

Invited Research Article

Finding forest management in prehistoric Amazonia

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ABSTRACT

This paper addresses a topic highlighted in recent arguments by Amazonian scholars: the extent to which forms of forest management in prehistory influenced the past and present composition of *terra firme* and riverine forests. New information on palm phytolith characteristics enabled phytolith analysis on soils sampled from underneath forests in western and central Amazon. We evaluated whether three major economic palms, *Oenocarpus bataua*, *O. bacaba*, and *Euterpe precatoria*, thought to have been significantly enriched by human activities, demonstrated such enrichment. All three palms are hyperdominant species today. We also examined expanded modern phytolith reference collections in a possible context of human management of other arboreal species that involved changes in overall forest structure and diversity during the past several thousand years. Results indicate little to no enrichment of the palms and largely stable forest structure and diversity in *terra firme* forests through time. Although much research remains, results of this study indicate that prehistoric human modification of Amazonian forest and creation of species hyperdominance was less influential than currently proposed by some Amazonian scholars. Findings contribute toward resolving questions concerning the temporal and spatial scale and characteristics of pre-Columbian human impacts across Amazonia. They also suggest cross-disciplinary insights surrounding the proposed new geological epoch of the Anthropocene.

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1. Introduction

The Amazon Basin, an area approximately the size of the continental United States, is presently home to the largest contiguous expanse of Neotropical forest and much of the New World's biological diversity (Fig. 1). The cultural complexity of pre-Columbian societies in Amazonia, together with their relationships with the natural environment, are enduring questions. Archaeologists have abandoned the older idea that prehistoric Amazonia supported mainly small and highly mobile human populations who exerted little influence on the environment (Meggers, 1954, 1971). Evidence accumulated over the last 10–20 years makes it clear that, by 3000–500 calendar years ago (hereafter, cal BP), several Amazonian regions were occupied by large and culturally-complex pre-Columbian human societies who transformed their natural environments in sometimes profound ways. The evidence includes landscape alterations in the form of raised agricultural fields, fish weirs, mound settlements, roads, geometric earthworks called geoglyphs, and the presence of highly modified anthropic

soils called *terra pretas* or “Amazonian Dark Earths” (Fig. 1) (e.g., Arroyo-Kalin, 2010; Blatrix et al., 2018; De Souza et al., 2018; Denevan, 2011; Erickson, 2000, 2008; Heckenberger et al., 2003; Lombardo et al., 2013; Neves et al., 2004; Neves and Petersen, 2006; Pärssinen et al., 2009; Roosevelt, 1991; Schaaf et al., 2012; Watling et al., 2017; Whitney et al., 2013; Woods et al., 2012). These features are documented largely along major rivers and their tributaries, in seasonal savannas/areas of poor drainage, or in highly seasonal interfluvial (*terra firme*) forests.

These findings have led some investigators to hypothesize, largely by extrapolating from available data from fluvial zones and studies of modern floristic composition of selected forests, that anthropogenic landscapes were widespread across Amazonia at the end of the prehistoric era (e.g., Balée, 2010, 2013; Clement et al., 2015; Dull et al., 2010; Erickson, 2008; Heckenberger, 2013; Heckenberger et al., 2003; Levis et al., 2012, 2017; Watling et al., 2017). An initial formulation of this view of Amazonia as a “domesticated” or “manufactured” landscape called for widespread forest clearance with fire for agriculture across most of the Basin (e.g., see W. Woods cited in Romero, 2012). Scholars have proposed that prehistoric fires and forest clearing were on such a massive scale that post-Columbian reforestation was a significant contributor to decreasing atmospheric CO₂ levels and the onset of the ‘Little Ice Age’ (Dull et al., 2010; Nevle et al., 2011; Koch et al.,

