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 continental-level 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 large-scale 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 cagayanensis* 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

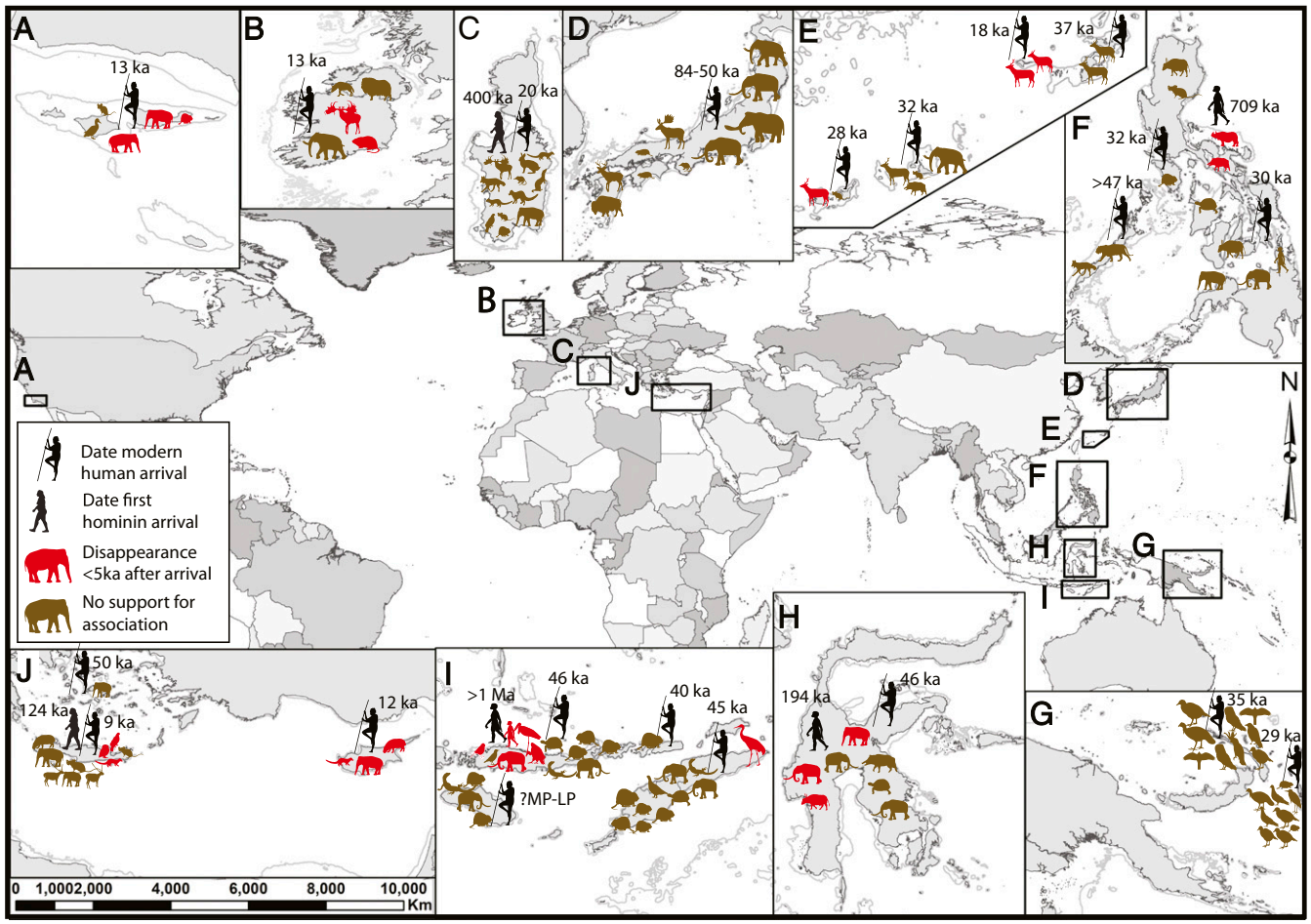


Fig. 1. Oceanic island groups with a documented record of Pleistocene hominins and faunal extinction. Clockwise from the top are San Miguel, Santa Rosa, and Santa Cruz (*A*); Ireland (*B*); Sardinia (*C*); Honshu, Shikoku, and Kyushu (*D*); Ishigaki, Miyako, Kume, and Okinawa (*E*); Luzon, Mindanao, 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).

