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Human contribution to Amazonian plant diversity: legacy of pre-Columbian land use in modern plant communities

Encarni Montoya[1,*], Umberto Lombardo[2], Carolina Levis[3,4], Gerardo A. Aymard[5] & Francis E. Mayle[6].

1 Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), 08028 Barcelona, Spain. Email: emontoya@ictja.csic.es
2 Institute of Geography, University of Bern, 3012 Bern, Switzerland. Email: umberto.lombardo@giub.unibe.ch
3 Instituto Nacional de Pesquisas da Amazônia – INPA, Brazil
4 Wageningen University & Research – WUR, The Netherlands. Email: carollevis@gmail.com
5 CiProgress Greenlife, Bogotá, D.C., Colombia. Email: cuyuni24@hotmail.com
6 University of Reading, RG6 6AB Reading, UK. Email: f.mayle@reading.ac.uk
* Corresponding author: emontoya@ictja.csic.es

Abstract

Amazonia is the world's largest tropical forest and is globally important in terms of its ecosystem services and extraordinarily high levels of biodiversity. The origin of this biodiversity has long been attributed to purely natural drivers, with little consideration given to the legacy of millennia of human land use. Here, the potential contribution of pre-Columbian human activity (prior 1492 CE) to current patterns of plant diversity in Amazonia is explored via long-term (palaeoecology, archaeology) and short-term (botany, plant ecology) studies. The aim of the chapter is to examine the information available to date and discuss recent advances and persisting shortcomings relevant to the extent to which pre-Columbian human societies influenced patterns of Amazonian plant diversity. This topic has been the subject of long-standing scientific debate over several decades, and among diverse disciplines. In recent years, this debate has intensified following the development of new techniques and data. The findings indicate that humans have had an impact upon Amazonian plant diversity for over 13,000 years. Late Pleistocene/early Holocene humans domesticated numerous plant species and may have inadvertently caused long-lasting ecosystem changes by contributing to Pleistocene megafauna extinction. Based on our literature review, we identify four key types of pre-Columbian anthropogenic impact, leaving a clear legacy upon current patterns of plant diversity: i) construction of vast earthworks, which has altered forest and savannah cover through changes in micro-topography, fire use and hydrology, ii) widespread distribution and dispersal of domesticated plants, iii) the creation of exceptionally fertile, anthropogenic soils, which enabled continuous, intensive agro-forestry, and iv) the enrichment of plant communities with edible and useful species. We argue that knowledge of the degree to which humans have shaped plant diversity over the past several millennia has relevance for developing sustainable land use and improving our understanding of the likely responses of Amazonian ecosystems to environmental and anthropogenic disturbance.

Keywords: anthropogenic soils, archaeology, biogeography, botany, edible plants, indigenous peoples, land use, landscape transformation, palaeoecology, plant composition

1. Introduction

Amazonia contains the largest area of tropical rainforest on Earth (6 million km^2), encompassing Amazonia *sensu stricto* (Olson et al. 2001; Keller et al. 2004) and three peripheral regions: the Guayana Shield and Plateau, the Andean foothills, and the Gurupi basin (*sensu* ter Steege et al. 2013; Antonelli et al. 2018; Alves Valles et al. 2018). This vast area is characterised by high levels of biodiversity, which have long been the focus of scientific interest across disciplines (Antonelli et al. 2018). Yet, the origin and patterns of Neotropical diversity have largely been explored in the context of natural processes and drivers, with little consideration given to the potential role of humans, despite the ancient human occupancy of the Americas (Goulding et al. 2003; Lyons et al. 2016).

Humans have interacted with tropical forests for at least 100 millennia (Roberts et al. 2016,2017). While the type and scale of these activities has varied across the world, sometimes leading to significant landscape impact (van der Kaars et al. 2017), the oldest evidence of human occupation in the tropical Americas dates back to 13,000 cal yr BP (calibrated years before 1950 CE) (Roosevelt et al. 2002). We hypothesize that early scattered human populations may have been responsible for some of the current patterns of forest biodiversity and structure in Amazonia, even when they attained low population densities (Goldberg et al. 2016).

The disappearance of Pleistocene megafauna in South America, for instance, was roughly coeval with the arrival of humans (Barnosky and Lindsey 2010). As ecological engineers, megafauna had profound impacts on biodiversity, plant distribution, forest structure, nutrient cycling and carbon storage in Amazonia (Barnosky and Lindsey 2010; Doughty et al. 2013, 2016). While it could be argued that their extinction entailed a shift in the natural dynamics of Amazonian ecosystems and led to long-lasting effects on present-day ecosystems, the role of humans in this process has yet to be fully resolved (Barnosky and Lindsey 2010), and therefore will not be discussed in this chapter. Besides megafauna depletion, it also has been suggested that early Amazonian hunter-gatherers may also have modified the distribution and density of edible and useful tree species (Balée 1994; Lauterjung et al. 2018).

A clear example of direct anthropogenic influence on current Amazonian plant diversity emerges from studies of domestication of globally important crops (Clement et al. 2010; Doughty 2010; Piperno 2011; Watling et al. 2018). Humans are known to have managed Amazonian landscapes since the early-mid Holocene (Levis et al. 2018), through practices that involved (i) the transformation of soil properties, through the addition of nutrients or hydrological changes in watersheds (Glaser and Birk 2012; Lombardo et al. 2011a; Rostain 2010), (ii) the domestication and cultivation of edible species (Bush et al. 1989; Clement 1999; Perry et al. 2007; Hilbert et al. 2017), (iii) the contribution to the dispersal success of selected species (Shepard and Ramirez 2011), and (iv) the elimination of competitors or predators of selected species (Bruno et al. 2003; Posey 1985). Beyond the global importance of Amazonian crop staples such as manioc (*Manihot esculenta*, also known as *cassava* or *yuca*), for instance, special attention has been paid to the potential impact of humans on the abundance and distribution of several species of palm (Arecaceae), which have been widely used by indigenous peoples, both in the past (Morcote-Ríos and Bernal 2001) and present (Smith 2015). As we explain below, Arecaceae contains a large number of Amazonian hyperdominant species (ter Steege et al. 2013), whose unusually high abundance has been attributed, in some cases, to their relationship with humans (Levis et al. 2017). It is therefore not surprising that several authors have explored the potential anthropogenic influence on the current distribution, or domestication routes, of some of the most useful palm species (Rull and Montoya 2014; Bush and McMichael 2016; Galluzzi et al. 2015; Clement et al. 2017).

We attribute the ongoing controversy over the relationship between past human activities and Amazonian plant diversity to multiple factors: (i) a scarcity of data and differing land-use practices compared to extra-tropical regions (Whitehouse and Kirleis 2014); ii) the massive depopulation of Amazonia over the last 500 years, which gives the impression of an 'empty' pristine wilderness (Denevan 1992a); and (iii) a disconnect between scientific fields, and lack of interdisciplinary research, which led to an unbalanced understanding of human-environment interactions through time (Barlow et al. 2012; Maezumi et al. 2018). To fill this knowledge gap, we here review key lines of evidence from multiple scientific fields -archaeology, biogeography, botany, ecology, and palaeoecology - to examine the potential legacy of past human land use upon Amazonian plant diversity.

2. Historical scientific background and hypotheses

The extraordinarily biodiverse rainforests of Amazonia have long been considered by Europeans to be evidence of a largely untouched pristine wilderness, ever since the Columbian Encounter (Jameson 1858; Denevan 1992a). Despite early European reports of numerous settlements of high population density (Medina 1934), this view of Amazonia as a pristine wilderness was at least partially due to the absence of the elaborate and ornate stone architecture, urban plazas, or population centres that characterised Peru and Mexico at the time of the Columbian Encounter. Later, the romantic idea of the 'noble savage' living in harmony with the surrounding environment, akin to a 'Garden of Eden', was embraced by European societies that spread the 'pristine myth' during the following centuries (Hemming 2006; Redford 1991).

In this sense, historical records from the 19th century described the Amazonian peoples as sparse, scattered populations, largely confined to the banks of major rivers (Jameson 1858; Medina 1934; Denevan 1996; Livi-Bacci 2016). After the Columbian Encounter, there was widespread depopulation of the most accessible sites, due to a combination of population collapse (arising from the introduction of European diseases and slavery) and abandonment to avoid further interactions with Europeans (Dobyns 1966; Crosby 2004; Chambouleyron et al. 2011). The net effect of site abandonment was that lands formerly cleared and/or cultivated underwent secondary succession (Chambouleyron et al. 2011). Consequently, the 'wilderness' described by European naturalists in the 19th century as pristine, was actually, in many cases, secondary forest regrowth (Loughlin et al. 2018). It was in this framework that research programmes on pre-Columbian environmental-human interactions began to develop during the second half of the 20th century.

Observations of lifestyles and land-use practices of modern Amazonian indigenous groups formed the basis of theories, hypotheses, and assumptions developed by anthropologists and cultural ecologists. They observed that Amazonia was populated by small and mobile indigenous groups, mostly hunter-gatherers, and linked the low level of social complexity of these populations with limited agricultural potential due to low soil fertility and high rainfall (Meggers 1954), and scarcity of protein (Gross 1975). According to Meggers, the archaeological evidence of pre-Columbian complex societies in Amazonia (e.g. Marajó Island, Meggers 2001) was best explained by the migration of complex societies from the Andes, rather than *in situ* cultural development. Meggers thought that, once these groups from the Andes settled in Amazonia, the harsh, 'unproductive' Amazonian environment led to cultural regression towards simpler societies such as the small indigenous groups we see in modern Amazonia. On the other hand, Lathrap (1970) disagreed with Meggers' view, instead arguing that the *várzea* (the white-water river floodplains) was relatively fertile and nutrient-rich, enabling social complexity to emerge along the large rivers of Amazonia. Both of these scenarios of social complexity are consistent with 'environmental determinism', by which human development and activities are controlled by the physical environment (Meggers 1954).

