

No evidence for widespread island extinctions after Pleistocene hominin arrival

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The arrival of modern humans into previously unoccupied island ecosystems is closely linked to widespread extinction, and a key reason cited for Pleistocene megafauna extinction is anthropogenic overhunting. A common assumption based on late Holocene records is that humans always negatively impact insular biotas, which requires an extrapolation of recent human behavior and technology into the archaeological past. Hominins have been on islands since at least the early Pleistocene and Homo sapiens for at least 50 thousand y (ka). Over such lengthy intervals it is scarcely surprising that significant evolutionary, behavioral, and cultural changes occurred. However, the deep-time link between human arrival and island extinctions has never been explored globally. Here, we examine archaeological and paleontological records of all Pleistocene islands with a documented hominin presence to examine whether humans have always been destructive agents. We show that extinctions at a global level cannot be associated with Pleistocene hominin arrival based on current data and are difficult to disentangle from records of environmental change. It is not until the Holocene that large-scale changes in technology, dispersal, demography, and human behavior visibly affect island ecosystems. The extinction acceleration we are currently experiencing is thus not inherent but rather part of a more recent cultural complex.

Holocene | island biogeography | human colonization | megafauna | extinction

When humans first arrived on the islands of New Zealand, they encountered a diverse and rich ecosystem including nine species of moa (1). Within 200 y of human arrival, all these were extinct (2), alongside at least 25 other vertebrates (3). Over the late Holocene, this sequence of events played out across more than 40 islands of the Pacific: On average, almost 50% of Pacific island birds have become extinct following human colonization (4), with the bulk of these extinctions occurring prior to European contact (5, 6). These patterns mirror the extinction records of Indian Ocean islands, such as the Mascarenes and Madagascar (7, 8), suggesting a global pattern of island extinction immediately following human colonization.

Islands are particularly prone to widespread extinction and extirpation of biota because of their smaller resident faunas and populations, lower genetic diversities, susceptibility to stochastic processes, less opportunity for recolonization, and higher levels of endemism compared to continents (9). The stunning extinction record of the Pacific and Indian Ocean islands is attributed to human activities, especially overhunting, habitat alteration, and introduction of invasive species (2, 10, 11). The chronology of island extinctions and human colonization have provided an enticing analog for understanding megafauna extinctions on the continents (3). Martin (12, 13) formulated the overkill hypothesis with explicit reference to anthropogenic extinctions on Madagascar and New Zealand, respectively, arguing that similar mechanisms could be invoked to explain African and North and South American megafauna extinctions.

Island records have subsequently often been considered ideal models for understanding how Pleistocene extinctions unfolded on the continents (14-19), despite the acknowledged and significant differences that exist between island and continental ecosystems (3, 20). Today, island extinctions are overwhelmingly interpreted

Significance

We provide global assessment of the possible link between Pleistocene hominin arrival and island extinction. The existing records on islands around the world do not support a significant and detrimental impact on island biotas following island colonization prior to the Holocene. This suggests that models using island extinctions as evidence in support of anthropogenic megafaunal overhunting, or as extensions of continentallevel extinctions, need to be reconsidered.

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as a continuation of a global extinction event initiated more than 50,000 y ago by humans (21–25). Well-known records of island extinctions, in which a close association between human arrival and faunal extinction have been firmly established, continue to be widely cited in support of anthropogenic extinction scenarios on other landmasses (e.g., refs. 24–26). Island extinction records are thus a key component in the debate over causes of megafauna losses.

The hypothesis that humans are the primary driver of island extinctions relies on penecontemporaneous records indicating human arrival into virgin ecosystems (i.e., those without prior human contact) closely linked with extinction (19, 21, 26). However, although many islands have been considered in appraising global extinction scenarios (e.g., refs. 2, 4-8, 10, 11), those considerations have focused almost entirely on those with a Holocene human presence. Despite the importance of Pleistocene islands for this paradigm, and the growing archaeological record of island colonization events during the Quaternary, few islands with Pleistocene records have been explicitly included in any global assessment of Quaternary extinctions. This is important because technologies, behaviors, and even the hominin species involved are not homogenous across islands. Hominins have visited or lived on oceanic islands since at least the early Pleistocene (27-29), and Homo sapiens for at least 50 thousand y (ka) (30), and during this time, many significant evolutionary, behavioral, and cultural changes have occurred (31). A review of whether an association between hominin arrival and extinction exists for all islands occupied during the Pleistocene is a critical first step in addressing this deficit.

Here, we examine whether any data support the hypothesis that Pleistocene hominin arrival on an island is coincident with the disappearance of insular taxa. We examine the archaeological and paleontological records of all islands with a documented Pleistocene hominin presence and some record of faunal extinction. We treat oceanic islands (islands that have never been connected to continental landmasses during the Quaternary) and continental islands (promontories that were connected to continents during the Last Glacial Maximum (LGM) and earlier periods of time but are islands today) separately. We also explore data relating to largescale geologic events (e.g., vulcanism) and the apparent ecological impact of different hominins on island ecosystems. We restricted our assessment to establishing whether a temporal overlap exists between taxon extinction and hominin arrival. We do not argue that this implies a causal relationship between arrival and extinction; rather, we take it as the first indication that such a relationship might exist. This allows us to evaluate the suggestion that modern humans and our immediate antecedents have always had a negative influence on virgin island ecosystems (e.g., refs. 15, 19, 23, 32, 33; see also ref. 34). This long-term perspective is a necessary step in understanding the impacts of humans on modern ecosystems globally and informing island conservation efforts today (11, 35).

Results

Islands Prior to H. sapiens. The earliest records of hominins on oceanic islands (Figs. 1 and 2) are represented by simple toolkits recovered from early to middle Pleistocene deposits on Flores (>1 Ma) (29) and Sulawesi (194 to 118 ka) (36) and cut-marked rhino bones and stone tools associated with a variety of fossil faunas from Luzon, Philippines (~709 ka) (28). It is possible that extinction of Nesorhinus philippinensis and Celebochoerus cagavanensis in Luzon are broadly synchronous with first hominin arrivals (Figs. 1 and 2), but at present, the evidence is based only on a single-dated locality, providing no firm insights into length of coexistence. It seems that much of the Philippines megafauna might have been extinct by 50 to 60 ka, and no clear extinctions are linked to Homo luzonensis. A giant rat (Batomys species [sp.]) and a dwarf buffalo (Bubalus sp.) are from the same palimpsest bone beds as the H. luzonensis fossils. They are not present in later deposits at Callao Cave or in any other sites so far excavated in Luzon, suggesting they might have gone extinct before the end of the Pleistocene. On Flores, there are no known extinctions closely associated with the first hominin appearance. Sulawesi shows no clear temporal associations between the arrival of an as-yet unidentified hominin and faunal losses, although the extinction of a stegodon (Stegodon sp.) and a buffalo (Bubalus grovesi) may be associated if minimum ages are close to the true ages. The only extinct taxon recorded on Naxos (Paleoloxodon lomolinoi) occurred well after the arrival of hominins. In Sardinia, the appearance of hominins is likewise associated with no losses. On Crete, however, the extinction of two birds (Athene cretensis and Aquila chrysaetos simurgh) and a mustelid (Lutrogale cretensis) could be synchronous with hominin arrival. On continental islands, the earliest record of hominins come in the form of Homo erectus on Java at 1.3 Ma (27) and Homo ? antecessor in Britain, perhaps as early as 1 Ma (37). Taiwan also has an as-yet unassigned hominin dated to perhaps as early as 450 ka (38). While no extinctions are recorded coincident with these arrivals (Fig. 3), they occurred during periods when the islands were connected to continental landmasses (Fig. 4) and should be understood in the context of range expansions of these hominins rather than colonization of virgin ecosystems. While the paleontological and archaeological records are admittedly limited, on this evidence seven extinctions across three islands may be the result of pre-sapiens hominin arrival.

Oceanic Islands with H. sapiens. The earliest direct evidence of H. sapiens on oceanic islands dates to around 50 ka and are situated in Asia (Fig. 1). Extinctions temporally associated with first arrivals in the broadest possible sense considered here (i.e., within 5,000 y) include the loss of two proboscideans (Mammuthus columbia and Mammuthus exilis) and a vole (Microtus miguelensis) from the California Channel Islands, a giant deer (Megaloceros giganteus) and a lemming (Dicrostonyx torquatus) from Ireland, an elephant from Sulawesi (Elephas/Paleoloxodon large sp.), and a crane (Grus sp.) from Timor. On Flores, a stork (Leptoptilos robustus), a vulture (Trigonoceps sp.), a songbird (confer Acridotheres), a stegodon (Stegodon florensis insularis), and Homo floresiensis disappear close to the first H. sapiens arrival as well as being coeval with a volcanic eruption on the island (Fig. 2). In the Philippines, H. luzonensis continued to inhabit Luzon until or shortly before 55 ka, with the first evidence of modern humans in the Philippines (on Palawan) currently around >47 ka (39). On only two islands, Cyprus and Kume, is there any evidence that all recorded island extinctions occur shortly after human arrival. Based on these data, most known extinctions on oceanic islands cannot be correlated with Pleistocene hominin arrival or separated from nonanthropogenic processes.

Continental Islands with H. sapiens. On continental islands, the earliest record of H. sapiens is Sumatra at 73 to 63 ka (40), although it was not an island at this time: As noted above, human arrival on these islands occurred during connections with continental landmasses and should be interpreted in this light (Figs. 3 and 4). Extinctions in Borneo and Sumatra are very poorly documented, especially with reference to extinctions on Java. Most large mammals such as rhinos, tigers, and tapirs, resident when modern humans arrived, all survived at least until very recently. Extinctions on Java occurred prior to the first documentation of likely H. sapiens on the island and have been tied to faunal turnover events resulting from episodic connection to the Southeast Asian mainland during glacial periods (41). These extinctions were likely triggered by the loss of extensive savannahs on the island and replacement by closed forests (42). Likewise, in Britain, most extinctions occurred prior to the arrival of H. sapiens. Extinctions during island phases are perhaps due to the expansion of the British-Irish Ice Sheet (43); however, most extinctions likely occurred during connections with the mainland (Fig. 4) and should be understood within the context of European continental extinctions (44). These have generally been attributed to environmental change

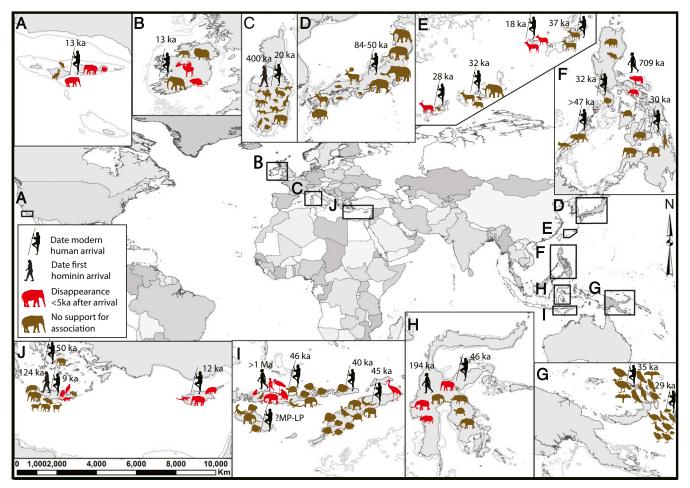


Fig. 1. Oceanic island groups with a documented record of Pleistocene hominins and faunal extinction. Clockwise from the top are San Miguel, Santa Rosa, and Santa Cruz (A); Ireland (B); Sardinia (C); Honshu, Shikoku, and Kyushu (D); Ishigaki, Miyako, Kume, and Okinawa (E); Luzon, Mindanao, Mindoro, and Palawan (F); New Ireland and Buka (G); Sulawesi (H); Timor, Alor, Flores, and Sumba (I); and Cyprus, Crete, and Naxos (J). MP, middle Pleistocene; LP, late Pleistocene.

(44). Almost all Pleistocene extinctions on New Guinea occurred a considerable time after human arrival, with both extinctions and arrival likely occurring while a connection with Australia existed (Fig. 4). Two extinctions (Hulitherium tomassetti and Casuarius lydekkeri) may be considered coeval with human arrival if the minimum ages are close to the true ages of the fossils. Likewise, on Kangaroo Island, three marsupial species (Procoptodon browneorum, Procoptodon gilli, and Procoptodon sp. indeterminant) could have disappeared close in time with first human arrival, provided minimum ages are considered close to true ages. Only two marsupials (Protemnodon anak and Simosthenurus occidentalis) disappeared from Tasmania close in time to the first human records on the island and neither of them are associated with archaeological records. Continental islands were islands for very little of the Pleistocene, and although some extinctions appear coincident with the beginning of insularity, most likely they occurred during periods of connection with continents (Fig. 4). Thus, the mechanisms underlying these extinctions are unlikely to be directly comparable to those acting on oceanic islands.

Summary of Extinctions. If Pleistocene hominin populations, including Pleistocene members of our own species, were as destructive as humans in the late Holocene, their impacts should be particularly visible in the records of isolated oceanic islands. This was not observed in our data. Only on Cyprus and Kume do the data support all recorded extinctions coeval with human arrival.

All other Pleistocene extinctions on oceanic islands appear unrelated as to the cause or staggered, at least within the chronological resolution currently available (see also ref. 45). Oceanic and distant continental island cumulative extinctions are modest in absolute terms-the maximum recorded are 12 each for Sardinia and Flores. Both islands are relatively large and not particularly isolated, although separated by deep-sea passages from nearby continents. Extinctions on continental shelf islands, when well represented and constrained, are staggered and appear largely confined to periods of connections with the mainland. Separations from the nearest continent was relatively uncommon across continental islands, at least during the last 500 ka, and largely dependent on interglacial conditions and associated with significant environmental changes (42, 44). In continental islands with good fossil records (e.g., Java and Britain), extinctions are numerous, but their causes should be considered largely as an extension of the mechanisms underlying continental losses (42, 44).

Discussion

Faunal turnovers are common on oceanic islands and extinctions are a natural process as ecosystems move toward equilibrium, even on very large islands (46, 47). Smaller and more isolated islands severely impact genetic diversity, precipitating extinctions even in the absence of humans (e.g., ref. 48). This process can be intensified by rising sea levels in an effect known as relaxation (49).

