

The deep human prehistory of global tropical forests and its relevance for modern conservation

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Significant human impacts on tropical forests have been considered the preserve of recent societies, linked to large-scale deforestation, extensive and intensive agriculture, resource mining, livestock grazing and urban settlement. Cumulative archaeological evidence now demonstrates, however, that *Homo sapiens* has actively manipulated tropical forest ecologies for at least 45,000 years. It is clear that these millennia of impacts need to be taken into account when studying and conserving tropical forest ecosystems today. Nevertheless, archaeology has so far provided only limited practical insight into contemporary human–tropical forest interactions. Here, we review significant archaeological evidence for the impacts of past hunter-gatherers, agriculturalists and urban settlements on global tropical forests. We compare the challenges faced, as well as the solutions adopted, by these groups with those confronting present-day societies, which also rely on tropical forests for a variety of ecosystem services. We emphasize archaeology's importance not only in promoting natural and cultural heritage in tropical forests, but also in taking an active role to inform modern conservation and policy-making.

By 2050, it is estimated that over half of the world's population will live in the tropics, with many people relying on tropical forests as a source of freshwater and agricultural and urban land, as well as timber, medicine and food¹. The expansion of human populations into tropical forest environments has seen them become some of the most threatened ecosystems in the world^{2,3}. Every day, c. 320 km² of tropical rainforest is destroyed, significantly impacting human populations, along with 135 plant, animal and insect species⁴. The ongoing viability of dry tropical forests is also under serious threat⁵. These alterations affect ecosystems that are central to the stability of Earth's atmosphere and climate⁶, as well as key providers of economic goods and ecosystem services².

Focus on recent impacts to tropical forests has tended to promote these ecosystems as pristine and relatively untouched until recent centuries or even decades. Nevertheless, cumulative archaeological interest, spurred on by the application of novel methods of site discovery⁷, archaeological science research (for example, refs 8–11) and palaeoenvironmental reconstruction (for example, refs 12,13), have increasingly demonstrated tropical forests to be dynamic 'artefacts' of millennia of human–forest interaction^{14,15}. Attempts to investigate the relationship between, on the one hand, prehistoric fire regime alteration, cultivation¹⁶, extensive sedentary settlement and enduring landscape modification^{17,18}, and, on the other, sustainable past subsistence, water-use and intensive human occupation, have so far been limited. This is despite recent calls from UNESCO¹⁹ and a broad range of researchers^{20,21} to actively involve archaeologists in conservation and policy-making in tropical forests.

Awareness of long-term anthropogenic impacts to tropical forests has only gradually emerged. As recently as the 1980s and 1990s, anthropologists argued that tropical forests were unattractive environments for human occupation (for example, ref. 22). This view was further promoted by archaeologists, who, for example, saw tropical forests as barriers to the expansion of Late Pleistocene *Homo sapiens* foragers²³, and also deemed them incapable of supporting agricultural populations²⁴. This bias has been exacerbated by the generally poor preservation of organic archaeological remains

in tropical forest environments (for example, ref. 25). Accordingly, scholarly assumptions about the timing of significant anthropogenic impacts on tropical forests generally point to the post-industrial era or, at the earliest, the colonial era of European 'discovery'^{26,27}. Clearly, the accumulating database of archaeological and palaeoecological evidence for pre-industrial and pre-colonial tropical forest occupation and transformation has not been effectively communicated beyond a restricted set of sub-disciplines (though see refs 28–31). As a consequence, this evidence has only played a small role in discussions about the start date or characteristics of the Anthropocene (for example, ref. 32, but see ref. 33).

Here, we review evidence that has accumulated, primarily in recent decades, for the long-term human transformation of tropical forest ecosystems. Our review is not exhaustive, but rather seeks to highlight how recent studies, drawing on a suite of new archaeological science and palaeoecological methods, have dramatically altered understanding of tropical forest prehistories and histories globally. We focus on three modes of human impact that, over the long-term, stack up as broad but non-synchronous phases: a phase marked by deliberate forest burning, species translocation and management of forest biota; a phase of agricultural cultivation and enduring landscape modification; and a phase of urban occupation and transformation of tropical forests. As will be seen, these modes are not mutually exclusive. We conclude by examining the implications of new archaeological and palaeoecological perspectives on the long-term prehistory of tropical forests for contemporary agendas of conservation, management, and resilience building.