The role of 'environmental determinism' in Amazonia, however, has been increasingly challenged thanks to the emergence of evidence for complex pre-Columbian urban systems in riverine settings, *terra firme* (upland interfluve), and wetland areas. Such evidence includes anthropogenic soils (*terra pretas*) and a diverse range of artificial earthworks, including fishery ponds, ring ditches, large habitation mounds and raised fields (Heckenberger and Neves 2009; Blatrix et al. 2018; Carson et al. 2016; Iriarte et al. 2012; Lombardo et al. 2011b; Prestes-Caneiro et al. 2016; Rostain 2010; de Souza et al. 2018) - the most impressive of which are the geometric geoglyphs of Acre and the urban road and plaza network of the Upper Xingu (Heckenberger et al. 2003,2008; Watling et al. 2017). The best evidence for social complexity comes from Marajó Island and Santarém (Roosevelt 1991; Stenborg et al. 2012) in Brazil, and the Llanos de Moxos in Bolivia (Lombardo and Prümers 2010). The existence of archaeological evidence of large cultural diversity has promoted a shift in how the Amazonian forests are traditionally perceived. Thus, the general view of pre-Columbian Amazonia has been shifting from the traditional paradigm of virgin wilderness toward a radically different view of Amazonia as a human-created, domesticated landscape or cultural parkland (Denevan 1992a; Heckenberger et al. 2003; Balèe and Erickson 2006; Erickson 2006) - especially among the archaeologists and anthropologists.

3. The debate reactivated

This progressive accumulation of archaeological and ethnobotanical data has led to the development of a new research program for Amazonia within the natural and social sciences called Historical Ecology, which attempts to understand the cumulative effects of centuries and millennia of interactions between past societies and environments (Balée 2006, 2013). Currently, a scientific debate has been reactivated and focused on critical questions related to the scale of human activities and their impact on the vegetation that remain unanswered. The debate is directly related to whether or not there is enough evidence accumulated to infer the main drivers of the ecological dynamics for the entire region, which results in open questions in and outside academia. The uncertainty about the spatial extent of human legacy on Amazonian plant diversity can be exemplified with the following questions: Can we assume that a particular spot of Amazonia is pristine in the absence of evidence of pre-Columbian human impact? Or should we assume that people significantly impacted all areas of Amazonia, in which case no place in Amazonia should be considered pristine? Clearly, these hypotheses have profound consequences in the way Amazonian vegetation diversity should be perceived nowadays and in the future.

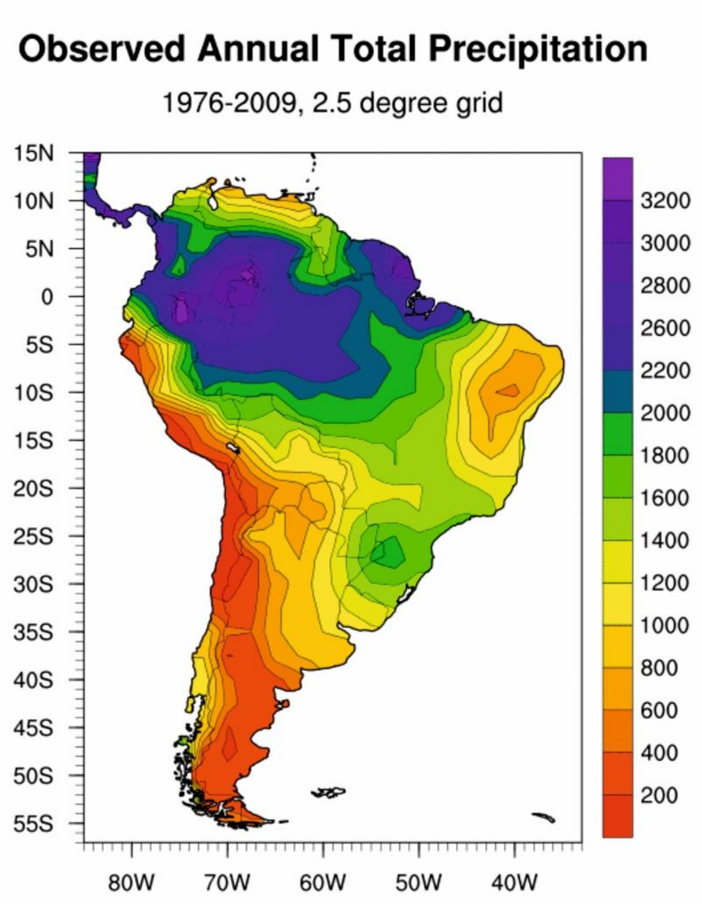

Figure 1. Map of observed annual total precipitation in South America during the time interval between 1976 and 2009 at 2.5 degree grids resolution. Source: NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at https://www.esrl.noaa.gov/psd, based on Liebmann & llured, 2005).

Besides the contribution of archaeology and anthropology to the subject, additional input has come from the study of long-term (palaeoecology) and short-term (botany, ecology) dynamics of Amazonian vegetation. Even though Neotropical palaeoecology began in the late 1960s, most studies focused on unravelling vegetation responses to climate change, especially during the last Ice Age (Colinvaux 2007). It was not until the 1990s that most palaeoecologists routinely included charcoal analysis to infer past fire regimes as disturbance drivers of the vegetation. Recent studies indicate that natural fires are rare in the wettest parts of Amazonia under today's climatic conditions (e.g. eastern Ecuador), and are normally associated with human-caused ignition (Figure 1; Bush et al. 2007a; de Toledo and Bush 2007; Mayle and Power 2008). In this sense, Charles Lyell's principle of uniformitarianism (summarised as the present is the key to the past; Tomkeieff 1962) is often used to interpret the occurrence of high fire incidence in Amazonian palaeoecological records as indication of human presence (Bush et al. 2016). Two hypothetical scenarios are provided below to exemplify potential interpretations of human presence based on the charcoal record. First, an abrupt increase in past fire regime in study sites nowadays inhabited and with no further major changes in the record (thus, maintaining a similar signal since the former and abrupt increase), can be indicative of the presence of indigenous peoples (Bush et al. 2007a; de Toledo and Bush 2007; Montoya and Rull 2011). Second, past high fire regimes in todays' uninhabited locations (presenting low charcoal values nowadays) might point to abandoned settlements (Carson et al. 2014). However, assuming human presence as the exclusive driver of fire occurrence may result in wrong interpretations, as the (past and present) natural flammability potential of the ecosystems must also be considered. For instance, SW Amazonia was characterised by a climate much drier in the mid Holocene relative to now, supporting more flammable dry forests and savannahs than today's rainforests. Thus, peaks in mid Holocene fire frequency in this region could have been caused by natural processes, with or without any human intervention (Mayle and Power 2008). Such differences in the interpretations of the same proxy highlight the importance of developing a truly multi-factor scenario for palaeoecological reconstructions, considering the role of several drivers and their different importance as forcing factors through time (Rull 2018). Also, it manifests the shortcomings of using only one proxy to infer human presence. Besides charcoal particles, the occurrence of pollen grains from cultivated plants in sedimentary archives, even in low abundances as in the case of maize, is considered direct evidence of human occupation (Liu and Colinvaux 1988).

The increase of multiproxy investigations, as well as the development of new techniques including phytoliths (microscopic biogenic silica formed in plants, which enables reconstructions of past vegetation), non-pollen palynomorphs (microscopic remains of biological origin other than pollen and pteridophyte spores preserved in palynological slides), and remote sensing and GIS, have provided clear evidence of pre-Columbian occupation in several areas previously thought to be uninhabited (Piperno et al. 2002; Lombardo et al. 2013a; Palace et al. 2017). Site selection is crucial, as searching for palaeoecological sites near to archaeological sites would enable direct comparison and integration of different lines of evidence. In this sense, the creation of truly inter-disciplinary studies and networks has enabled the development of a more holistic, accurate picture of the human dimension to Amazonian biodiversity and ecology than has previously been possible (Mayle and Iriarte 2014; Lombardo et al. 2011b, Clement et al. 2015a). Such an improvement is essential for deciphering past land use, especially for those archaeological sites where long-term human impacts upon the environment are subtle or difficult to determine in sedimentary profiles (Kelly et al. 2018). Nevertheless, given the heterogeneity and spatial magnitude of Amazonia, the current debate does not deal with the pre-Columbian population density *per se*, but whether or not the indigenous peoples had a long-lasting effect on the Amazonian vegetation that could be recognised or inferred throughout the basin. Specifically, the controversy centres on the magnitude, spatial extent, and type of pre-Columbian anthropogenic impacts and the legacy of those impacts observable within the floristic and structural patterns of vegetation across Amazonia today (Tollefson 2013; Bush et al. 2015; Clement et al. 2015a, b; McMichael et al. 2015a; Piperno et al. 2015).

3.1. *Broad-scale patterns*

Amazonian landscapes have been managed by humans over at least the past 13,000 years of occupation, although the intensity and type of management likely varied through the Holocene (Roosevelt 2013). Through time, some ecosystems and plants were modified by humans to make them more productive and more suitable for the resource needs of human societies (Clement et al. 2015a). As a general pattern, Amazonian people today often cut and burn the vegetation, plant useful species, and alter soils to improve their drainage and fertility, resulting in considerable transformation of forests near their homes (Levis et al. 2018). Recent archaeological and anthropological studies have shown that small-scale clearing and burning activities by indigenous communities have not been practised with the same magnitude over the last several millennia (Siren 2014; Riris 2018). Based on modelling data, interviews with current indigenous settlements, and the review of historical records literature, these studies suggest more extensive slash-and-burn forest clearing activities after the European Encounter compared to the pre-Columbian period than previously thought (Siren 2014; Riris 2018). Anthropogenic soils (*terra preta* and *terra marrom,* also known as Amazonian Dark Earth - ADE -, and *terra mulata* respectively), indigenous pottery, mounds, raised fields and charcoal integrated with pollen and phytolith records of cultivated plants (Neves et al. 2003; McKey et al. 2010; Iriarte et al. 2012, Bush et al. 2007a; McMichael et al. 2012a,b; Morcote-Ríos and Leon-Sicard 2012; Morcote-Ríos et al. 2013; Piperno et al. 2015) have been used to detect past human activities. Reconstructing past forest management practices, however, may require other techniques, such as an assessment of the distribution and abundance of useful (in the sense of socio-economically important or used by peoples for different reasons) tree species in modern vegetation, on the assumption that such distributions are not explainable by natural ecological processes alone but are instead a legacy of historic forest management practices (Balée, 1993; Levis et al. 2012; Clement 2014).