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ENVIRONMENTAL SCIENCES

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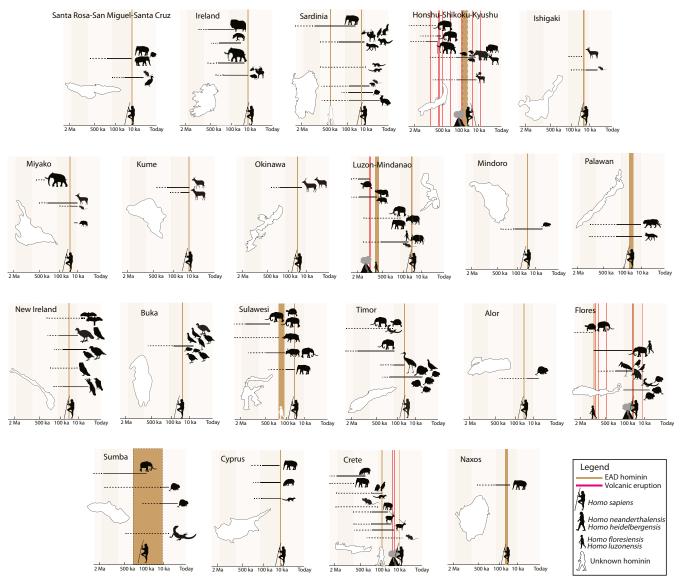


Fig. 2. Extinction chronology (right end of horizontal bars) shown with respect to the first hominin and *H. sapiens* arrival (vertical bars and boxes) to oceanic islands. Outlines for island groups are shown as one island during LGM connection. Extinct taxon LADs are represented by horizontal lines. In cases in which the LAD was highly imprecise, occurrence was represented by a dashed line only. Where dates had been provided for individual taxa, associated sedimentary contexts, and/or sites, this was represented by a dashed line progressing to a solid line, with the end of the solid line representing the LAD. Taxa on one island sharing LADs close in time (at a level indistinguishable on the scale used here) were grouped together. Horizontal lines are only illustrative of prior occurrence and are not lengthened to scale. More details on how this figure was constructed are presented in *SI Appendix, Supplementary Information Text*, and dates and associated references are listed in *SI Appendix*, Table S1.

The size of an island and thus diversity of its resources are likely the most important factors for successful hominin colonization, with a lack of terrestrial protein an obvious challenge (50, 51). Specialization in marine resources can remove this limitation (51). Other raw material limitations include lithics, bamboo and/or wood, and availability of fresh water; these provide some measure of how, where, and which islands had exploitable resources. In oceanic islands, the availability of freshwater may have been the biggest limitation for occupation, as many tiny islands were not settled until very late in the Holocene, when strategies for capturing freshwater became available, even if marine protein was abundant (52).

In Martin's overhunting concept (12–14), island extinctions were regarded as accelerated versions of mainland losses, with the added feature that there was very little choice of what to hunt. K-selected taxa are considered most vulnerable to extinction from

overhunting in megafauna extinction models (53). However, oceanic island conditions independent of humans tend to favor r-selected taxa, such that large, slow-breeding species are less likely to be found on islands than continents. Notable exceptions include tortoises and proboscideans; although, the latter exhibit dwarfing on islands, potentially signaling an evolutionary shift in response to insular conditions (54). Nevertheless, island overhunting remains one of the key factors explaining Pleistocene and Holocene extinctions (6, 10, 11).

Early hominins on islands such as *H. floresiensis* and *H. luzonensis* exploited a range of terrestrial fauna (28, 55). While access to maritime resources was available to *H. erectus* on Java (56), there is no unambiguous evidence that anything other than terrestrial resources were consumed (57). There is evidence from Callao Cave that a hominin hunted or scavenged the Philippine brown deer (*Rusa marianna*) and the Philippine warty pig (*Sus philippensis*).

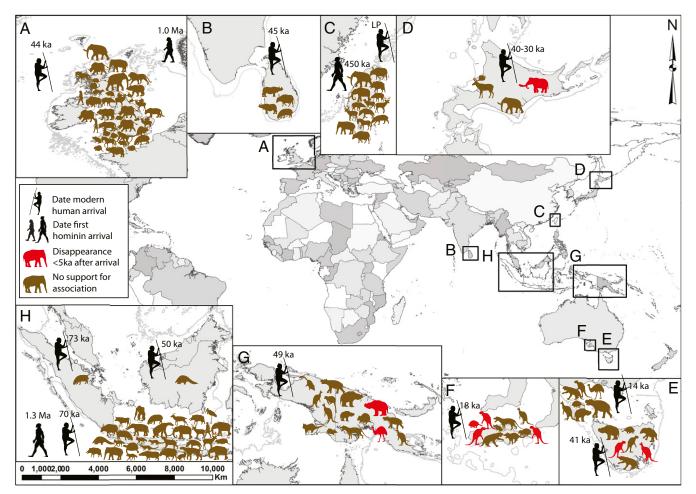


Fig. 3. Continental island groups with a documented record of Pleistocene hominins and faunal extinction. Clockwise from the top are Britain (A); Sri Lanka (B); Taiwan (C); Hokkaido (D); King Island and Tasmania (E); Kangaroo Island (F); New Guinea (G); and Borneo, Java, and Sumatra (H). LP, late Pleistocene.

Both species are still extant on Luzon. Zooarchaeological records from Borneo and Java indicate that *H. sapiens* used a range of techniques to hunt and trap terrestrial, aquatic, and arboreal vertebrates (58, 59). The introduction of ranged weaponry (e.g., bows, arrows, and spears) more broadly across Southeast Asia seems to have had an impact on the diversity of fauna hunted and especially arboreal taxa such as monkeys and civets. However, those species hunted most intensively, such as long-tailed macaques, leaf monkeys, and binturongs, are still extant today (59).

Pleistocene records associated with *H. sapiens* in oceanic islands in Wallacea are dominated by marine fish and shellfish and include early evidence of pelagic fishing and complex fishing technologies (57). A notable exception is Sulawesi, where cave art dated to ~44 ka depicts therianthropes in a hunting scene with anoa and Sulawesi warty pigs (60), and the earliest archaeological deposits are dominated by babirusa (*Babyrousa babyrussa*) and anoa (*Bubalus depressicornis*) (61). Both taxa are extant on the island. On Okinawa of the central Ryukyus, the Jōmon people hunted wild boars (*Sus scrofa*) intensively, which became smaller until 6 ka. Subsistence shifted to shellfish, and wild boars became larger again (62), suggesting that cultural and/or environmental controls may have existed on some islands to curb overhunting to extinction.

While three terrestrial taxa are recorded as going extinct at the same time as human arrival on the California Channel Islands, there is no indication that mammoths were ever hunted, and subsistence focused on marine resources (63). Similarly, archaeological records on Tasmania show that only small to medium animals were hunted, and there is no evidence that any extinct species were exploited by humans or that people were responsible for their extinction (64, 65). Archaeological records from Cyprus suggest largescale extinctions directly following human arrival around 12 ka (66), and this is one of only two islands where a convincing overlap exists between island extinction and first human arrival.

Extinctions, when present and tied to subsistence activities, are difficult to disentangle from records of environmental change. In the Tabon Caves in Palawan, Philippines, the first humans arrived at ~47 ka, when forest cover on the island was limited and open woodland dominated. Late Pleistocene forager communities predominately hunted deer (67). In the early Holocene, rainforests expanded, and Palawan lost more than 80% of its landmass because of rising sea levels. Deer populations diminished, and the bearded pig became the principal large mammal resource. By \sim 3 ka, deer populations were extinct. While humans hunting played a significant role in their disappearance, gross changes in climate and environment also impacted population resilience (67), as demonstrated by the continuing survival of deer on three islands in the Calamian group still supporting more open environments.

Hominins also became extinct on at least some islands in the Pleistocene (Fig. 1), and several archaeological records appear to represent island abandonment. The tiny island of Kisar in Wallacea, for example, was first occupied about 16 ka. Human occupation was only successfully achieved following the establishment of extensive maritime trading networks, and island abandonment in the early Holocene may have been linked to the collapse of these networks (51). Kangaroo Island preserves the

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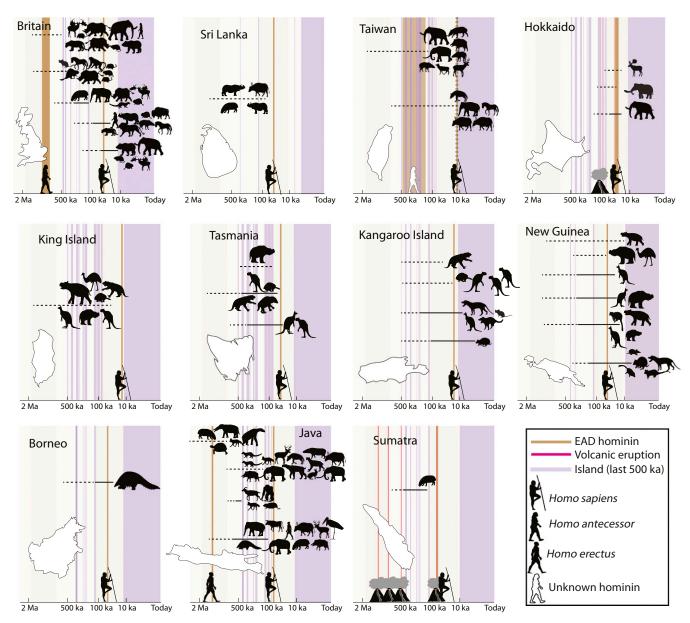


Fig. 4. Extinction chronology (right end of horizontal bars) shown with respect to first hominin and *H. sapiens* arrival (vertical bars and boxes) to continental islands. Purple vertical bars represent periods when these landmasses were islands. Extinct taxon LADs are represented by horizontal lines. In cases in which the LAD was highly imprecise, occurrence was represented by a dashed line only. When dates had been provided for individual taxa, associated sedimentary contexts, and/or sites, this was represented by a dashed line progressing to a solid line, with the end of the solid line representing the LAD. Taxa on one island sharing LADs close intime (at a level indistinguishable on the scale used here) were grouped together. Horizontal lines are only illustrative of prior occurrence and are not lengthened to scale. More details on how this figure was constructed is presented in *SI Appendix*, *Supplementary Information Text*, and dates and associated references are listed in *SI Appendix*, Tables S1 and S2.

best direct positive evidence of abandonment. There, records suggest that Indigenous Australian occupation ceased by around 4 ka, and although transient visits (or perhaps continued limited settlement) may have continued for a further 2,000 y (68), by the time Europeans arrived there were no human inhabitants on the island. Cyprus shows that after pygmy hippos became extinct human presence was limited until the Early Neolithic (66).

Because of their size and isolation, islands, especially small distant islands, are particularly prone to random events. We found few instances in which volcanic activity was perhaps coeval with extinction (Figs. 2 and 4); however, these events were also indistinguishable in time from the first arrival of humans on islands. The Quaternary history of large-scale volcanic eruptions have been particularly well investigated in Honshu, Shikoku, Kyushu, and Hokkaido (69), and eruptions seem not to be synchronous with the extinctions of mammalian species (Figs. 2 and 4). This also applies to the eruption record for Flores. The effects of major eruptions on local extinctions are difficult to assess, even for relatively well-documented major eruptions that occurred on islands in historic times. Nevertheless, studies of the ecological impacts of volcanic eruptions have indicated short recovery times and no long-term changes in mammal communities (70).

The arrival of humans on islands in the Holocene is often considered synchronous with large-scale extinctions of insular endemics. These extinctions are conceptually associated with human agency through mechanisms such as overhunting, habitat alteration, and the introduction of domestics and commensals (2–4). The latter arguably have had a much greater impact on

island extinctions than overhunting, particularly for small mammals and birds but also larger mammals. On Miyako Island of the Ryukyus, for example, endemic deer (Capreolus tokunagai) were not displaced by first human arrival, but rather, their extinction coincides with the human introduction of suids in the late Pleistocene or early Holocene (71). As a result, what happened on islands in the Holocene has often provided the theoretical and practical framework for understanding extinction processes associated with people (11). This makes sense when considering the Holocene expansion of H. sapiens into previously unreachable or untenable regions. It also applies to continental islands, where insular conditions and technological changes were coincident with the onset of the Holocene (e.g., ref. 72). However, the Pleistocene record is significantly more ambiguous regarding the impacts of hominins on island biota. This is due to factors intimately tied to subsistence strategies, technological and behavioral changes occurring throughout the Pleistocene, and the distinct nature of islands and their resources globally.

Our data shows that hominins, including our own species, have not always had the negative impacts on island ecosystems that humans have today. Rather, extinctions accelerated beginning in the early to late Holocene, following expanded migration opportunities, increased seafaring and thus dispersal abilities, the introduction of widespread land clearance, the introduction of commensals and synathropics, increased human densities, and the development of technologies allowing for the overexploitation of animal populations. Acknowledging that humans may not have always been detrimental to virgin ecosystems is important for identifying instances in which they have had a more passive or even beneficial impact. Such cases are critical for comparative studies aimed at identifying the factors increasing extinction risks of endemic island faunas. It is only through this process that we can hope to preserve the biodiversity that remains on islands today.

Materials and Methods

The aim of our study was to examine the coincidence of Pleistocene, as opposed to Holocene, hominin arrival with disappearance, so we restricted our analyses only to islands with evidence of Pleistocene hominin presence. For each island, we recorded the earliest appearance date (EAD) of the first hominin species on the island, as well as the EAD of *H. sapiens* (if different) on that island (*SI Appendix*, Table S1). In many instances, EADs were indirectly inferred based on archaeological records and the most widely accepted species attributions available (source references in *SI Appendix*). For each island, we also compiled a list of every extinct vertebrate (i.e., mammals, birds, and reptiles) taxon recorded from the literature, as well as its last appearance date (LAD) (*SI Appendix*, Table S1). Most species considered here have no direct dates associated with their remains, let alone their last appearance. Many are from sites that exceed the radiocarbon dating window, were historically collected with minimal stratigraphic information, and/or

- M. Bunce et al., Extreme reversed sexual size dimorphism in the extinct New Zealand moa Dinornis. Nature 425, 172–175 (2003).
- G. L. W. Perry et al., A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes). *Quat. Sci. Rev.* 105, 126–135 (2014).
- D. K. Grayson, The archaeological record of human impacts on animal populations. J. World Prehist. 15, 1–68 (2001).
- A. G. Boyer, W. Jetz, Extinctions and the loss of ecological function in island bird communities. *Glob. Ecol. Biogeogr.* 23, 679–688 (2014).
- A. G. Boyer, Consistent ecological selectivity through time in Pacific Island avian extinctions. Conserv. Biol. 24, 511–519 (2010).
- D. W. Steadman, Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. Science 267, 1123–1131 (1995).
- A. S. Cheke, J. P. Hume, Lost Land of the Dodo: The Ecological History of the Mascarene Islands (T and AD Poyser, 2008).
- B. E. Crowley, A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat. Sci. Rev.* 29, 2591–2603 (2010).
- W. G. Lee, "Islands" in *Encyclopedia of Biological Invasions*, D. Simberloff, M. Rejmánek, Eds. (University of California Press, 2011), pp. 391–395.
- J. A. Alcover, A. Sans, M. Palmer, The extent of extinctions of mammals on islands. J. Biogeogr. 25, 913–918 (1998).
- J. R. Wood et al., Island extinctions: Processes, patterns, and potential for ecosystem restoration. Environ. Conserv. 44, 348–358 (2017).
- 12. P. S. Martin, Africa and Pleistocene overkill. Nature 212, 339-342 (1966).

have, at best, indirect dates associated with the strata from which they were found. The actual appearance and disappearance of taxa will be earlier and later than the EAD and LAD, respectively, because of the Signor-Lipps effect (73). Moreover, paleontological sites with good faunal sequences are rare, particularly for smaller islands (74, 75), such that the absolute number of dated occurrences for fossils on an island will usually be limited compared to continents and prohibiting the use of statistical techniques to accurately estimate extinction times. Thus, currently available data do not allow us to confidently assign last appearance datums or estimate true extinction windows for almost all taxa. Use of commonly applied data quality criteria or auditing of dating methods would require us to reject most islands from our examination and almost all species. However, the null hypothesis we test in this study is that there is evidence of hominin-driven extinctions following first Pleistocene arrival on an island. This can be achieved using available datasets (albeit weakly and subject to retesting once further data becomes available), as for any given island, a lack of reliable dates does not support the null hypothesis.

