

Review

Tropical Trees as Time Capsules of Anthropogenic Activity

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After the ice caps, tropical forests are globally the most threatened terrestrial environments. Modern trees are not just witnesses to growing contemporary threats but also legacies of past human activity. Here, we review the use of dendrochronology, radiocarbon analysis, stable isotope analysis, and DNA analysis to examine ancient tree management. These methods exploit the fact that living trees record information on environmental and anthropogenic selective forces during their own and past generations of growth, making trees living archaeological ‘sites’. The applicability of these methods across prehistoric, historic, and industrial periods means they have the potential to detect evolving anthropogenic threats and can be used to set conservation priorities in rapidly vanishing environments.

Trees of the Tropics in Prehistory and History

Tropical forests harbor over half of the world’s biodiversity, providing fundamental ecosystem services of local and global significance [1]. However, every day 32 000 hectares of tropical forests are deforested [2], threatening mass extinctions and the disappearance of these ecosystems if no urgent conservation actions are taken. Contrary to the common image of ‘pristine’ forests prior to these industrial-era threats (e.g., [3]), prehistoric human impacts on tropical forests are far more significant than once thought [4]. Multidisciplinary archaeological and paleoenvironmental datasets have demonstrated tropical tree domestication, massive landscape and forest cover modifications, and even the formation of vast, preindustrial cities in the midst of tropical forests [5–7]. This is particularly the case in the Amazon Basin, where ‘Garden Cities’, horticultural landscapes, and preferential selection of specific plant species are known to have supported millions of Indigenous peoples [8,9]. Significantly, here, as elsewhere, these prehistoric practices are now known to have left their mark on modern tropical forest composition and nutrient cycles [6,10]. This means that plants growing in these environments today are not just endangered natural biota but also crucial legacies of cultural heritage that record the past impacts of climate change and anthropogenic actions in the tropics.

While growing attention has been placed on using genetic variation among modern domesticates and the current distribution of their wild relatives to determine the scale and nature of past human interactions with certain crops, there has been relatively little focus on the application of multidisciplinary approaches to examine the most prominent structural constituents of tropical forests, trees. Trees are capable of surviving for centuries in the landscape, taking carbon from the air and water and essential mineral nutrients from the soil. Trees incorporate these resources into their wood during growth [11], with input varying from year to year depending on factors like nutrient availability, sunlight intensity, and rainfall amount and seasonality. Their incremental growth rings thus reflect their abiotic and biotic environment throughout their lifespan and enable chronological records of changes in growing conditions to be reconstructed. Scientists can accordingly sample and analyze modern trees to reconstruct how forests have changed and evolved in response to external factors, including human societies.

Highlights

Tropical forests now known to be key sites of ancient human occupation and modification from the Late Pleistocene, intensifying into the Late Holocene.

Dendrochronology and radiocarbon dating demonstrate that living tropical trees can provide ‘stratigraphic records’ of human influences on growth patterns over the past millennium.

Stable isotope analysis of tree rings identify climate-related influences on tree growth, enabling differentiation of natural- versus human-induced forest disturbance.

Genetic studies of modern trees can reconstruct impacts of past human activity on the population structure of species that have been deforested (‘selected against’) or promoted (‘selected for’) by humans.

Tropical trees are not just key organisms for global climate, biodiversity, and carbon stock but also represent surviving ‘time capsules’ of cultural heritage.

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As scientific methods have evolved and come of age, the suite of methods available for studying trees as time capsules of broader natural and historical processes has expanded. Here, we explore some of the key methods that are currently available for exploring ‘tree history’, including dendrochronology, radiocarbon dating, stable isotope analysis, and genetic analysis. Using findings from a range of multidisciplinary case studies, we demonstrate that ancient trees are still preserved in tropical forests and are the last living witnesses of various Late Holocene climatic oscillations and natural forest disturbances, as well as past changes in human land use and management practices [12,13]. Much work in this regard has been focused on the Amazon Basin, due to its global significance to nutrient cycling, biodiversity, and climate [14,15] as well as its recent history of major upheavals as a result of changes in human technology, land use, and sociopolitical organization [9,16,17] – including the arrival of colonialism and global demand for forest products such as rubber [18]. However, for the purpose of this review we try to go beyond the Amazon Basin and draw on work from other parts of the tropics where possible. In highlighting the potential and challenges of diverse, cross-disciplinary methods in reconstructing ‘living archaeologies’ in the tropics, we hope to encourage the extension of these approaches to cover more species and tropical regions. Finally we provide some insights into changing forest management through time and the relevance of information about the past to conservation policy today.