Although Amazonian forests have been shown to be very diverse, some tree species are consistently more abundant than would be expected from chance alone (ter Steege et al. 2013). An estimated 11,676 tree species, belonging to 1225 genera and 140 families, make up Amazonian forests (ter Steege et al. 2016), yet over half the stems belong to just 227 species. This subset of disproportionately common trees has been dubbed the "hyperdominants" (ter Steege et al. 2013). The contribution of rare species to this diversity has been recognized (Wills et al. 2006), but their spatial distribution remains poorly understood (Zizka et al. 2018). Likewise, the distribution range of some Amazonian tree species extends across the entire Amazon basin, but most are restricted to much smaller areas (Kristiansen et al. 2009). A similar imbalance is observed in species to genus ratios. Over half of all Amazonian tree species belong to genera with 100 or more species, while the majority of genera (52%) have ten or fewer species (Gentry 1993; Dexter and Chave 2016). Some of these hyperdominants are tree species with some evidence of domestication that dominate large forest areas, especially in those locations near archaeological sites (Levis et al. 2017). Ancient forest management may at least partly explain the hyperdominance of these species, corroborated by pollen evidence for the cultivation and domestication of several tree species before European conquest (Maezumi et al. 2018). However, some ecologists (Barlow et al. 2012) argue that large monodominant stands of a given species do not necessarily imply human intervention, but instead a natural phenomenon whereby particular edaphic and/or hydrological conditions favour only that species. In addition to studies dealing with the dominance of certain species within vegetation plots, it has been argued that useful tree species with some evidence of domestication (e.g., *Bertholletia excelsa*, *Theobroma cacao, Bactris gasipaes, Inga* (*edulis*) *ynga* and *Crescentia cujete*) were likely dispersed across Amazonia by past societies (Morcote-Rios and Bernal 2001; Guix 2005; Shepard and Ramirez 2011; Thomas et al. 2012, 2015; Levis et al. 2017, Moreira et al. 2017, Clement et al. 2017). Moreover, genetic and morphological variation of fruit shapes and types between Amazonian regions illustrates how humans have been important drivers of fruit shape diversity and distribution over several millennia (Moreira et al. 2017; Clement et al. 2017). In this sense, management and domestication of Amazonian ecosystems and their constituent flora by past peoples would have contributed to explain current ecological patterns.

Predictions of where humans transformed Amazonian ecosystems also remain controversial because vast portions of Amazonia have not been studied to date (McMichael et al. 2017a). Knowledge of Amazonia's environmental and human history has increased significantly in recent decades, but unfortunately remains geographically patchy. Particular regions have received far less scientific attention than others due, for example, to political turmoil (i.e Colombia and Venezuela), bureaucracy (Rull et al. 2008), or lack of roads/trails preventing access. Even for those areas which are accessible and have been studied, a lack of evidence of landscape domestication may arise from i) the use of inappropriate proxies or lack of an inter-disciplinary research strategy, ii) the absence of long-lasting effects clearly visible today (e.g., forest recovery after land abandonment), or iii) a poor visibility of past land use in the palaeo record (e.g. lack of charcoal due to poor flammability, use of cultigens/domesticates which are poorly preserved/represented in the palaeoecological record). Nevertheless, some insights about the human contribution to biodiversity, understood hereafter in terms of species abundance and plant community assemblages, can be obtained. For instance, humans controlled local-scale forest expansion around past occupation sites in some forest-savannah ecotones (Carson et al. 2014) and expanded the distribution and abundance of socio-economically important tree species across the region (Balée 2013). Legacies of past human activities, such as landscapes and plant populations with different degrees of domestication, are commonly found near archaeological sites with and without *terra preta* (Levis et al. 2017, 2018). Moreover, remote-sensing data have revealed past human influence on forest structure (Palace et al. 2017; Stenborg et al. 2018). In *terra preta* sites, forest biomass and tree height were found to be lower compared to random sites (Palace et al. 2017). Large-scale studies have described a widespread distribution, although heterogeneous, of archaeological sites (Clement et al. 2015a; McMichael et al. 2017a, see also Figure 2) and socio-economically important plants across Amazonia (Levis et al. 2017). Balée (1989, 2013) estimated that around 11% of forest has been transformed by the long-term process of plant cultivation and forest management among indigenous peoples. However, caution must be taken when considering this rough estimate, as it is based on a list of potential useful species that encompasses species with and without known active management, and extrapolates sub-regional data across the large extent of the entire Amazon basin. In addition, modern assemblages with useful, hyperdominant trees may not necessarily derive from pre-Columbian activities, but could be historically more recent, for instance from the last few centuries (McMichael et al. 2017b).

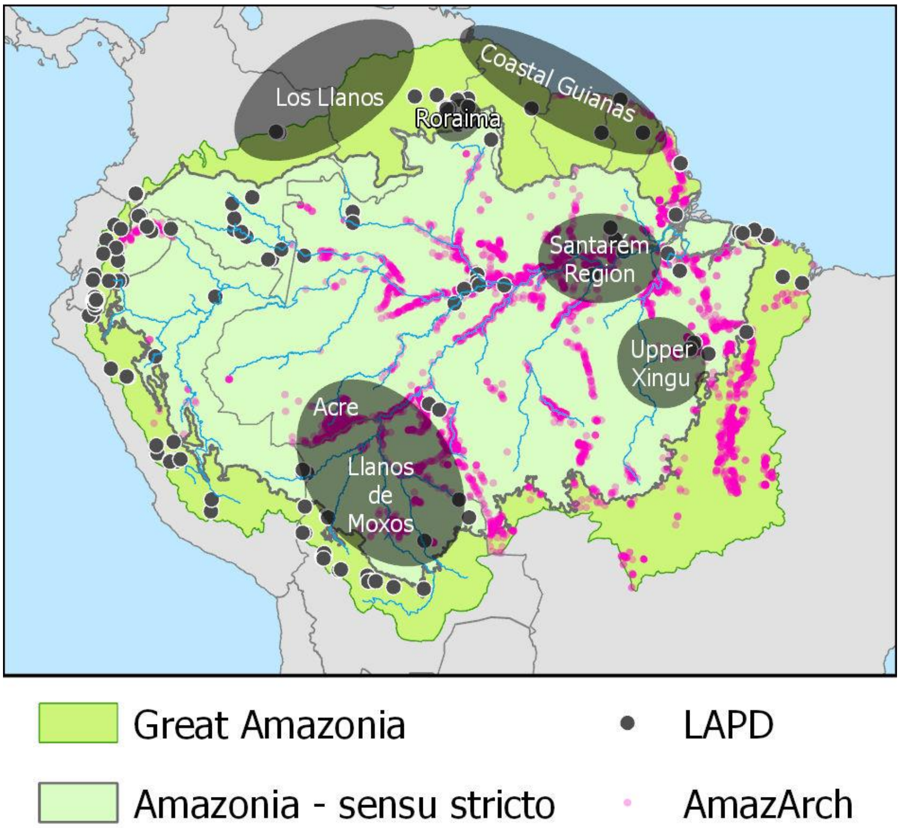

Figure 2. Map of Amazonia (following Eva et al. 2005) showing the archaeological sites contained in the database AmazonArch and the palaeoecological records uploaded in LAPDB (Latin American Pollen Database; Flantúa et al. 2015). The main regions mentioned in the text are marked with dark shades. Modified from Lombardo et al. (2018b).

To prevent unwarranted extrapolations and assumptions, the spatial extent and heterogeneity of the entire Amazonia must first be established and understood, as the evidence obtained and interpretations made in a given region are not necessarily representative of other regions in the basin. Furthermore, palaeoecological evidence of past human land use can be highly localised: clearly evident at some sites, but absent from others only a few kilometres (km) away (Bush et al. 2007a). In addition, the magnitude of human impact upon vegetation is not necessarily correlated with human population density, and some types of land use, especially those not requiring fire, may not be recognisable with current palaeoecological techniques. For instance, Bush and Silman (2007) reconstructed the regional fire and vegetation history to infer associated human presence and activity using 22 palaeoecological records of lakes of western and eastern Amazonia. The study perfectly shows the danger of extrapolations to supra-local scale data from "dot-data maps", and highlights the need for (i) incorporating climate seasonality information to infer fire origins, and (ii) sampling away from human-inhabited areas to prevent over-estimates regarding human occupation and impact (Bush and Silman 2007). In another study, Bush et al. (2007b) employed a multi-site approach with different lacustrine sequences near an archaeological site in Peruvian Amazonia (total study area of 50 km radius), which again demonstrated highly localised land use. Similarly, McMichael et al. (2012a), using phytolith and charcoal data from 55 soil cores, found low frequencies of charcoal and lack of phytoliths of maize and cultivated plants in most soil samples of western and interfluvial parts of the basin. These findings were used to support the hypothesis that wetter and remoter forests were occupied by smaller human groups that created only sporadic and highly localised impacts on the vegetation (Bush et al. 2015; McMichael et al. 2012a,b; Piperno et al. 2015). However, care must be taken again, highlighting the danger of extrapolations from point data, and also avoiding the implicit unwarranted assumption that absence of charcoal signifies absence of human occupation or land use (Watling et al. 2017) - especially in wet areas where forests are not easily burned.

Below we review evidence of past land use in those areas of Amazonia where most archaeological studies have been undertaken: southern (including southwestern), central, and eastern (including coastal and Guianas) Amazonia (Figure 2).

3.2. Regional patterns

3.2.1. Eastern Amazonia: Coastal regions of Amazonia and the Guiana Shield

Coastal Amazonia includes raised fields, which are artificially elevated berms used for agriculture, in both French Guiana (Rostain 2008) and the island of Marajó, in the mouth of the Amazon River (Schaan 2008). Data indicate that a mixed diet with maize, fruits and legumes (*Acronomia aculeata*, *Euterpe oleracea*, *Inga* spp., *Spondias mombin* and *Byrsonima sp.*) and fish sustained pre-Columbian societies on Marajó Island, and likely other complex societies in coastal regions as well (Roosevelt 2013). Today, these Marajó mounds are covered by secondary forests enriched with edible species (Roosevelt 2013). The coasts of the Guianas and areas north of the mouth of the Amazon river underwent major earthwork engineering, including mounds and raised fields to avoid seasonal flooding (Rostain 1991; Iriarte et al. 2012). Inter-disciplinary studies of the French Guiana raised fields have shown that they were cultivated in pre-Columbian times without the use of fire (Iriarte et al. 2012), demonstrating the danger of relying on charcoal alone to infer the scale of pre-Columbian land use or population density. The modified landscape and soil left a long-term legacy upon the composition of the vegetation community (Rostain 2010). These earthworks not only altered the vegetation composition, but also had long-lasting effects on ecosystem structure and functioning (which are still evident today) due to the introduction of ecosystem engineers such as ants, termites, earthworms, and woody plants in raised fields that persisted well after humans abandoned them (McKey et al. 2010).