We only considered taxa identified to a level that would allow us to definitively assess whether extinction had occurred. In most cases, this was possible to do at the species level, although, where relevant, we also estimated extinction occurrence at higher taxonomic levels (e.g., family-level extinctions in the case of Stegodontidae). Nonvolant taxa were considered extinct on an island if they not only had disappeared from that island but were also absent from the island's nearest biogeographical source region. This is because, from an island biogeography perspective, the presence of regional species pools means that island recolonization could occur at any point, in which case the loss of the island population of a species would not count as a permanent extinction but rather a transient one. Thus, extirpated but extant taxa were only considered truly extinct from an island if there was no potential for recolonization of that species from a nearby source. This definition means that many well-established island extirpations (e.g., Palawan deer from Palawan in the Philippines, tigers from Borneo, mountain goats from Vancouver Island, brown bears from the Alexander Archipelago, etc.) are not considered in our analyses. For volant animals, taxa were only considered if they represented true endemic or resident taxamigratory birds were not counted in our assessments. As such, our extinction estimates represent a minimum of insular vertebrate biodiversity loss on islands, and it is highly likely that the number of true extinctions was greater on all islands. Additional methods and considerations are discussed in SI Appendix, Supplementary Information Text.

Data Availability. All study data are included in the article and/or SI Appendix.

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- P. S. Martin, "Prehistoric overkill" in *Pleistocene Extinctions: The Search for a Cause*, P. S. Martin, H. E. Wright Jr., Eds. (Yale University Press, 1967), pp. 75–120.
- P. S. Martin, "Prehistoric overkill: The global model" in *Quaternary Extinctions: A Prehistoric Revolution*, P. S. Martin, R. G. Klein, Eds. (University of Arizona Press, 1984), pp. 354–403.
- 15. J. M. Diamond, Man the exterminator. Nature 298, 787-789 (1982).
- P. S. Martin, D. W. Steadman, "Prehistoric extinctions on islands and continents" in Extinctions in Near Time, R. D. E. MacPhee, H.-D. Sues, Eds. (Springer, 1999), pp. 17–55.
- B. W. Brook, D. M. J. S. Bowman, The uncertain blitzkrieg of Pleistocene megafauna.
- J. Biogeogr. 31, 517–523 (2004). 18. P. S. Martin, Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of
- America (University of California Press, 2005). 19. D. A. Burney, T. F. Flannery, Fifty millennia of catastrophic extinctions after human
- contact. *Trends Ecol. Evol.* 20, 395–401 (2005).
 20. D. K. Grayson, D. J. Meltzer, A requiem for North American overkill. *J. Archaeol. Sci.* 30, 585–593 (2003).
- C. Sandom, S. Faurby, B. Sandel, J.-C. Svenning, Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. Biol. Sci.* 281, 20133254 (2014).
- L. J. Bartlett *et al.*, Robustness despite uncertainty: Regional climate data reveal the dominant role of humans in explaining global extinctions of late Quaternary megafauna. *Ecography* **39**, 152–161 (2016).

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Louys et al. No evidence for widespread island extinctions after Pleistocene hominin arrival

- S. K. Lyons et al., The changing role of mammal life histories in late Quaternary extinction vulnerability on continents and islands. *Biol. Lett.* 12, 20160342 (2016).
- C. N. Johnson et al., Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–275 (2017).
- C. N. Johnson, Ecological consequences of late Quaternary extinctions of megafauna. Proc. Biol. Sci. 276, 2509–2519 (2009).
- Y. Malhi et al., Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Natl. Acad. Sci. U.S.A. 113, 838–846 (2016).
- S. Matsu'ura et al., Age control of the first appearance datum for Javanese Homo erectus in the Sangiran area. Science 367, 210–214 (2020).
- T. Ingicco et al., Earliest known hominin activity in the Philippines by 709 thousand years ago. Nature 557, 233–237 (2018).
- A. Brumm et al., Hominins on Flores, Indonesia, by one million years ago. Nature 464, 748–752 (2010).
- S. Kealy, J. Louys, S. O'Connor, Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. J. Hum. Evol. 125, 59–70 (2018).
- S. Mcbrearty, A. S. Brooks, The revolution that wasn't: A new interpretation of the origin of modern human behavior. J. Hum. Evol. 39, 453–563 (2000).
- J. M. Diamond, The present, past and future of human-caused extinctions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 325, 469–476, discussion 476–477 (1989).
- G. Haynes, Extinctions in North America's late glacial landscapes. Quat. Int. 285, 89–98 (2013).
- J. T. Faith, J. Rowan, A. Du, W. A. Burr, The uncertain case for human-driven extinctions prior to Homo sapiens. Quat. Res. 96, 88–104 (2020).
- T. J. Braje, T. P. Leppard, S. M. Fitzpatrick, J. M. Erlandson, Archaeology, historical ecology, and anthropogenic island ecosystems. *Environ. Conserv.* 44, 286–297 (2017).
- G. D. van den Bergh et al., Earliest hominin occupation of Sulawesi, Indonesia. Nature 529. 208–211 (2016).
- N. Ashton et al., Hominin footprints from early Pleistocene deposits at Happisburgh, UK. PLoS One 9, e88329 (2014).
- 38. C.-H. Chang et al., The first archaic Homo from Taiwan. Nat. Commun. 6, 6037 (2015).
- F. Détroit et al., Upper Pleistocene Homo sapiens from the Tabon cave (Palawan, the Philippines): Description and dating of new discoveries. C. R. Palevol 3, 705–712 (2004).
- K. E. Westaway et al., An early modern human presence in Sumatra 73,000-63,000 years ago. Nature 548, 322–325 (2017).
- G. D. van den Bergh, J. de Vos, P. Y. Sondaar, The late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 171, 385–408 (2001).
- J. Louys, P. Roberts, Environmental drivers of megafauna and hominin extinction in Southeast Asia. Nature 586, 402–406 (2020).
- J. R. Stewart, The progressive effect of the individualistic response of species to Quaternary climate change: An analysis of British mammalian faunas. *Quat. Sci. Rev.* 27, 2499–2508 (2008).
- A. J. Stuart, Late Quaternary megafaunal extinctions on the continents: A short review. Geol. J. 50, 338–363 (2015).
- R. D. E. MacPhee, "Insulae infortunatae: Establishing the chronology of late Quaternary mammal extinctions in the West Indies" in *American Megafaunal Extinctions at the End of the Pleistocene*, G. Haynes, Ed. (Springer, 2009), pp. 169–193.
- R. H. MacArthur, E. O. Wilson, The Theory of Island Biogeography (Princeton University Press, 1967).
- M. L. Rosenzweig, Species Diversity in Space and Time (Cambridge University Press, 1995).
- R. L. Rogers, M. Slatkin, Excess of genomic defects in a woolly mammoth on Wrangel island. *PLoS Genet.* 13, e1006601 (2017).
- J. R. Karr, Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* 63, 1975–1978 (1982).
- F. Aziz et al., Early dispersal of man on islands of the Indonesian Archipelago: Facts and controls. Anthropol. Sci. 103, 349–368 (1995).
- S. O'Connor et al., Kisar and the archaeology of small islands in the Wallacean Archipelago. J. Island Coast. Archaeol. 14, 198–225 (2019).

- S. M. Fitzpatrick, V. D. Thompson, A. S. Poteate, M. F. Napolitano, J. M. Erlandson, Marginalization of the margins: The importance of smaller islands in human prehistory. J. Island Coast. Archaeol. 11, 155–170 (2016).
- B. W. Brook, D. M. J. S. Bowman, One equation fits overkill: Why allometry underpins both prehistoric and modern body size-biased extinctions. *Popul. Ecol.* 47, 137–141 (2005).
- P. Raia, C. Barbera, M. Conte, The fast life of a dwarfed giant. *Evol. Ecol.* 17, 293–312 (2003).
- 55. G. D. van den Bergh et al., The Liang Bua faunal remains: A 95k.yr. sequence from Flores, East Indonesia. J. Hum. Evol. 57, 527–537 (2009).
- J. C. A. Joordens, F. P. Wesselingh, J. de Vos, H. B. Vonhof, D. Kroon, Relevance of aquatic environments for hominins: A case study from Trinil (Java, Indonesia). J. Hum. Evol. 57, 656–671 (2009).
- S. O'Connor, J. Louys, S. Kealy, S. C. Samper Carro, Hominin dispersal and settlement east of Huxley's line: The role of sea level changes, island size, and subsistence behavior. *Curr. Anthropol.* 58, 5567–5582 (2017).
- N. Amano et al., Subsistence strategies and environment in late Pleistocene early Holocene Eastern Java: Evidence from Braholo cave. Quat. Int. 416, 46–63 (2016).
- R. J. Rabett, P. J. Piper, The emergence of bone technologies at the end of the Pleistocene in Southeast Asia: Regional and evolutionary implications. *Camb. Archaeol. J.* 22, 37–56 (2012).
- 60. M. Aubert et al., Earliest hunting scene in prehistoric art. Nature 576, 442-445 (2019).
- S. O'Connor, D. Bulbeck, "Homo sapiens societies in Indonesia and South-Eastern Asia" in *The Oxford Handbook of the Archaeology and Anthropology of Hunter-Gatherers*, V. Cummings, P. Jordan, M. Zvelebil, Eds. (Oxford University Press, 2014), pp. 346–367.
- M. Fujita, S. Yamasaki, H. Sugawara, M. Eda, Body size reduction in wild boar (Sus scrofa) from the late Pleistocene Maehira Fissure Site in Okinawa-jima Island, Japan, with relevance to human arrival. Quat. Int. 339–340, 289–299 (2014).
- T. C. Rick, J. M. Erlandson, R. L. Vellanoweth, T. J. Braje, From Pleistocene mariners to complex hunter-gatherers: The archaeology of the California Channel Islands. J. World Prehist. 19, 169–228 (2005).
- R. Cosgrove et al., Overdone overkill–The archaeological perspective on Tasmanian megafaunal extinctions. J. Archaeol. Sci. 37, 2486–2503 (2010).
- M. S. Lima-Ribeiro, J. A. F. Diniz-Filho, Obstinate overkill in Tasmania? The closest gaps do not probabilistically support human involvement in megafaunal extinctions. *Earth Sci. Rev.* 135, 59–64 (2014).
- 66. A. Simmons, R. D. Mandel, "Site formation processes at Akrotiri Aetokremnos, Cyprus: Why is the site so controversial?" in Géoarchéologie des îles de Méditerrané; M. Ghilardi, Ed. (CNRS éditions, 2016), pp. 57–72.
- J. Ochoa, P. J. Piper, "Holocene large mammal extinctions in Palawan Island, Philippines" in *Climate Change and Human Responses: A Zooarchaeological Perspective*, G. G. Monk, Ed. (Springer, 2017), pp. 69–86.
- 68. S. Bowdler, The bass strait Islands revisited. Quat. Int. 385, 206-218 (2015).
- H. Machida, F. Arai, Atlas of Tephra in and Around Japan (University of Tokyo Press, 2003).
- N. A. Famoso, Mammalian community response to historic volcanic eruptions. *Mamm. Biol.* 100, 219–230 (2020).
- A. Kawamura, C.-H. Chang, Y. Kawamura, Middle Pleistocene to Holocene mammal faunas of the Ryukyu Islands and Taiwan: An updated review incorporating results of recent research. *Quat. Int.* **397**, 117–135 (2016).
- 72. A. J. Stuart, *Pleistocene Vertebrates in the British Isles* (Longman Financial Service, 1982).
- 73. P. W. Signor III, J. H. Lipps, "Sampling bias, gradual extinction patterns, and catastrophes in the fossil record" in *Geological Implications of Impacts of Large Asteroids* and Comets on the Earth, L. T. Silver, P. H. Schultz, Eds. (Geological Society of America Special Publication, 1982), vol. 190, pp. 291–296.
- 74. J. P. Hume, "Contrasting taphofacies in ocean island settings: The fossil record of Mascarene vertebrates" in *Proceedings of the International Symposium Insular Vertebrate Evolution: The Palaeontological Approach*, J. A. Alcover, P. Bover, Eds. (Societat d'Història Natural de les Balears, Palmer de Mallorca, Spain, 2005), pp. 129–144.
- 75. J. Louys et al., Differential preservation of vertebrates in Southeast Asian caves. Int. J. Speleol. 46, 379–408 (2017).



Supplementary Information for

No evidence for widespread island extinctions after Pleistocene hominin arrival

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Supplementary text Tables S1 to S2 SI References

Supplementary Information Text

Defining what constitutes an island often poses difficulty as any strict definition will likely either be so broad as to encompass virtually all landmasses on Earth, or too specific, whereby areas that are classically thought of as islands are excluded (1, 2). Rosenzweig (1, p. 211) suggested that, in a biological sense, islands could be defined as a "self-contained region whose species originate entirely by immigration from outside the region". Whittaker and Fernández-Palacios (2) criticized this definition for being too restrictive and that it excluded real islands with high levels of endemism. They used a much broader and more classic definition-essentially that of a landmass surrounded by water-and thus included Australia under their 'island continent' subcategory. Because our intent is to examine extinctions on islands as opposed to continents, we restricted our analyses to geographical areas that are considered true islands today, following classic definitions (e.g. 2) and excluding all continents. Islands were considered for their present geography without any consideration of any local Quaternary geomorphological evolution, meaning that the Muria Volcano for example, which has long been isolated from the rest of what is now Java and on which a Pleistocene fauna contemporaneous to *Homo erectus* has been recovered, is here considered as part of Java. However, major geomorphological events were considered (see below). Our criteria resulted in the examination of 32 islands and islandcomplexes, the largest sample size of its kind.

