Environmental drivers of megafauna and hominin extinction in Southeast Asia

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Summary paragraph

Southeast Asia has emerged as an important region for understanding hominin and mammalian migrations and extinctions. High-profile discoveries show Southeast Asia was home to at least five members of the genus *Homo*¹⁻³. Significant turnover in Pleistocene megafauna is linked with these hominins or climate change⁴, although the region is often left out of discussions of megafauna extinctions. Establishing the environmental context of hominin evolution and its association with faunal changes have long been informed by stable isotope methodologies in the traditional evolutionary core of Africa^{5,6}. However, such studies have been largely neglected in Southeast Asia. Here, we present the first large-scale dataset of stable isotope data for Southeast Asian mammals spanning the Quaternary. Our results demonstrate that Early Pleistocene forests gave way to savannahs by the Middle Pleistocene leading to the spread of grazers and extinction of browsers, although geochronological limitations mean that not all samples can be resolved to glacial/interglacial periods. Savannahs retreated by the Late Pleistocene and completely disappeared by the Holocene, replaced by highly stratified closed canopy rainforest. This resulted in the ascendancy of rainforest-adapted species, including our own, at the expense of savannah and woodland specialists, such as *Homo erectus*. Megafauna today are restricted to rainforests and severely threatened by anthropogenic deforestation.

Main Text

Southeast Asia, comprising northern Indochinese and southern Sundaic subregions (Fig. 1), is characterised by extensive dipterocarp rainforests which host some of the most species-rich ecosystems on Earth. Yet, the exposure of a now-submerged Sundaland continental shelf during periods of lower sea level is argued to have catalysed severe environmental change, most notably the development of a central savannah corridor stretching from Indochina to Java^{7,8}. Supported by changes in the Inter-Tropical Convergence Zone, significantly reducing precipitation over much of Southeast Asia, the expansion of drier, grassland environments are argued to have channelled earlier members of *Homo* and large grazing taxa throughout much of mainland and island Southeast Asia⁹⁻¹¹. Disappearance of the corridor and expansion of the modern rainforest was proposed to have led to extinction or range reduction of many of its former travellers⁴. Conversely, it is also associated with population expansion of rainforest species such as the Bornean orangutan and the Asian golden cat^{12,13}. Given the emerging cosmopolitan nature of Pleistocene Southeast Asia, testing this hypothesis

will make a major contribution to global understandings of how hominin taxa had different ecological tolerances or capacities¹⁸ and the role of climate change in driving megafaunal extinctions¹⁹.

Despite evidence suggesting more open environments during the Pleistocene^{7,8,16}, the extent, and even existence, of the Southeast Asian savannah corridor remains hotly debated, with modelling and long-distance pollen data suggesting rainforest coverage even at the peak of the Last Glacial Maximum (LGM)¹⁷⁻²¹. Testing these propositions has been hindered by limited palaeoenvironmental data associated with local records and a lack of a widespread palaeoecological assessment. Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analyses have long been used to reconstruct major environmental events on local, continental, and global scales. Built on the principle that plants have distinct $\delta^{13}\text{C}$ depending on their photosynthetic pathway, while $\delta^{18}\text{O}$ varies with environmental water, research has focused on the degree to which medium-large bodied mammals associated with hominins show evidence for more humid C_3 forest and woodland ecologies versus open, drier C_4 'savannah' biomes (e.g. ref²²). The application of isotope analyses in Southeast Asia has been historically absent though recent studies have begun analysing fossil mammals as palaeoenvironmental indicators (Extended Data Table 1). Importantly, modern baseline data necessary to properly interpret the fossil record and to put the deep-time record of geobiology into a modern context has been almost entirely missing.

To address this deficit, we report $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data for 269 modern and historical specimens representing 63 mammals found in Southeast Asia. We compare these to 644 previously published $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossil taxa spanning the Early Pleistocene to today. For consistency and comparability, in all cases, the $\delta^{13}\text{C}$ values have been corrected to $\delta^{13}\text{C}_{\text{diet}}$. Our combined dataset represents the largest compilation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data from mammals in Asia, allowing us to examine broad trends in the distribution of C_3 and C_4 plants associated with faunal communities and hominins.