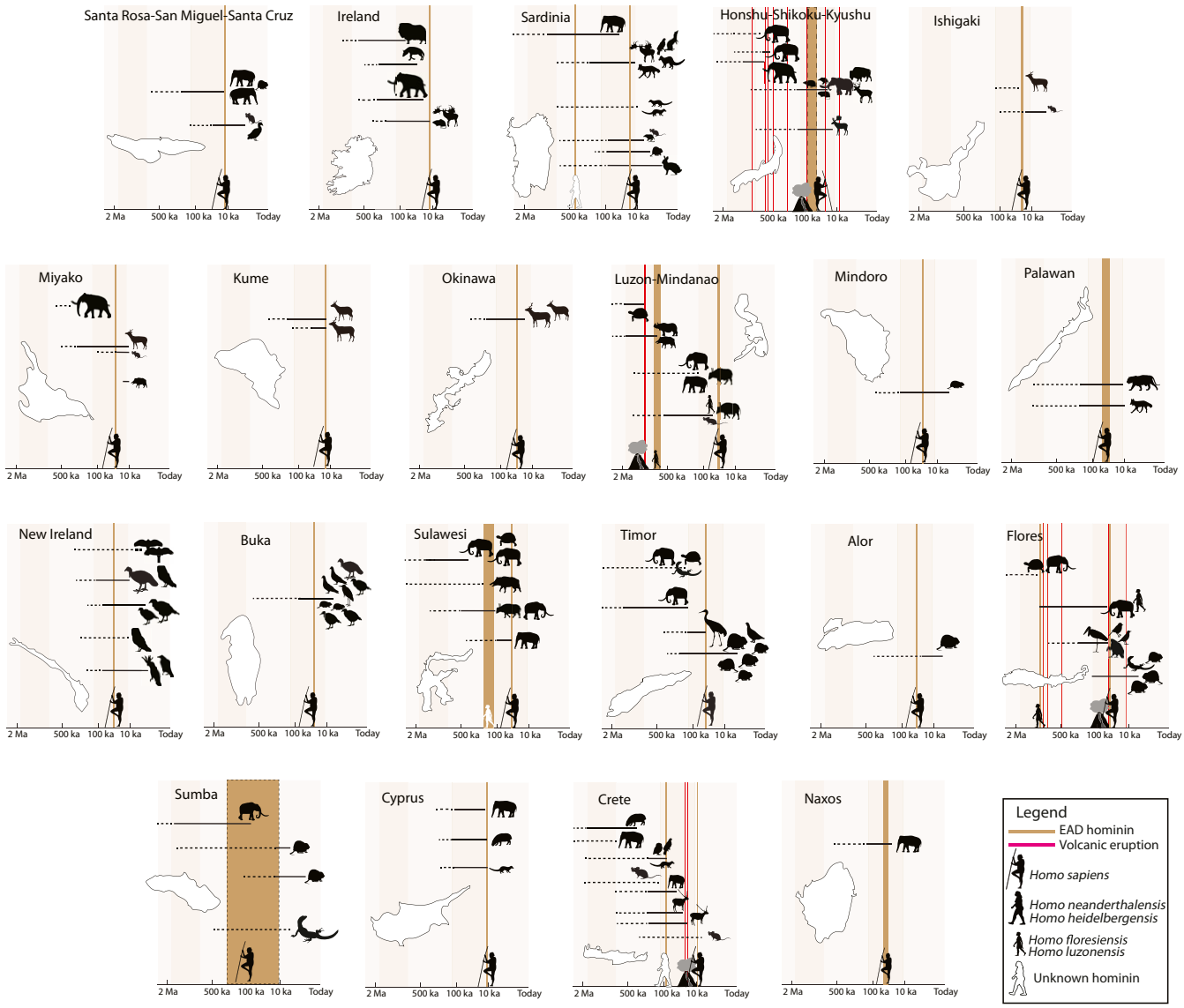


Fig. 2. Extinction chronology (right end of horizontal bars) shown with respect to the first hominin and *H. sapiens* arrival (vertical bars and boxes) to oceanic islands. Outlines for island groups are shown as one island during LGM connection. Extinct taxon LADs are represented by horizontal lines. 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*).