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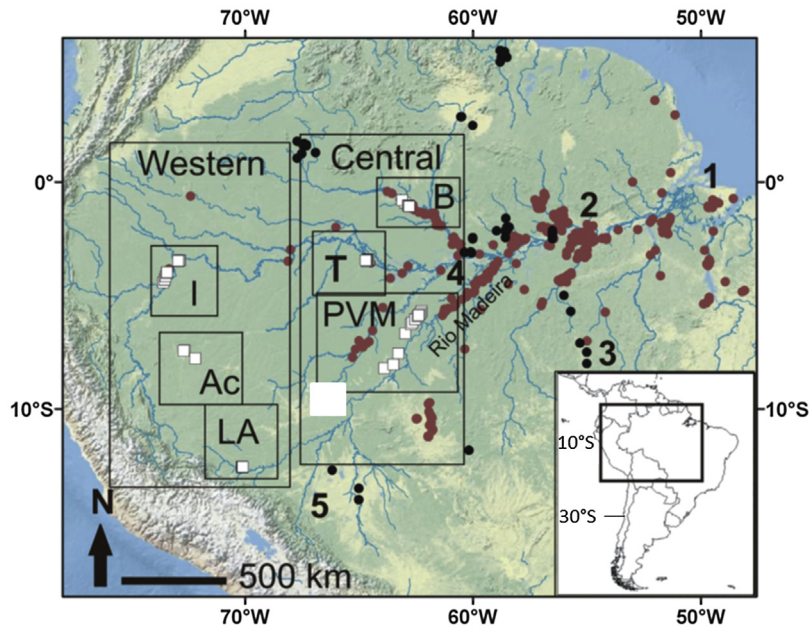


Fig. 1. Locations in western Amazonia and central Amazonia studied in this work are shown by white squares; PVM, Porto Velho to Manaus; LA, Los Amigos; T, Tefe. Other white squares are other terrestrial soil sites studied in [McMichael et al. \(2012a\)](#) that were not re-examined here (AC, Acre; I, Iquitos; B, Barcelos). Large white square is the approximate area of some geoglyphs. Numbers represent major pre-Columbian archaeological sites noted in the text (1, Marajó Island; 2, Santarém; 3, Upper Xingu; 4, Central Amazon Project; 5, Bolivian Beni). Brown circles are some known *terra preta* locations and black circles are some soil charcoal survey locations. The locations of the Rio Madeira and associated *terra preta*s are shown.

2019). However, neither lake and terrestrial soil paleo-vegetation and fire histories, nor peatland and ice core carbon source studies, nor correlations of climate and fire data, so far support widespread forest clearing or fire (e.g., [Bush et al., 2007, 2016](#); [Griscom and Ashton, 2006](#); [Kelly et al., 2018](#); [Maezumi et al., 2018a,b](#); [McMichael et al., 2012a,b](#); [Piperno, 2011](#); [Piperno et al., 2015](#); [Piperno and Becker, 1996](#); [Power et al., 2013](#); [Stocker et al., 2017](#); [Urrego et al., 2013](#); [Watling et al., 2017](#)).

Several investigators now instead hypothesize that widespread forms of agroforestry with planted, orchard-like formations or other forest management strategies involving the care and possible enrichment of several dozens of native species. Such proposed activities are thought to have led to human-created “hyperdominance” (after [ter Steege et al., 2013](#)) of some and forests with higher diversity than before human modification (e.g. [Balée, 2010, 2013](#); [Clement et al., 2015](#); [Erickson, 2008](#); [Levis et al., 2012, 2017, 2018](#); [Watling et al., 2017](#)). These arboreal formations are said to be still prominent and detectable in the modern vegetation (e.g., [Levis et al., 2012, 2017](#)). At this point, the evidence for these views relies largely on inventories of modern forest composition that are said to predict what were pre-Columbian activities (e.g., [Levis et al., 2012, 2017](#)), though modern vegetation surveys are typically conducted in areas with high densities of known archaeological sites ([McMichael et al., 2017](#)).