Our results show that during the Early Pleistocene, both C_3 and C_4 consumers were present in Southeast Asia (Fig. 2). However, these were unevenly distributed across the region (Extended Data Table 2), with C_3 consumers predominately found in Indochina ($\delta^{13}\text{C}_{\text{diet}}$ Q1–Q3: -29.3‰ – -26.4‰) and C_4 consumers in Sundaland ($\delta^{13}\text{C}_{\text{diet}}$ Q1–Q3: -20.0‰ – -13.3‰). The distribution of herbivores and omnivores across C_3 and C_4 ecosystems (Extended Data Fig. 1) was not significantly different during this period ($\chi^2(2, N=120)=1.95, p=0.377$). By the Middle Pleistocene, Sundaland records very few C_3 consumers (Extended Data Fig. 1 and 2), with most species falling into the C_4 range and, to a lesser extent, the mixed C_3 – C_4 feeder category (Q1–Q3: -15.8‰ – -13.3‰). The beginning of this period sees a peak in $\delta^{13}\text{C}_{\text{diet}}$ (Extended Data Fig. 2) corresponding to a shift of C_3 herbivores in Indochina towards higher $\delta^{13}\text{C}$ values ($\chi^2(2, N=308)=40.754, p<0.001$). This appears not to have affected omnivores whose distributions across both regions remain similar to their Early Pleistocene distribution ($\chi^2(2, N=39)=0.23, p=0.893$). Carnivores favour C_4 –grazers during this time ($\bar{x}=-14.6\text{‰}$, $N=7$). By the Late Pleistocene, most Sundanese and Indochinese herbivores and omnivores were consuming predominately C_3 resources ($\bar{x}_{\text{herbivore}}=-25.3\text{‰}$, $N=149$; $\bar{x}_{\text{omnivore}}=-22.3\text{‰}$, $N=38$). This stands in marked contrast to the carnivores, most of whom were still found in the C_4 end of the dietary spectrum ($\bar{x}_{\text{carnivore}}=-16.2\text{‰}$, $N=14$). By the Holocene, Southeast Asian mammals were consuming C_3 diets across the entire trophic spectrum ($\bar{x}_{\text{herbivore}}=-25.5\text{‰}$, $N=270$; $\bar{x}_{\text{omnivore}}=-23.5\text{‰}$, $N=38$; $\bar{x}_{\text{carnivore}}=-24.0\text{‰}$, $N=15$).

Beyond prominent C_3 and C_4 distinctions, we also find significant $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation within C_3 ecosystems. The lowest $\delta^{13}\text{C}_{\text{diet}}$ values ($<-29.0\text{‰}$) correspond to closed canopy and subcanopy habitats^{23,24}. Conversely, higher $\delta^{13}\text{C}$ values (-25.6 to -23.0‰) occur in open canopy forests or woodlands. High $\delta^{18}\text{O}$ values are also found in folivores that forage in the upper canopy, whereas those that prefer the understory have lower $\delta^{18}\text{O}$ values²⁵. In Southeast Asia, the distribution of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in browsers are significantly different across all sub-epochs (Kruskal-Wallis, $H_C=25.23, p$

<0.001; $H_0=27.34$, $p < 0.001$). Post-hoc analysis indicates that significant differences in environmental structure are present through time (Extended Data Fig. 3). In the Early Pleistocene, sites in Indochina have some understory browsers based on their $\delta^{13}\text{C}$ values. By the Middle Pleistocene, no understory browsers are recorded and only five individuals have values consistent with closed canopies. In the Late Pleistocene, sites in northern Indochina begin to record the first clear evidence of closed canopy forests. In the Holocene, browsers in both Indochina and Sundaland are occupying closed canopy rainforests, with both regions exhibiting highly negatively skewed distributions (-0.53 and -0.63, respectively). Increased forest stratification through time is suggested by the emergence of canopy specialists in the Holocene, supported by significantly higher $\delta^{18}\text{O}$ amongst species that forage in the lower, mid, and upper canopies, respectively (Kruskal-Wallis, $H=13.95$, $p=0.001$).

The regional shifts in C_3 and C_4 consumption across all taxa and the shifts in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ within browsing groups illustrate a common picture. Although subtle variation in atmospheric CO_2 partial pressure and $\delta^{13}\text{C}$ may have occurred over time, influencing interpretations of $\delta^{13}\text{C}$ as exactly equivalent to forest cover, these are not enough to obfuscate the magnitude of changes observed in terms of C_4 to C_3 abundance or environmental shifts within C_3 environments²². Our data show that mixed to closed canopy forests were present in Indochina during the Early Pleistocene, while Sundaland hosted open savannah grasslands. By the beginning of the Middle Pleistocene, both regions were dominated by open savannahs, although those of Indochina were more wooded than those of Sundaland with some open forests persisting. Closed canopy forests emerged in Indochina during the Late Pleistocene while Sundaland remained largely dominated by open canopy forests. By the Holocene, both regions were home to largely closed canopy forests.

These observed shifts are consistent with global Quaternary climate models indicating a significant change at the mid-Pleistocene transition. A shift from low amplitude 41,000-year to high amplitude 100,000-year cycles between 1.25 Ma and 700 ka were accompanied by significant decreases in sea surface temperatures, increases in ice volume, and heightened Asian aridity and monsoonal intensity²⁶. The change in glacial cycles, recorded in the benthic oxygen isotope record, coincides with our observed peak in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in Southeast Asian mammals (Extended Data Fig. 2). As drier conditions decreased in intensity, savannahs began to give way to forests (details in Methods). This process was further impacted at 400 ka by the subsidence of the Sunda shelf²⁷. This event significantly reduced exposed land and decreased albedo, leading to increased atmospheric convection and regional rainfall²⁸. Our data shows an accelerated decrease in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ at this time (Extended Data Fig. 2b, b), indicating a continued trend towards more favourable conditions for forests.