Tracking the Tempo and Conditions of Growth: Dendrochronology, Radiocarbon Dating, and Stable Isotope Analysis

The past decade has witnessed a significant upturn in the application of dendrochronology in the tropics. Despite initially being considered impossible due to a perceived lack of tropical environmental seasonality, dendrochronological study has now demonstrated that more than 200 tree species form annual rings in tropical regions [19]. While the annual nature of these rings has been debated, with some studies suggesting they may form over longer periods [20], the joint application of radiocarbon dating with dendrochronology has helped to develop robust time series of growth patterns [21,22]. Although primarily used to study carbon uptake in one of the most major, but also vulnerable, carbon stocks on the planet [23,24], radiocarbon dating of tree rings has also facilitated more accurate dating of tree-ring records where estimations based on ring counting are insecure. Moreover, while joint applications of dendrochronology and radiocarbon dating are currently rare [25], they have helped to identify tree records that cover significant periods of human social and political change in the tropics over the past millennium. For example, individual trees of the species *Bertholletia excelsa* have now been dated between 670 and 1000 years BP in upland forests (*terra firme*) in the Amazon Basin [26], meaning that their records span major historical overhauls in land use seen following the arrival of European colonialism and resulting mass mortality of Indigenous populations [27].

Once chronologies for tree growth have been established, joint analysis of multiple individuals can be used to analyze recruitment patterns in a tropical forest stand [28,29], growth patterns of individual trees [25,30], biomass productivity [31], and forest dynamics [32,33] in a given region at a high level of temporal constraint. These parameters can then be related to external factors, including human activities. Long-lived pioneer species, for example, benefit from additional light following gap formation, which can be caused by human burning activities or deforestation [34], enabling these species to grow into the forest canopy [25,30]. Sustained changes in tree diameter growth (i.e., release and suppression events), analyzed through the relative growth change rates of rings [35], can provide quantitative information about such events. For example, Caetano Andrade *et al.* [13] demonstrated reduced recruitment rates in a stand of *B. excelsa* in the vicinity of Manaus, Brazil at the beginning of the 19th century, arguing this was a product of the interruption of Indigenous management practices coincident with the collapse of pre-

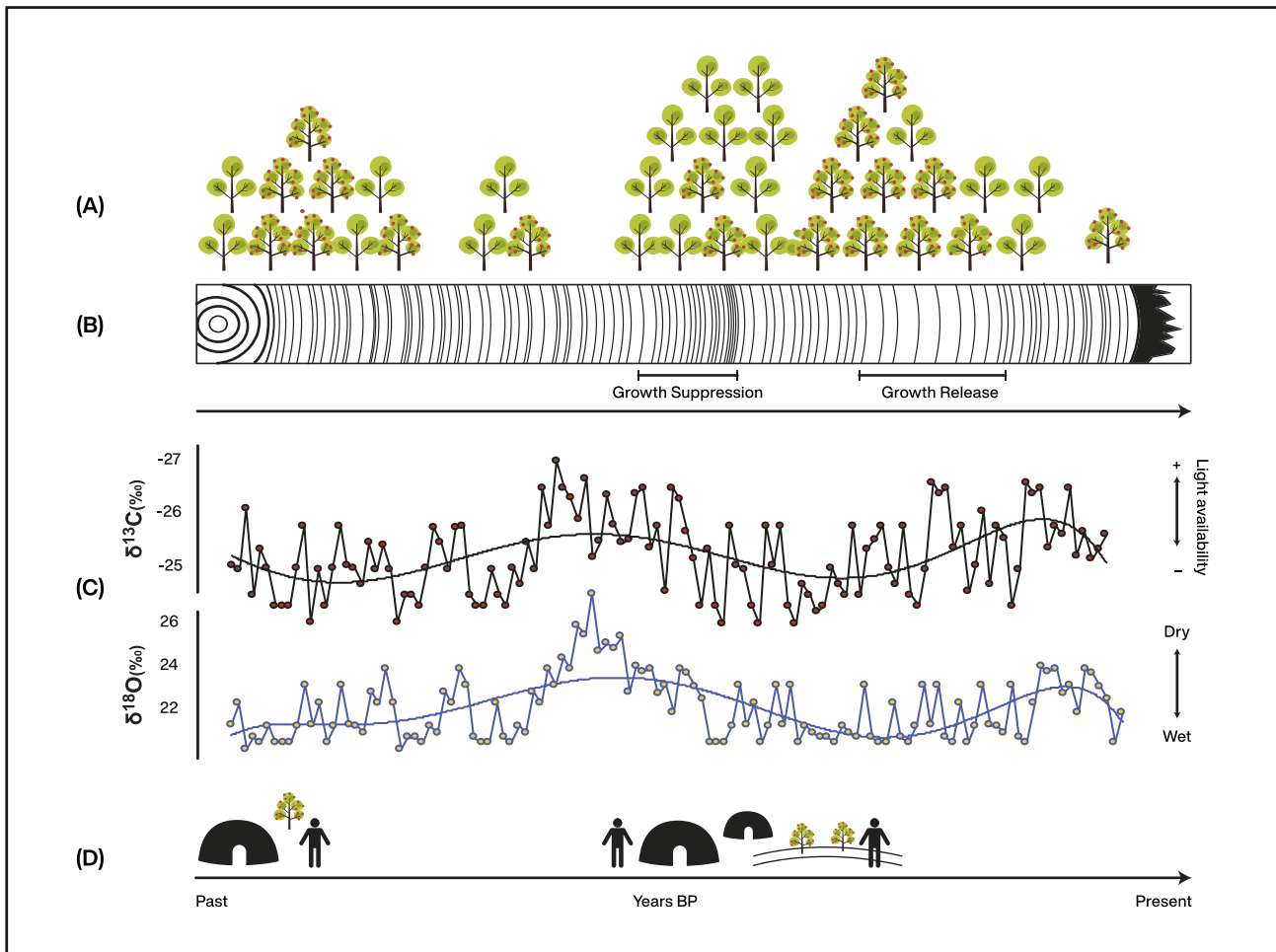
Columbian societies following the arrival of European populations [13]. This work highlights the presence of a long-term, living record of human–environment interactions in tropical tree populations.