We further divided islands into two groups: oceanic islands (islands that have never been connected to continental landmasses, at least since the Last Glacial Maximum [LGM]); and continental islands (promontories that were connected to continents during the LGM and earlier periods of time, but islands today). Connectivity was established by examining global bathymetric data using the gshhs high resolution world vector shoreline dataset version 2.3.7 (3; accessed 29th Jan 2018) and using Geographic Information Systems (GIS) to determine island areal extent based on the Miller et al. (2011) 'scaled' sea level curve (4) and the GEBCO 30-second arc dataset: GEBCO 2014 Grid (5), with a max low point of 120 m below present. These were drawn on maps as light grey contours and when contiguous with a continent, were considered continental islands, with the following caveats. Ireland was covered by the British-Irish Ice Sheet during the LGM and emerged from glaciation as an island between 20 and 18 ka, prior to the first record of post-LGM fauna and subsequent hominin presence (6-8). From the point of first colonisation considered here, Ireland falls into the oceanic island category. In Japan, the Tsugaru Strait (between Hokkaido and Honshu-Shikoku-Kyushu) and the Korean Strait (between the latter and Korean Peninsula) are generally considered not to have dried up during the LGM (9-13). Thus Honshu-Shikoku-Kyushu is classified here as an oceanic island, while Hokkaido falls into the continental island category.

Most continental islands considered here were islands during periods of high sea levels during the Quaternary, subject to bathymetric measurements and current understanding of geological history of the straits separating them from continents (14-19). Two notable exceptions are Britain and Sundaland (Java, Borneo, Sumatra). Britain first became an island approximately 450 ka following the first breach of the land bridge connecting it to the European mainland (20). For Sundaland, the subsidence of the low-lying continental shelf began approximately 400 ka, prior to which all major islands were connected (21). As a first level approximation of when continental islands were separated from the mainland over the last 500 ka, periods of insular conditions are shown in Figure 4 based on the Miller et al. (2011) 'scaled' sea level curve (4) and the GEBCO 30-second arc dataset: GEBCO 2014 Grid (5), with connection established for each island based on global bathymetric data and resolved at 1000 year level resolution (Table S2). For Britain and Sundaland, these are only shown back to MIS12 (other continental islands have no dated Pleistocene faunas older than MIS12). Because of this, for Britain, we only considered taxa dated to the stage just prior to the land bridge breach (i.e. the Anglian onwards), although we included the site of Ostend as it could potentially date to as late as MIS13 (22). We included all sites from Java due to the highly uncertain chronology of the earliest Pleistocene assemblages on that island.

Due to the limited availability of high-quality occurrence and geochronological data for most island systems considered, and given issues highlighted with 'big data' guantitative approaches to Quaternary extinction studies (23), we restricted our assessment to an examination of temporal overlap between taxon extinction (LAD) and hominin arrival (EAD). We do not argue this implies a causal relationship between arrival and extinction; rather, we take it as the first indication that such a relationship might exist. In order to determine overlap, hominin EADs and extinct species LADs were shown graphically for each island. Hominin EADs were represented as a vertical bar representing the 'arrival window' on the island, with uncertainty in EAD indicated by the width of the window, corresponding to published estimates (Table S1). Where this information was considered robust, the arrival window was represented as a vertical line only, and where information was considered highly uncertain, it is shown with a dashed border. Known past volcanic eruptions were shown similarly. In Japan, volcanic eruptions have been particularly well investigated, and are summarily given in (24). Based on this work, large-scale eruptions producing a huge amount of tephras are selected and shown in Figures 2 and 4. Extinct taxon LADs were represented by horizontal lines. In cases where the LAD was highly imprecise (e.g. 'Middle Pleistocene'), occurrence was represented by a dashed line only. Where dates had been provided for individual taxa, associated sedimentary contexts, and/or sites, this was represented by a dashed line progressing to a solid line, with the end of the solid line representing the LAD. Taxa on one island sharing LADs close in time (at a level indistinguishable on the scale used here) were grouped together. Extinction records are shown as solid and dashed lines, as opposed to points, for ease of visual interpretation and to indicate that each taxon would have been present on the island at some unestablished point prior to their extinction. The dearth of occurrence data for almost all taxa considered here makes it impossible to calculate exactly how long each taxon had been established on each island in a quantitatively rigorous manner, or how much confidence can be attributed to each LAD. Thus, horizontal lines are only illustrative of prior occurrence and are not lengthened to scale. Each extinct taxon and first hominin and Homo sapiens arrival was illustrated on a global map, one for oceanic islands and another for continental islands. To visually represent where extinctions and arrivals closely coincided in time (here assessed at <5 ka or occurring within the window of hominin arrival), extinct taxa were colored in red where this occurred.

Animal outlines used in our figures were either created ourselves, provided by courtesy of G.J. Price or downloaded from Phylopic.org. The latter are either in the public domain or are covered under Creative Commons licenses as follows: CC BY-SA 3.0 (Stegodon by Zimeces; Leptoptilos by L. Shyamal); CC BY 3.0 (Ardea by Rebecca Groom; Testudinidae by Andrew A. Farke; Elephas by T. Michael Keesey; Candiacervus by Zimices; Acrobates by Sarah Werning); CC BY-NC-SA 3.0 (Cuon by AnAgnosticGod (vectorized by T. Michael Keesey); Anas by Maija Karala; Panthera by Lukasiniho); CC BY-NC 3.0 (Mammuthus by Zimices; Chaeropsis by T. Michael Keesey (after Marek Velechovský); Leporidae by Sarah Werning; Accipiter by Shyamal; Rallidae by T. Michael Keesey (vectorization) and HuttyMcphoo (photography); Tyto by Unknown (photo), John E. McCormack, Michael G. Harvey, Brant C. Faircloth, Nicholas G. Crawford, Travis C. Glenn, Robb T. Brumfield & T. Michael Keesey; Equus by Mercedes Yrayzoz (vectorized by T. Michael Keesey); Alces by Rebecca Collins; Coelodonta by Rebecca Collins; Setonix by T. Michael Keesey (photo by Sean Mack); Caprinae by Zimices, based in Mauricio Antón skeletal; Bos by DFoidI (modified by T. Michael Keesey); Anthrocotherium by Dmitry Bogdanov; Homotherium by Zimices; Machairodontini by Dantheman9758 (vectorized by T. Michael Keesey); Sthenurine by Zimices; Dromaius by Darren Naish (vectorize by T. Michael Keesey); Palorchestes by Zimices; Sarcophilus by Sarah Werning).

Table S1. Reference data for Figures. The list of extinct species considered in our analyses for each island group as well as first hominin appearance, and *Homo sapiens* appearance are provided. References used for taxa are listed immediately after each taxon name, last appearance chronology provided after date listed. Volcanic eruption data from (24-29).

Island Group	Extinct Taxa Latest Published Date ¹	Hominin Earliest
San Miguel-Santa	Chendytes lawi (30) 3 ka cal BP (30)	Published Date ¹ Homo sapiens (33, 34)
Rosa-Santa Cruz	Peromyscus nesodytes (31) ?1 ka cal BP (31)	12-13 ka cal BP (33, 34)
	Mammuthus columbia (31) 14 ka cal BP ² (32)	
	Mammuthus exilis (31) 13 ka cal BP (31)	
	Microtus miguelensis (31) Terminal	
	Pleistocene (31)	
Ireland	Mammuthus primigenius (35) 25 ka cal BP ²	Homo sapiens (40) 13 ka
	(36)	cal BP (40)
	Crocuta crocuta (35) 38 ka cal BP (37)	
	Megaloceros giganteus (35) 13 ka cal BP (38)	
	Dicrostonyx torquatus (35) 12 ka cal BP (36) ²	
	Ovibos moschatus (35) 109-74 ka (39)	
Sardinia	Cynotherium sardous (41, 42) 11 ka cal BP	Hominin gen. et sp.
	(43)	indet.
	Praemegaceros cazioti (42) 10 ka cal BP (44)	(54) ~400 ka (54)
	Prolagus sardus (42) ~250 BP (45, 46)	Homo sapiens (55, 56)
	Microtus henseli (42) 3-2 ka cal BP (46)	~20 ka (55, 56)
	Rhagamys orthodon (42) ~5 ka (47)	
	Asoriculus similis (42) ~5 ka (47)	
	Mammuthus lamarmorai (42) 43 ka cal BP	
	(48)	
	Sardolutra ichnusae (42) LP (49)	
	Algarolutra majori (42) LP (50)	
	Megalenhydris barbaricina (42) 70-10 ka (51)	
	Enhydrictis galictoides (42) LP (52)	
	Aquila nipaloides (28) 17-9 ka cal BP (53)	
Honshu-Shikoku-	Stegodon aurorae (57) 0.7 Ma (57)	?Homo sapiens (63, 64)
Kyushu	Mammuthus trogontherii (58) 0.58 Ma (57)	84-50 ka (65)
	Stegodon orientalis (57) 0.55 Ma (57)	
	Palaeoloxodon naumanni (59) 20 ka cal BP	
	(59)	
	Cervus kazusensis (60) 20 ka cal BP (59)	
	Sinomegaceros yabei (59) 14 ka cal BP (59)	
	Bison priscus (59) 22-26 ka cal BP (59)	
	Anourosorex japonicus (59) 22 ka cal BP (59)	
	Myodes japonicus (61) 22 ka cal BP (59)	
	Microtus epiratticepoides (62) 20 ka cal BP	
	(59)	

Ishigaki	<i>Cervus</i> (<i>C. nippon</i> type) (66) >29 ka (66)	Homo sapiens (67) 28 ka
	Niviventer sp. (66) 2-4 ka cal BP (66, 67)	cal BP (67)
Miyako	Sus sp. (small form) (68) 10-11 ka cal BP (69)	Homo sapiens (70) 32 ka
	Diplothrix miyakoensis (66) 10-11 ka cal BP	cal BP (70)
	(69)	
	Capreolus tokunagai (66) 10-11 ka cal BP	
	(69)	
	Mammuthus trogontherii (58) MP (66)	
Kume	Muntacinae gen. et sp. indet. (66) 18 ka cal	Homo sapiens (71, 72) 18
	BP (71)	ka cal BP (71, 72)
	Cervus astylodon (66) 18 ka cal BP (71)	
Okinawa	Cervus astylodon (59, 66) 20 ka cal BP (59)	Homo sapiens (73, 74) 37
	Muntacinae gen. et sp. indet. (59, 66) 20 ka	ka cal BP (73, 74)
	cal BP (59)	
Luzon-Mindanao	Nesorhinus philippinensis (75) 709 ka (76)	Hominin gen. et sp.
	Stegodon luzonensis (77) MP (77)	indet. (76) 709 ka (76)
	Elephas beyeri (78) MP (78)	Homo luzonensis (85) 67
	Celebochoerus cagayanensis (79) 709 ka (76)	ka (86)
	Megalochelys sondaari (80) 1 Ma (81)	Homo sapiens (87) ~30 ka
	Batomys sp. (82) >52 ka (82, 83)	(87)
	Bubalus cebuensis (84) MP (84)	
	Bubalus sp. (83) >52 ka (83)	
	Homo luzonensis (85) ~55 ka (85)	
Mindoro	Crateromys paulus (88) ~2 ka (88)	Homo sapiens (89, 90)
		~32 ka (89, 90)
Palawan	Panthera tigris (64) ~11 ka (91)	Homo sapiens (93, 94)
	<i>Cuon</i> sp. (65) ~9.4 ka (92)	>47 ka (93)
New Ireland	Accipiter 'sp. 2' (95) Holocene (95)	Homo sapiens (95) 35 ka
	Accipiter 'sp. 3' (95) Holocene (95)	cal BP (95)
	Megapodius sp. (95) 10-14 ka cal BP (95)	
	Gallirallus sp. (95) <2 ka cal BP (95)	
	Porphyrio sp. (95) <1.6 ka cal BP (95)	
	<i>Cacatua</i> sp. (95) 1-5 ka cal BP (95)	
	<i>Tyto</i> 'sp. 1' (95) >10 ka cal BP (95)	
	<i>Tyto</i> 'sp. 2' (95) 5-10 ka cal BP (95)	
	Corvus sp. (95) 1-5 ka cal BP (95)	
Buka	<i>Megapodius</i> sp. n. (96) ~5 ka (97)	Homo sapiens (99) 29 ka
	<i>Hypotaenidia</i> sp. n. (96) ~5 ka (97)	RYBP (99)
	<i>Porphyrio</i> sp. n. (96) ~5 ka (97)	
	Pareudiastes sp. n. (96) ~5 ka (97)	
	<i>Nycticorax</i> sp. n. (96) ~5 ka (97)	
	Columbidae gen. et sp. n. (96) ~5 ka (97)	
	Columbidae gen. et sp. n. (96) ~5 ka (97)	

	Melomys spechti (98) ~5 ka (97)	
	Solomys spriggsarum (98) ~5 ka (97)	
Sulawesi	Stegoloxodon celebensis (100, 101) 400-600 ka (100) Stegodon sp. B (large-sized) (100) 354-484 ka (102, 103) Stegodon sp. (102) >194-118 ka (102) Elephas/Palaeoloxodon (large-sized) (100, 104) 35-50 ka (104) Celebochoerus heekereni (100, 102) >200 ka (100, 102) Bubalus grovesi (105) 94-115 ka (102)	Hominin gen. et sp. indet. (102) >194-118 ka (102) <i>Homo sapiens</i> (106) 46ka (107)
Timor	Megalochelys sp. (100) 400-600 ka (100) Coryphomys buehleri (108) ~2 ka (109) Coryphomys musseri (108) ~2 ka (109) Murine 'Gen. A' (108) late Holocene (108) Murine 'Gen. B' (108) late Holocene (108) Murine 'Gen. C' (108) late Holocene (108) Stegodon timorensis (110-113) >130 ka (113) Stegodon 'trigonocephalus' (114, 115) Pleistocene (114, 115) Varanus sp. nov. (116) Pleistocene (116) Megalochelys sp. (116) Pleistocene (116) Turnix sp. (117) 1.3 ka cal BP (117) Grus sp. (117) >42 ka (117)	Homo sapiens (118) 45 ka cal BP (118)
Alor	Alormys aplini (119) 3 ka cal BP (119)	Homo sapiens (120) 40 ka cal BP (120)
Flores	Papagomys theodorverhoeveni (121) ~3 ka (121, 122)Spelaeomys florensis (121) Holocene (121) Varanus hooijeri (123) Holocene (123) Hooijeromys nusatenggara (124) ~3 ka (122) Stegodon florensis insularis (3) 50 ka (122) Homo floresiensis (26) 50 ka (26) Trigonoceps sp. (125) 50 ka (125) Megalurus sp. (126) 60 ka (126) cf. Acridotheres (126) 50 ka (125) Leptoptilos robustus (125) 50 ka (125) Stegodon sondaari (127, 128) >1.07 Ma (129, 130) Megalochelys sp. (94) >1.07 Ma (129, 130)	Hominin gen. et sp. indet. (131) >1 Ma (131) <i>Homo floresiensis</i> (76) 193 ka (76) <i>Homo sapiens</i> (125, 132) ~46 ka (125, 132)
Sumba	Stegodon sumbaensis (100, 133) 125-186 ka (133)	Hominin gen. et sp. indet. (134) ?late Middle