Further inland, more evidence of human contribution to current plant diversity has been proposed in the Roraima savannahs, near the northeastern margin of Amazonia - specifically the Gran Sabana of the Venezuelan Guayana Shied (Figure 2). In this unusual treeless area located between the Amazon and the Orinoco basins and rainforests, an increase in fire frequency 2000 years ago was coeval with the arrival and establishment of a new type of vegetation in the Gran Sabana, the monospecific palm stands of *Mauritia flexuosa*, locally referred to as *morichales* (Montoya and Rull 2011; da Silva Meneses et al. 2013). It has been suggested that the vast expanses of *morichales* in Gran Sabana could be anthropogenic, whereby selective burning by humans facilitated their expansion at the expense of other species (Rull et al. 2013; Rull and Montoya 2014).

The large extent of "Los Llanos del Orinoco", or the Orinoquia savannah, has also been tentatively linked to past human activities (Berrío et al. 2012). Los Llanos is the largest savannah area in northwestern South America - a broad lowland zone that extends from northeastern Colombia to western Venezuela, occupying an area of ca. 532,000 km² (Huber et al. 2006). The Llanos vegetation is composed of a mosaic of savannahs, gallery forests, and dry semi-deciduous to evergreen forests (Aymard 2015). It has been proposed that humans played a key role in this region due to the occurrence of fire and humans in the adjacent Río Negro area, since the mid Holocene (Sanford et al. 1985; Sánchez et al. 2017). However, while humans may have modified these savannahs through use of fire and selection of economically important palms, this savannah biome is likely natural in origin, resulting from the combination of edaphic, hydrological, and climatic conditions unsuitable for forest growth (Huber et al. 2006). This is supported by drier late-glacial and early-mid Holocene conditions leading to savannah expansion and development of extensive dune fields (Sánchez et al. 2017). Because no palaeoecological record and charcoal analysis are available for a time period prior to human occupation, any inference of a fire regime shift (anthropogenically driven or not) remains elusive in this area. That being said, the hypothesis of humans driving savannah expansion has also been suggested for other treeless locations, such as the Amapá savannahs in eastern Brazil and the Venezuelan Gran Sabana (de Toledo and Bush 2007; Montoya et al. 2011) - although the presence of savannahs has been reported since the late Glacial (Rull et al. 2015). Today, savannahs might be expanding in floodplain ecosystems due to the close relationship of these ecosystems to fire (Flores et al. 2017) and their proximity to long-term human settlements along major Amazonian rivers (Denevan 1996). While humans may have been involved in the savannah expansion and maintenance in certain locations where forest-savannah transitions zones exist today, this assumption cannot be generalised to all Amazonian savannahs.

3.2.2. Central Amazonia

Central Amazonia hosts most of the anthropogenic soils, i.e. *terra preta* sites, mainly along the major water courses (Neves et al. 2004). Patches of *terra preta* are relatively large (1 to 2 hectares, sometimes reaching 90 hectares) and comprise very dark, fertile soil, and coincide with locations that were densely occupied by humans since at least 2500 cal yr BP (Neves et al. 2003). Prolonged occupation resulted in the enrichment of soil with high amounts of pottery sherds, calcium, phosphorous, charcoal and organic matter. The latter accounts for the soil's dark colour and high fertility (Glaser and Birks 2012). *Terra preta* sites are often surrounded by *terra marrom*, which is also an anthropogenic soil, similar to *terra preta*, but less dark and without pottery and less nutrient-rich. *Terra marrom* is believed to be formed in areas cultivated in the past. Past occupations and cultivation activities left very clear signals in terms of soil properties, abundance of charcoal (anthropogenic originated) and phytoliths. These proxies are increasingly used to infer past human presence and land use (Woods and Glaser 2004; Neves et al. 2003). However, the absence of charcoal and cultigen phytoliths does not necessarily imply the absence of people, as shown by Levis et al. (2012). Diverse plant communities, rich in socio-economically important plants, have been found near archaeological sites in central Amazonian old-growth forests (Levis et al. 2012; Junqueira et al. 2017), secondary forests (Junqueira et al. 2010), and home gardens (Lins et al. 2015). Many native crops cultivated today predominate on *terra preta* soils, implying that these soils may be considered reservoirs of agrobiodiversity (Clement et al. 2003; Junqueira et al. 2010, 2016). Moreover, multiple cultures contributed to the diversification of plant communities in *terra preta* sites by creating 'home gardens'. The latter were successively occupied by different pre-Columbian cultures and hold a greater variety of socio-economically important species than those occupied by a single cultural group (Lins et al. 2015). Some forests, therefore, may be perceived as mosaics of numerous and diverse vegetation patches with different degrees of cultural intervention (Levis et al. 2018).

Santarém (including Tapajós, Belterra Plateau and Monte Alegre areas), in Pará state, NE Brazil, is a region that deserves special attention. Since the 1920s, numerous pre-Columbian settlements have been discovered in this area, predominantly in *terra firme* (not in floodplains or *várzeas*) locations, and occasionally near the river banks (Stenborg 2009; Stenborg et al. 2018). These settlements are associated with *terra preta* and *terra marrom* soils, cavities or depressions (*poços de água*), and a system of roads that connected the settlements further inland. It has been suggested that these settlements, near the junction of major rivers, occupied a highly strategic location and facilitated efficient communication between several cultures along the north-south and east-west riverine axes (Stenborg et al. 2012, 2018). Besides the concentration of *terra pretas* and *terra marrom*, this area is also renowned for the longest human occupation history in Amazonia, extending to the beginning of the Holocene at the cave Pedra Pintada (Roosevelt et al. 1996). Recently published palaeoecological evidence (Maezumi et al. 2018) shows that, prior to the construction of *terra preta* soils (ca. 2000 cal yr BP), the peoples of Santarém had developed several agroforestry practices for subsistence since 4500 cal yr BP, which, by 2500 cal yr BP, had deeply altered the floristic composition of the forests via selective enrichment with edible plant species. Although this human intervention began 2500 cal yr BP, it is clearly evident in the composition of today's forests.

3.2.3. South and southwestern Amazonia

Southwestern Amazonia is one of the best studied regions of the basin. It has, by far, the clearest evidence of past human occupation and modification of the landscape, as pre-Columbian peoples built thousands of earthworks in this area - something easily visible in satellite imagery (Lombardo et al. 2011a). Acre State in western Brazil, for instance, is covered by more than 450 geometric structures called geoglyphs (Pärssinen et al. 2003). The forest surrounding these sites has been managed for millennia (Watling et al. 2017). Archaeobotanical studies detected changes in plant community composition, especially in palm abundance, when human activities intensified during the Holocene (McMichael et al. 2015b; Watling et al. 2017). In the Bolivian Amazon, much of which is covered by a seasonally flooded savannah called the *Llanos de Moxos*, raised fields (Rodrigues et al. 2018), monumental mounds (Lombardo and Prümers 2010), canals and causeways (Erickson 2001), fish weirs (Blatrix et al. 2018) and ring ditches (Carson et al. 2014) form a 100,000 km^2 anthropogenic landscape (Erickson 2008; Prümers and Betancourt 2014). Within this region, studies reveal interactions between pre-Columbian peoples and river networks over several millennia. People settled in this region more than 10,000 cal yr BP (Lombardo et al. 2013b), but abandoned the area around 4000 cal yr BP due to catastrophic flooding from the Río Grande (Lombardo et al. 2018a). These floods transformed the landscape in the southern *Llanos de Moxos* by building a sedimentary lobe of fertile and relatively well drained land that made possible the establishment of the populous, agriculture-based, monumental mounds culture in this region 2000 years later. Different cultures transformed the eastern *Llanos de Moxos* by building other types of earthworks – hundreds of canals, ring ditches and causeways (Lombardo et al. 2012). The *Llanos de Moxos* can therefore be considered to be probably the most spectacular example of pre-Colombian human-environment interactions anywhere in Amazonia.

Interestingly, centuries after the abandonment of anthropogenic mounds and soils, plant communities still hold legacies of past transformations (Erickson and Balée 2006; Quintero-Vallejo et al. 2015, Levis et al. 2017). For instance, southwestern Amazonian is the region where the highest abundance and diversity of native domesticated plants has been found (Levis et al. 2017). Important crops were first domesticated in this region, such as manioc (*Manihot esculenta*), peach palm (*Bactris gasipaes*) and hot peppers (*Capsicum baccatum*) (Clement et al. 2010; 2016), making this one of the most important domestication hotspots of South America (Piperno 2011; Watling et al. 2018). Genetic analysis also confirms that peach palm was first domesticated in southwestern Amazonia, followed by two dispersal events into western and eastern Amazonia (Clement et al. 2017). Today, domesticated plant diversity (Levis et al. 2017) and cultural diversity (Crevels and der Voort 2008) is striking in this region.

Further east, in the Upper Xingu River basin, ethnoarchaeological studies have mapped territorial polities, urbanism and extensive landscape transformations (e.g., roads, raised causeways and *terra preta*) covering an area of approximately 50,000 km^2 (Heckenberger et al. 2003, 2008). In addition, a recent study in the Upper Tapajós River basin using remote sensing, archaeological survey, and excavations has detected more than a hundred earthworks with ceramics and *terra preta*, confirming that the southern rim of the Amazon basin was densely settled between 750 and 500 yr BP (de Souza et al. 2018). These authors also estimated that approximately 400,000 km^2 of southern Amazonia was occupied by pre-Columbian earth-builders.