Recent research involving stable isotope transects across tree cores has documented climate-related variations in growing conditions. Stable oxygen isotope ($\delta^{18}\text{O}$) analyses of tropical tree cellulose, for example, have been drawn on to provide insights into changes in water sources [23] and demonstrate significant correlations with intra-annual rainfall variation [36–39]. By contrast, stable carbon isotope ($\delta^{13}\text{C}$) is more related to light availability and factors that control the stomatal conductance and rate of photosynthesis [11]. $\delta^{13}\text{C}$ variation can indicate changes in light availability (i.e., canopy structure) and periods of gap formation [40]. Together, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ can also help to identify seasonal climatic variations in tropical trees records [41,42] and have been used to provide insights into changes in complex climate systems (i.e., El Niño–Southern Oscillation, Asian Monsoon system) [39,43], as well as their potential impacts on human societies. For example, Buckley *et al.* used hydroclimate reconstruction from tropical southern Vietnamese tree rings to implicate increasingly long, severe droughts in the decline of the Greater Angkor urban network in Cambodia in the 14th century AD [44]. Similarly, Stahle *et al.* [45] related severe droughts to a series of historically important events across Mexico using a network of tree-ring chronologies [45]. Perhaps most importantly, however, is the fact that the combination of these climatic insights with growth pattern information from dendrochronology and radiocarbon dating within the same tree core allows the determination of whether human activity or climate change was the most probable cause of changes in past tree-growth patterns (Figure 1).

Examining Spatial and Temporal Changes in Demography and Relatedness: Modern Tree DNA

The analysis of the DNA of modern trees is a regular fixture of silviculture and an important tool for the selection of economically desirable traits (e.g., [46]). Work over the past two decades has also demonstrated the efficacy of genetic analysis as a tool for understanding the deep demographic histories of particular tree species, and their relationship to external factors, such as climate change and human activities (e.g., [47–50]). This work initially focused on DNA coming from organelles (mitochondrial and chloroplast DNA), as they have smaller and more structurally simple DNA than the vast nuclear genomes of many trees [51,52]. Such approaches enable the observation of broad population-level trends when enough individuals are sampled. For example, the analysis of chloroplast DNA in trees such as the white elm (*Ulmus laevis*) around the Mediterranean, white spruce (*Picea glauca*) in Alaska, and ulmo (*Eucryphia cordifolia*) in temperate South America has been used to support the hypothesized contraction of tree populations into environmental refugia during the Last Glacial Maximum [53–55]. Similarly, studies of microsatellite variation in tree chloroplasts have been drawn on to help to determine the geographic patterns of domestication of certain important species. For example, the organelle DNA of a number of economically important tree species, such as papaya (*Carica papaya*), tree gourd (*Crescentia cujete*), chocolate tree (*Theobroma cacao*), peach palm (*Bactris gasipaes*), inga (*Inga edulis*), brazil nut (*B. excelsa*), and cupuassu (*Theobroma grandiflorum*) [56–58], has been demonstrated to correlate with areas of intense precolonial human occupation in various parts of Central and South America [58,59].