	Milimonggamys juliae (133) 54-222 cal AD (133) Raksasamys tikusbesar (133) 1935–1700 cal BC (133) Varanus cf. hooijeri (133) Holocene (133)	Pleistocene and early Upper Pleistocene (134)
Cyprus	Hippopotamus minor (135) 12 ka cal BP (136, 137, 138) Palaeoloxodon cypriotes (139) 12 ka cal BP (136, 138) Genetta plesictoides (140) 11 ka (140)	Homo sapiens (136) 12 ka cal BP (136, 138)
Crete	Candiacervus cf. reumeri (25, 141) 21.5 ka (142) Candiacervus sp. (25, 141) 33.5 ka (143) Palaeoloxodon creutzburgi (25, 141) 49 ka (142) Mus minotaurus (25, 144) Neolithic (Jarman cited in 143) Lutrogale cretensis (25, 141) 87 ka (143) Athene cretensis (145) 87 ka (143) Aquila chrysaetos simurgh (145) 87 ka (143) Hippopotamus creutzburgi (146) 378 ka (143) Kritimys catreus (144) MP (144) Mammuthus creticus (147) EP (147)	Hominin gen. et sp. indet. (148) ~85-124 ka (148) <i>Homo sapiens</i> (149) 9 ka cal BP (149)
Naxos	Palaeoloxodon lomolinoi (150) 116-30 ka (150)	<i>Homo</i> sp. (151) 50-38 ka (151)
Britain	Mammuthus trogontherii (152) ~700-500 ka (MIS17-13) (153) Sorex savini (152) ~700-500 ka (MIS17-13) (153) Pliomys episcopalis (154) ~500 ka (MIS13) (153) Ursus deningeri (154) ~500 ka (MIS13) (153) Panthera cf. gombaszoegensis (154) ~500 ka (MIS13) (153) Stephanorhinus sp. A (154) ~500 ka (MIS13) (153) Stephanorhinus hundsheimensis (154) ~500 ka (MIS13) (153) Megaloceros verticornis (155) ~300 ka (MIS10-6) (155) Megaloceros dawkinsi (154) ~500 ka (MIS13) (154)	Homo ?antecessor (154) 1-0.78 Ma (154) Homo sapiens (163) 44- 41 ka cal BP (163)

	(164)	ka (165)
Sri Lanka	Hippopotamus amphibius (164) ?Pleistocene	Homo sapiens (165) ~45
	(156)	
	Pitymys arvaloides (152) ~400 ka (MIS11)	
	Panthera pardus (159) ~45 ka (159)	
	(152)	
	Arvicola cantiana (152) ~100 ka (MIS5c)	
	(155)	
	<i>Cyrnaonyx antiqua</i> (155) ~300 ka (MIS10-6)	
	<i>Equus ferus</i> (161) ~40 ka (161)	
	Bison priscus (159) ~28 ka (159)	
	<i>Crocuta crocuta</i> (161) ~35 ka (161) <i>Panthera leo</i> (161) >39 ka (161)	
	Microtus gregalis (159) ~47 ka (159)	
	Dicrostonyx torquatus (159) ~22 ka (159)	
	Ochotona pusilla (159) \sim 22 ka (159)	
	Megaloceros giganteus (162) \sim 12.5 ka (162)	
	Coelodonta antiquitatis (161) ~35 ka (161)	
	(160)	
	<i>Mammuthus primigenius</i> (160) 14 ka cal BP ²	
	Ursus spelaeus (159) ~18 ka (159)	
	(158)	
	Homo cf. neanderthalensis (158) ~38-36 ka	
	(157)	
	Hippopotamus amphibius (157) ~120 ka	
	(157)	
	Stephanorhinus hemitoechus (157) >87 ka	
	Palaeoloxodon antiquus (157) >87 ka (157)	
	(156)	
	Macaca sylvanus (152, 154) ~400 ka (MIS11)	
	(MIS11) (154)	
	Stephanorhinus kirchbergensis (154) ~400 ka	
	(154)	
	Equus hydruntinus (154) ~400 ka (MIS11)	
	(MIS11) (154)	
	Apodemus maastrichtiensis (154) ~400 ka	
	(156)	
	Trogontherium cuvieri (152) ~400 ka (MISII) (154)	
	<i>Talpa minor</i> (152) ~400 ka (MIS11) (154)	
	(154)	
	(MIS13) (154) Sorex runtonensis (154) ~400 ka (MIS11)	
	(NAIC12) (1E4)	

		1 1
	Rhinoceros sinhaleyus (164) ?Pleistocene	
	(164)	
	Rhinoceros kagavena (164) ?Pleistocene	
	(164)	
	Bibos sinhaleyus (164) ?Pleistocene (164)	
Taiwan	Crocuta crocuta (166) LP (166)	<i>Homo</i> sp. (167) 130-450
	Stegodon sp. (166) MP (166)	ka (167)
	Palaeoloxodon sp. (166) LP (166)	Homo sapiens (168) LP
	Mammuthus sp. (166) MP (166)	(168)
	Equus dalianensis (166) LP (166)	
	<i>Tapirus</i> sp. (166) MP (166)	
	Potamochoerus sp. (166) MP (166)	
	<i>Sus houi</i> (166) MP (166)	
	Sus australis (166) MP (166)	
	Muntiacus bohlini (166) MP (166)	
	Elaphurus formosanus (166) MP (166)	
	Bubalus teilhardi (166) LP (166)	
	Bubalus youngi (166) LP (166)	
Hokkaido	Mammuthus primigenius (59) 23 ka cal BP	?Homo sapiens (169,
	(59)	170) ~30-40 ka (169, 170)
	Palaeoloxodon naumanni (59) 35 ka cal BP	
	(59)	
	Sinomegaceros yabei (59) ?60-25 ka (59)	
King Island	Megalibgwilia sp. (171) Pleistocene (171)	Homo sapiens (179) ~14
	Simosthenurus occidentalis (172-	ka (179)
	176) Pleistocene (172-176)	
	Diprotodon optatum (177) Pleistocene (177)	
	Dromaius ater (175) Pleistocene (175)	
	Zygomaturus trilobus (175, 177, 178)	
	Pleistocene (175, 177, 178)	
	Thylacoleo carnifex (175) Pleistocene (175)	
	Protemnodon anak (172-176) Pleistocene	
	(172-176)	
Tasmania	Megalibgwilia sp. (174-176, 180) 60-52 ka	Homo sapiens (181) 41 ka
	(174-176, 180)	cal BP (181)
	?Zygomaturus trilobus (176) >75 ka (176)	
	Metasthenurus newtonae (174-176, 180) 60-	
	52 ka (174-176 <i>,</i> 180)	
	Palorchestes azael (174-176, 180) 60-52 ka	
	(174-176, 180)	
	Protemnodon anak (176) 43-41 ka cal BP	
	(176)	
	Simosthenurus occidentalis (181) 45-53 ka	
1	cal BP (181)	

	<i>Thylacoleo carnifex</i> (181) 57-49 ka (181)	
Kangaroo Island New Guinea	Initiacities cannifex (181) 57-49 ka (181)Megalibgwilia sp. indet. (182) >20 ka (182)Thylacinus cynocephalus (182) 7 ka BP (182)Sarcophilus harrisii (182) 7 ka BP (182)Potorous platyops (182) 1 ka BP (183)Thylacoleo carnifex (182) >45 ka (146)Lagorchestes leporides (182) 7 ka BP (182)Procoptodon browneorum (182, 185) >20 ka(182)Procoptodon gilli (182, 185) >20 ka (182)Protemnodon sp. indet. (182) >20 ka (182)Pseudomys gouldii (182) 7 ka BP (182)Dendrolagus noibano (186) 29-18 ka cal BP ² (187, 188)	Homo sapiens (185) 18 ka BP (185) Homo sapiens (199) 49- 43 ka cal BP (199)
	(187, 188)Protemnodon tumbuna (186) 29-18 ka cal BP^2 (187, 188)Protemnodon nombe (186) >29 ka cal BP^2 (187, 188)Diprotodontid (186) 29-18 ka cal BP^2 (187, 188)Protemnodon hopei (189) ~20 ka (187)Maokopia ronaldi (189) ~20 ka (187)Hulitherium tomassetti (190) >50 ka (191)Casuarius lydekkeri (192) >50 ka (191)Casuarius lydekkeri (192) >50 ka (191)Kolopsis watutense (193) Pleistocene (193)Thylogale christenseni (189) 3.5 ka cal BP(187)Thylacinus cynocephalus (194) <5 ka cal BP	
Borneo	Manis palaeojavanica (200) ~35 ka (200)	Homo sapiens (201) ~50 ka (201)
Java	Xenocyon trinilensis (202) 0.54-0.43 Ma (203) Xenocyon merriami (204) EP (204) Cuon priscus (204) MP (204) Cervus zwaani (205, 206) MP (205, 206) Stegodon hypsilophus (202) MP (202) Sinomastodon bumiajuensis (202) EP (202)	Homo erectus (221) 1.3 Ma (221) Homo sapiens (222) ~70 ka (222)

	Hexaprotodon simplex (202) EP (202)	
	Elephas hysudrindicus (202) 117-108 ka	
	(207)	
	Manis palaeojavanica (202) 117-108 ka	
	(207)	
	Pachycrocuta brevirostris (202) MP (163,	
	208)	
	Bos palaesondaicus (202) 117-108 ka (207)	
	<i>Homo erectus</i> (207) 117-108 ka (207)	
	Stegodon sp. (208) MP (208)	
	Stegodon trigonocephalus (202) 117-108 ka	
	(207)	
	Duboisia santeng (202) 0.54-0.43 Ma (203)	
	Hexaprotodon sivajavanicus (202, 209) 117-	
	108 ka (207)	
	Bubalus palaeokerabau (207) 117-108 ka	
	(207)	
	Sus sangiranensis (210) MP (210)	
	Sus macrognathus (207) 117-108 ka (207)	
	Axis lydekkeri (211) 117-108 ka (207)	
	Lutrogale palaeoleptonyx (212) MP (212)	
	Lutrogale robusta (213) MP (214)	
	Rattus trinilensis (212) 0.54-0.43 Ma (203)	
	Colossochelys sp. (211) EP (211)	
	Merycopotamus dissimilis (211) MP (211)	
	Caprolagus sivalensis (211) MP (211)	
	Homotherium ultimum (215) MP (211)	
	Hemimachairodus zwierzyckii (216) MP (216)	
	Nestoritherium sivalense (211) EP (217)	
	Megantereon megantereon (211) MP (218)	
	Epileptobos groeneveldtii (212) MP (212)	
	Meganthropus palaeojavanicus (219) 0.54-	
	0.43 Ma (203)	
	Leptoptilos titan (220) Late Pleistocene (216)	
Sumatra	Hexaprotodon sp. (223) ~130 ka (223)	Homo sapiens (224) 73-
		63 ka (224)

¹Rounded values listed, refer to references for exact dates.

²Radiocarbon dates calibrated here using OxCal v. 4.4 (225) and the IntCal20 calibration curve (Reimer et al., 2020). Rounded median ages listed, refer to references for original radiocarbon results.

Table S2. Times when each continental island was an island in the last 500 ka, calculated based on the Miller et al. (4) 'scaled' sea level curve and the GEBCO 30-second arc dataset GEBCO_2014 Grid, with connection established for each island based on global bathymetric data and resolved at 1000 year level resolution.

Island	Depth below modern sea-level to establish connection	Times (ka) when an island in last 500 ka
Britain (*first separated 450 ka)	Between -31 and -31 m	0-11
		116-127
		130
		199-203
		209-217
		236-242
		311
		313
		315-316
		319-334
		397-417
		450*
Hokkaido	Between -50 and -51 m	0-12
		75
		80-85
		92-105
		113-131
		192-220
		233-243
		282-287
		308-335
		387-390
		392-422
		424
		483+
Kangaroo Island	Between -28 and -29 m	0-11
		116-127
		199-203
		209-217
		236-241
		315
		319-334
		397-417
		489-492
King Island	Between -53 and -54 m	0-12
		74-75

		80-85
		91-106
		111-131
		192-220
		229
		233-243
		282-288 300
		303
		307-335
		386-424
		482+
New Guinea	Between -12 and -13 m	0-9
		119-127
		324-333
		400-415
Sri Lanka	Between -3 and -4 m	0-2
		5
		120-126
		324
		326-329
Sumatra (*first separated 400 ka)	Between -23 and -24 m	0-10
		116-127
		199-201
		210
		214-217
		237-241
		319
		321-334
		397-400*
Borneo (*first separated 400 ka)		0-11
		115-128
		130
		199-203
		208-218
		235-242
		311
		313
		315-316
		319-334
		396-400*
Java (*first separated 400 ka)		

		94-97
		99-100
		102-103
		102-103
		114-128
		130-131
		192
		194
		196-218
		234-243
		283-286
		308-316
		318-335
		393
		395-400*
Taiwan	Between -50 and -51 m	0-12
		75
		80-85
		93-105
		113-131
		192-219
		233-243
		283-287
		308-335
		388-390
		392-422
		424
		483
Tasmania	Between -58 and -59 m	0-13
		74-86
		88-108
		110-131
		192-220
		229
		233-244
		282-291
		300-336
		382
		384
		386-424
		482+

SI References

SI References

- 1. M.L. Rosenzweig, Species Diversity in Space and Time (Cambridge University Press, 1995).
- 2. R.J. Whittaker, J.M. Fernández-Palacios, Island Biogeography: Ecology, Evolution, and Conservation (Oxford University Press, 2007).
- 3. P. Wessel, W.H.F. Smith, A global self-consistent, hierarchical, high-resolution shoreline database. J. Geophys. Res. 101, 8741-8743 (1996).
- K.G. Miller et al., A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. Oceanograph. 24, 40-53 (2011).
- 5. W.H.F. Smith, D.T. Sandwell, Global sea floor topography from satellite altimetry and ship depth soundings. Science, 277, 1956–1962 (1997).
- R.J. Edwards, A.J. Brooks, "The island of Ireland: drowning the myth of an Irish land-bridge?" in Mind the Gap: Postglacial Colonisation of Ireland, J.L. Daveport, D. Paddy Sleeman, P.C. Woodman, Eds (The Irish Naturalists' Journal, 2008), pp. 19-34.
- 7. C.D. Clark et al., Pattern and timing of retreat of the last British-Irish Ice Sheet. Quat. Sci. Rev., 44, 112-146 (2012).
- 8. J.L. Peters et al., Maximum extent and dynamic behaviour of the last British–Irish Ice Sheet west of Ireland. Quat. Sci. Rev, 128, 48-68 (2015).
- 9. Y. Kawamura, Succession of the mammalian fauna in Japan since the Last Glacial Period. The Earth Monthly (Gekkan Chikyu) 7, 349–353 (1985).
- 10. Y. Kawamura, Quaternary rodent faunas in the Japanese Island (Part 2). Mem. Faculty Sci. Kyoto Univ. Ser. Geol. Mineral. 54, 1–235 (1989).
- Y. Kawamura, Last Glacial and Holocene land mammals of the Japanese Islands: Their fauna, extinction and immigration. The Quat. Res. (Daiyonki-Kenkyu) 46, 171–177 (2007).
- 12. T. Oba, Comment for sea level change. The Quat. Res. (Daiyonki-Kenkyu), 26, 243–250 (1988).
- 13. T. Oba, in Sea and Civilization (Lectures on Civilization and Environment), (Asakura-shoten, 1995), pp. 49–65.
- A. Sahni, H.C. Mitra. Lower Miocene (Aquitanien-Burdigalian) palaeobiogeography of the Indian subcontinent. Geologische Rundschau 69.3, 824-848 (1980).
- 15. J. Malavieille et al., Arc-continent collision in Taiwan: New marine observations and tectonic evolution. Special Papers-Geol. Soc. Am. 187-211 (2002).
- 16. V.E. Neall, S.A. Trewick, The age and origin of the Pacific islands: a geological overview. Phil. Trans. R. Soc. B. 363, 3293-3308 (2008).