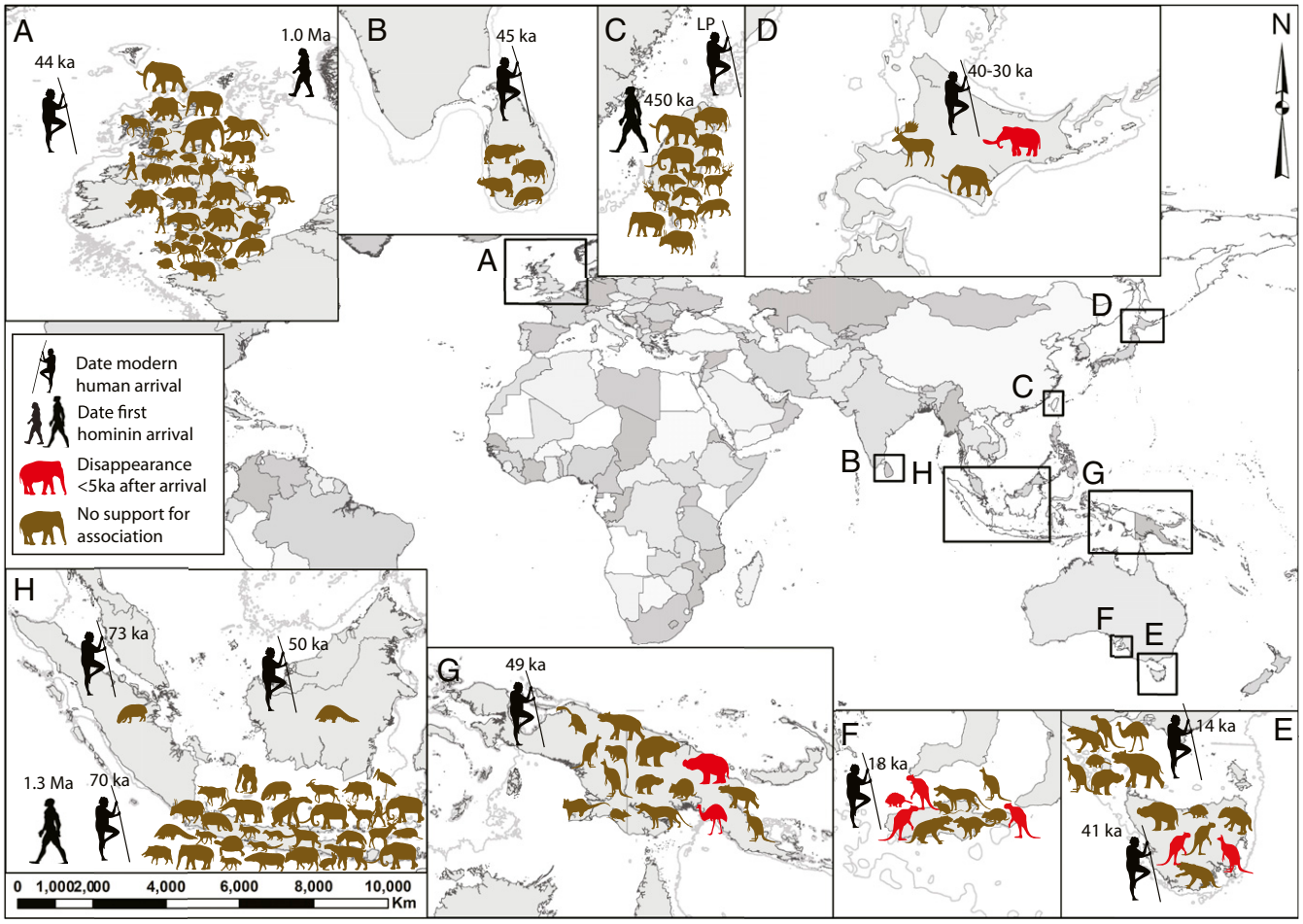


Fig. 3. Continental island groups with a documented record of Pleistocene hominins and faunal extinction. Clockwise from the top are Britain (*A*); Sri Lanka (*B*); Taiwan (*C*); Hokkaido (*D*); King Island and Tasmania (*E*); Kangaroo Island (*F*); New Guinea (*G*); and Borneo, Java, and Sumatra (*H*).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

