4-fold greater

mass compared to *Phanourios*, the elephant's extinction probability was lower than for the hippopotamus across the range of human population sizes eliciting some extinction risk (Fig. 3). Here, *Phanourios* extinction risk began to increase once the human population on the island exceeded 3,000, and was near certain at human population sizes of ~ 4,500 (Fig. 3). The extinction risk of *Palaeoloxodon* similarly began to rise at human population sizes > 3,000, but increased more slowly than for *Phanourios*, eventually achieving near-certain extinction risk at an island-wide human population of around 7,500 (Fig. 3). The time to drive the population of *Phanourios* to extinction correspondingly declined from around 800 years at a human population of ~ 3,700, to < 100 years at a human population of 4,500 (Fig. 3). Meanwhile, the time to drive the population of *Palaeoloxodon* to extinction declined from around 800 years at a human population of ~ 6,300, to < 100 years at a human population of just over 7,000 (Fig. 3).

Figure 3. Probability of quasi-extinction (E_Q) of dwarf hippopotamus (*Phanourios minor*) and dwarf elephant (*Palaeoloxodon cypriotes*) as a function of the number of people living on Cyprus (left axis; red), and median number of years to extinction for each species (right axis; blue).
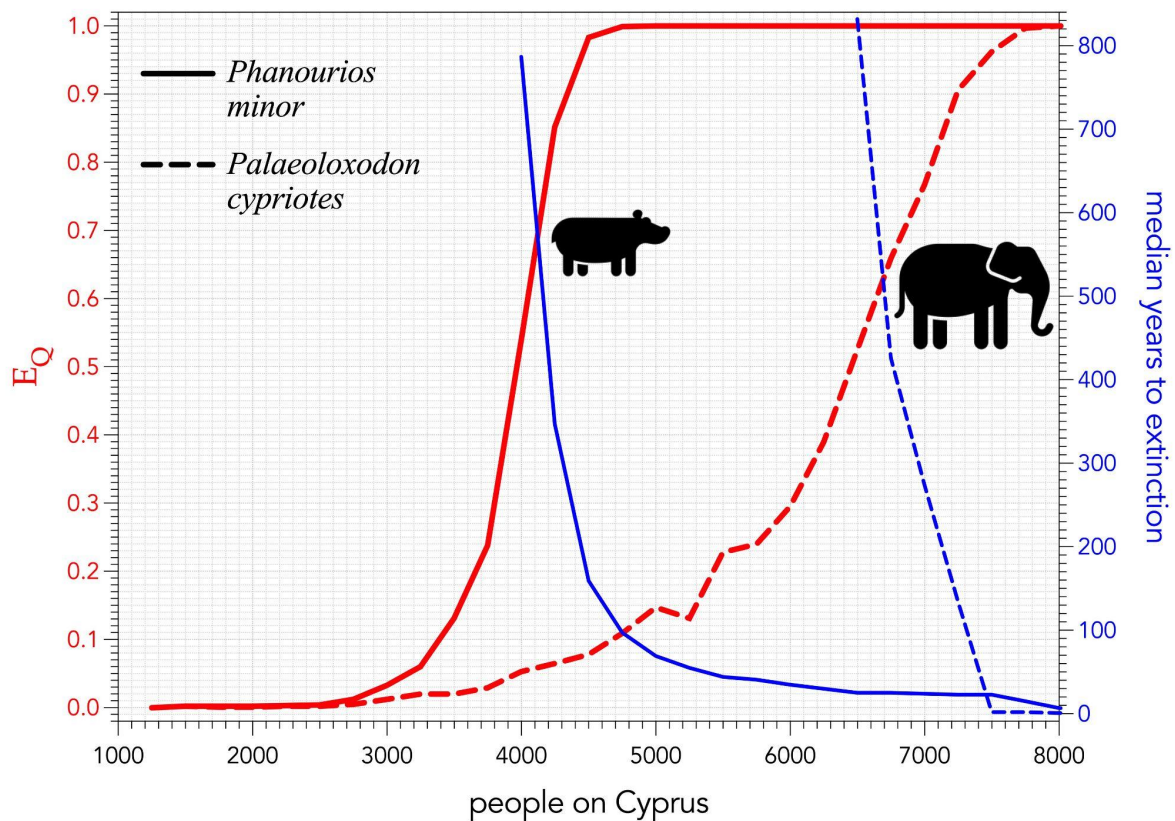
Discussion

Conclusions drawn about the role of palaeo-human exploitation on the extinction of megafauna species are too often predicated on an uncritical comparison of uncertain chronologies, and do not typically examine the ecological plausibility of extinctions based on predator-prey dynamics or human energetic requirements[42]. Our stochastic model not only demonstrates that 3000–7000 pre-agropastoralist humans on Cyprus could have driven both dwarf hippopotamus and dwarf elephants to extinction, within < 1000 years, the predicted

chronology of extinctions (first hippopotamus, then elephants) matches the Signor-Lipps-corrected extinction sequence derived from independent palaeontological evidence. Indeed, median human population sizes predicted for Cyprus during the Late Pleistocene have been estimated in the several thousands, from initial arrival at 14.3–13.2 ka to settlement of the entire island in as little as 200 years[27]. Rapid growth during that time also estimates that the human population could have numbered > 10,000 within < 400 years from initial arrival (median = 4300 after 400 years[27]). Clearly, these human population sizes were therefore sufficient to drive both the dwarf hippopotamus and dwarf elephant to extinction according to our conservative models.