- 17. S.L. Baldwin, P.G. Fitzgerald, L.E. Webb. Tectonics of the New Guinea region. Ann. Rev. Earth and Plan. Sci. 40 (2012).
- D. B. Seymour, G.R. Green, C.R. Calver. The Geology and Mineral Deposits of Tasmania: A Summary, (Vol. 72. Dept. of Infrastructure, Energy and Resources, 2006).
- B. Daily et al. "Geology and geomorphology" in Natural History of Kangaroo Island. Vol. 2, M.J. Tyler, C.R. Twidale, J.K. Ling, Eds, (Royal Society of South Australia Adelaide, 1979), pp. 1-38.
- 20. S. Gupta et al., Two-stage opening of the Dover Strait and the origin of island Britain. Nat. Comm. 8.1 1-12 (2017).
- 21. A.C. Sarr et al., Subsiding Sundaland. Geology, 47, 119-122 (2019).
- 22. L.C. Maul, S.A. Parfitt, Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. Quat. Int. 228 91-115 (2010).
- G.J. Price et al., Big data little help in megafauna mysteries. Nature 558, 23-25 (2018).
- 24. H. Machida, F. Arai, Atlas of Tephra in and around Japan, revised edition (University of Tokyo Press, 2003).
- 25. A.A.E. van der Geer, M. Lomolino, G.A. Lyras, Islands before man: the speciesarea relationship during the late Pleistocene. *J. Biogeogr.* 44, 995–1006 (2017).
- 26. T., Sutikna *et al.*, Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. *Nature* **532**, 366-369 (2016).
- 27. A. Brumm *et al.*, Age and context of the oldest known hominin fossils from Flores. *Nature*, **534**, 249-253 (2016).
- 28. E. Olausson, Tephrochronology and the Late Pleistocene of the Aegan Sea *Opera Botanica* **30**, 29-39 (1971).
- 29. C.A. Chesner, W.I. Rose, Stratigraphy of the Toba tuffs and the evolution of the Toba caldera complex, Sumatra, Indonesia. *Bull. Volcanol.*, **53**, 343-356 (1991).
- 30. T.L Jones *et al.*, The protracted Holocene extinction of California's flightless sea duck (*Chendytes lawi*) and its implications for the Pleistocene overkill hypothesis. *Proc. Nat. Acad. Sci.* **105**, 4105-4108 (2008).
- T.C. Rick *et al.*, Flightless ducks, giant mice and pygmy mammoths: Late Quaternary extinctions on California's Channel Islands. *World Archaeol.* 44, 3-20 (2012).
- L.D. Agenbroad, Giants and pygmies: mammoths of Santa Rosa Island, California (USA). *Quat. Int.* 255, 2-8 (2012).
- 33. J.R. Johnson, T.W. Stafford, Jr., H.O. Ajie, D.P. Morris. "Arlington Springs revisited", in Proceedings of the Fifth California Islands Symposium, D. Browne,

K. Mitchell, H. Chaney, Eds. (Santa Barbara Museum of Natural History, 2002), pp. 541-545.

- 34. J.M. Erlandson *et al.*, Paleoindian seafaring, maritime technologies, and coastal foraging on California's Channel Islands. *Science*, **331**, 1181-1185 (2011).
- N.T. Monaghan, "Irish Quaternary vertebrates" in Advances in Irish Quaternary Studies, P. Coxon, S. McCarron, F. Mitchell Eds. (Atlantis Press, Paris, 2017), pp. 255-291.
- 36. P. Woodman, M. McCarthy, N. Monaghan, The Irish Quaternary Fauna Project. *Quat. Sci. Rev.* 16, 129–159 (1997).
- A.J Stuart, A.M. Lister, New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. *Quat. Sci. Rev.* 96, 108–116 (2014).
- 38. A.M. Lister, A.J. Stuart, The extinction of the giant deer *Megaloceros giganteus* (Blumenbach): New radiocarbon evidence. *Quat. Int.* **500**, 185-203 (2019).
- 39. A.M. Lister, R. Grün, Mammoth and musk ox ESR-dated to the early Midlandian at Aghnadarragh, county Antrim, Northern Ireland, and the age of the Fermanagh Stadial. *Geol. J.* **50**, 306–320 (2015).
- 40. M. Dowd, R.F. Carden. First evidence of a Late Upper Palaeolithic human presence in Ireland. *Quat. Sci. Rev.* **139**, 158-163 (2016).
- 41. G.A. Lyras, A.A.E. van der Geer, M.D. Dermitzakis, J. de Vos, *Cynotherium sardous*, an insular canid (Mammalia: Carnivora) from the Pleistocene of Sardinia (Italy), and its origin. *J. Vert. Paleontol.* 26, 735–745 (2006).
- 42. A.A.E. van der Geer, M. Lomolino, G.A. Lyras, Islands before man: the speciesarea relationship during the late Pleistocene. J. Biogeogr. 44, 995–1006 (2017).
- G. Klein Hofmeijer, Late Pleistocene deer fossils from Corbeddu Cave -Implications for human colonization of the island of Sardinia, Thesis, University of Utrecht (1996).
- 44. G. Klein Hofmeijer *et al.* La fine del Pleistocene nella Grotta Corbeddu in Sardegna. *Rivista di Scienze Preistoriche*, **41**, 1-36 (1987).
- 45. F. Cetti, I Quadrupedi di Sardegna (G. Piatolli, Sassari, Italy, 1774).
- 46. F. Delussu, "Lo stato attuale degli studi sulle faune oloceniche della Sardegna centro-settentrionale" in Atti del 2. Convegno Nazionale di Archeozoologica, Asti 14016 Novembre 1997, (Abaco, Forl., Italy, 2000), pp. 183-192.
- 47. M. Sanges, J.A. Alcover, Noticia sobre la micro-fauna vertebrada holocenica de la grotta Su Guanu o Gonagosula (Oliena, Sardenya). *Endins* **7**, 57-62 (1980).
- 48. R. Melis, M.R. Palombo, Sedimentary sequences and paleoclimate evidences in the Middle-Late Pleistocene of Sardinia. AIQUA, FStato delle conoscenze e nuovi dati, Bari, 24–25 giugno 2002, 26–7 (2002).
- 49. G.F. Willemsen, A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geol.* **101**, 1–115 (1992).

- 50. A. Malatesta, G.F. Willemsen, Algarolutra g.n. established for a fossil otter of the Sardinia island. *Geol. Romana* **25**, 285–286 (1986).
- G.F. Willemsen, A. Malatesta, *Megalenhydris barbaricina* sp. nov., a new otter from Sardinia. *Verhandelingen der Koninklijke Akademie van Wetenschappen* (Ser. B), 90, 83–92 (1987).
- 52. M.R Palombo, Biochronology of the Plio-Pleistocene terrestrial mammals of Sardinia: the state of the art. *Hellenic J. Geosci.* **41**, 47-66 (2006).
- 53. A. Louchart, C. Bedetti, M. Pavia, A new species of eagle (Aves: Accipitridae) close to the Steppe Eagle, from Pleistocene of Corsica and Sardinia, France and Italy. *Palaeontographica Abteilung A Paläozoologie, Stratigraphie*, **272**, 121-148 (2005).
- 54. F. Martini, "Early human settlement in Sardinia: the Palaeolithic industries" in Sardinia in the Mediterranean, a Footprint in the Sea, R. Tykot, T.K. Andrews Eds. (Sheffield Academic Press, Monographs in Mediterranean Archaeology 2, 1992), pp. 40-48.
- 55. P. Sondaar *et al.*, The human colonization of Sardinia: a Late—Pleistocene human fossil from Corbeddu cave. *C. R. Acad. Sci. Ser. II* **320**, 145-150 (1995).
- 56. H. Dawson, Mediterranean Voyages: The Archaeology of Island Colonisation and Abandonment (Left Coast Press, Walnut Creek, California, 2014).
- 57. S. Konishi, S. Yoshikawa, Immigration times of the two proboscidean species, *Stegodon orientalis* and *Palaeoloxodon naumanni*, into the Japanese Islands and the formation of land bridge. *Earth Sci. (Chikyu Kagaku)* **53**, 125–134 (1999).
- 58. H. Taruno, Y. Kawamura, "Mammoths of East Asia: Revisions of their taxonomy, chronospatial distribution, and immigration into Japan" in Jubilee Publication in Commemoration of Prof. Kamei Tadao's 80th Birthday (Publication Committee for the Commemoration of Prof. Kamei Tadao's 80th Birthday, Tokyo, 2007), pp. 59–78.
- 59. Y. Kawamura, R. Nakagawa, Terrestrial mammal faunas in the Japanese Islands during OIS 3 and OIS 2. *BAR Int. S.* **2352**, 33–54 (2012).
- 60. Y. Kawamura, "Fossil record of sika deer in Japan" in Sika Deer: Biology and Management of Native and Introduced Populations, D.R. McCullough, S. Takatsuki, K. Kaji, Eds. (Springer, New York, 2009), pp. 11–25.
- 61. Y. Kawamura, "Holocene and Late Pleistocene mammalian remains from Kazaana Cave" in Search for Japanese Pleistocene Human Remains in the Kitakami Mountains: Excavations of the Abakuchi and Kaza-ana Cave Sites in Ohasama, Iwate Prefecture, Y. Dodo, W. Takigawa, J. Sawada Eds. (Tohoku University Press, Sendai, 2003), pp.284-386.
- 62. Y. Kawamura, T. Kamei, H. Taruno, Middle and Late Pleistocene mammalian faunas in Japan. *The Quat. Res. (Daiyonki-Kenkyu)*, **28**, 317–326 (1989).

- 63. T. Inada, "Human history of the Palaeolithic Period and the Japanese Islands" in Lectures on Archaeology in Japan 1. Palaeolithic Period (Part 1), T. Inada, H. Sato Eds. (Aoki-shoten, Tokyo, 2010), pp. 3–39.
- 64. K. Matsufuji, "Establishment of Late Palaeolithic culture in East Asia" in Lectures on Archaeology in Japan 1. Palaeolithic Period (Part 2), T. Inada, H. Sato Eds. (Aoki-shoten, Tokyo, 2010), pp. 583–606.
- 65. T. Yanagida, "Regional chronology in the Tohoku District" in Regional Chronology of the Palaeolithic Period, M. Anzai, H. Sato, Eds. (Doseisha, Tokyo, 2006), pp.141–172.
- 66. A. Kawamura, C.H. Chang, Y. Kawamura, Middle Pleistocene to Holocene mammal faunas of the Ryukyu Islands and Taiwan: An updated review incorporating results of recent research. *Quat. Int.* **397**, 117-135 (2016).
- 67. Okinawa Prefectural Archaeological Center, Shiraho-Saonetabaru Cave Site: Report on the Range Confirmation Research Excavation of the Important Site I (Okinawa Prefectural Archaeological Center, Nishihara, 2017).
- A. Kawamura, Y. Kawamura, M. Namiki, Early Holocene wild boar remains from Tsudupisuki-abu Cave on Miyako Island of the Southern Ryukyus, Japan. *Quat. Int.* 455, 18–29 (2017).
- 69. Palynosurvey Co. Ltd, "Natural science analyses of Tsudupisuki-abu Cave" in Arafu Site, Tsudupisuki-abu Cave and Tomori-Motojima Site: Report on the Excavation Research of the Archaeological Sites in Miyakojima City (Miyakojima City Board of Education, Miyakojima, 2015), pp.120–141.
- Department of Education, Okinawa Prefectural Government, Pinza-Abu: Reports on Excavation of the Pinza-Abu Cave (Department of Education, Okinawa Prefectural Government, Naha, 1985).
- H. Otsuka, T. Nakamura, T. Ota, ¹⁴C ages of vertebrate fossil beds in the Ryukyu Islands, South Japan. *Summaries of Researches Using AMS at Nagoya University*, 19, 135–153 (2008).
- 72. I. Oshiro, T. Nohara, Distribution of Pleistocene terrestrial vertebrates and their migration to the Ryukyus. *Tropics*, **10**, 41-50 (2000).
- 73. H. Takamiya, M. Kin, M. Suzuki, Excavation report of the Yamashita-cho Cave Site, Naha-shi, Okinawa. J. Anthropol. Soc. Nippon, 83, 125-130 (1975).
- 74. Y. Kaifu, M. Fujita, Fossil record of early modern humans in East Asia. *Quat. Int.* 248, 2-11 (2012).
- 75. P-O. Antoine *et al.*, A new rhinoceros clade from the Pleistocene of Asia sheds light on mammal dispersals to the Philippine. *Zool. J. Linn. Soc.* 10.1093/zoolinnean/zlab009 (2021).
- 76. Ingicco, T. et al. Earliest known hominin activity in the Philippines by 709 thousand years ago. *Nature*, **557**, 233-237 (2018).