4. Towards a common view

Determining the extent of the human footprint on current Amazonian biodiversity is essential for the development of appropriate conservation and management strategies, as this information is directly relevant for ascertaining the degree of resilience of plant communities to drivers of change (Maslin et al. 2005). First, studying vegetation response to past climatic conditions as a rough analogue for predicted responses to future projected climate change (e.g. with respect to drought) may inform the development of appropriate mitigation or adaptation strategies (Mayle and Power 2008; IPCC 2013; Nolan et al. 2018). This palaeoecological information has been proposed to establish adequate restoration strategies (Bush et al. 2014), and has also been inadequately used by companies for exploitation activities (Bush and Silman 2007). Second, some of the pre-Columbian practices have been proposed for a future sustainable economy such as the creation of new *terra preta* soils for agriculture (Glaser et al. 2001). However, this initiative is in its infancy and further information and deeper knowledge are required before its viability can be ascertained (Renard et al. 2012; Bezerra et al. 2016).

However, this determination of the past human footprint in Amazonia is not always an easy task. As argued above, not all the aforementioned human activities left an impact upon the vegetation that remains preserved in the sedimentary record (Kelly et al. 2018). Neither the proxy preserved in the sedimentary records has to be indicative about the same environmental driver in different settings, preventing extrapolations. The examples discussed in this chapter show, for instance, that the presence of charcoal particles is indicative of fire occurrence (environmental process) - but does not imply an anthropogenic origin (environmental driver) *per se*. This calls for alternative approaches to investigate past human presence and activities, as well as other drivers of landscape change in sedimentary archives (Rull 2018). With respect to palaeoecological proxies, the search for pollen grains and phytoliths from either edible or cultivated plants, and disturbance indicators such as *Cecropia* sp. (Marchant et al. 2002), has yielded important information concerning pre-Columbian land use. Yet, it still has important limitations which need to be overcome. A particular challenge, for example, is differentiating between disturbances which are anthropogenic *versus* those which are natural, especially in geomorphologically dynamic environments such as southwestern Amazonia (Lombardo 2014,2016,2017). In most cases, the information obtained in palaeoecological records can only provide coarse evidence of human land use (Bush and Colinvaux 1988), which results in general (not detailed) interpretations of human-driven modification of the landscape (Bush et al. 2007b,2016). Accurate evaluation of the legacy of past indigenous peoples within current ecosystems – particularly regarding species richness – requires interdisciplinary studies that combine long- and short- term data such as archaeological, palaeoecological, and modern vegetation inventories (e.g., Maezumi et al. 2018).

Climatic conditions also differ largely within Amazonia (Figure 1), preventing supra-local extrapolations in most cases (i.e., to make basin-wide extrapolations from local-scale or region-specific data). For instance, equatorial western Amazonia is one of the wettest regions of the basin, containing forests which experience no dry season (i.e. months with < 100 mm precipitation). In such areas, it has been argued that slash-and-burn deforestation was difficult without readily available stones (for the production of axes) and given the poor flammability of vegetation under wet conditions (Bush et al. 2015). Clearly, absence of charcoal in these wet aseasonal regions would not necessarily signify absence of human occupation or land use, in which case alternative lines of evidence of human occupation would need to be found (Kelly et al. 2018). Although Charles Lyell’s analogue model is certainly useful for inferring the past, it does not necessarily hold true for all regions or time periods, especially with respect to slash-and-burn agriculture, which, prior to the introduction of metal by Europeans, was likely far less common in pre-Columbian times than today (Lathrap et al. 1985; Denevan 1992b). Instead, agroforestry systems which did not require forest clear-cutting and shifting cultivation was likely a much more common form of land use in pre-Columbian times than today (Denevan et al. 1984; Peters 2000; Levis et al. 2018; Maezumi et al. 2018). Therefore, forest enrichment of socio-economically important and edible plants could have been a much more common form of land use than burning in pre-Columbian times (Politis 1996; Maezumi et al. 2018). To deal with this issue, a major challenge for palaeoecologists is to increase the taxonomic resolution of their vegetation proxies to species level, in order to identify socio-economically useful plant species (Rull 2014). Another limitation that requires attention is the poor understanding of the spatial scale of human settlements and its signal in sedimentary archives. Whereas archaeology generally focuses on the local area of habitation, palaeoecological records are collected from water bodies that might be capturing a regional signal depending on the basin size. This feature of the palaeoecological records result in the difficulty of quantifying the spatial scale represented by a pollen or charcoal record. In addition, archaeological and palaeoecological archives differ in the chronological resolution that can be achieved. Given these differences, it is often challenging to effectively integrate data from different disciplines. So far, what it is clear is that more interdisciplinary collaboration is needed (Mayle and Iriarte 2014).

Following the accumulation of relevant data over the last decades, the dichotomy between the extreme and exclusive views of pristine or manufactured parklands has shifted to whether the heterogeneous past human impact was or was not strong throughout the basin (e.g., McMichael et al. 2012b). An additional conclusion from these studies relates to the spatial scale considered. Taking into account the size of Amazonia, the number of both archaeological and palaeoecological studies published so far is very limited. This is shown in Figure 2, where vast areas lack sampling points. Even within well-studied regions it is clear how little overlap exists between palaeoecological studies (concentrated toward the margin of Amazonia) and archaeological sites (distributed along the main rivers) (Lombardo et al. 2018b). In this sense, some authors argue that small sample sizes, lack of interdisciplinary (multi-proxies) overlap, and the proxies used to date are insufficient to i) detect subtle human activities across vast areas, ii) reveal the diversity of ancient domestication and management processes, and finally iii) extrapolate results from one region to the entire heterogeneous Amazonia (Stahl 2015; Clement et al. 2015a; Montoya 2018; Lombardo et al. 2018b). Caution must be taken especially regarding this last argument: whereas in archaeological studies there is a *priori* assumption of human presence, this is not necessarily the case in palaeoecology. However, given the water resources supply that lakes offer, it is not rare to expect a higher likelihood of human presence near the locations where the sedimentary records are retrieved.

Although this chapter has focused on the human contribution to diversity prior to the arrival of Europeans (pre-1492 CE), we must remember that the anthropogenic legacy upon Amazonian plant communities did not stop at the contact eve. The colonial period and, more recently, globalization, have produced important biotic interchanges that has contributed to Amazonian plant diversity by the introduction of exotic cultigens (e.g., sugar, banana) and animals from elsewhere. On the one hand, the deforestation of vast areas of the Amazonia involving fire– for industrialised agriculture and cattle ranching (Carmenta et al. 2018) – is rapidly altering the composition, structure and functioning of rainforest ecosystems in recent decades (Longo et al. 2018). On the other hand, increased indigenous political activism, the establishment of protective laws, and the recognition of indigenous territories (indigenous lands), may lead to the expansion of indigenous forest management (Muehlebach 2001). We will need to await the consequences of these changes for the future of Amazonia's biodiversity.

5. Final remarks

Pre-Columbian human impact on Amazonian plant diversity has been occurring since humans first arrived on the continent, and a clear legacy of this disturbance remains in today's forests. Late Pleistocene/early Holocene human practices such as the onset of plant domestication and cultivation, and perhaps the anthropogenic influence on the terminal Pleistocene megafaunal extinctions, had long-lasting impacts still evident in today's ecosystems. The scientific debate about the presence, population density, and impact of pre-Columbian peoples upon their rainforest environment prior to the arrival of Europeans has now extended to studies of the human legacy on current Amazonian plant diversity. Some of the interpretations obtained are the result of studies developed in specific locations and cannot be extrapolated to other areas or the entire region given the spatial extent and heterogeneity of Amazonia. Nevertheless, based on the available evidence, a potential human contribution to current diversity recognisable in an Amazonian context (supra-regionally, in a wider scale of more than a single site), would be suggested by the following general processes: i) construction of vast earthworks, which has altered forest versus savannah cover via changes to micro-topography, fire use and hydrology, ii) widespread distribution and dispersal of domesticated plants, iii) change in soil properties, and iv) enrichment of plant communities with edible and useful species.

To obtain a better understanding of the degree to which pre-Columbian peoples have shaped Amazonia's plant diversity (and where), a greater range of complementary approaches and techniques are needed from different disciplines. First, greater sampling density is needed across Amazonia. New study sites should prioritise random locations as well as sites deliberately located close to and far from archaeological sites. In order to improve our understanding of the historical human role in Amazonian biodiversity, one must consider the characteristics of the study area (climate, landscape and cultures) to determine whether broader scale extrapolations are warranted (e.g. with respect to fire regime). Thus, independent proxies are needed to determine the degree to which disturbances, such as fire, are anthropogenic or natural (climate driven). These include a combination of climatic proxies (speleothems, biomarkers), soil properties (isotopic composition), and evidence of direct human presence (non-pollen palynomorphs, biomarkers). Increased understanding of the degree to which current patterns of Amazonian biodiversity were shaped by pre-Columbian indigenous peoples, and the process by which this was achieved, may provide important insights into elucidating rainforest resilience to future land-use and climate change, as well as the development of long-term, sustainable land-use strategies.

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References

Alvez-Valles CM, Balslev H, García-Villacorta R et al (2018) Palm species richness, latitudinal gradients, sampling effort, and deforestation in the Amazon region. Acta Bot Bras, doi: 10.1590/0102 33062017abb0400.

Antonelli A, Zizka A, Carvalho FA et al (2018) Amazonia is the primary source of Neotropical biodiversity. P Natl Acad Sci USA, https://doi.org/10.1073/pnas.1713819115

Aymard G (2015) Bosques de los Llanos de Venezuela: estructura, composición florística, diversidad y estado actual de conservación: Tierras Llaneras de Venezuela. In: López-Falcón R, Hétier JM, López-HD et al (eds), IRD-CIDIAT, Mérida, Venezuela, p241-268.

Balée W (1989) The Culture of Amazonian Forests. In: Posey DA and Balée W (edds) Resource Management in Amazonia: Indigenous and Folk Strategies. NY: NYGB Press, p 1–21.

Balée W (1993) Indigenous Transformation of Amazonian Forests: An Example from Maranhão, Brazil. L'Homme 33, 231–254.

Balée W (1994) Footprints of the forest: Ka'apar ethnobotany-the historical ecology of plant utilization by an Amazonian people. Columbia University Press.

Balée W (2006) The Research Program of Historical Ecology. Annu Rev Anthr 35: 75–98.

Balée W (2013) Cultural forests of the Amazon: a historical ecology of people and their landscapes. The University of Alabama Press, Tuscaloosa, USA.