Early impacts

In the last ten years, the archaeologically acknowledged human inhabitation of tropical forests has quadrupled in age. There is now clear evidence for the use of tropical forests by our species in Borneo^{12,13,34} and Melanesia³⁵ by c. 45 ka, in South Asia by c. 36 ka³⁶, and in South America by c. 13 ka³⁷. There are suggestions of earlier rainforest occupation c. 125 ka in Java^{38,39}, c. 60 ka in the Philippines⁴⁰, c. 100 ka in China⁴¹, and in Africa, perhaps from the

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first appearance of *H. sapiens*, c. 200 ka⁴², though further research is required to verify these cases⁴³ (note 'ka' represents thousands of calibrated/uncalibrated years ago; where this refers to radiocarbon dates it is equivalent to calibrated years BP). Early modern humans adapted to diverse tropical forest formations, ranging from the sub-zero temperatures of montane forests to dense, humid, evergreen rainforests, undertaking sophisticated forest mammal hunting and plant processing (for example, ref. 44). Moreover, people did not just adapt passively to these environments, but from the onset modified them in fundamental ways^{10,45}, with outcomes that have affected the natural histories of these forests to the present day.

In Southeast Asia, mounting evidence points to deliberate anthropogenic biomass burning in order to create forest-edge habitats from the first human arrival c. 45 ka^{13,35} (Fig. 1). This may reflect reliance on starchy forest-edge plants and bearded pigs that were attracted to canopy openings¹². In tropical Australia, the decline of *Araucaria* and rise of Eucalypts and *Casuarina* have been correlated with the advent of anthropogenic biomass burning after 40 ka^{46–48}. Human landscape impacts have also been documented in the montane tropical forests of the New Guinea Highlands from 45–35 ka, even retarding vegetation re-colonization in the region following the Last Glacial Maximum⁴⁹. That early foragers could have played a significant role in reshaping newly colonized landscapes is also supported by evidence that later foragers did. For example, the first colonists of the eastern Caribbean in the mid-Holocene brought their foraging, collecting and hunting lifestyles with them, and engaged in modification and management of tropical ecosystems that is reflected in significant shifts in pollen and phytolith datasets⁵⁰.

Still debated, but potentially even more significant in terms of long-term impact, is human involvement in Late Pleistocene tropical forest megafaunal extinctions, which are argued to have had anthropogenic, climatic or multivariate causes, and to have resulted in major changes to ecosystem structure⁴⁷. While discussions of megafaunal extinctions in tropical forests have been relatively limited, these environments possessed diverse megafauna, some of which persists in parts of Africa and Asia⁵¹. In the New Guinea Highlands there is evidence for megafauna, including extinct marsupials (such as *Maokopia ronaldii* and *Thylogale hopeii*), at West Balim River c. 30 ka and at Nombe c. 25 ka, with their gradual demise occurring after human arrival and subsequent biomass burning^{49,52}. In the Amazon basin, megafaunal extinctions, such as those of large mastodons (*Haplomastodon waringi*) and ground sloths (*Erethotherium laurillardii*), significantly altered biodiversity, vegetation distributions, nutrient cycling and carbon storage in the region, with effects persisting to the present day⁵³, though the role of humans in this process has yet to be fully explored (for example, ref. 54).

Tropical forest foragers also reshaped landscapes through the active long-distance translocation of species. In Melanesia, people translocated small mammals for reliable protein from 20 ka⁵⁵. The result is that species such as bandicoot (*Perameles* sp.) and cuscus (*Phalanger* sp.) are now widely distributed across Melanesian islands, including the Bismarck Archipelago, where they are not endemic. Yams (*Dioscorea alata*) are present on both sides of Wallace's Line by 45 ka^{34,56}. By the terminal Pleistocene or early Holocene, a web of translocations seems to have carried economically important plants, including the sago palm (*Metroxylon sagu*), yams (*D. alata*) and *Dioscorea hispida*, taro (*Colocasia esculenta*) and swamp taro (*Alocasia longiloba*), to the coastlands and islands of Southeast Asia, the Philippines and Wallacea, and possibly also into North Australia^{57–59} (Fig. 1). Modification of the distribution and density of edible and economic tree species has also been observed among Amazonian hunter-gatherers⁶⁰.