- 77. J. de Vos, A. Bautista, Preliminary notes on the vertebrate fossils from the Philippines. *Proc. Soc. Philippine Archaeol.* **1**, 46–62 (2003).
- G.H.R. von Koenigswald, Fossil Mammals from the Philippines (National Research Council of the Philippines, University of the Philippines, Diliman, Special reprint, 1956)
- T. Ingicco *et al.*, A new species of *Celebochoerus* (Suidae, Mammalia) from the Philippines and the palaeobiogeography of the genus *Celebochoerus* Hooijer, 1948. *Geobios* 49, 285-291(2016).
- K. Hans-Volker, U. Staesche, Fossile Riesen-Landschildkröten von den Philippinen und ihre paläogeographische Bedeutung. *Geologisches Jahrbuch* 160, 171-197 (2006).
- W.U. Schoell, P. Militante-Matias, A. Peleo, *Stegodon* fossil remains from the Plio-Pleistocene Laguna Formation, Antipolo, Rizal. *Nat. Appl. Sci. Bull.* **39**, 217-236 (1987).
- 82. L.R. Heaney, P.J. Piper, A.S. Mijares, The first fossil record of endemic murid rodents from the Philippines: A late Pleistocene cave fauna from northern Luzon. *Proc. Biol. Soc. Washington*, **124**, 234-247 (2011).
- 83. A.S. Mijares, *et al.*, New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. *J. Hum. Evol.* **59**, 123-132 (2010).
- D.A Croft, L.R. Heaney, J.J. Flynn, A.P. Bautista, Fossil remains of a new, diminutive *Bubalus* (Artiodactyla: Bovidae: Bovini) from Cebu island, Philippines. *J. Mammal.* 87, 1037-1051 (2006).
- 85. F. Détroit *et al.*, A new species of *Homo* from the Late Pleistocene of the Philippines. *Nature*, **568**, 181–186 (2019).
- A.S. Mijares *et al.*, New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. J. Hum. Evol. 59, 123–132 (2010).
- A.S.B. Mijares, Unearthing Prehistory: The Archaeology of Northeastern Luzon, Philippine Islands (British Archaeological Reports Limited, Oxford, Vol. 1613, 2007).
- M.C. Reyes *et al.*, First fossil evidence of an extinct cloud rat (*Crateromys paulus*) (Chordata: Mammalia: Rodentia, Muridae) from Ilin Island, Mindoro (Philippines): Insights on *Crateromys paulus* diversity. *Proc. Biol. Soc. Washington* 130, 84-97 (2017).
- 89. A. Pawlik, P. Piper, The Philippines from c. 14,000 to 4,000 cal. bp in regional context. *Cambr. Archaeol. J.* **29**, 1–22 (2018).
- 90. C. Boulanger *et al.*, Coastal subsistence strategies and mangrove swamp evolution at Bubog I Rockshelter (Ilin Island, Mindoro, Philippines) from the Late Pleistocene to the mid-Holocene. *J. Is. Coast. Archaeol.* **14**, 584-604 (2019).

- 91. P.J. Piper *et al.*, The first evidence for the past presence of the tiger *Panthera tigris* on the island of Palawan, Philippines: Extinction in an island population. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **264**, 123-127 (2008).
- 92. P.J. Piper et al., Palaeozoology of Palawan Island, Philippines. Quat. Int. 233, 142-158 (2011).
- 93. Détroit, F. *et al.*, Upper Pleistocene *Homo sapiens* from the Tabon cave (Palawan, The Philippines): description and dating of new discoveries. *C. R. Palevol* **3**, 705-712 (2004).
- 94. A.F. Pawlik, P.J. Piper, A.S.B. Mijares, "Modern humans in the Philippines: colonization, subsistence and new insights into behavioural complexity" in Southern Asia, Australia and the Search for Human Origins, R. Dennell, M. Porr Eds. (Cambridge Uni Press, Cambridge, 2014), 135-147.
- 95. D.W. Steadman, J.P. White, J. Allen, Prehistoric birds from New Ireland, Papua New Guinea: extinctions on a large Melanesian island. *Proc. Natl. Acad. Sci.* U.S.A. 96, 2563-2568 (1999).
- 96. D.W. Steadman, Extinction and biogeography of tropical Pacific birds. (University of Chicago Press, 2006).
- 97. S.K. Wickler, The prehistory of Buka: A stepping stone island in the Northern Solomons. (Terra Australis 16, The Australian National University, 2001).
- T. F. Flannery, S. Wickler, Quaternary murids (Rodentia: Muridae) from Buka Island, Papua New Guinea, with descriptions of two new species. *Aust. Mammal.* 13, 127-139 (1990).
- 99. S. Wickler, M. Spriggs, Pleistocene human occupation of the Solomon Islands, Melanesia. *Antiquity*, **62**, 703-706 (1988).
- 100. G. D. van den Bergh, The Late Neogene elephantoid-bearing faunas of Indonesia and their palaeozoogeographic implications: a study of the terrestrial faunal succession of Sulawesi, Flores and Java, including evidence for early hominid dispersal east of Wallace's Line. *Scripta Geologica*, **117**, 1-419 (1999).
- 101. G.N Markov, H. Saegusa, On the validity of *Stegoloxodon* Kretzoi, 1950 (Mammalia: Proboscidea). Zootaxa, **1861**, 55-56 (2008).
- 102. G.D. van den Bergh, *et al.* Earliest hominin occupation of Sulawesi, Indonesia. *Nature*, **529**, 208-211 (2016).
- 103. G.D. van den Bergh *et al.*, The fossil terrestrial fauna record of Sulawesi and hominin colonization. Paper presented at the 3rd Southeast Asian Gateway Evolution Meeting 28 August 1 Sept 2017, Bogor, Indonesia (2017).
- 104. A. Brumm *et al.*, A reassessment of the early human archaeological record at Leang Burung 2, a Late Pleistocene rock-shelter site on the Indonesian island of Sulawesi. *PLoS ONE* **13**, e0193025 (2018).

- R. Rozzi, A new extinct dwarfed buffalo from Sulawesi and the evolution of the subgenus *Anoa*: An interdisciplinary perspective. *Quat. Sci. Rev.* 157, 188-205 (2017).
- M. Aubert *et al.*, Pleistocene cave art from Sulawesi, Indonesia. *Nature*, 514, 223–227 (2014).
- 107. A. Brumm *et al.*, Oldest cave art found in Sulawesi. *Sci. Adv.* **7**, eabd4648 (2021).
- 108. K.P. Aplin, K.M. Helgen, Quaternary murid rodents of Timor Part I: new material of *Coryphomys buehleri* Schaub, 1937, and description of a second species of the genus. *Bull. Am. Mus. Nat. Hist.* **341**, 1-80 (2010).
- 109. I. Glover, Archaeology in Eastern Timor (Terra Australis 11, Australian National University, 1986).
- S. Sartono, *Stegodon timorensis*: a pygmy species from Timor (Indonesia). *Proc. Koninklijke Nederlandse Akademie van Wetenschappen, B.* **72**, 192-202 (1969).
- 111. D.A. Hooijer, *Stegodon* from Timor. *Proc. Koninklijke Nederlandse Akademie van Wetenschappen, B.* **72**, 201-210 (1969).
- 112. D.A. Hooijer Stegodon trigonocephalus florensis Hooijer and Stegodon timorensis Sartono from the Pleistocene of Flores and Timor. I & II. Proc. Koninklijke Nederlandse Akademie van Wetenschappen, B. **75**, 12-33 (1972).
- 113. J. Louys, G.J. Price, S. O'Connor, Direct dating of Pleistocene stegodon from Timor Island, East Nusa Tenggara. *PeerJ* **4**, e1788 (2016).
- 114. D.A. Hooijer, *Stegodon trigonocephalus florensis* Hooijer and *Stegodon timorensis* Sartono from the Pleistocene of Flores and Timor. *The Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, **75**, 12-33 (1972).
- 115. D.A. Hooijer, The Stegodon from Timor. *The Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, **72**, 201-210 (1969).
- 116. D.A. Hooijer *Varanus* (Reptilia, Sauria) from the Pleistocene of Timor. *Zoologische Mededelingen* **47**, 445-448 (1972).
- H.J. Meijer, J. Louys, S. O'Connor, First record of avian extinctions from the Late Pleistocene and Holocene of Timor Leste. *Quat. Sci. Rev.* 203, 170-184 (2019).
- 118. S. Hawkins *et al.*, Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. *Quat. Sci. Rev.* **171**, 58-72 (2017).
- 119. J. Louys *et al.*, New genus and species of giant rat from Alor Island, Indonesia. J. Asia-Pacific Biodiv. **11**, 503-510 (2018).
- S. Kealy, *et al.*, Forty-thousand years of specialised maritime subsistence near a changing shoreline on Alor Island (Indonesia). *Quat. Sci. Rev.* 249, 106599 (2020).

- 121. E. Locatelli, R.A. Due, G.D. van den Bergh, L.W. Van Den Hoek Ostende, Pleistocene survivors and Holocene extinctions: the giant rats from Liang Bua (Flores, Indonesia). *Quat. Int.* **281**, 47-57 (2012).
- 122. E.G. Veatch *et al.*, Temporal shifts in the distribution of murine rodent body size classes at Liang Bua (Flores, Indonesia) reveal new insights into the paleoecology of *Homo floresiensis* and associated fauna. *J. Hum. Evol.* **130**, 45-60 (2019).
- 123. G.D. van den Bergh *et al.*, The Liang Bua faunal remains: a 95 k. yr. sequence from Flores, East Indonesia. *J. Hum. Evol.* **57**, 527-537 (2009).
- 124. G. Musser, The giant rat of Flores and its relatives east of Borneo and Bali. *Bull. Am. Mus. Nat. Hist.* **169**, 67-176 (1981).
- 125. T. Sutikna *et al.*, The spatio-temporal distribution of archaeological and faunal finds at Liang Bua (Flores, Indonesia) in light of the revised chronology for *Homo floresiensis*. J. Hum. Evol. **124**, 52-74 (2018).
- 126. H.J.M. Meijer *et al.*, Late Pleistocene songbirds of Liang Bua (Flores, Indonesia); the first fossil passerine fauna described from Wallacea. *PeerJ* **5**, e3676 (2017).
- 127. H.J.M. Meijer, L.W. van den Hoek Ostende, G.D. van den Bergh, J. de Vos, The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*. J. *Biogeogr.* 37, 995-1006 (2010).
- 128. A. Brumm *et al.*, Age and context of the oldest known hominin fossils from Flores. *Nature*, **534**, 249-253 (2016).
- 129. D. Yurnaldi, R. Setiawan, E.Y. Patriani, The magnetostratigraphy and the age of So'a Basin fossil-bearing sequence, Flores, Indonesia. *Indon. J. Geosci.* **5**, 221-234 (2018).
- 130. G.D. van den Bergh *et al.*, An update of the stratigraphic framework of the So'a Basin on Flores, with implications for first hominin arrival and faunal turnover. Abstract, International Conference on *Homo luzonensis* and the Hominin Record of Southeast Asia (Diliman, Quezon City, Philippines, 2020).
- 131. A. Brumm *et al.*, Hominins on Flores, Indonesia, by one million years ago. *Nature* **464**, 748-752 (2010).
- 132. Callaway, E. Human remains found in hobbit cave. *Nature News*, 10.1038/nature.2016.20656 (2016).
- 133. S.T. Turvey *et al.* Quaternary vertebrate faunas from Sumba, Indonesia: implications for Wallacean biogeography and evolution. *Proc. R. Soc. B.*, **284**, 20171278 (2017).
- 134. T. Simanjuntak, F. Sémah, C. Gaillard, The Palaeolithic in Indonesia: nature and chronology. *Quat. Int.* **223-224**, 418-421 (2010).
- 135. G.J. Boekschoten, P.Y. Sondaar, On the fossil Mammalia of Cyprus. *Proc. Koninklijke Nederlandse Akademie van Wetenschappen* **75**, 306-338 (1972).

- 136. A. Simmons, Faunal Extinctions in an Island Society: Pygmy Hippopotamus Hunters of Cyprus (Kluwer Academic/Plenum Publishers, New York, 1999).
- 137. A. Simmons, Akrotiri-Aetokremnos (Cyprus) 20 years later: an assessment of its significance. *Eurasian Prehist.* **10**, 139-155 (2013).
- 138. A. Simmons, R. Mandel, "Site formation processes at Akrotiri Aetokremnos, Cyprus: Why is the site so controversial?" in Géoarchéologie des îles de Méditerrané, M. Ghilardi, Eds. (CNRS éditions, 2016), pp. 57-72.
- 139. A. Athanassiou *et al.*, Cranial evidence for the presence of a second endemic elephant species on Cyprus. *Quat. Int.* **379**, 47-57 (2015).
- G.E., Theodorou *et al.*, A Late Pleistocene endemic genet (Carnivora, Viverridae) from Aghia Napa, Cyprus. *Bull. Geol. Soc. Greece*, 40, 201-208 (2007).
- 141. J. De Vos, The endemic Pleistocene deer of Crete. *Verhandeling der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Eerste reeks, Deel* **31**, 100 (1984).
- 142. G. Belluomini, L. Delitala, Datazione di resti ossei e denti del Pleistocene superiore e dell'Olocene dell'area mediterranea con il metodo della racemizzazione degli aminoacidi. Geograf. *Fis. Din. Quat.* **6**, 21–30 (1983).
- 143. D. Reese, G. Belluomini, M. Ikeya, "Absolute dates for the Pleistocene fauna of Crete", in Pleistocene and Holocene Fauna of Crete and its First Settlers Reese, D.S. Reese Ed. (Prehistory Press, Madison, 1996), pp. 47–52.
- 144. D. Mayhew, The endemic Pleistocene murids of Crete I-II. *Proc. Koninklijke Nederlandse Akademie van Wetenschappen*, **80**, 182-214 (1977).
- 145. P.D.M. Weesie, A Pleistocene endemic island form within the genus *Athene: Athene cretensis* n. sp. (Aves, Strigiformes) from Crete. *Proc. Koninklijke Nederlands Akademie van Wetenschappen Amsterdam B.*, **85**, 323-336 (1982).
- 146. G.J. Boekschoten, P.Y. Sondaar, The Pleistocene of the Katharo Basin (Crete) and its hippopotamus. *Bijdragen tot de Dierkunde*, **36**, 7-17 (1966).
- 147. V.L. Herridge, A.M. Lister, Extreme insular dwarfism evolved in a mammoth. *Proc. R. Soc. B.* **279**, 3193-3200 (2012).
- C. Runnels, C. DiGregorio, K.W. Wegmann, S.F. Gallen, T.F. Strasser, E. Panagopoulou, Lower Palaeolithic artifacts from Plakias, Crete: implications for hominin dispersals. *J. Eurasian Prehist.* 11, 129–152 (2014).
- F. Facchini, G. Giusberti, "Homo sapiens sapiens remains from the island of Crete", in Continuity or Replacement: Controversies in Homo sapiens Evolution, G. Bräuer, F.H. Smith, F.H. Eds. (A.A.Balkema, Rotterdam, 1992), pp. 189–208.
- 150. A.A.E. van der Geer *et al.*, A dwarf elephant and a rock mouse on Naxos (Cyclades, Greece) with a revision of the palaeozoogeography of the Cycladic

Islands (Greece) during the Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **404**, 133-144 (2014).