Elsewhere, the zooarchaeological record of large-mammal remains during the Late Upper Palaeolithic (14.0 ka–12.6 ka) is influenced strongly by cost-benefit regimes arising from human decision making, meaning that the abundance of zooarchaeological remains do not necessarily reflect animal densities in the landscape[13]. As such, the higher relative return rate of hippopotamus compared to elephants (expressed as ψ in the model) was an important determinant of the relative extinction chronology of the two species. However, ψ was a weak driver of variation in extinction risk predicted by our model (Fig. 4). Instead, the most important determinant of extinction risk for both species was the proportion of edible meat that could be derived from a single carcass (η). While we determined η from measured edible proportions of several Arctic species, it is possible that pre-agropastoralists on Cyprus were able to obtain higher portions, thereby reducing the number of individual hippopotamus or elephants killed to supply their human energetic requirements.

We also incorporated a function that increased the proportion of 'other' meat sources in the diet as megafauna were depleted, based on empirical data that hunter-gatherers of the Late Pleistocene pursued and exploited a broad range of prey[74]. But this function was partially arbitrary because we do not know the shape of the relationship between megafauna abundance and reliance on other meat sources. However, traditional diets of Indigenous peoples in North America favour large species (particularly mammals)[82], and both modelling and empirical data suggest that the distribution of body sizes in archaeological inventories match those built from food-recall and harvest surveys[82]. This latter evidence supports the assumption in the model that palaeolithic peoples would have preferentially selected megafauna over other meat sources until rarity of the former forced them to rely more on the latter.

While the initial (pre-human) population sizes of both species of course influence extinction risk, there was only a modest influence of initial population size of hippopotamus on that species' extinction rate. The lack of a strong influence of the initial population size of elephants on that species' extinction rate is partially a function of the two-prey model favouring hippopotamus as human prey over elephants. Further, while our estimates of initial population size were derived from ecological theory, population densities would have varied spatially according to habitat diversity and island topography, including the presence of a large mountain range (Troödos Mountains) in the western region of Cyprus. While fossil sites for *Phanourios* and *Palaeoloxodon* remains span most of the island (Appendix III Fig. S5; Table S1), there are still large spatial gaps within the Troödos Mountains region and the far northeast (Fig. S5).

We did not incorporate any theoretical prediction of how environmental change might have exacerbated the extinction risk our model predicted. Climate hindcasts from the HadCM3 atmosphere-ocean general circulation model[79] for Cyprus during the period from 14 ka to 10 ka predicted a mean temperature rise of ~ 1.5 °C (Fig. 1) and a 44-mm increase in annual precipitation. However, the temporally finer-resolution (seamless) TraCE21ka climate model[80,81] predicts a more dynamic climate during this same period, with a ~ 1 °C rise during the latter half of the Bølling-Allerød interstadial (14.6 ka–12.9 ka), followed by a ~ 1.4 °C decline during the Younger Dryas, and then a ~ 2.0 °C rise by 10 ka (Fig. 1). With increasing evidence for extinction synergies[83] between human over-exploitation and environmental change in the demise of late Quaternary megafauna extinctions[2-4,6-8], such simultaneous temperature and precipitation fluctuations could have exacerbated the extinction risk of both dwarf hippopotamus and elephants on Cyprus. Indeed, there is evidence for human- and climate-mediated collapse of ecological networks in ancient Egypt[84], and Saltré et al.[8] concluded that combinations of aridification and human presence contributed to the local extinction of many megafauna species in Sahul. Our predictions of extinction risk arising solely from human over-exploitation should therefore be considered conservative.

In addition to the feasibility of pre-agropastoralist humans driving both megafauna species on Cyprus to extinction demonstrated by our conservative models, we also argue that it was an attractive destination for early palaeolithic explorers. The notion that Cyprus was an "impoverished" landscape[29-31,85-87] is not supported either by climate models hindcasting net primary production[27] or from archaeobotanical records[88,89]. Indeed, evidence from pollen analysis of the early Holocene suggests that Cyprus was covered by dense forests of typical Mediterranean trees and shrubs (e.g., carob *Ceratonia siliqua*, cypress *Cupressus* spp., juniper *Juniperus* spp., kermes oak *Quercus coccifera*, Aleppo oak *Q. infectoria*, bay laurel *Laurus nobilis*, olive *Olea europaea*, oriental plane *Platanus orientalis*)[88,89]. Eratosthenes reported in the 3rd Century BC that the island was "thickly overgrown with forests"[90], even in the arid central plain of Mesaoria[91]. In the Classical period, Cyprus was referred to as a 'green island', exporting timber and specialising in ship building[92]. Such a diverse, prey-filled landscape would therefore have been a highly sought destination once discovered by palaeolithic peoples[27].

Author contributions

CJAB led the analysis, with contributions from FS and CR. TM, CR, and FS provided data. CJAB, TM, and CR drafted the first version of the manuscript. All authors contributed to writing the manuscript.

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