Balée W, Erickson CL (2006) Time, Complexity, and Historical Ecology. Columbia University Press. New York, USA.

Barlow J, Gardner T A, Lees AC et al (2012) How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. Biol Conserv 151: 45-49.

Barnosky AD, Lindsey EL (2010) Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. Quat Int217: 10-29.

Berrío JC, Wouters H, Hooghiemstra H et al (2012) Using paleoecological data to define main vegetation dynamics along the savannah-forest ecotone in Colombia: Impliactions for accurate assessment of human impacts. In: Myster RW (ed) Ecotones between forest and grassland. Springer, New York, p 209–225.

Bezerra J, Turhout E, Melo Vasquez I et al (2016) The promises of the Amazonian soil: shifts on discourses of Terra Preta and biochar. J Environ Pol Plann, DOI: 10.1080/1523908X.2016.1269644

Blatrix R, Roux B, Béarez P et al (2018) The unique functioning of a pre-Columbian Amazonian floodplain fishery. Sci Rep 8: 5998.

Bruno JF, Stachowicz JL, Bertness MD (2003) Inclusion of facilitation into ecological theory. TRENDS Ecol Evol 18: 119-125.

Bush MB, Colinvaux PA (1988) A 7000-year pollen record from the Amazon lowlands, Ecuador. Vegetatio 76: 141-154.

Bush MB, Silman MR (2007) Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. Front. Ecol. Envir. 5: 457-465.

Bush MB, McMichael CHN (2016) Holocene variability of an Amazonian hyperdominant. J Ecol 104: 1370-1378.

Bush MB, Piperno DR, Colinvaux PA (1989) A 6,000 year history of Amazonian maize cultivation. Nature 340: 303-305.

Bush MB, Silman MR, de Toledo MB et al (2007a) Holocene fire and occupation in Amazonia: records from two lake districts. Philos Trans R Soc B-Biol Sci 362: 209-218.

Bush MB, Silman MR, Listopad CMCS (2007b) A regional study of Holocene climate change and human occupation in Peruvian Amazonia. J Biogeogr 34: 1342-1356.

Bush MB, Restrepo A, Collins AF (2014) Galápagos history, restoration and a shifted baseline. Rest. Ecol. 22: 296-298.

Bush MB, McMichael CH, Piperno DR et al (2015) Anthropogenic influence on Amazonian forest in pre-history: an ecological perspective. J Biogeogr 42: 2277-2288.

Bush MB, Correa-Metrio A, McMichael CH et al (2016) A 6900-year history of landscape modification by humans in lowland Amazonia. Quat Sci Rev 141: 52-64.

Carmenta R, Coudel E, Stewards AM (2018) Forbidden fire: Does criminalising fire hinder conservation efforts in swidden landscapes of the Brazilian Amazon? The Geographical Journal 184: 1–15.

Carson JF, Whitney BS, Mayle FE et al (2014) Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. P Natl Acad Sci USA 111: 10497-10502.

Carson JF, Mayle FE, Whitney BS et al (2016) Pre-Columbian ring ditch construction and land use on a “chocolate forest island” in the Bolivian Amazon. J Quat Sci 31: 337-347.

Chambouleyron R, Barbosa BC, Bombardi FA et al (2011) ‘Formidable contagion’: epidemics, work and recruitment in Colonial Amazonia (1660–1750). Hist Cienc Saúde-Manguinhos 18: 987–1004.

Clement CR (1999) 1492 and the loss of Amazonian crop genetic resources. I. The relation between domestication and human population decline. Econ Bot 53: 188–202.

Clement CR (2014) Landscape domestication and archaeology. In: Smith C (ed) Encyclopedia of Global Archaeology New York: Springer, p 4388-4394.

Clement CR, McCann JM, Smith NJ (2003) Agrobiodiversity in Amazonia and its relationship with dark earths. In: Lehmann J, Kern, DC, Glaser B, Woods, WI (eds) Amazonian dark earths: origin, properties, management. Berlin: Springer, p 159-178.

Clement CR, de Cristo-Araújo M, Coppens d'Eeckenbrugge G et al (2010) Origin and domestication of native Amazonian crops. Diversity 2: 72-106.

Clement CR, Denevan WM, Heckenberger MJ et al (2015a) The domestication of Amazonia before European conquest. Proc R Soc B-Biol Sci 282: 20150813.

Clement CR, Denevan WM, Heckenberger MJ et al (2015b) Response to comment by McMichael, Piperno and Bush. Proc R Soc B-Biol Sci 282: 20152459.

Clement CR, Rodrigues DP, Alves-Pereira A et al (2016) Crop domestication in the upper Madeira River basin. Bol Mus Para Emílio Goeldi Cienc Hum 11: 193-205.

Clement CR, Cristo-Araújo M, Coppens d'Eeckenbrugge G et al (2017) Origin and Dispersal of Domesticated Peach Palm. Front Ecol Evol 5: 148.

Colinvaux P (2007) Amazon Expeditions: My quest for the Ice-Age Equator. Yale University Press, New Haven & London.

Crevels M, Van der Voort H (2008) The Guaporé-Mamoré region as a linguistic area. In: Muysken P (ed) From Linguistic Areas to Areal Linguistics. Amsterdam: John Benjamins Press, p 151–179.

Crosby AW (2004) Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge University Press, Cambridge, UK.

Denevan WM (1992a) The pristine myth: The landscapes of the Americas in 1492. Ann Assoc Am Geogr 82: 369-385.

Denevan WM (1992b) Stone vs metal axes: the ambiguity of shifting cultivation in prehistoric amazonia. J Steward Anthropol Soc 20: 153-165.

Denevan WM (1996) A bluff model of riverine settlement in prehistoric Amazonia. Ann Assoc Am Geogr 86: 654-681.

Denevan WM, Treacy JM, Alcorn JB e al (1984) Indigenous agroforestry in the Bora Indian management of swidden fallows. Interciencia 9: 346–357.

Dexter K, Chave J (2016) Evolutionary patterns of range size, abundance and species richness in Amazonian angiosperm trees. PeerJ 4: e2402.

Dobyns HF (1966) Estimating Aboriginal American population: an appraisal of techniques with a New Hemispheric estimate. Current Anthropology 7: 395–416.

Doughty CE (2010) The development of agriculture in the Americas: an ecological perspective. Ecosphere 1: art21.

Doughty CE, Wolf A, Malhi Y (2013) The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. Nat Geosci 6: 761-764.

Doughty CE, Wolf A, Morueta-Holme N et al (2016) Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. Ecography 39: 194-203.

Erickson CL (2001) "Pre-Columbian roads of the Amazon." Expedition 43: 21-30.

Erickson CL (2006) The domesticated landscapes of the Bolivian Amazon. In: Balée W, Erickson CL (eds) Time and complexity in historical ecology: Studies in the neotropical lowlands. Columbia University Press. New York, USA, p 235-278.

Erickson CL (2008) Amazonia: the historical ecology of a domesticated landscape. In: Silverman H, Isbell WH (eds) Handbook of South American archaeology. Berlin, Springer, p 157-183.

Erickson CL, Balée WL (2006) The historical ecology of a complex landscape in Bolivia. In: Balée W, Erickson CL (Eds) Time and complexity in historical ecology: Studies in the Neotropical Lowlands. New York: Columbia University Press, p 187–233.

Eva HD, Huber O, Achard F et al (2005) Synthesis of the results from an expert consultation workshop organized by the European Commission in collaboration with the Amazon Cooperation Treaty Organization – JRC Ispra, 7-8 June 2005. Luxembourg, EC: 40

Flantua SGA, Hooghiemstra H, Grimm EC et al (2015) Updated site compilation of the Latin American Pollen Database. Rev Palaeobot Palynol 223: 104–115.

Flores BM, Holmgren M, Xu C et al (2017) Floodplains as an Achilles' heel of Amazonian forest resilience. P Natl Acad Sci USA 114: 4442-4446.

Galluzzi G, Dufour D, Thomas E et al (2015) An Integrated Hypothesis on the Domestication of *Bactris gasipaes*. PLoS ONE 10: e0144644.

Gentry A H (1993) A field guide to the families and genera of woody plants of Northwest South America. Washington, D.C.: Conservation International.

Glaser B, Birk JJ (2012) State of the scientific knowledge on properties and genesis of Anthropogenic Dark Earths in Central Amazonia (terra preta de Índio), Geochim Cosmochim Acta 82: 39-51.

Glaser B, Haumaier L, Guggenberger G et al (2001) The "terra preta" phenomenon: a model for sustainable agriculture in the humid tropics. Naturwissensch 88: 37-41.

Goldberg A, Mychajliw AM, Hadly EA (2016) Post-invasion demography of prehistoric humans in South America. Nature 532: 232-235.

Goulding M, Barthem R, Ferreira EJG (2003) The Smithsonian Atlas of the Amazon. Washington DC, Smithsonian Books.

Gross DR (1975) Protein capture and cultural development in the Amazon Basin. Am Anthropol 77: 526-549.

Guix JC (2005) Evidence of Old Anthropic Effects in Forests at the Confluence of the Caurés and Negro Rivers, NW Amazonia: The Role of Indians and Caboclos. Grup Estud Ecológicos 8: 1–27.

Heckenberger MJ, Kuiluro A, Kuikuro UT et al (2003) Amazonia 1492: Pristine Forest or Cultural Parkland? Science 301: 1710-1714.

Heckenberger MJ, Russell JC, Fausto C et al (2008) Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon. Science 321: 1214-1217.

Heckenberger M, Neves EG (2009) Amazonian archaeology. Annu Rev Anthropol 38: 251-266.

Hemming J (2006) Romance and Reality: the first European vision of Brazilian Indians. In: Posey, DA, Balick MJ (eds) Human Impacts on Amazonia: The role of traditional ecological knowledge in conservation and development. Columbia University Press, New York, p 5-16.

Hilbert L, Góes Neves E, Pugliese F et al (2017) Evidence for mid-Holocene rice domestication in the Americas. Nat Ecol Evol 1: 1693-1698.

Huber O, Duno de Stefano R, Aymard G et al (2006) Flora and vegetation of the Venezuelan Llanos: A review: Neotropical savannas and dry forests: plant diversity, biogeography and conservation In: Pennington RT, Lewis GP, Ratter JA (eds). Taylor & Francis Group, LLC de Boca Ratón, Florida, p 95–120.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Iriarte J, Power MJ, Rostain S et al (2012) Fire-free land use in pre-1492 Amazonian savannas. P Natl Acad Sci USA 109: 6473-6478.