The distribution of sites suggests that, at their maximum, savannahs extended from Indochina down into Sundaland, enabling the dispersal of large-bodied grazers across this vast region. The expansion of these ecosystems coincides with the time of maximum hominin diversity in the region². During the Middle and beginning of the Late Pleistocene, the dramatic decline of C_4 habitats occurs at a time of disappearance of almost all hominin taxa present in Southeast Asia. Seemingly, these populations were unable to flexibly shift to the expanding tropical rainforest habitats that came to dominate Southeast Asia (Table 1), highlighting their likely status as mixed savannah/woodland-specialists¹⁰. By contrast, the arrival of *Homo sapiens* in the region c. 72-45 ka is linked to the expanded presence of tropical lowland evergreen rainforest. Although savannah settings did perhaps persist in some patches and were almost certainly used by our species, *Homo sapiens* expanded its niche in Southeast Asia to make use of rich rainforest and marine habitats^{14,29}. The ability to specialize in such environments becomes increasingly evident into the Terminal Pleistocene and Holocene³⁰.

Beyond hominins, these environmental shifts played a major role in mammalian turnover more broadly. During the Early Pleistocene, most mammals occupied a broad ecospace of open forests, the only exception being perissodactyls that were restricted to closed forests (Extended Data Fig. 4). The expansion of C_4 environments and loss of closed forests between the Early and Middle Pleistocene saw mammals occupy one of two ecospace – open forests or savannahs. Rodents, primates, and perissodactyls retreated to open forests while carnivores, artiodactyls, and proboscideans took advantage of the savannahs. The loss of closed forests likely had a role in the extinction of the largest ape to ever have existed *Gigantopithecus blacki* (Table 1). Based on stable isotope data, associated fauna, and tooth morphology, this species specialised on rainforest conditions in northern Indochina and its extinction during the Middle Pleistocene was likely driven by loss of its preferred habitats⁴. These changes likely also contributed to the extinction of other Early Pleistocene browsers such as *Ailuropoda wulingshanensis* and *Sus peii* (Table 1). The large-scale distribution of savannahs during the Middle Pleistocene, when most of the now island region was directly connected, produced novel faunal communities across Sundaland such as the Trinil H.K., Kedung Brubus, and Ngandong faunas, through exchange with Indochina and local endemism¹¹.

A return shift towards denser tropical canopies from the late Middle Pleistocene onwards in turn led to extinctions of the now widely dispersed grazing specialists. Artiodactyls shift significantly towards open canopy forest environments (Extended Data Fig. 4), and this period records the last appearance of grazers such as *Bubalus palaeokerabau* and *Duboisia santeng* (this ecospace also hosts primates and rodents, unchanged from the Middle Pleistocene). However, this pales in comparison to the enormous shift in diet exhibited by proboscideans, corresponding to the loss of grazing taxa including *Elephas hysundricus* and *Stegodon trigonocephalus* (Table 1). From this point onwards, elephants and their kin became restricted to closed forests. Rhinos and tapirs return to closed forests by the Late Pleistocene, although they were impacted by loss of rainforests during the LGM, with Sumatran rhinos, for example, showing genetic decline corresponding to this period³¹. The Late Pleistocene sees a significant move towards forest ecosystems for carnivores and a major extinction event for the open-adapted hyenas. Finally, the Holocene witnessed the persistence of major forested ecospace, open and closed canopy forests. Primates also demonstrate a shift towards more closed forests at this time.

There is a significant positive correlation between conservation and extinction status in Southeast Asian mammals for both $\delta^{13}C$ and $\delta^{18}O$ ($\tau_c = 0.14$, $p < 0.001$; $\tau_o = 0.16$, $p < 0.001$), indicating that the loss of drier and more open environments is associated with higher extinction risks. This correlation remains significant even if only modern species are considered; however, the trend is reversed such that rainforest-adapted taxa are correlated with higher levels of conservation risk ($\tau_c = -0.18$, $p < 0.001$; $\tau_o = 0.09$, $p = 0.006$). Thus, our data shows that Early-Middle Pleistocene megafauna extinctions affected C_4 adapted taxa the most, as they faced the re-expansion of Late Pleistocene forest and the loss of the savannahs that had sustained them. Today, by contrast, rainforest species are at the greatest risk of extinction. This highlights the dominant role of environmental change in the fortunes of large bodied mammals. The modern rainforests of Southeast Asia harbour some of the most critically endangered animals in the world. They are at significant risk from overhunting and loss of habitat through deforestation³², representing an anthropogenically-influenced return to grassland ecosystems in which these rainforest taxa were notably absent. Our long-term perspective thus provides critical insights relevant to conservation priorities today. For example, orangutan (*Pongo* spp.) diets differ significantly across all sub-epochs (Kruskal-Wallis, $H=11.11$, $p = 0.011$), with mean $\delta^{13}C$ values the lowest during the Holocene. These changes are likely tied to increased exploitation and land clearing by people during the mid to late Holocene, driving orangutans deeper into rainforests where they are isolated and vulnerable³³.