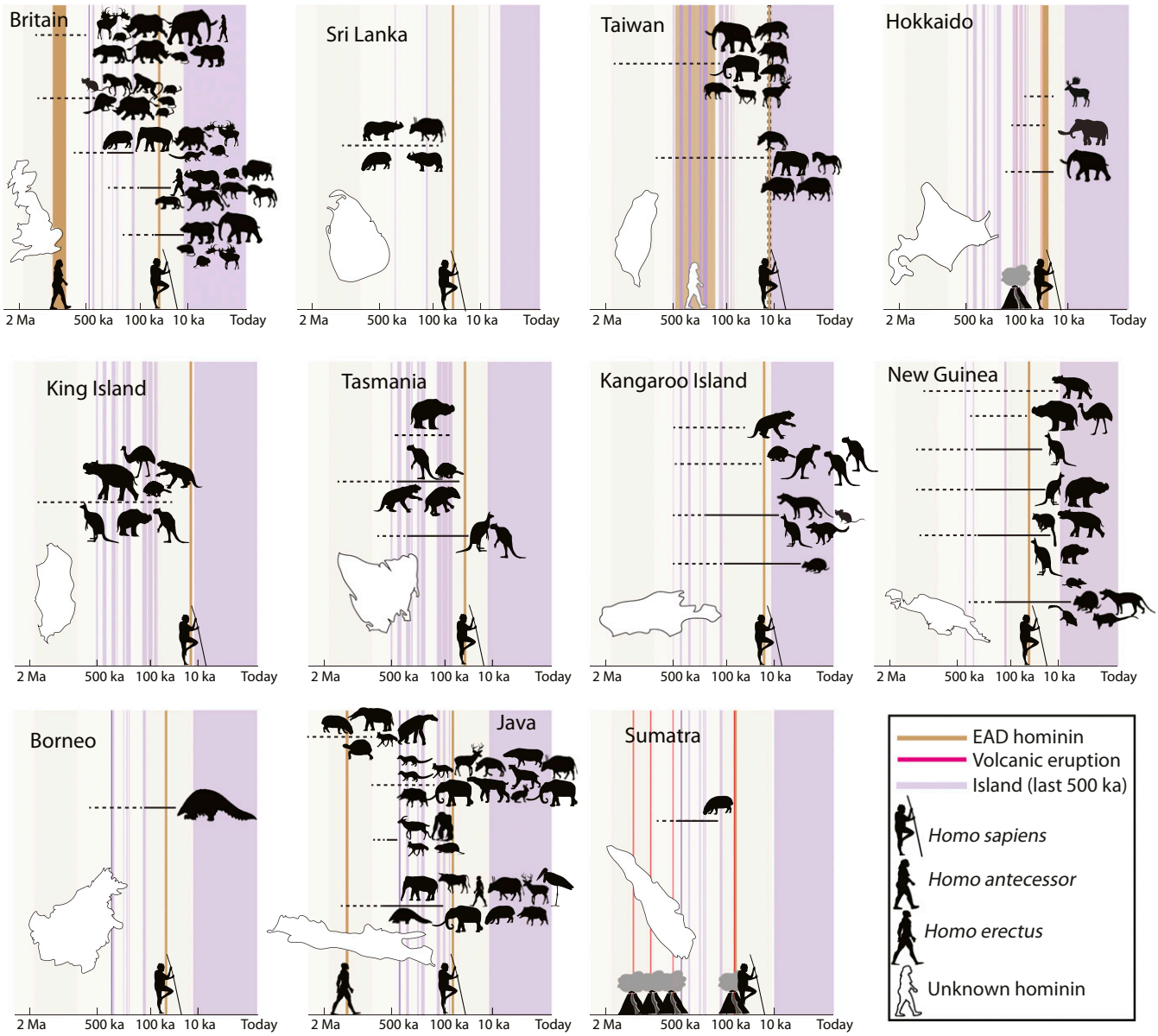


Fig. 4. Extinction chronology (right end of horizontal bars) shown with respect to first hominin and *H. sapiens* arrival (vertical bars and boxes) to continental islands. Purple vertical bars represent periods when these landmasses were islands. Extinct taxon LADs are represented by horizontal lines. 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 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 taxa—migratory 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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1. M. Bunce *et al.*, Extreme reversed sexual size dimorphism in the extinct New Zealand moa *Dinornis*. *Nature* **425**, 172–175 (2003).
2. 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).
3. D. K. Grayson, The archaeological record of human impacts on animal populations. *J. World Prehist.* **15**, 1–68 (2001).
4. A. G. Boyer, W. Jetz, Extinctions and the loss of ecological function in island bird communities. *Glob. Ecol. Biogeogr.* **23**, 679–688 (2014).
5. A. G. Boyer, Consistent ecological selectivity through time in Pacific Island avian extinctions. *Conserv. Biol.* **24**, 511–519 (2010).
6. D. W. Steadman, Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* **267**, 1123–1131 (1995).
7. A. S. Cheke, J. P. Hume, *Lost Land of the Dodo: The Ecological History of the Mascarene Islands* (T and AD Poyser, 2008).
8. B. E. Crowley, A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat. Sci. Rev.* **29**, 2591–2603 (2010).
9. W. G. Lee, "Islands" in *Encyclopedia of Biological Invasions*, D. Simberloff, M. Rejmánek, Eds. (University of California Press, 2011), pp. 391–395.
10. J. A. Alcover, A. Sans, M. Palmer, The extent of extinctions of mammals on islands. *J. Biogeogr.* **25**, 913–918 (1998).
11. 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).
13. 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.
14. 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).
16. 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.
17. 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).
21. 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).
22. 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).

23. 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).
24. C. N. Johnson *et al*., Biodiversity losses and conservation responses in the Anthropocene. *Science* **356**, 270–275 (2017).
25. C. N. Johnson, Ecological consequences of late Quaternary extinctions of megafauna. *Proc. Biol. Sci.* **276**, 2509–2519 (2009).
26. 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).
27. 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).
28. T. Ingicco *et al*., Earliest known hominin activity in the Philippines by 709 thousand years ago. *Nature* **557**, 233–237 (2018).
29. A. Brumm *et al*., Hominins on Flores, Indonesia, by one million years ago. *Nature* **464**, 748–752 (2010).
30. 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).