Jameson W (1858) Excursion made from Quito to the River Napo, January to May, 1857. J Royal Geogr Soc Lond 28: 337–349.

Junqueira AB, Shepard GH, Clement CR (2010) Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. Biodivers Conserv 19: 1933–1961.

Junqueira AB, Souza NB, Stomph TJ et al (2016) Soil fertility gradients shape the agrobiodiversity of Amazonian homegardens. Agric Ecosyst Environ 221: 270–281.

Junqueira AB, Levis C, Bongers F et al (2017) Response to Comment on “Persistent effects of pre-Columbian plant domestication on Amazonian forest composition”. Science 358: aan8837.

van der Kaars S, Miller GH, Turney CSM et al (2017) Humans rather than climate the primary cause of Pleistocene megafaunal extinction in Australia. Nat Commun 8: 14142.

Keller MA, Alencar A, Asner GP et al (2004) Ecological research in the large-scale biosphere atmosphere experiment in Amazonia (LBA): early results. Ecol Appl 14: S3–S16.

Kelly TJ, Lawson IT, Roucoux KH et al (2018) Continuous human presence without extensive reductions in forest cover over the past 2500 years in an aseasonal Amazonian rainforest. J Quat Sci 33: 369-379.

Kristiansen T, Svenning JC, Grandez C et al (2009) Commonness of Amazonian palm (Arecaceae) species: cross-scale links and potential determinants. Acta Oecologica-Int J Ecol 35: 554-562.

Lathrap DW (1970) The upper Amazon. Southampton, Thames and Hudson.

Lathrap DW, Gebhart-Sayer A, Mester AM (1985) The roots of the Shipibo art style: three waves on Imiríacocha, or there were "Incas" before Incas. J Lat Am Lore 11: 31-119.

Lauterjung MB, Bernardi AP, Montagna T et al (2018) Phylogeography of Brazilian pine (*Araucaria angustifolia*): integrative evidence for pre-Columbian anthropogenic dispersal. Tree Genet Genomes 14: 36.

Levis C, de Souza PF, Schietti J et al (2012) Historical human footprint on modern tree species composition in the Purus-Madeira interfluve, Central Amazonia. PLoS One 7: e48559.

Levis C, Costa FRC, Bongers F et al (2017) Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. Science 355: 925-931.

Levis C, Flores BM, Moreira PA et al (2018) How people domesticated Amazonian forests. Front Ecol Evol 5: 171.

Liebmann B, Allured D (2005) Daily precipitation grids for South America. Bull Amer Meteor Soc 86: 1567-1570.

Lins J, Lima HP, Baccaro FB et al (2015) Pre-Columbian Floristic Legacies in Modern Homegardens of Central Amazonia. PLoS ONE 10: e0127067.

Liu KB, Colinvaux PA (1988) A 5200-year history of Amazonian rain forest. J Biogeogr 15: 231-248.

Livi-Bacci M (2016) The Depopulation of Upper Amazonia in Colonial Times. Revista de Indias 76: 419-448.

Lombardo U (2014) Neotectonics, flooding patterns and landscape evolution in southern Amazonia. Earth Surf Dyn 2: 493-511.

Lombardo U (2016) Alluvial plain dynamics in the southern Amazonian foreland basin. Earth Surf Dyn 7: 453-467.

Lombardo U (2017) River logjams cause frequent large-scale forest die-off events in Southwestern Amazonia. Earth Surf Dyn 8:565-575.

Lombardo U, Prümers H (2010) Pre-Columbian human occupation patterns in the eastern plains of the Llanos de Moxos, Bolivian Amazonia. J Archaeol Sci 37: 1875-1885.

Lombardo U, Canal-Beeby E, Fehr S et al (2011a) Raised fields in the Bolivian Amazonia: a prehistoric green revolution or a flood risk mitigation strategy? J Archaeol Sci 38: 502-512.

Lombardo U, Canal-Beeby E, Veit H (2011b) Eco-archaeological regions in the Bolivian Amazon. Geographica Helvetica 66: 173-182.

Lombardo U, May JH, Veit H (2012) Mid- to late-Holocene fluvial activity behind pre-Columbian social complexity in the southwestern Amazon basin. Holocene 22: 1035-1045

Lombardo U, Denier S, May J-H, et al (2013a) Human-environment interactions in pre-Columbian Amazonia: The case of the Llanos de Moxos, Bolivia. Quat Int 312: 109–119.

Lombardo U, Szabo K, Capriles JM et al (2013b) Early and Middle Holocene Hunter-Gatherer Occupations in Western Amazonia: The Hidden Shell Middens. PLoS ONE 8: e72746.

Lombardo U, Rodrigues L, Veit H (2018a) Alluvial plain dynamics and human occupation in SW Amazonia during the Holocene: A paleosol-based reconstruction. Quat Sci Rev 180: 30-41.

Lombardo U, McMichael C, Tamanaha EK et al (2018b) Mapping pre-Columbian land use in Amazonia. PAGES magazine 26: 14-15.

Longo M, Knox RG, Levine NM et (2018) Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. New Phytol, doi: 10.1111/nph.15185

Loughlin NJD, Gosling WD, Mothes P et al (2018) Ecological consequences of post-Columbian depopulation in the Andean-Amazonian corridor. Nat Ecol Evol 2: 1233-1236.

Lyons SK, Amatangelo KL, Behrensmeyer AK et al (2016) Holocene shifts in the assembly of plant and animal communities implicate human impacts. Nature 529: 80-83.

Maezumi SY, Whitney B, Mayle F et al (2017) Reassessing climate and pre-Columbian drivers of paleofire activity in the Bolivian Amazon. Quat Int, doi: 10.1016/j.quaint.2017.11.053

Maezumi SY, Alves D, Robinson M et al (2018) The legacy of 4500 years of polyculture agroforesty in the Eastern Amazon. Nat Plants, DOI: 10.1038/s41477-018-0205-y

Marchant R, Almeida L, Behling H et al (2002) Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev Palaeobot Palynol 121: 1–75.

Maslin M, Malhi Y, Phillips O et al (2005) New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest. Trans Inst Br Geogr 30: 477-499.

Mayle FE, Power MJ (2008) Impact of a drier Early-Mid-Holocene climate upon Amazonian forests. Philos Trans Royal Soc B 363: 1829-1838.

Mayle FE, Iriarte J (2014) Integrated palaeoecology and archaeology – a powerful approach for understanding pre-Columbian Amazonia. J Archaeol Sci 51: 54-64.

McKey D, Rostain S, Iriarte J et al (2010) Pre-Columbian agricultural landscapes, and self-organized patchiness in Amazonia. P Natl Acad Sci USA 107: 7823-7828.

McMichael CH, Piperno DR, Bush MB et al (2012a) Sparse pre-Columbian human habitation in western Amazonia. Science 336: 1429–1431.

McMichael CH, Bush MB, Piperno DR et al (2012b) Spatial and temporal scales of pre-Columbian disturbance associated with western Amazonian lakes. Holocene 22: 131-141.

McMichael CH, Piperno DR, Bush MB (2015a) Comment on Clement et al. 2015 “The domestication of Amazonia before European conquest”. Proc Royal Soc B 282: 20151837.

McMichael CH, Piperno DR, Neves EG et al (2015b) Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. Front Ecol Evol 3: 1–15.

McMichael CH, Matthews-Bird F, Farfan-Rios W et al (2017) Ancient human disturbances may be skewing our understanding of Amazonian forests. Proc Natl Acad Sci USA 114: 522-527.

McMichael CH, Feeley KJ, Dick CW, Piperno DR, Bush MB (2017) Comment on “Persistent effects of pre-Columbian plant domestication on Amazonian forest composition”. Science 358: eaan8347.

Medina JT (1934) The discovery of the Amazon according to the account of Friar Gaspar de Carvajal and other documents. New York, NY: The American Geographical Society.

Meggers BJ (1954) Environmental limitation on the development of culture. Am Anthropol 56: 801-824.

Meggers BJ (2001) The mystery of the Marajoara: an ecological solution. Amazoniana 16: 421-440.

Montoya E (2018) Historia de la Amazonía: contribución de la paleoecología al debate de ocupación precolombina y sus efectos en el ecosistema. Ecosistemas 27: 18-25.

Montoya E, Rull V (2011) Gran Sabana fires (SE Venezuela): a paleoecological perspective. Quat Sci Rev 30: 3430-3444.

Montoya E, Rull V, Nogué S (2011) Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): palynological evidence from El Paují record. Palaeogeogr Palaeoclimatol Palaeoecol 310: 413-426.

Morcote-Ríos G, Bernal R (2001) Remains of palms (Palmae) at archaeological sites in the New World: a review. Bot Rev 67: 309-350.

Morcote-Ríos G, León-Sicard T (2012) Las *Terras Pretas* del Igarape Takana: un sistema de cultivo precolombino en Leticia Amazonas –Colombia. Universidad Nacional de Colombia, Facultad de Ciencias.

Morcote-Ríos G, Raz L, Giraldo-Cañas D et al (2013) Terras Pretas de Índio of the Caquetá-Japurá River (Colombian Amazonia), Tipití: J Soc Anthropolof Lowland South Am 11: 30-39.

Moreira PA, Aguirre-Dugua X, Mariac C et al (2017) Diversity of Treegourd (Crescentia cujete) Suggests Introduction and Prehistoric Dispersal Routes into Amazonia. Front Ecol Evol 5: 150.

Muehlebach A (2001) "Making Place" at the United Nations: Indigenous Cultural Politics at the U. N. Working Group on Indigenous Populations. Cult. Anthropol. 16: 415-448.

Neves EG, Petersen JB, Bartone RN et al (2003) Historical and socio-cultural origins of Amazonian Dark Earths. In: Lehmann J, Kern DC, Glaser B, Woods WI (eds) Amazonian Dark Earths: origin, properties, management. Berlin: Springer, p 29–50.

Neves EG, Petersen JB, Bartone RN et al (2004) The Timing of Terra Preta Formation in the Central Amazon: Archaeological Data from Three Sites. In: Glaser B, Woods WI (eds) Amazonian Dark Earths: Explorations in Space and Time. Springer Berlin Heidelberg, p 125-134.