Farming in the forest

The montane rainforests of New Guinea provide some of the earliest evidence for agricultural experimentation anywhere in the

world^{18,58}. At Kuk Swamp, terminal Pleistocene human foragers moved and tended tropical plants such as yam (*Dioscorea* sp.), banana (*Musa* spp.) and taro (*Colocasia* sp.) until these species were fully 'domesticated' by the early–mid Holocene^{8,61}. Both recent and ancient agricultural practices in this and other tropical forest regions were, however, combined with hunting/fishing and gathering. For example, while there was large-scale land management at Kuk Swamp, other surrounding sites demonstrate continued evidence for small mammal hunting^{62,63}. Studies of early human activities in rainforest environments have helped to blur the boundaries between tropical forest hunter-gatherers and farmers, revealing sophisticated subsistence practices, such as transplantation and cultivation extending back to at least the early Holocene. Such studies highlight how even these small populations may have altered tropical forest environments (Fig. 2).

The eventual domestication of tropical forest plants and animals, together with the incorporation of plants and animals domesticated outside of tropical forest environments, and the emergence of agricultural systems, reflect new thresholds in the intensifying relationship between humans and tropical forest environments. The scale of human selection on tropical forest species can be seen in the number of them that are central to global cuisine today, including sweet potato, manioc, chilli, black pepper, mango, yams, pineapple and banana⁶⁴ (Fig. 3). While domesticated tropical forest fauna are fewer in number, the now globally distributed domestic chicken also most probably had a tropical forest origin in the form of the jungle fowl⁶⁵. Despite new crops, however, increasingly settled tropical forest communities also continued to practice the same agroforestry systems developed by their forebearers, with a focus on the management of various tree species. For example, the first Polynesian occupants of the Chatham Islands brought with them translocated tree crops, which were important to arboriculture and agroforestry strategies (with lasting impacts on conservation efforts in these islands)⁶⁶. Likewise, stands of Brazil nut (*Bertholletia excelsa*) in the Amazon closely map onto ancient human settlements⁶⁷, reflecting long-term human interaction with and management of this species.

In addition to species domestication and translocation, the development of indigenous tropical forest agricultures during the Holocene also led to the intensive drainage and modification of soils. We have already mentioned the distinctive aspects of early Holocene indigenous agriculture in Melanesia, which involved the formation of drainage ditches to prevent waterlogging of soils in planting areas⁶¹. In Amazonia, evidence from the Llanos de Mojos⁶⁸ and Guyanas⁶⁹ highlights how populations adapted to flooding conditions in order to intensify agricultural production. In areas now dominated by tropical rainforest, pre-Columbian settlement and fire-intensive land-use practices resulted in the formation of expanses of fertile anthropic soils (Fig. 2) known as *terras pretas* and *terras mulatas*^{10,17}. These may have been re-utilized as fertile soilscape legacies by populations in the past, just as they are employed in the present.

Over their human history, tropical forests have also been influenced by expansions of neighbouring farming groups and crops. In Amazonia, the adoption of Mesoamerican maize (*Zea mays*) dates back to at least 6,000 years BP⁷⁰, and the plant was an important part of regional diets by the late Holocene⁷¹. In Africa, Bantu agriculturalists farming pearl millet and cattle appear to have expanded into the tropical rainforests of western and central Africa, c. 2.5 ka, when their extent was greatly contracted²⁴. This expansion is suggested to have resulted in severe erosion and forest fragmentation in eastern and central Africa⁷². Similarly, the arrival of rice and millet agriculture in the tropical forests of Southeast Asia is associated with large-scale forest clearance, particularly within the more deciduous forests to the north of the equatorial belt in mainland Southeast Asia, which would have been easier to burn^{73,74}.