Robust palaeoecological datasets are essential if we are to understand the changing adaptations of hominin and other megafauna during the Quaternary. While such records have long been available from Africa, they have been conspicuously absent from Southeast Asia until recently. Our results demonstrate that the coming and going of extensive savannah environments played a major role in hominin and mammalian Pleistocene biogeography, with savannah/woodland specialists being usurped by rainforest-adapted species as these habitats disappeared following the LGM. Of the high hominin diversity in the region, it was only our species, *Homo sapiens*, which sufficiently adapted to these changing conditions. Perhaps ironically, it is now a return to grassland conditions, with human development, plantations, and population growth as its primary driver, that stands as the greatest threat to some of the most critically endangered mammals in the world, as well as the long-term sustainability of human populations in the region and across the tropics as a whole. Work such as this helps to place these threats in their long-term context, demonstrating how, while our own species' fortunes changed for the better with the arrival of the typical endemic rainforest communities, it is now in danger of destroying them forever.

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Fig. 1: Locality map showing the biogeographic subregions examined, land extent during the Last Glacial Maximum, and the proposed extent of the 'savannah' corridor after ref⁷.

Fig. 2: Distribution of $\delta^{13}\text{C}$ values across different geological sub-epochs. Green bars represent herbivores, blue omnivores, and yellow carnivores. Shaded boxes represent division between forests (100% C_3 consumers) and grasslands (100% C_4 consumers). All large herbivore $\delta^{13}\text{C}_{\text{enamel}}$ values were adjusted by -14‰ ; omnivores, rodents, pigs, and primates were adjusted by -11‰ ; Carnivora by -9‰ ; $\delta^{13}\text{C}_{\text{hair/horn}}$ values were adjusted by -3.1‰ ; post-1930 samples were adjusted by 1.5‰ . VPDB, Vienna PeeDee Belemnite.

Table 1: Extinct megafauna and their last appearance dates, with corresponding site (listed in brackets) and approximate Marine Isotope Stage(s) for these sites. Average carbon and oxygen stable isotope values are provided, with $\delta^{13}\text{C} < 21\text{‰}$ considered typical of C_3 dominated ecosystems.

Taxon	Common name	Last Appearance Date	Marine Isotope Stage	Mean $\delta^{13}\text{C}$	N _{δ13C}	Mean $\delta^{18}\text{O}$	N _{δ18O}
<i>Ailuropoda baconi</i>	Bacon's giant panda	10-12 ka (Gulin)	MIS1	-25.6	4	-7.0	4
<i>Ailuropoda wulingshanensis</i>	Wulingshan panda	1.2 Ma (Sanhe)	MIS35-40	-25.7	1	-7.7	1
<i>Axis lydekkeri</i>	Lydekker's deer	108-117 ka (Ngandong)	MIS5	-13.8	7	-4.2	7
<i>Bubalus palaeokerabau</i>		108-117 ka (Ngandong)	MIS5	-14.6	19	-4.7	19
<i>Crocota crocuta ultima</i>	Spotted hyena	25-18 ka (Boh Dambang)	MIS2	-14.8	12	-6.3	4
<i>Duboisia santeng</i>	Dubois' antelope	0.54-0.43 Ma (Trinil)	MIS12-14	-14.0	3	-4.1	3
<i>Elephas hysudrindicus</i>		108-117 ka (Ngandong)	MIS5	-15.0	12	-4.6	12
<i>Gigantopithecus blacki</i>		400-320 ka (Hejiang Cave)	MIS9-11	-26.6	17	-6.4	17
<i>Homo erectus</i>		108-117 ka (Ngandong)	MIS5	-16.5	7	-6.3	7
<i>Megatapirus augustus</i>	Giant tapir	10-12 ka (Gulin)	MIS1	-30.2	3	-6.5	3
<i>Pachycrocota brevirostris</i>	Short-faced hyena	196 and 143 ka (Changyang)	MIS6	-22.7	1	-9.8	1
<i>Sinomastodon bumiajuensis</i>		1.2-1.9 Ma (Sangiran)	MIS35-72	-16.5	8	-5.0	8
<i>Stegodon orientalis</i>		10-12 ka (Gulin)	MIS1	-25.5	20	-6.8	20
<i>Stegodon trigonocephalus</i>		108-117 ka (Ngandong)	MIS5	-14.4	55	-6.1	55
<i>Stegoloxodon indonesicus</i>		>1.5 Ma (Kaliglagah Fm)	>MIS50	-27.7	5	-5.7	5
<i>Sus brachygnathus</i>		0.54-0.43 Ma (Trinil)	MIS12-14	-17.8	3	-6.3	3
<i>Sus peii</i>		630-810 ka (Sanhe Cave)	MIS15-20	-25.8	1	-7.5	1
<i>Sus xiaozhu</i>		320-400 ka (Hejiang Cave)	MIS9-11	-23.5	1	-7.8	1
<i>Tapirus sinensis</i>	Chinese tapir	< 280-88 ka (Lower Pubu Cave)	< MIS5	-29.5	4	-10.7	4