- 151. T. Carter *et al.*, The Stélida Naxos archaeological project: new data on the Middle Palaeolithic and Mesolithic cyclades. *Antiquity*, **88**, 341 (2014).
- 152. A.J. Stuart, Pleistocene vertebrates in the British Isles (Longman Financial Service, 1982).
- 153. L.C. Maul, S.A. Parfitt. Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. *Quat. Int.* **228**, 91-115 (2010).
- 154. J.R. Stewart, The progressive effect of the individualistic response of species to Quaternary climate change: an analysis of British mammalian faunas. *Quat. Sci. Rev.* **27**, 2499-2508 (2008).
- 155. A.M. Lister, A. Brandon. A pre-Ipswichian cold stage mammalian fauna from the Balderton Sand and Gravel, Lincolnshire, England. *J. Quat. Sci.* **6** 139-157 (1991).
- 156. A. Turner, The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. J. Quat. Sci. 24, 991-1005 (2009).
- 157. A. Currant, R. Jacobi, A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quat. Sci. Rev.* **20**, 1707-1716 (2001).
- 158. M.J. White, P.B. Pettitt, The British Late Middle Palaeolithic: an interpretative synthesis of Neanderthal occupation at the northwestern edge of the Pleistocene world. *J. World Prehist.* **24**, 25-97 (2011).
- 159. J. R. Stewart *et al.*, "The mammalian faunas of Europe during oxygen isotope stage three" in Neanderthals and Modern Humans in the European Landscape during the Last Glaciation, T.H. Van Andel, W. Davies, Eds. (McDonald Institute for Archaeological Research, 2003), pp. 103-130.
- 160. A. J. Stuart *et al.*, The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. *Quat. Sci. Rev.* **21**, 1559-1569 (2002).
- 161. R.Dinnis, A. Pate, N. Reynolds, Mid-to-late Marine Isotope Stage 3 mammal faunas of Britain: a new look. *Proceedings of the Geologists' Association* **127**, 435-444 (2016).
- 162. A.M. Lister, A.J. Stuart. The extinction of the giant deer *Megaloceros giganteus* (Blumenbach): New radiocarbon evidence. *Quat. Int.* **500**, 185-203 (2019).
- 163. T. Higham *et al.*, The earliest evidence for anatomically modern humans in northwestern Europe. *Nature*, **479**, 521-524 (2011).
- 164. A.R. Sumanarathna, J. Katupotha, K. Abeywardhana, B. Madurapperuma, Extinction of Quaternary mammalian habitats of megafauna in Sabaragamuwa Basin, Sri Lanka. *J. Eco Astron.* **1**, 16- 31 (2017).

- O. Wedage *et al.*, Late Pleistocene to early-Holocene rainforest foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena. *Quat. Sci. Rev.* 231, 106200 (2020).
- 166. A. Kawamura, C.H. Chang, Y. Kawamura, Middle Pleistocene to Holocene mammal faunas of the Ryukyu Islands and Taiwan: An updated review incorporating results of recent research. *Quat. Int.*, **397**, 117-135 (2016).
- 167. C.H. Chang *et al.*, The first archaic *Homo* from Taiwan. *Nature Comm.* **6**, 1-10 (2015).
- C.M. Lien, "Chang-pin culture of Taiwan and characteristics of its lithic industry" in Emergence and Diversity of Modern Human Behavior in Paleolithic Asia, Y. Kaifu, M. Izuho, T. Goebel, H. Sato, A. Ono Eds. (Texas A&M, College Station, 2014), pp. 239-249.
- 169. Y. Terasaki, "Regional chronology in the Hokkaido District" in Regional Chronology of the Palaeolithic Period, M. Anzai, H. Sato Eds. (Doseisha, Tokyo, 2006), pp. 275–314.
- T. Yamahara, Y. Terasaki, "Hokkaido" in Lectures on Archaeology in Japan 1. Palaeolithic Period (Part 1), T. Inada, H. Sato Eds. (Aoki-shoten, Tokyo, 2010), pp. 265–308.
- 171. H.H. Scott, C.E. Lord, Studies in Tasmanian mammals living and extinct. No. 5. Zaglossus harrissoni sp. nov. Pap. Proc. R. Soc. Tasm. 13-15 (1922).
- 172. H.H. Scott, Memoir on *Macropus anak* from King Island. *Queen Vict. Mus. Brochure* 1905.
- 173. H.H. Scott, Some paleontological notes. *Queen Vict. Mus Brochure* **6**, 1917.
- 174. R.H. Tedford, A review of the macropodid genus *Sthenurus*. *Univ. Calif. Pubis. Geol. Sci.* **57**, 1-72 (1966).
- 175. J.H. Hope, Mammals of the Bass Strait islands. *Proc. Roy. Soc. Vict.* **85**, 163–195 (1973)
- C.S.M. Turney *et al.*, Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction. *Proc. Natl. Acad. Sci. U.S.A.* 105, 12150–12153 (2008).
- 177. D. M. D'Costa, J. Grindrod, R. Ogden, Preliminary environmental reconstructions from late Quaternary pollen and mollusc assemblages at Egg Lagoon, King Island, Bass Strait. *Austral Ecol.* **18**, 351-366 (1993).
- 178. J. N. Jennings, The coastal geomorphology of King Island, Bass Strait, in relation to changes in relative level of land and sea. *Rec. Queen Vict. Mus.* **11**, 1-39 (1959).
- 179. R. Sim, A. Thorne, Pleistocene human remains from King Island, southeastern Australia. *Aust. Archaeol.* **31**, 44-51 (1990).

- E. D. Gill, M. R. Banks, Cainozoic History of Mowbray Swamp and Other Areas of North-western Tasmania (Museum Committee, Launceston City Council, 1956).
- 181. R. Cosgrove, *et al.*, Overdone overkill the archaeological perspective on Tasmanian megafaunal extinctions. *J. Archaeol. Sci.* **37**, 2486-2503 (2010).
- 182. M.C. McDowell, Late Quaternary Faunal Responses of Environmental Change and Isolation on a Large Australian Land-bridge Island, Thesis, Flinders University of South Australia (2013).
- 183. S.J. Adams, M.C. McDowell, G.J. Prideaux, Understanding accumulation bias in the ecological interpretation of archaeological and paleontological sites on Kangaroo Island, South Australia. *J. Archaeol. Sci. Rep.*, **7**, 715-729 (2016).
- 184. R.T. Wells *et al.*, Late Pleistocene megafauna site at Black Creek Swamp, Flinders Chase National Park, Kangaroo Island, South Australia. *Alcheringa Special Issue* 1, 367–387 (2006).
- 185. M.C. McDowell *et al.*, Re-evaluating the Late Quaternary fossil mammal assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna. *J. Quat. Sci.* **30**, 355–364 (2015).
- 186. T.F. Flannery, M.J. Mountain, K. Aplin, Quaternary kangaroos (Macropodidae: Marsupialia) from Nombe rock shelter, Papua New Guinea, with comments on the nature of megafaunal extinction in the New Guinea Highlands. *Proc. Linn. Soc. N.S.W.* **107**, 75-97 (1983).
- 187. A. Sutton *et al.*, Archaeozoological records for the highlands of New Guinea: a review of current evidence. *Aust. Archaeol.* **69**, 41-58 (2009).
- 188. M.J. Mountain, Highland New Guinea Hunter-Gatherers: The Evidence of Nombe Rockshelter, Simbu, with Emphasis on the Pleistocene. Thesis. Australian National University (1991).
- 189. G.S. Hope, T.F. Flannery, Boeadi, A preliminary report of changing Quaternary mammal faunas in subalpine New Guinea. *Quat. Res.* 40, 117-126 (1993).
- T.F. Flannery, M. Plane, A new Late Pleistocene diprotodontid (Marsupialia) from Pureni, Southern Highlands Province, Papua New Guinea. *BMR J. Aust. Geol. Geophys.* 10, 65-76 (1986).
- 191. S.G. Haberle, Late Quaternary vegetation change in the Tari Basin, Papua New Guinea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **137**, 1-24 (1998).
- 192. P.V. Rich, M. Plane, N. Schroeder, A pygmy cassowary (*Casuarius lydekkeri*) from late Pleistocene bog deposits at Pureni, Papua New Guinea. *BMR J. Aust. Geol. Geophys.* 10, 377-389 (1988).
- 193. H.S. Hardjasasmita, Fosil diprotodontid: *Zygomaturus* Owen 1859 dari Nimboran, Irian Jaya. *Pertemuan Ilmiah Arkeologi*, **3**, 999-1004 (1985).

- 194. M-J. Mountain, Highland New Guinea Hunter-Gatherers: The Evidence of Nombe Rockshelter, Simbu, with Emphasis on the Pleistocene, Thesis, Australian National University (1991).
- 195. P.F. Murray, The smallest New Guinea zygomaturines derived dwarfs or relict plesiomorphs?. *Beagle: Rec. Mus. Art Gall. N.T.*, **9**, 89-110 (1992).
- 196. K.P. Aplin, J.M. Pasveer, W.E. Boles, Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. *Rec. West. Aust. Mus. Suppl.* 57, 351-387 (1999).
- 197. J.M. Pasveer, S.J. Clarke, G.H. Miller, Late Pleistocene human occupation of inland rainforest, Bird's Head, Papua. *Archaeol. Oceania*, **37**, 92-95 (2002).
- B.P. Kear, K.P. Aplin, M. Westerman, Bandicoot fossils and DNA elucidate lineage antiquity amongst xeric-adapted Australasian marsupials. *Sci. Rep.* 6, 37537 (2016).
- 199. G.R. Summerhayes *et al.*, Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science*, **330**, 78-81 (2010).
- P.J. Piper, R.J. Rabett, E.O. Cranbrook, New discoveries of an extinct giant pangolin (*Manis* cf. *palaeojavanica* Dubois) at Niah Cave, Sarawak, Borneo: biogeography, palaeoecology and taxonomic relationships. *Sarawak Mus. J.* 84, 207-226 (2007).
- 201. T. Higham *et al.*, "Radiocarbon Dating" in Archaeological Investigations in the Niah Caves, Sarawak, G. Barker, and L. Farr Eds. (McDonald Institute for Archaeological Research, Oxford, 2016), pp. 219-232.
- 202. van den Bergh, G.D. de Vos, J., Sondaar, P.Y. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **171**, 385-408 (2001).
- 203. J.C.A. Joordens *et al.*, *Homo erectus* at Trinil on Java used shells for tool production and engraving. *Nature*, **518**, 228-231 (2015).
- 204. R. Volmer *et al.*, When did *Cuon* reach Java?–Reinvestigation of canid fossils from *Homo erectus* faunas. *Geobios* **55**, 89-102 (2019).
- Y. Zaim *et al.*, A new antler specimen from the 1936 Perning hominid site, East Jawa, Indonesia, attributable to *Axis lydekkeri* (Martin, 1886). *J. Miner. Technol.* 10, 45-52 (2003).
- 206. F. Aziz, "New insights on the Pleistocene Fauna of Sangiran and other hominid sites in Asia" in Sangiran: Man, Cluture, and Environment in Pleistocene Times, T. Simanjuntak, B. Prasetyo, R. Handini Eds. (Yayasan Obor, Indonesia, 2007), pp. 154-171.
- 207. Y. Rizal *et al.*, Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. *Nature*, **577**, 381-385 (2020).

- 208. A. Bouteaux, A.-M. Moigne, New taphonomical approaches: The Javanese Pleistocene open-air sites (Sangiran, central Java). *Quat. Int.* **223–224**, 220–225 (2010).
- 209. J.A. de Visser, The extinct genus *Hexaprotodon* Falconer & Cautley, 1836 (Mammalia, Artiodactyla, Hippopotamidae) in Asia: paleoecology and taxonomy. Dissertation, University of Utrecht (2008).
- 210. H. S. Hardjasasmita, Taxonomy and phylogeny of the Suidae (Mammalia) in Indonesia. *Scripta Geologica*, **85**, 1-68 (1987).
- 211. A.A. van der Geer, G. Lyras, J. de Vos, D. Dermitzakis, Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands (John Wiley, New York, 2010).
- 212. J. de Vos, P.Y. Sondaar, G.D. van den Bergh, F. Aziz, The *Homo* bearing deposits of Java and its ecological context. *Courier Forschung-Institut Senkenberg* **171**, 129-140.
- G.H.R. von Koenigswald, Beitrage zur Kennunis der fossilen Wirbeltiere Javas. Wetenschappelijke Mededeelingen Dienst Mijnbouw Nederlandsch-Indië
 23, 1–127 (1933).
- 214. G.A. Lyras, A.A. van der Geer, L. Rook, Body size of insular carnivores: evidence from the fossil record. *J. Biogeogr.* **37**, 1007-1021 (2010).
- B. Kurtén, The sabre-toothed cat *Megantereon* from the Pleistocene of Java. *Zoologische Mededelingen* 38, 101-104 (1962).
- C. Hertler, R. Volmer, Assessing prey competition in fossil carnivore communities—a scenario for prey competition and its evolutionary consequences for tigers in Pleistocene Java. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 257, 67-80. (2008).
- 217. D.A. Hooijer, The geological age of *Pithecanthropus*, *Meganthropus* and *Gigantopithecus*. *Am. J. Phys. Anthropol.* **9**, 265-282 (1951).
- 218. F. Aziz, "New Insight on the Pleistocene Fauna of Sangiran and Other Hominid Sites in Java" in *Sangiran: Man, Culture, and Environment in Pleistocene Times,* Proceedings of the International Colloquium on Sangiran Solo, Indonesia (1998).
- 219. C. Zanolli *et al.* Evidence for increased hominid diversity in the Early to Middle Pleistocene of Indonesia. *Nat. Ecol. Evol.* **3**, 755-764 (2019).
- 220. A. Wetmore, Avian remains from the Pleistocene of central Java. J. *Paleontol.* **14**, 447–450 (1940).
- 221. S. Matsu'ura *et al.*, Age control of the first appearance datum for Javanese *Homo erectus* in the Sangiran area. *Science*, **367**, 210-214 (2020).
- 222. M.J. Morwood, *et al.*, Climate, people and faunal succession on Java, Indonesia: evidence from Song Gupuh. *J. Archaeol. Sci.* **35**, 1776-1789 (2008).

- 223. J. Louys *et al.*, Quaternary extinction of large rainforest herbivores on Indonesia's largest island, Sumatra. *J. Vert. Paleont.* (Program and Abstracts, 2019), 144-145 (2019).
- 224. K.E. Westaway, *et al.*, An early modern human presence in Sumatra 73,000-63,000 years ago. *Nature* **548**, 322-325 (2017).
- 225. C.B. Ramsey, Bayesian analysis of radiocarbon dates. *Radiocarbon*, **51**, 337-360 (2009).
- 226. P.J. Reimer *et al.*, The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, **62**, 725-757 (2020).