Figure 1 | Tropical Australasian Pleistocene and Holocene sites with evidence for human presence, forest disturbance and plant translocation. Tropical Australasia showing Pleistocene sites with reasonably certain modern human presence, Pleistocene and Holocene vegetation disturbance by fire atypical of the longer Pleistocene record, or where humans are directly implicated, and locations with evidence for economically useful plants found both sides of the biogeographical discontinuity of Wallace’s Line. Top: late Pleistocene; bottom: early Holocene 11,000–5,000 BP. The figure is compiled based on data from Barker *et al.*¹¹⁸, Denham⁵⁸, Hunt *et al.*¹³, Hunt and Premathilake⁵⁹, Hunt and Rabett¹¹⁹, Marwick *et al.*¹²⁰, Mijares *et al.*⁴⁰, Moss and Kershaw⁴⁷, Paz⁵⁶, Kershaw *et al.*¹²¹, van der Kaars *et al.*¹²², Storm *et al.*³⁸, Summerhayes *et al.*³⁵ and Westaway *et al.*³⁹

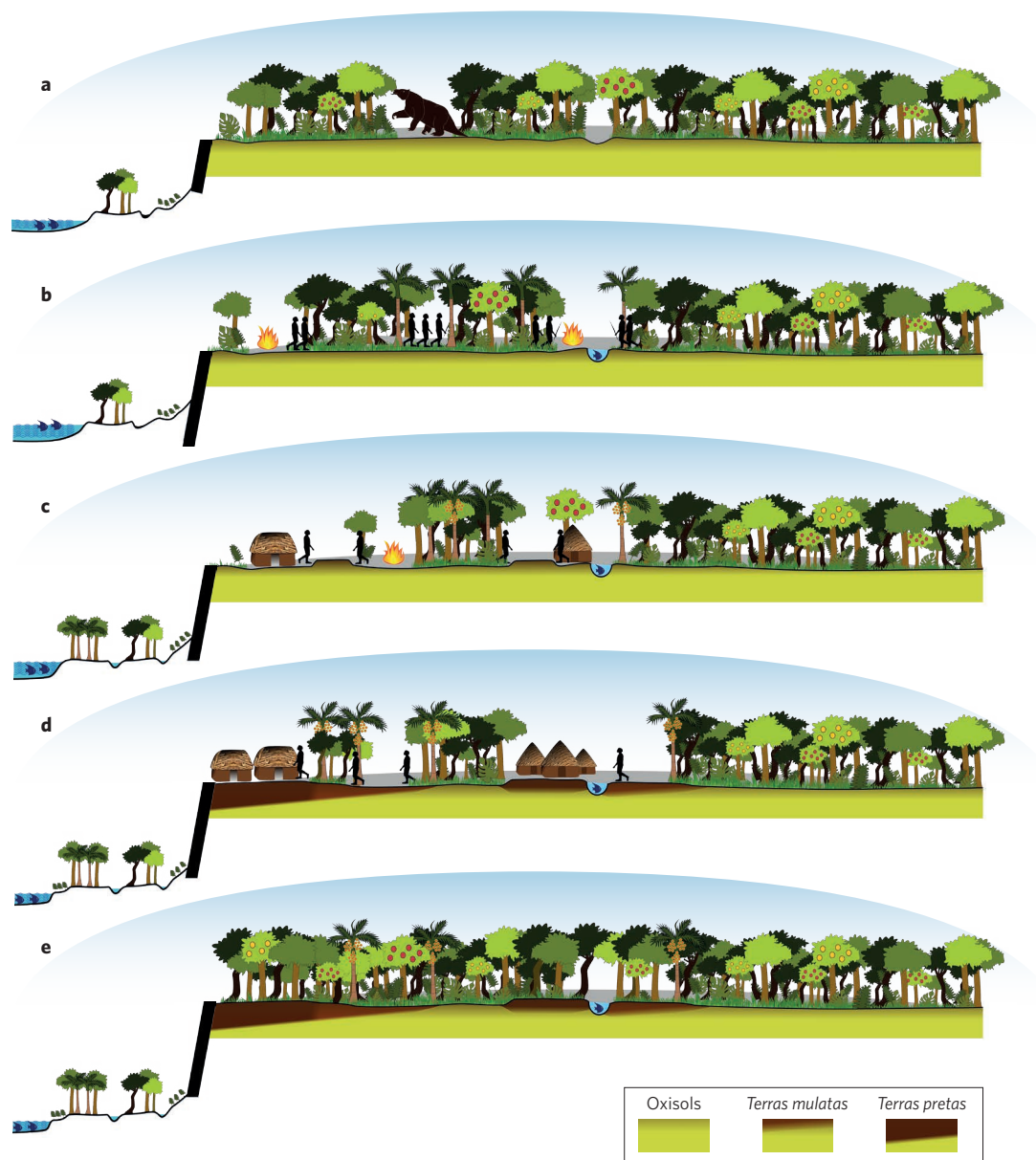


Figure 2 | A model of anthropic impact on tropical forest environments based on Amazonia. **a**, Pre-human tropical forest with natural gap dynamics, including megafaunal impacts. **b**, Nomadic foraging groups utilizing plant (including tree) and animal resources and, where desirable, forming gaps through forest burning. **c**, Initial sedentism with house gardens and slight soil modification. **d**, Increased sedentism and population growth with corresponding soil modification, swidden plots, slash and burn impacts, and small regrowth of trees on old plots. **e**, Abandonment leading to forest regrowth and the legacy of anthropic soils. Note the central role played by aquatic resources and alluvial environments for the selection of appropriate environments for human habitation.