Methods

The process of photosynthesis produces strong isotopic fractionation of ^{13}C depending on the photosynthetic pathway used by the plant^{34,35}. There is a large and non-overlapping distinction between C_3 and C_4 plants³⁶. Depletion is on average, -5‰ in C_4 and -19‰ in C_3 plants, relative to atmospheric $\delta^{13}\text{CO}_2$ (c. -6.5‰ prior to the industrial era). This distinction has been used in the tropics and subtropics to determine the relative proportion of C_4 grassland to C_3 woodland or forest in mammalian (including hominin) diets and thus their inferred associated environments³⁴⁻⁴⁰. Under C_3 forest settings, there is a further canopy influence on the isotopic composition of plants. Lower light levels and trapping of respired CO_2 leads to an even stronger depletion in ^{13}C in soils, leaves, fruits, and therefore mammals found in subcanopy environments^{23,41,42}. This 'canopy effect' has been observed in temperate, subtropical, and tropical forests⁴²⁻⁴⁷. The distribution of $\delta^{13}\text{C}$ in tropical forest mammal communities has a long left tail (highly negative skew) reflecting the abundance of browsers feeding in the canopy top, gaps in the canopy, and subcanopy frugivores who have higher $\delta^{13}\text{C}$ values than browsers feeding only in the subcanopy²³⁻²⁵.

Measurements of $\delta^{18}\text{O}$ in vegetation and animals can also provide important insights into palaeoenvironments and the presence of closed canopy forests. The critical site of isotope fractionation in vegetation is the leaf, with evaporation leading to a loss of lighter ^{16}O and concomitant enrichment in ^{18}O (ref⁴⁸). The degree of $\delta^{18}\text{O}$ enrichment in leaf water is thus negatively related to relative humidity, with increasing humidity resulting in decreased $\delta^{18}\text{O}$ values and vice versa⁴⁹⁻⁵¹. Due to differences in evaporative potentials across different strata in the canopy and between different plant parts found at different heights, CO_2 and vegetation $\delta^{18}\text{O}$ will differ based on vertical stratification⁵²⁻⁵⁴. In tropical systems, $\delta^{18}\text{O}$ of vegetation, recorded with high fidelity in the tissues of mammals that obtain most of their water requirements from plants, provide information on evaporative potential or source-effect of rainfall as well as the vertical structure of forests^{25,52,53,55-58}. Notably, folivores that forage in the canopy top will have higher $\delta^{18}\text{O}$ than those that prefer the subcanopy²⁵.

Historical mammal specimens were selected for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis of tooth enamel from the collections of the Zoologische Staatssammlung München (ZSM), Germany, the Muséum National d'Histoire Naturelle (MNHN), Paris, France, the American Museum of Natural History (AMNH), New York, United States of America, and the Lee Kong Chian Natural History Museum (LKCNHM), Singapore. Specimens with full adult dentition in occlusion and with clear provenance and collection information were preferentially selected. In collaboration with the curatorial teams of each institution, specimens were only sampled where duplicate specimens existed for the same taxa. Sampling was done under the CITES registration of Griffith University, Australia (no. AU 062) and the Department of Archaeology, Max Planck Institute for the Science of Human History (no. DE 215-07). Specimens were identified based on existing labels within the museum collections with taxonomy updated according to latest available systematic information.

Sampled teeth were cleaned using portable air-abrasion to remove any adhering external material. Enamel powder for bulk analysis was obtained using gentle abrasion with a diamond-tipped drill along the full length of the buccal surface in order to ensure a representative measurement for the entire period of enamel formation. All enamel powder was pretreated to remove organic or secondary carbonate contaminants following established protocols. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H_2O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H_2O (as per. refs^{59,60}). When comparing the novel data presented here with that from the existing literature it is worth noting that different pretreatment protocols have been applied in each case, though for tooth

enamel pre-treatment induced variation is limited ($<0.5\%$ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ^{61,62}), and these differences have a negligible effect on the scale of the questions examined here⁶³.

Following reaction with 100% phosphoric acid, gases evolved from the samples were analysed for their stable carbon and oxygen isotopic measurements using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were compared against International Standards (IAEA-603 ($\delta^{13}\text{C} = 2.5$; $\delta^{18}\text{O} = -2.4$); IAEA-CO-8 ($\delta^{13}\text{C} = -5.8$; $\delta^{18}\text{O} = -22.7$); USGS44 ($\delta^{13}\text{C} = -42.2$)) and in-house standard (MERCK ($\delta^{13}\text{C} = -41.3$; $\delta^{18}\text{O} = -14.4$)). Replicate analysis of MERCK standards suggests that machine measurement error is c. $\pm 0.1\%$ for $\delta^{13}\text{C}$ and $\pm 0.2\%$ for $\delta^{18}\text{O}$. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard ($n = 20$, $\pm 0.2\%$ for $\delta^{13}\text{C}$ and $\pm 0.2\%$).