31. 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).
32. 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).
33. G. Haynes, Extinctions in North America's late glacial landscapes. *Quat. Int.* **285**, 89–98 (2013).
34. 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).
35. 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).
36. G. D. van den Bergh *et al*., Earliest hominin occupation of Sulawesi, Indonesia. *Nature* **529**, 208–211 (2016).
37. 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).
39. 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).
40. K. E. Westaway *et al*., An early modern human presence in Sumatra 73,000-63,000 years ago. *Nature* **548**, 322–325 (2017).
41. 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).
42. J. Louys, P. Roberts, Environmental drivers of megafauna and hominin extinction in Southeast Asia. *Nature* **586**, 402–406 (2020).
43. 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).
44. A. J. Stuart, Late Quaternary megafaunal extinctions on the continents: A short review. *Geol. J.* **50**, 338–363 (2015).
45. 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.
46. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, 1967).
47. M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge University Press, 1995).
48. R. L. Rogers, M. Slatkin, Excess of genomic defects in a woolly mammoth on Wrangel island. *PLoS Genet.* **13**, e1006601 (2017).
49. J. R. Karr, Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* **63**, 1975–1978 (1982).
50. F. Aziz *et al*., Early dispersal of man on islands of the Indonesian Archipelago: Facts and controls. *Anthropol. Sci.* **103**, 349–368 (1995).
51. S. O'Connor *et al*., Kisar and the archaeology of small islands in the Wallacean Archipelago. *J. Island Coast. Archaeol.* **14**, 198–225 (2019).
52. 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).
53. 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).
54. 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).
56. 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).
57. 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**, S567–S582 (2017).
58. 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).
59. 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).
61. 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.
62. 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).
63. 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).
64. R. Cosgrove *et al*., Overdone overkill–The archaeological perspective on Tasmanian megafaunal extinctions. *J. Archaeol. Sci.* **37**, 2486–2503 (2010).
65. 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.
67. 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).
69. H. Machida, F. Arai, *Atlas of Tephra in and Around Japan* (University of Tokyo Press, 2003).
70. N. A. Famoso, Mammalian community response to historic volcanic eruptions. *Mamm. Biol.* **100**, 219–230 (2020).
71. 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).