Although DNA from the mitochondria and chloroplasts of long-lived species may be considered to provide only coarse temporal insights into the influence of external factors on population fragmentation, effective sampling strategies have proved that such methodologies can provide insights into human-linked population changes on decadal scales. This method has



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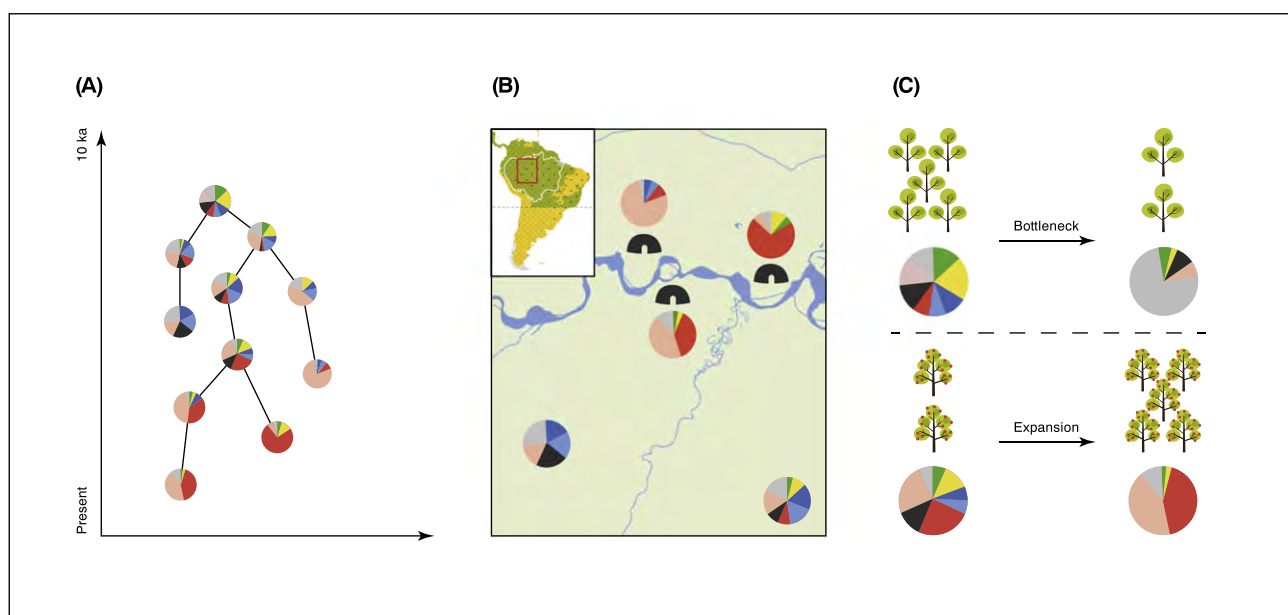
Figure 1. Tree Rings Document Impacts of Humans and Climate on Tree Growth. (A) Patterns of recruitment for a given tree population that is favored by human presence over time (represented by trees with fruits) and other trees growing in the same area (represented by trees without fruits). (B) The capacity of tree-ring analysis to date a tree and to reconstruct changes in growth patterns of individual trees, revealing periods of rapid growth (release events) and periods of decreased growth (suppression events) related to forest disturbances and competition of the economically useful fruiting trees favored by humans with other trees (i.e., canopy dynamics) in the past. (C) Records from stable carbon and oxygen isotope analysis in tree rings, represented by hypothetical data, provide information related to past environmental and climatic conditions. (D) Contextual information from archaeology and history further enables distinction between climate change and human behavior as primary drivers of changes in tree growth and population dynamics.

been used to demonstrate that recent industrial logging activities have reduced genetic diversity, increased inbreeding, and elevated the genetic differentiation between different isolated populations as tree population size and densities have decreased, forming bottlenecks akin to those seen following major climatic disruptions [60]. For example, when chloroplast DNA from mahogany trees (*Swietenia macrophylla*) was compared between recently logged areas and adjacent undisturbed areas across seven regions of the Amazon, this revealed clear patterns of population restriction and genetic homogenization in logged populations [61,62]. A series of factors can contribute to the resilience of forests to genetic fragmentation, such as gene flow via dispersal [63,64] and generation overlap among fast-growing species (e.g., [48,65,66]). Nevertheless, providing that the behaviors of the studied species are well known, this work highlights the fact that analysis of the DNA of living trees can permit inferences about past human selection and disturbance.

With the emergence of technologies that enable the rapid sequencing of the entire nuclear genomes of individual trees, alongside sophisticated statistical approaches [67], the demographic information available from the DNA of modern trees has increased significantly in the past decade. This is a product of higher mean numbers of alleles, higher mean allelic richness, and a higher percentage of polymorphic loci in the datasets available for analysis [52]. With thousands to millions of sequenced markers that are easily obtained across many individuals, one can detect divergent lineages [68,69] and identify candidates for domestication alleles that have been favored by anthropogenic selection and accumulated in domesticated populations [49,70] (Figure 2). For example, genomic analysis of the chocolate tree (*T. cacao* L.) revealed the selection of genes likely to be involved in the process of bitterness reduction, as well as disease resistance [50]. Similar results might be expected for tree species known to have been translocated by humans – for example, paper mulberry (*Broussonetia papyrifera*), in the Pacific – and represents an important avenue of future genetic research that has often focused on more ‘traditional’ domesticated species [71]. However, it has also been demonstrated that low genetic diversity is correlated with human disturbance, meaning that species intensively logged by humans should record ‘bottlenecks’ in their genetic history (Figure 2). For example, Derero *et al.* [72] note the lowest nuclear and chloroplast genetic diversity in populations of Sudan teak (*Cordia africana*), a declining forest tree in Ethiopia disturbed during the establishment of coffee plantations three decades prior. Interpretations of human influence on tree genetic diversity will, however, be reliant on comparison with detailed climatic and archaeological datasets for contextualization.