Fossil $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were compiled from existing published sources⁶⁴⁻⁷⁶. These cover 31 sites across Indochina and Sundaland, representing the largest compilation of stable isotope data from anywhere in Asia. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis of fossil tooth enamel has shown to preserve ecological distinctions back into the Miocene^{77,78}. The bioapatite of tooth enamel has fewer substitutions, less distortion and larger crystals than that found in bone and dentine, making it more resistant to taphonomic alteration^{79,80}. Although we have not been able to check the state of each tooth sampled in the studies we have compiled, a number of studies have studied the potential for taphonomic change in fossil enamel in hydrologically active tropical settings using chemical and physical analysis^{14,81}. They found limited alteration to fossil enamel structure in both open air and cave contexts in South and Southeast Asia dating back to the Pleistocene and concluded there was no reason to assume alteration to the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Furthermore, several studies from which the compiled data were taken applied similar approaches to demonstrate taphonomic integrity^{65,73,76}.

Where serially sampled values were provided, we calculated the mean for both carbon and oxygen isotopes for each specimen. To enable comparison of our $\delta^{13}\text{C}$ dataset with existing fossil enamel $\delta^{13}\text{C}$ in the literature we performed a series of data corrections. We made no adjustment for the Suess effect for specimens collected prior to 1931 as $\delta^{13}\text{C}$ CO_2 in 1930 differs from pre-industrial values by just c. 0.2% ⁸². This is, as far as can be confidently ascertained from existing museum records, after or around the time of the death of most individuals sampled in our dataset. For specimens with known collection dates after 1930 we applied an offset of 1.5% , and for modern data sourced from published sources, we followed the authors' application of this offset. Another approach is to correct modern samples using the atmospheric $\delta^{13}\text{C}$ values by year, using a dataset spanning 1850-2015⁸³ (Graven et al. 2017). The use of different corrections produced statistically indistinguishable values ($r = 0.99$, $p < 0.0001$), lending confidence to the modern $\delta^{13}\text{C}$ values used in our analyses. In order to convert all existing faunal data into an estimated $\delta^{13}\text{C}$ of diet, a correction was applied to all fossil and modern enamel, apatite, bone, horn, and hair samples.

Hair and horn samples were adjusted by -3.1% following refs^{64,84,85}. Enamel, apatite, and bone samples from both ruminant and non-ruminant large-bodied herbivores were adjusted by -14% . This corresponds to a collagen to diet offset of $\sim 5\%$ (following ref⁷⁶) and a carbonate to collagen offset of between $7-8\%$ and 9% for non-ruminants and ruminants, respectively^{85,87}. Because they have similar carbonate to collagen offsets (wild omnivores (5.5%), omnivorous rodents (5.5%), captive pigs (6.0%), hominoids (6.0%), and cercopithecines (5.9%) – see ref⁸⁷), all omnivores, rodents, pigs, and primates in our dataset were adjusted by -11% . Several taxa in Asia belonging to the Carnivora are herbivores (e.g. giant panda, red panda). Diet-apatite offset values are determined largely by digestive physiology, with differences in metabolic breakdown, and in particular degree of fermentation, a likely explanation for differences between carnivores and herbivores^{86,88}. Fermentation processes, in turn,

are controlled by gut microbiota⁸⁹. We assigned offset values for herbivorous Carnivora based on comparative gut microbe diversity and physiology^{90,91}. On this basis, giant and red pandas are similar to other typical carnivores (see fig. S2 in ref⁹⁰). Thus, all Carnivora were adjusted by -9‰, as the carnivore carbonate to collagen offset is lower than those observed in other mammals⁸⁶.

All statistical analyses were run in PAST ver. 2.17c⁹². Univariate statistics for each geological sub-epoch and region and trophic group listed are provided in Extended Data Tables 2 and 3, respectively. In order to test whether or not the distribution of herbivores and omnivores were bimodal for the Early and Middle Pleistocene, we subjected each group (i.e. Early Pleistocene herbivores, Early Pleistocene omnivores, Middle Pleistocene herbivores, Middle Pleistocene omnivores) to a k-means cluster analysis, setting the number of clusters to two. We then counted the number of values falling into the first and second clusters, corresponding to C₃ and C₄ peaks, respectively. Division across all groups was very similar, with the division between clusters discernible in all but one case at -20.0‰ $\delta^{13}\text{C}$. The only exception was the Middle Pleistocene herbivores, where the division occurred between -19.3‰ and -19.5‰. Full counts were used in the χ^2 test (Extended Data Table 4). For consistency, we use a cut-off at -20.0‰ across all groups; however, even when using the value of -19.4‰ for Middle Pleistocene herbivores, they are still significantly different than their Early Pleistocene counterparts ($\chi^2(2, N=208) = 48.195, p < 0.001$).