In the Caribbean archaic and ceramic periods, meanwhile, communities brought a variety of exogenous domesticates, including wild avocado (*Persea americana*), manioc (*Manihot esculenta*), dog (*Canis lupus familiaris*) and guinea pig (*Cavia porcellus*), into island tropical forests⁷⁵. Early Polynesians similarly carried a range of domesticated crops, animals, and commensals that have contributed to the alteration of tropical forests across the region^{76,77}. On Tonga, for example, tropical forest tree species declined in abundance following Polynesian colonization⁷⁸. Extinctions also ensued. Estimates suggest that avian extinctions from the tropical Pacific after Polynesian colonization and prior to European arrival numbered in the hundreds, if not thousands⁷⁹.

Nevertheless, outside of more vulnerable island contexts, the adaptation of non-endemic domesticates to tropical forest

environments did not generally result in significant or lasting environmental degradation in pre-industrial times. Indeed, most communities entering these habitats were initially at low population densities and appear to have developed subsistence systems that were tuned to their particular environments. This stands in stark contrast to the more recent effects of industrial monoculture and extensive cattle ranching in tropical forest settings. These practices, which induce rampant clearance, reduce biodiversity, provoke soil erosion and render landscapes more susceptible to the outbreak of wild fires (for example, refs 80,81), represent some of the greatest dangers facing tropical forests. Pre-industrial farming in tropical forests, which often employed fire in controlled fashion (for example, refs 17,82), by contrast, relied on an intimate knowledge of forest dynamics and successful integration within the whole ecological