‘Tree Houses’: Living Trees as Cultural Heritage

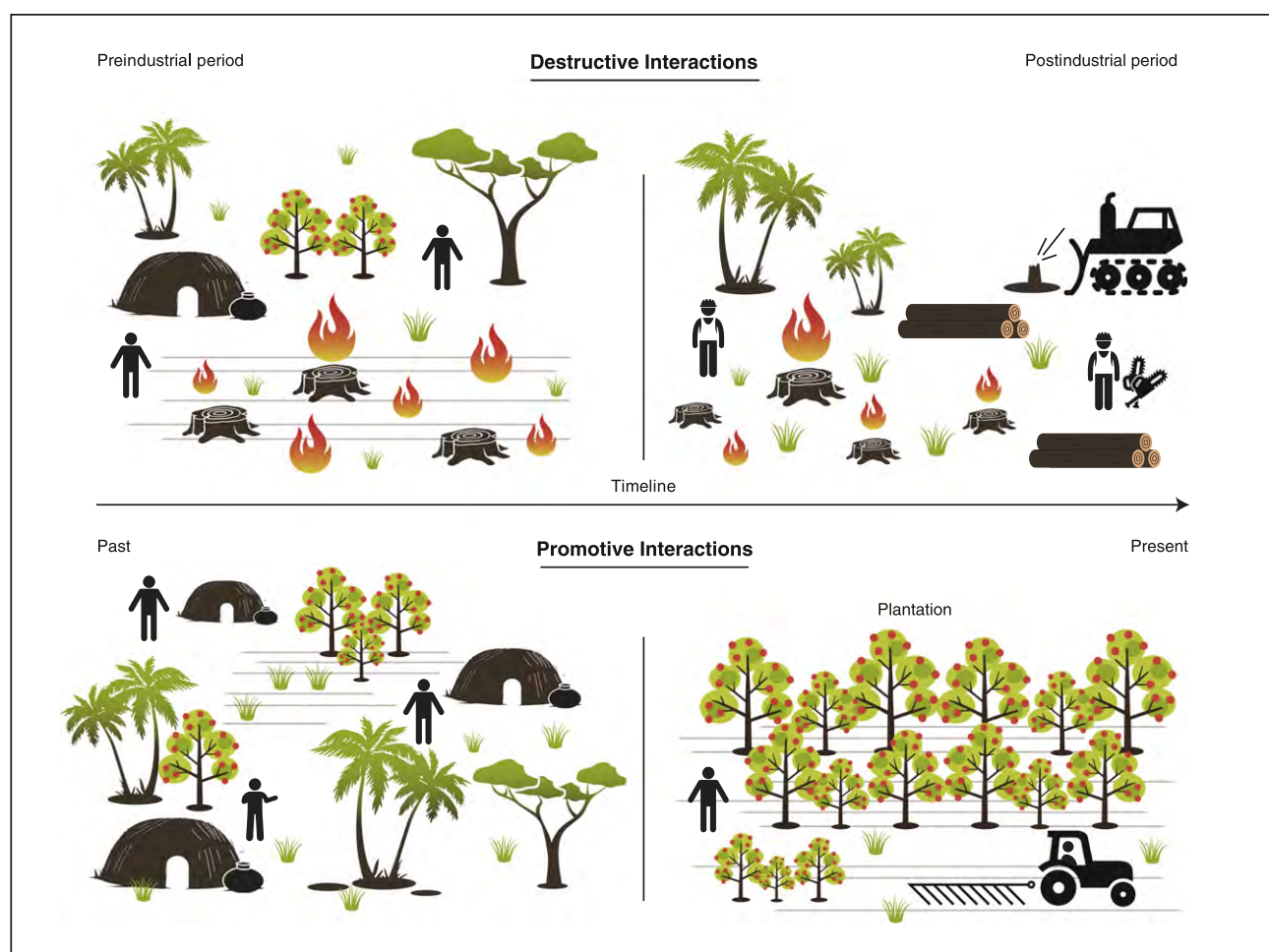
While changes in forest structure and tree growth have traditionally been linked by ecologists to climate fluctuations and natural disturbances, particularly in the supposedly ‘pristine’ tropics, it