Nolan C, Overpeck JT, Allen JRM et al (2018) Past and future global transformation of terrestrial ecosystems under climate change. Science 361: 920-923.

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51: 933–938.

Palace MW, McMichael CNH, Braswell BH et al (2017) Ancient Amazonian populations left lasting impacts on forest structure. Ecosphere 8: e02035.

Pärssinen M, Ranzi A, Saunaluoma S et al (2003) Geometrically patterned ancient earthworks in the Rio Branco Region of Acre, Brazil: New evidence of ancient chiefdom formations in Amazonian interfluvial *terra firme* environment. In: Pärssinin M, Korpisaari A (eds) Western Amazonia - Amazônia Ocidental. Multidisciplinary Studies on ancient Expansionistic Movements, Fortifications and Sedentary Life. Helsinki, Renvall Institute for Area and Cultural Studies, University of Helsinki, p 97-133.

Peters CM (2000) Precolumbian silviculture and indigenous management of neotropical forests. In: Lentz DL (ed) Imperfect Balance: Landscape Transformations in the Precolumbian Americas. New York, NY: Columbia University Press, p 203–223.

Perry L, Dickau R, Zarrillo S et al (2007) Starch Fossils and the Domestication and Dispersal of Chili Peppers (*Capsicum* spp. L.) in the Americas. Science 315: 986-988.

Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics. Curr Anthropol 52: S453-S470.

Piperno DR, Holst I, Wessel-Beaver L et al (2002) Evidence for the Control of Phytolith Formation in Cucurbita Fruits by the Hard Rind (Hr) Genetic Locus: Archaeological and Ecological Implications. Proc Natl Acad Sci USA 99: 10923-10928.

Piperno DR, McMichael C, Bush MB (2015) Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon basin at the end of prehistory? Holocene 25: 1588-1597.

Politis GG (1996) Moving to produce: Nukaka mobility and settlement patterns in Amazonia. World Archaeol 27: 492-511.

Posey DA (1985) Indigenous management of tropical forest ecosystems: the case of the Kayapó Indians of the Brazielian Amazon. Agroforestry Systems 3: 139-158.

Prestes-Caneiro G, Béarez P, Bailon S et al (2016) Subsistence fishery at Hatahara (750-1230 CE), a pre-Columbian central Amazonian village. J Archaeol Sci: Reports 8: 454-462.

Prümers H Jaimes Betancourt C (2014) 100 años de investigación arqueológica en los Llanos de Mojos. Arqueoantropológicas 4: 11-53.

Quintero-Vallejo E, Klomberg Y, Bongers F et al (2015) Amazonian dark earth shapes the understory plant community in a Bolivian forest. Biotropica 47: 152–161.

Redford KH (1991) The ecologically noble savage. Cult Surv Q 1: 46-48.

Renard D, Iriarte J, Birks JJ et al (2012) Ecological engineers ahead of their time: the functioning of pre-Columbian raised-field agriculture and its potential contributions to sustainability today. Ecol Eng 45: 30-44.

Riris P (2018) Assessing the impact and legacy of swidden farming in neotropical interfluvial environments through exploratory modelling of post-contact Piaroa land use (Upper Orinoco, Venezuela). Holocene 28: 945-954.

Roberts P, Boivin N, Lee-Thorp J, Petraglia M, Stock J (2016) Tropical forests and the genus *Homo*. Evol. Anthr. 25: 306-317.

Roberts P, Hunt C, Arroyo-Kalin M et al (2017) The deep human prehistory of global tropical forest and its relevance for modern conservation. Nat Plants 3: 17093.

Rodrigues L, Lombardo U, Veit H (2018) Design of pre-Columbian raised fields in the Llanos de Moxos, Bolivian Amazon: Differential adaptations to the local environment? J Archaeol Sci: Reports 17: 366-378.

Roosevelt AC (1991) Moundbuilders of the Amazon: geophysical archaeology on Marajo Island, Brazil. Academic Press. San Diego, CA, USA.

Roosevelt AC (2013) The Amazon and the Anthropocene: 13,000 years of human influence in a tropical rainforest. Anthropocene 4: 69-87.

Roosevelt AC, Lima da Costa M, lopes Machado C et al (1996) Paleoindian cave dwellers in the Amazon: the peopling of the Americas. Science 272: 373-384.

Roosevelt AC, Douglas J, Brown L (2002) Migrations and adaptations of the first Americans: Clovis and pre-Clovis viewed from South America. In: Jablonski N (ed) The First Americans: The Pleistocene Colonization of the New World. Mem. Cal. Acad. Sci., vol. 27. University of California, Berkeley, p 159–236.

Rostain S (1991) Les champs surélevés amérindiens de la Guyane, Coll° La Nature et l'Homme, Centre ORSTOM de Cayenne/Institut Géographique National, Cayenne.

Rostain S (2008) Agricultural earthworks on the French Guiana Coast. In: Silverman H, Isbell WH (eds) Handbook of South American archaeology. Berlin, Springer, p 217-233.

Rostain S (2010) Pre-Columbian earthworks in coastal Amazonia. Diversity 2: 331-352.

Rull V (2014) Time continuum and true long-term ecology: from theory to practice. Front Ecol Evol 2: 75.

Rull V 2018. Strong fuzzy EHLFS: a general conceptual framework to address past records of environmental, ecological and cultural change. Quaternary 1: 10.

Rull V, Montoya E (2014) *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. Quat Sci Rev 99: 17-33.

Rull V, Vegas-Villarrúbia T, Nogué S et al (2008) Bureaucratic Obstruction of Conservation Science in the Guayana Highlands. Conserv Biol 22: 508-509.

Rull V, Montoya E, Nogué S et al (2013) Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. Perspect Plant Ecol Evol Syst 15: 338-359.

Rull V, Montoya E, Vegas-Vilarrúbia T et al (2015) New insights on paleofires and savannisation in northern South America. Quat Sci Rev 122: 158-165.

Sánchez F, Fernández J, Gassón R et al (2017) Paleoecología y ocupación humana durante el Holoceno en los Llanos del Orinoco: una revisión y nuevos datos. Biollania 15: 297-333.

Sanford RL, Saldarriaga J, Clark KE et al (1985) Amazon rain-forest fires. Science 227: 53-55.

Schaan D (2008) The nonagricultural chiefdoms of Marajó Island. In: Silverman H, Isbell WH (eds) Handbook of South American archaeology. Berlin, Springer, p 339-357.

Shepard Jr GH, Ramirez H (2011) “Made in Brazil”: Human dispersal of the Brazil Nut (*Bertholletia excelsa*, Lecythidaceae) in ancient Amazonia. Econ Bot 65: 44-65.

da Silva Meneses MEN, Lima da Costa M, Behling H (2013) Late Holocene vegetation and fire dynamics from a savanna-forest ecotone in Roraima state, northern Brazilian Amazon. J S Am Earth Sci 42: 17-26.

Siren A (2014) History of natural resource use and environmental impacts in an interfluvial upland forest area in western Amazonia. Fennia 192: 36-53.

Smith N (2015) Palms and people in the Amazon. Geobotany Studies: Basics, Methods and Case Studies. Springer.

de Souza JG, Schaan DP, Robinson M et al (2018) Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. Nat Commun 9: 1125.

Stahl PW (2015) Interpreting interfluvial landscape transformations in the pre-Columbian Amazon. Holocene 25: 1598-1603.

ter Steege H, Pitman NCA, Sabatier D et al (2013) Hyperdominance in the Amazonian tree flora. Science 342: 1243092.

ter Steege H, Vaesen RW, Cárdenas-López D et al (2016) The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. Sci Rep 6: 29549.

Stenborg P (2009) Points of convergence-routes of divergence: Some considerations based on Curt Nimuendajú's archaeological work in the Satarém-Trombetas Area and Amapá. In: Whitehead NL, Alemán SW (eds) Anthropologies of Guayana: cultural spaces in northeastern Amazonia. The University of Arizona Press, Tucson, USA, p 55-73.

Stenborg P, Schaan DP, Amaral-Lima M (2012) Precolumbian land use and settlement pattern in the Santarém region, lower Amazon. Amazônica 4: 222-250.

Stenborg P, Schaan DP, Figueiredo CG (2018) Contours of the Past: LiDAR Data Expands the Limits of Late Pre-Columbian Human Settlement in the Santarém Region, Lower Amazon. J Field Archaeol 43: 1-14.

Thomas E, van Zonneveld M, Loo J et al (2012) Present spatial diversity patterns of Theobroma cacao L. in the neotropics reflect genetic differentiation in Pleistocene refugia followed by human-influenced dispersal. PLoS One 7: e47676.

Thomas E, Alcázar Caicedo C, McMichael CH et al (2015) Uncovering spatial patterns in the natural and human history of Brazil nut (Bertholletia excelsa) across the Amazon Basin. J Biogeog 42: 1367-1382.

de Toledo MB, Bush MB (2007) A Mid-Holocene environmental change in Amazonian savannas. J Biogeog 34: 1313-1326.

Tollefson J (2013) Footprints in the forest. Nature 502: 160-162.

Tomkeieff SI (1962) Unconformity - an historical study. Proc GeolAssoc 73: 383-417.

Watling J, Iriarte J, Mayle FE et al (2017) Impact of pre-Columbian "geogliph" builders on Amazonian forests. Proc Natl Acad Sci USA 114: 1868-1873.

Watling J, Shock MP, Mongeló GZ, Almeida FO, Kater T, De Oliveira PE, et al (2018) Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. PLoS ONE 13: e0199868

Whitehouse NJ, Kirleis W (2014) The world reshaped: practices and impacts of early agrarian societies. J Archaeol Sci 51: 1-11.

Wills C, Harms KE, Condit R et al (2006) Nonrandon processes maintain diversity in tropical forests. Science 311: 527–531.

Woods WI, Glaser B 2004. Towards an Understanding of Amazonian Dark Earths. In: Glaser B, Woods, WI (eds) Amazonian Dark Earths: Explorations in Space and Time. Springer Berlin Heidelberg, p 1-8.

Zizka A, ter Steege H, Do Céo M et al (2018) Finding needles in the haystack: Where to look for rare species in the American tropics. Ecography 41: 321–330.