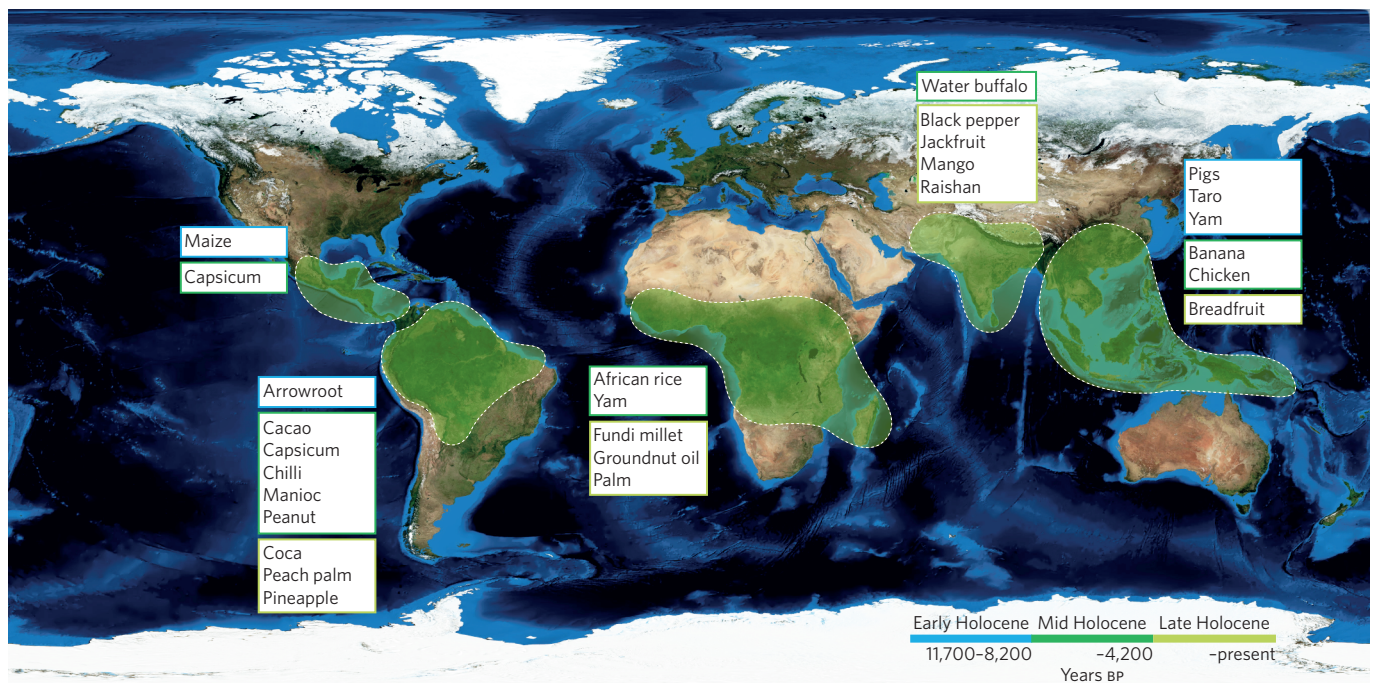


Figure 3 | Map of the temporal and geographical origins of selected domesticated plant and animal resources coming from tropical forest regions during the early (11,000–8,200 ka), middle (8,200–4,200 ka) and late Holocene (4,200 ka onwards). Temporal periods have been defined on the basis of Walker *et al.*¹²³ Temporal and geographical information comes from Pearsall¹²⁴, Clement *et al.*¹²⁵, Piperno¹²⁶, Denham⁵⁸, Kingwell-Banham and Fuller¹²⁷, Storey *et al.*¹²⁸, Fuller and Hildebrand¹²⁹, Hunt and Rabett¹¹⁹ and Nagarajan *et al.*¹³⁰ Image reproduced with permission from Reto Stöckli, NASA Earth Observatory.

system, and largely appears to have encouraged more flexible and resilient farming systems based around polyculture.

Forests of ruins or sustainable urbanism

Public perceptions of archaeology in tropical forests often revolve around ‘lost’ temples that are only now being ‘discovered’, with romantic visions of vanished cities abandoned to the jungle⁸³. In places such as Cambodia, however, these perceptions are deeply political and firmly grounded in colonialism⁸⁴. Evocative images of the rise, fall, and sudden ‘collapse’ of societies in these environments also owe much to twentieth century archaeological suggestions that large, permanent settlements could not be maintained due to the low fertility of tropical soils⁸⁵. Nevertheless, over the last two decades, archaeological data, including canopy-penetrating LiDAR (light detection and ranging) mapping, have revealed previously unimagined scales of human settlement in the Americas and Southeast Asia^{7,86}. Indeed, extensive settlement networks in the tropical forests of Amazonia, Southeast Asia, and Mesoamerica clearly persisted for much longer than the modern industrial and urban settlements in these environments have currently been present^{18,87}.

Several challenges face urban populations in tropical forest environments today. For instance, floods and mudslides pose one of the greatest threats to modern urban settlements in tropical settings⁸⁸. In 1999, a high-magnitude storm in the Vargas region of northern Venezuela triggered flash floods and mudslides that killed between 10,000 and 15,000 people and destroyed *c.* 40,000 homes in one of the worst natural disasters in the recorded history of the Americas⁸⁸. Past urban populations clearly acknowledged such challenges and worked to mitigate them. For example, communities in and around the great temple-cities of the Angkor period in Cambodia developed large-scale hydrological infrastructure to both ensure access to water and divert excess flow away from settlements⁷ (Fig. 4). Similarly, archaeological evidence from *c.* 1.3 ka in Mesoamerica