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Figure 2. Tree DNA Records Past Human Impacts on Population Structure. Graphic of the potential contributions of living-tree genetic analysis to the study of past tree populations in the form of (A) ancestral relationships and estimates of genetic diversity through time that may be linked to human factors (e.g., management following the arrival of humans in South America), where the pink and red colors represent alleles related to some phenotypical characteristic that has a particular value to human selection and dispersal (e.g., fruit size, fruit sweetness). (B) Spatial mapping of the genetic diversity of populations of the same species and its correlation with human presence and activities as revealed by archaeology. (C) Full-genome analysis of bottlenecks (for trees unfavored and deforested by humans through time) and expansion (for trees selected and promoted by humans through time).

is now clear that humans have manipulated tropical forests in some parts of the world since the Late Pleistocene [73,74] and by the Late Holocene were in some regions having large-scale effects linked to the emergence of vast urban networks [4,75,76]. Trees can provide a number of benefits to humans (sometimes referred to as ‘ecosystem services’), finding use as food, medicine, manufacturing, construction, thatching, and firewood [77]. In the Amazon and other tropical forests, tree management practices include the cutting of non-useful competing plants, opening of the forest canopy, liana cutting, and fire management (see [5] for detailed examples). Depending on the utility to humans of particular species, management practices can aim at either the promotion (i.e., selection, protection) or non-promotion (i.e., elimination) of particular trees (Figure 3). Given that current tropical forest species distributions, abundance, and structure can reflect past transitions in human forest management [6,10] and that the methodologies outlined above can illuminate such past events, one must conclude that living trees not only have significant ecological value but are also standing repositories of cultural information.



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Figure 3. How Humans Promote or Suppress Trees, Past and Present. Schematic of the various destructive and promotive interactions humans may have with tropical forest systems and their impacts through time. The nature and scale of these activities will have varied across prehistoric, historic, and postindustrial timeframes. Understanding of these activities and their relationship with the tree species studied will be essential to properly interpret the methodologies displayed in Figures 1 and 2 (see also Table 1).

The information that can be obtained about past human relationships with tropical trees will depend on the lifespan, growth patterns, reproductive strategies, and dispersal tactics of individual tree species. Living trees in the tropics are already beginning to provide exciting insights into past human settlement and land use, particularly in the context of precolonial and colonial forms of land use. This is particularly the case in the Amazon Basin. Here, it is now increasingly recognized, by archaeologists and ecologists alike, that Indigenous peoples managed and altered tropical forest structure and species prior to the arrival of Europeans. For example, at least 85 tree species have undergone some degree of domestication [6]. The dominance of some of these species, such as açai (*Euterpe precatoria*), piquiarana (*Caryocar glabrum*), the rubber tree (*Hevea brasiliensis*), and the iconic brazil nut (*B. excelsa*), across the Amazon Basin is likely to have links with Indigenous selection, with the brazil nut being used by humans for at least 11 000 years [78]. Recent dendrochronological and anthracological work has highlighted the degree to which colonial expansion, decimation of Indigenous people due to European diseases, slavery, and warfare, and new forms of land use have altered forest management and tree growth in the Amazon [13,79]. Taking a more wide-reaching approach across the tropics, Vlam *et al.* [29] analyzed incremental cores from 1154 trees from 12 species in Bolivia, Cameroon, and Thailand to estimate the ages of trees across in three different tropical forests. They argued that recruitment patterns discovered for shade-intolerant species in West Cameroon and Central Bolivia were potentially linked to the abandonment of agricultural fields in recent history, with long-term anthropogenic dynamics influencing disturbance–recovery cycles in tropical forests in the same way as those prominently documented in temperate climates.

In this way, the increasingly widespread multidisciplinary analysis of tropical trees holds much potential to yield broader insights into how these organisms have responded to different histories of human land management on global scales. When compared with the Amazon Basin, for example, ecologists and archaeologists have been much more resistant to the idea that humans have played a significant role in shaping the long-term structure and species diversity of Central African tropical forests [80], with most arguing that climate dynamics alone – from the Last Glacial Maximum through to the Late Holocene – have dictated fluctuations in their extent and composition [81]. The dominance of climate change as a sole driver is beginning to be contested, however, notably in the case of the study of the forest retreat witnessed during the Late Holocene ‘Rainforest Crisis’ about 2600 to 2000 cal. years BP, although this continues to be hotly debated [82,83]. While this question may be accessible from a tree DNA approach, it is unlikely that the multidisciplinary suite presented here will be applicable to such long timescales. Nevertheless, as in the neotropics, recent dendrochronological work has documented clear changes in land use and forest management between Indigenous activities and the onset of colonial governance in Africa. Morin Rivat *et al.* [12] analyzed the population and demographic structure of four light-dependent pioneer species, the ordeal tree (*Erythrophloeum suaveolens*), afromosia (*Pericopsis elata*), afara (*Terminalia superba*), and African whitewood (*Triplochiton superba*), using tree-ring studies and age-growth models [84–87], finding that individuals younger than 165 years were absent. The authors argued that changes in political organization in the 19th century, primarily as a consequence of the expansion of European presence and administration, resulted in less itinerancy and disturbance in the forest compared with preceding Indigenous activities. They suggested that this in turn caused a lack of regeneration of these historically managed tree populations.