Each epoch and sub-epoch of the Quaternary samples vastly different temporal scales and includes different numbers of glacial/interglacial cycles. Thus, grouping sites by geological group may mask or extenuate vegetation trends that are not reflective of the past 2.6 million years. In order to examine long term trends in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ through the Quaternary, for sites with published age estimations (Extended Data Table 5), we calculated the average $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values across all taxa for each site. Next, we assigned each site to successive time bins of equal duration spanning the Pleistocene. We examined time bins under three different geochronological scenarios related to the range of ages available for each site: (i) the minimum age of the site; (ii) the median age; and (iii) the maximum age. The number of time bins equalled the smallest division of the Quaternary that included at least one site in each bin. This resulted in seven bins of 321 ka duration for minimum ages; six bins of 428 ka for median age; and five bins of 513.8 for maximum ages. We applied a Locally Weighted Scatterplot Smoothing Spline^{93,94} with a smoothing factor set at 0.9. The 95% confidence interval for the curve was based on 999 random replicates using resampling of residuals⁹². We compared our results to the Lisiecki Raymo benthic oxygen isotope stack⁹⁵ adjusted to the same temporal scale.

Most sites in Southeast Asia are derived from Late Pleistocene cave deposits, so there is unevenness in temporal sampling across the Quaternary, and/or they have poor constraints on their geological ages. At the extreme, geochronological constraints of these vertebrate deposits make it impossible to exclude the possibility that the fossils are sampling dry or wet states in some unexpected way, such that the patterns we observe could represent artefacts of taphonomic or sampling biases rather than broad environmental changes. Taphonomic bias could result from a restriction of fossil accumulation in caves to dry phases, as has been observed in South Africa for example⁹⁶. Sampling bias could include the collection or analysis of only certain taxa from deposits. However, the possibility that the pattern we observe is artefactual can be discounted for several reasons. First, regarding taphonomy, low $\delta^{13}\text{C}$ values are recovered from samples from both cave and open-air sites (e.g. Baxian and Cipeundeuy, respectively), and equally, higher $\delta^{13}\text{C}$ values have also been recovered from both types of sites (e.g. Khok Sung and Pha Bong). Second, regarding sampling, several taxa, including the most commonly represented in our dataset (i.e. bovids and cervids), span the range of $\delta^{13}\text{C}$ values of rainforest and savannah. Third, taphonomic and sampling biases would need to be structured in such a way that they provide a peak in $\delta^{13}\text{C}$ values at the beginning of the Middle Pleistocene. There are no structural biases

in Middle Pleistocene sites that would differentiate them from Early and Late Pleistocene sites in this way. More importantly, the patterns we observe are fully consistent with major climatic changes in Southeast Asia reported by other proxies.

The climate in Southeast Asia is governed by the position of the Inter-Tropical Convergence Zone (ITCZ), which determines where precipitation from the East Asian and the Australian-Indonesian monsoons occurs⁹⁷. Changes in the position of the ITCZ during the Pleistocene have significantly impacted regional precipitation patterns and vegetation. The Mid-Pleistocene Transition initiated high amplitude 100,000-year glacial-interglacial cycles that were accompanied by heightened Asian aridity and monsoonal intensity²⁶, corresponding with the peak in our $\delta^{13}\text{C}_{\text{diet}}$ values. Following this, at the Mid-Brunhes Event between MIS13 and 11, interglacial conditions in high latitudes became warmer and more comparable to Holocene conditions⁹⁸. However, cave speleothem records from Southeast Asia indicate that neither ITCZ activity nor its position responded to this event^{99,100}, although quite variable interglacial conditions were recorded. Major changes to the ITCZ are however observed following deglaciations, where environmental changes linked to the Earth's precession cycle and insolation intensity shifted and trapped the ITCZ in a southern position, precipitating millennia-long intervals of reduced monsoon rainfall^{99,100}. Decreasing trends in global glacial ice volume during the Late Pleistocene correspond to decreasing maximum peaks in oxygen isotopes over successive interglacials, explaining the decrease in drier conditions we observe during this time. This would have been accentuated from ~400 ka by the initiation of Sunda shelf subsidence²⁷. This reinforces the idea that the broad trends we observe in Southeast Asian vegetation were driven by global-scale climatic changes and regional-scale geological events. Nevertheless, such events can still produce variable conditions locally, for example, the distribution of rainfall in Southeast Asia today is also strongly dependent on topographical relief as well as the position of the ITCZ⁹⁷. This can cause local scale (temporal and/or spatial) environmental heterogeneity that may not be congruent with the larger scale patterns we observe. For example, some palaeoecological records show that patches of both savannah and rainforests were present in Southeast Asia during Late Pleistocene¹⁰¹⁻¹⁰⁸. However, their impact on hominin and mammal biogeography must be understood in broader temporal and spatial environmental contexts. It is further worth noting that only palaeoecological records such as ours provide direct insights into the environments actually used by mammals and hominins, as they come from the animals themselves, rather than via indirect proxies.