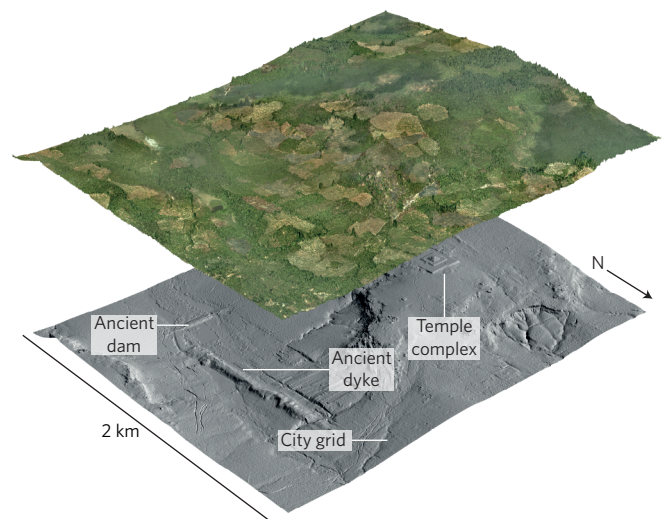


Figure 4 | LiDAR-derived bare earth model of urban and hydraulic infrastructure at a city on Phnom Kulen, ~35 km north of Angkor Wat. Penny *et al.*¹³¹ have demonstrated that the area shown here was subject to intensive land use for several centuries between the eighth and twelfth centuries CE, punctuated by episodes of severe erosion.

and Southeast Asia suggests both wetland modification and raised fields were deployed to minimize the impact of flooding on settlements^{89,90}. Nevertheless, in some cases, the ongoing danger of this high-water-flow system could not be contained, with disastrous consequences. Such impacts have been observed, for example, in the remains of the settlements of the Khmer Empire, where hydraulic systems ultimately failed⁷. The archaeological record offers both mitigation strategies and cautionary tales.

Another major challenge to sustaining large populations in tropical forest habitats is the soil erosion that results from forest clearance and large-scale agricultural systems^{91,92}. In Mesoamerica, certain Mayan communities appear to have ‘gardened’ the local forest for their resources rather than practicing forest clearance and monoculture farming⁹³. This facilitated the long-term sustainable support of large populations. Southern Mayan cities, or at least their ruling elites, perhaps did over-stretch under duress from climate change, but an overall decrease in population, with perhaps significant effects on the erosive potential of the landscape⁹¹, occurred alongside increased resilience and population growth in the northern Maya region^{90,94}. In Amazonia, dense pre-colonial populations relied on various combinations of fire-intensive cultivation practices, raised agricultural fields, capture and management of aquatic riverine resources, and foraging for wild fauna and plants^{17,68,95}. This agroforestry system helped produce fertile soils and enhanced long-term forest biodiversity. Deforestation appears to have been sufficiently limited that evidence of significant human-induced erosion in Amazonia is so far scant.

Many other archaeological and palaeoecological intersections demonstrate the fine balance between large human populations and their tropical forest environments. For instance, current evidence would suggest that a tendency towards sprawling was already present in early tropical urbanism⁹⁶. This is mirrored to a significant degree in the modern world and is reflected in concerns about the sustainability of sprawling megacities resulting in continual degradation of environments at the ever-expanding urban fringe⁹⁷. The decline of early, low-density megacities with dense urban cores and massive state-sponsored hydraulic infrastructure often appears to have been strongly correlated with climate change^{98,99}. On the other hand, diversification, decentralization and ‘agrarian urbanism’ seem to have contributed to overall resilience^{100,101}.

Implications for the twenty-first century

Although tropical forests were once seen as pristine, they are increasingly becoming recognized as outcomes of long-standing human modification, management and transformation. New methods and emerging datasets are demonstrating unequivocally that their enduring transformation by past human populations has much greater antiquity than previously thought. Yet despite the contemporary threat to tropical forests, and the need for concerted cross-disciplinary efforts to address the challenges they face, growing archaeological datasets have to date played only a relatively minor role in shaping contemporary discussions, debate, and policy-making. This is in part a result of limited archaeological survey and exploration of tropical forests relative to other environments. It is also due to the fact that few ecologists and conservationists have engaged with mounting evidence for the long-term human impact of tropical forest environments (however, see refs 15,31,102).