Concluding Remarks and Future Perspectives

Despite the fact that tropical forests are broadly neglected in studies of human prehistory and history, archaeological research into human subsistence, land use, and social organization across the global tropics has begun to attract significant attention [4,73,76,88]. This research is

Outstanding Questions

Are more combined studies of dendrochronology, radiocarbon dating, stable isotope analysis, and DNA analysis of modern trees feasible across the tropics? These methods are underutilized together to obtain maximum insights into how human societies influenced past tropical tree populations. However, many tropical tree taxa now known to be sources of food, construction, and symbolism to large prehistoric and historical human societies, representing important targets for future work.

How many long-lived tree species with annual growth rings exist in the tropics? Radiocarbon dating and dendrochronology combine to determine whether rings are annual in tropics, as well as the overall age of trees. Trees dating to ca 1000 years old have now been found in the Amazon Basin but it remains to be seen how common such ages are across the tropics.

How did changes in human land use influence tree growth and population structure in precolonial, colonial, and industrial periods in the tropics and can we pinpoint an early-onset ‘Anthropocene’ in these organisms? Multidisciplinary analyses of tree growth and population structure that span at least the last five centuries can be used to investigate the scale of tropical forest loss and regrowth with various social, economic, and political upheavals that, in some cases, have been proposed to be so significant as to represent the onset of the ‘Anthropocene’.

Can long-lived tropical trees also be used to look at differing prehistoric human management in the tropics (e.g., how did Amazonian ‘Garden Cities’ impact different tree species relative to modern day urbanism)? Where datasets of human–tropical forest interactions from living trees extend beyond historical records, they can provide a major step change in how we understand the sustainability of different types of human land use through time. For example, it would be possible to determine how different forms of urbanism (e.g., dispersed versus nucleated) influenced tree growth, recruitment, and diversity over space and time, with implications for modern urban planning and priorities.

increasingly supported by a diversity of multidisciplinary methodologies, including remote sensing [89], diverse archaeobotanical analyses [79], and genetics and genomics [90,91]. This review demonstrates that such investigations need not solely focus on obvious settlement structures, landscape modifications, or materials excavated from archaeological sites, but that cross-disciplinary studies of living trees can also yield significant insights into past human forest management and ecosystem alterations. DNA studies of modern and archaeological plants are being increasingly drawn on to document trends in the domestication and management of certain key crops, such as maize [92], and important tree species, such as annatto (*Bixa orellana*) [93], peach palm (*B. gasipaes*) [94], and papaya (*C. papaya*) [56]. Meanwhile, dendrochronology and stable isotope analysis have been frequently used in temperate, and increasingly tropical [39,40], environments to study either human or climatic impacts on forest development (e.g., [95,96]). These approaches are, however, yet to be thoroughly combined in the analysis of different species of living tropical trees on a wide scale to document changing temporal and geographical trends in the management of different taxa (domesticated and non-domesticated) and the relative impacts of human and climatic influences on forest structure and population dynamics (Table 1).

The novel combination of specialist dendrochronological, stable isotope, and plant genetic methodologies should also occur alongside robust appreciation of other, more traditional, archaeological and paleoecological methods. Microbotany, including pollen and phytolith analysis, can be used to reconstruct tropical vegetation structure and anthropogenic management at increasingly high resolution. For example, Maezumi *et al.* [79] demonstrate that changing proportions of economically useful plants in Lake Caranã in the Amazon Basin fluctuate strongly correlated with human burning and remain reflected in floral diversity in the region today. Meanwhile, anthracological analyses of lake and archaeological sediments reveal changing human fire management regimes through time [97–99]. Alongside detailed archaeological and historical contextual information, these methods provide an important anchor for dendrochronological, radiocarbon dating, and stable isotope approaches to studies of the relative importance of anthropogenic and climatic forces in shaping tree growth patterns in the past (Figure 1) and genetic analyses investigating the association of human activities with tree population bottlenecks (Figure 2). In doing so, broader insights into land use and paleoenvironmental change can be used to develop more resolved insights of tree population structure, growth patterns, and distribution and their association with past human societies.