For canopy specific analyses, herbivores with $\delta^{13}\text{C}$ values less than -23‰ were considered to belong to the browsing trophic group. Browsers were further subdivided into subcanopy (< -32‰ $\delta^{13}\text{C}$), mid-canopy (-32 – -29‰ $\delta^{13}\text{C}$), and top canopy browsers (-29 – -25.6‰ $\delta^{13}\text{C}$). Oxygen values for these were examined to determine forest stratification, with higher $\delta^{18}\text{O}$ predicted to occur in top canopy folivores, and lower $\delta^{18}\text{O}$ in subcanopy browsers²⁵.

Analysis of changes in isotopes across mammalian orders and trophic groups proceeded in two concurrent steps: between the same order over different periods, and between different orders in the same period. Summary statistics for the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for each of these is provided in Extended Data Table 6. Statistical significance was assessed via Kruskal-Wallis test with differences deemed significant at $\alpha = 0.05$. Changes across orders are illustrated in Extended Data Fig. 4.

In order to assess the relationship between conservation risk and environmental preference, we determined the conservation status for each taxon confidently identified to species from the IUCN Red List of Threatened Species¹⁰⁹. We determined extinction times for Southeast Asian megafauna through an extensive literature survey, with sites and dates listed in Table 1 sourced from refs^{68,72,74,110-121}. We calculated whether a correlation between conservation risk and extinction status, and $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, existed using Kendall's Tau with significance assessed at $\alpha = 0.05$. In order to examine

current threats to Southeast Asian mammal biodiversity, we examined the same dataset but removed extinct species from the list.

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Data availability

All data generated and used during this study are included in this published article (and its supplementary information files).

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Author contributions

JL conceived this research and conducted the statistical analyses. PR performed the stable isotope analyses. Both authors contributed equally to study design, data acquisition, interpretation of data, and writing of the final manuscript.

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The authors declare no competing interests. Both authors can be contacted for correspondence or material requests.

Materials and Correspondence

All accession numbers, and data generated and used during this study are included in this published article (and its supplementary information files).

Extended Data Fig. 1: Distribution of $\delta^{13}\text{C}$ across the Quaternary shown with a jitter plot and corresponding Kernel density for Indochina (blue) and Sundaland (red). Kernel densities exaggerated vertically such that the peak for both provinces are equal. Shaded boxes represent division between forests (left) and grasslands (right). VPDB, Vienna PeeDee Belemnite.

Extended Data Fig. 2: Temporal trends of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ under different geochronological scenarios. A) $\delta^{13}\text{C}$ assuming minimum age for each site; B) $\delta^{18}\text{O}$ assuming minimum age for each site; C) $\delta^{13}\text{C}$ assuming median age for each site; D) $\delta^{18}\text{O}$ assuming median age for each site; E) $\delta^{13}\text{C}$ assuming maximum age for each site; F) $\delta^{18}\text{O}$ assuming maximum age for each site. Each panel shown relative to the Lisiecki Raymo benthic oxygen isotope stack. VPDB, Vienna PeeDee Belemnite. The 95% confidence interval for each curve was based on 999 random replicates using resampling of residuals.

Extended Data Fig. 3: Distribution of $\delta^{13}\text{C}$ values for browsers across (Indochina: dark green; Sundaland: light green) sites through Southeast Asia. Horizontal line represents the -29‰ zone indicating the beginning of subcanopy and closed canopy environments. Long lower whiskers in the box and whisker plot, indicating a very negatively skewed distribution, are most closely associated with highly stratified forests. The boxes show the median and the lower (25%) and upper (75%) quartiles; the whiskers encompass the minimum and maximum values. VPDB, Vienna PeeDee Belemnite. Independent sample sizes Juyuandong n=4, Longudong n=26, Mohui n=5, Sanhe n=25,

Semedo n=6, Sangiran n=4; Upper Pubu n=4, Khok Sung n=5; Pha Bong n=15; Tham Wiman Nakin n=10; Baxian n=32, Boh Damman n=18, Nam Lot n=39, Quzai n=32, Sibrambang n=6, Wajak n=4, Cipeundeuy n=2; Indochina n=74, Sundaland n=158.

Extended Data Fig. 4: Changes in mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for mammals classified at the ordinal level. Continuity (non-significant differences in mean) of $\delta^{13}\text{C}$ within orders between epochs are illustrated with arrows at the top of each plot. Continuity between orders in a single epoch are illustrated with circles bounding similar $\delta^{13}\text{C}$ means. Variation within orders and epochs indicated at 1 S.D. VPDB, Vienna PeeDee Belemnite.

Extended Data Table 1: Sites included in the analyses with corresponding sources for the isotope data.

Extended Data Table 2: Univariate statistics for each geological sub-epoch and biogeographical province.

Extended Data Table 3. Univariate statistics for each geological sub-epoch and trophic group.

Extended Data Table 4: Count data for Early and Middle Pleistocene herbivores and omnivores.

Extended Data Table 5: Age ranges for fossil sites and the time bins they were allocated to for each age modelling scenario.

Extended Data Table 6: Stable isotope values for different orders of mammals across different geological epochs of the Quaternary.