Some important strides have nonetheless been made. Increasing numbers of world heritage sites are now being accepted from tropical forest habitats, ranging from early *H. sapiens* cave sites in Sri Lanka¹⁰³ to large-scale field systems in Bolivia¹⁰⁴. UNESCO¹⁹ is now actively seeking to create joint world heritage sites of natural and cultural importance in tropical forest regions so that archaeological sites and their forest contexts are mutually protected within the framework of the United Nations 2030 Sustainable Development Programme¹⁰⁵. Ecological restoration projects are also drawing on archaeological data. In the tropical forests of Hawaii, for example, wild flowering plants identified in archaeobotanical assemblages have been successfully reintroduced into regions from which they had been extirpated by the twenty-first century¹⁰⁶.

Ancient tropical forest urban centres are also attracting broader attention in terms of their potential to shed light on contemporary challenges. For example, the extensive urban fringes around many

ancient tropical forest urban centres are being drawn upon within present-day urban planning research (for example, ref. 97). The role of such peri-urban interfaces in local resilience, in addressing vulnerability of urban centres to climate change, and in supporting current livelihoods and food security are of increasing interest, with archaeological data from tropical regions providing useful case studies of long-term dynamics⁹⁷. Also of interest have been tropical rainforest anthrosols, such as the fertile *terra preta* soils of the pre-Columbian Amazon. Research into these pre-Columbian soilscape legacies has both encouraged the search for pan-tropical analogues^{107,108} and inspired attempts to recreate similarly fertile soils¹⁰⁹.

Tropical forest archaeology is now past its pioneering stage. Although its development over the past decades has been enabled by new methods within and beyond the discipline of archaeology, the role of deforestation in revealing previously hidden ancient structures underlines the urgency of drawing on the past to inform present-day policy and planning. This urgency is fully felt by indigenous and traditional populations in tropical regions, many of whose livelihoods and cultural existence are intimately linked to tropical forest environments. For instance, Mbuti populations in Central Africa have been gradually evicted from the tropical evergreen rainforests of this region over the last decade or so¹¹⁰, sometimes in the name of nature conservation. This has led not only to loss of traditional ecological knowledge but also to pervasive malnutrition and disease among some groups¹¹¹. In the Brazilian Amazon, the impact of expanding infrastructure on populations is severe¹¹² and current debates examine the ethics of contract archaeological work in environmental licencing of large-scale infrastructure projects¹¹³. Threats to indigenous and traditional populations, their livelihoods, and their knowledge systems are global in scope and need to be factored into any attempts to marry archaeological practice and policy relating to tropical forests.

Archaeological and palaeoecological data relating to ancient tropical forest problematizes the notion of any return to pristine conditions. If past human populations have in many cases altered tropical forests in ways that have rendered them more useable for human inhabitation—improving ecosystem services in modern parlance—then perhaps restoration is a problematic goal, at least if such practices are aimed at restoring to some ‘original’ condition. Archaeological research instead promotes recognition and, in some cases, conservation of ‘novel ecosystems’^{114,115} that have helped to sustain human populations over the long term. The championing of novel ecosystems and abandonment of traditional conservation goals are controversial ideas, but are clearly amongst a number of key debates that archaeologists might usefully weigh in on as part of wider, interdisciplinary discussions about tropical forests.

In conclusion, we suggest that emerging understanding of the long-term history of tropical forests points to a number of core recommendations. Foremost amongst these is that indigenous and traditional peoples—whose ancestors’ systems of production and knowledge are slowly being decoded by archaeologists—should be seen as part of the solution and not one of the problems of sustainable tropical forest development. Second, there is a need for greater dissemination of the findings of archaeology beyond the discipline in order to enable broader understanding of long-term human alteration of tropical forest regions, and informed consideration of its implications. Third, we should continue to advance along the path of more regular and intensive exchange between archaeologists, ecologists, anthropologists, biologists and geographers, engaging beyond academia with international bodies such as UNESCO and FAO^{19–21,116,117}. To this end, we advocate holding further regular meetings dedicated to a holistic and pantropical approach to the study of the archaeology of tropical forest biomes, as well as undertaking to achieve broader engagement between archaeologists and stakeholders.

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Author contributions

P.R. conceived of the manuscript, wrote the manuscript and conceived of and produced Figs 2 and 3. C.H. wrote the manuscript and conceived of and produced Fig. 1. M.A.-K. wrote the manuscript and conceived of and produced Figs 2 and 3. D.E. wrote the manuscript and conceived of and produced Figs 3 and 4. N.B. conceived of the manuscript, wrote the manuscript and conceived of Figs 2 and 3.

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Competing interests

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