We argue that such an integrated approach has much to offer for studies of the human past in the tropics, though currently remains underapplied (see Outstanding Questions). Detailed dendrochronological analysis of tropical trees is beginning to provide new insights into how transitions from indigenous to colonial land use have altered the growth patterns of certain species in Central Africa and the Amazon Basin [12,13]. Extending such analyses to other areas of the world and different species of trees has the potential to further elucidate the impacts of social, political, and economic upheaval on forests around the world (see Outstanding Questions). Moreover, the combination with integrated DNA research holds promise for more resolved insights into human management of particular species over significant periods of time. First, full genome analysis and high-resolution dendrochronological comparison of climate and anthropogenically driven growth patterns in certain parts of the world offer the possibility of reconstructing the significance of changes in agriculture, forest selection, and land management across precolonial, colonial, and industrial periods to tree regeneration and population diversity – potentially contributing to arguments of an early onset of the ‘Anthropocene’ in tropical contexts [27,74] (see Outstanding Questions). Second, the discovery of tropical trees dated to ca 1000 years ago, and constraint on tree life cycles and reproductive patterns, raises the possibility of studying

Table 1. Different Methodologies for Analyzing Living Trees, Their Shortcomings, and the Possible Information They Can Provide in Relation to Past Human Interactions with Tropical Forest Environments

Methodology	Sample type	Shortcomings and considerations	Potential	Insight into past human activity	Refs
Tree-ring analysis	Tree core obtained using borer or entire disk obtained from logging or natural death	Tree rings must be present and annually formed Growth of the sampled species must in some way be relatable to human activity Large sample size needed to cross-date individual trees and reconstruct demographic changes Wood samples collected with a borer may hide irregular anatomical features of the wood, such as false rings and eccentric pith	Enables reliable, annually resolved information on tree growth	Analysis of ring width and 'release' or 'suppression' events can evidence human management or abandonment Shade-intolerant species can present recruitment pattern associated with human presence Species used for nutrition by humans will generally be favored during periods of human presence	[12,13,28–30,32]
Radiocarbon dating	Cellulose extracted from rings of tree core or entire disk	Expensive, depending of the number of samples Must be calibrated, which can result in a wide uncertainty of cal. years BP	Enables validation of the annuity of tree-ring formation Where tree rings are irregular or not seasonally representative, radiocarbon dating provides direct assessment of age	Can give insights into recent carbon cycling ('bomb curve' studies), which may be relatable to recent regional and global human activity	[21,22]
Stable oxygen isotope ($\delta^{18}\text{O}$) analysis	Cellulose extracted from rings of tree core or entire disk	Requires labor-intensive cellulose extraction methodology Can be difficult to interpret the primary driver of change without baseline data	Provides insights into the water source of a tree as well as precipitation seasonality and amount	Climatic information can be used to infer whether dendrochronologically determined demographic changes in tree populations are linked to climatic changes or anthropogenic activity	[11,23,37–39,44]
Stable carbon isotope ($\delta^{13}\text{C}$) analysis	Cellulose extracted from rings of tree core or entire disk	Requires labor-intensive cellulose extraction methodology Can be difficult to interpret the primary driver of change without baseline data	Provides insights into the carbon cycling of a tree that can be linked to local environmental changes (sunlight, deforestation, climate)	Environmental information can be used to infer whether dendrochronologically determined demographic changes in tree populations are linked to climate change or anthropogenic activity	[11,24,41]
DNA analysis	Young leaves or cambium	Difficult to date observed genetic variation Issues interpreting the causes of population structure	Can be used to infer spatial and temporal genetic variation for populations of a given species	Where tree species is 'promoted' or 'suppressed' by humans, genetic variation can be correlated with anthropogenic activities DNA from dated trees enables association of genetic patterns with temporal demographic changes, which can be related to human environmental manipulation (i.e., planting, plant transportation, and cultivation of individuals)	[51,52,58,65]

variation in prehistoric human impacts on certain tree species. Of particular interest could be a comparison of how Garden Cities or 'low-density agrarian urbanism' [4,75] characteristic of early tropical forest use compares with more 'traditional' dense urban land use in this regard (see Outstanding Questions).

Beyond specific research questions and areas, however, perhaps one of the most significant aspects of the research discussed here is the way it forces us to reconsider prevalent ideas

concerning archaeological ‘sites’ and ‘materials’. In the face of massive deforestation threats, the UNESCO World Heritage program has promoted the protection of 107 forest sites covering a combined 750 000 km² across the globe. More than 50% of these are tropical and found in Latin America and the Caribbean [100]. Traditionally, arguments for protection have been focused on the ecosystem services provided by these crucial environments in the form of clean drinking water, nutrient cycling, food sources, construction materials, biodiversity, and protection against natural disasters. We must, however, not ignore another contribution of living tropical trees – that they act as cultural heritage repositories of knowledge about how human action has shaped the forests in which people reside today and on which a large fraction of humanity depends. Our sentiment echoes increasing calls by UNESCO to focus on combined cultural and natural heritage protection areas across the tropics [100,101]. By 2050, over half of the world’s human population will live in the tropics [102], placing new burdens on already stressed tropical forest resources. In this context, and with the development of novel multidisciplinary approaches to the study of these environments, it is essential that archaeologists and ecologists work together to preserve not only the natural benefits provided by tropical trees but also the centennial and millennial scale records of human activities and knowledge that are imprinted within them.

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