An alternative viewpoint is that, although the cultural practices depicted above no doubt existed in some Amazonian forests, much more paleo-environmental and archaeological research is required, particularly in the vast and understudied interfluves, for conclusions regarding the spatial and temporal scale, characteristics, and degree of human influence (e.g., [Bush et al., 2015](#); [McMichael et al., 2015a, 2017](#); [Piperno et al., 2015](#)). We consider that modern floristic analyses are insufficient as documentation of the dynamics of the prehistoric past. Reasons include: 1) a lack of consideration of possible historical period disturbances, which were profound in some regions and could be mistaken for prehistoric legacies, 2) the paucity of information—due to sparse archaeobotanical data and spotty early historic-period records (see

[Miller and Nair, 2006](#))—concerning which and how many of the numerous tree species whose distributions and abundance are assumed to be modern relicts of past forest management were actively managed in prehistory, 3) a poor understanding of the natural distributions and abundance of many species in different habitats and climates through time, making uncertain whether their present abundance and distribution relates more to human activity, natural habitat preferences (e.g., swamps), or climate change during the past few thousand years, and 4) that differences among the forests in rainfall and its seasonality, soil quality, floristic composition, and distance to water bodies including lakes may have influenced human habitation.

For example, examining fossil pollen in 13 lake records from western Amazonia, [Bush and McMichael \(2016\)](#) found that increased abundance during the last 3000 years of a now-hyperdominant palm, *Iriartea deltoidei* Ruiz & Pav., likely related to increased precipitation rather than human influence. Another example is that high densities in certain areas today of the babaçu palm (*Attalea speciosa* Mart. ex Spreng.), used heavily by [Balée \(1989\)](#) for estimating the extent of prehistoric human disturbance, probably resulted from its invasion following swidden cultivation and cattle ranching during the past 500 years ([Forline, 2008](#)). Similarly, recent studies of Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.) stands in mature *terra firme* forests along the Madeira River in Brazil, thought by some to be a legacy of prehistoric nut management, date from the rubber boom ([Scoles and Gribel, 2011](#)). In a region of southeastern Peru the Brazil nut occurs in low densities indicative of limited ancient human influence there ([Porcher et al., 2018](#)).

Therefore, among the major research questions requiring further study are the spatial scale, degree, and persistence through time of various types of management of perennial tree species. How to best document these activities, however, is less clear. This uncertainty is due in part to the fact that they could be ‘silent’, since some major economic tree fruit and nut species produce few to no recognizable phytoliths and pollen ([Piperno, 2006](#); [Piperno et al., 2015](#)). Examples include Brazil nut, rubber (*Hevea brasiliensis* Müll.

Arg.), and cacao (*Theobroma cacao* L.). Table 1 lists other species considered useful and potentially enriched by humans in prehistory (largely after Levis et al., 2012, 2017) that will not provide useful phytolith records. On the other hand, critical and readily detected economic taxa include palms (Arecaceae family), which are prolific phytolith producers in all structures of the plant. Also importantly, because palms always produce abundant and diagnostic phytoliths negative evidence can be brought to bear, since their absence or rare frequencies through time indicates they were not growing nearby the locales and/or were not being enriched by human populations, also suggesting no human settlement nearby (e.g., McMichael et al., 2015a; Piperno et al., 2015).

Given the growing importance of considering possible forest exploitation that did not involve cultivation of annual plants and significant clearings for agricultural plots, paleo-ecologists should seek to develop new approaches for detecting and documenting those practices. This paper describes one such beginning effort through re-examinations and expansions of modern phytolith reference collections and re-analyses of soil phytoliths sampled from underneath Amazonian forests. In particular, it addresses the following research questions: 1) Can some economically important palm genera be identified and quantified in soil profiles, such that hypotheses discussed above about prehistoric influences on their present distributions and abundances can be empirically evaluated, and 2) Can prehistoric management of Amazonian forests overall be evaluated through analysis of non-palm woody phytoliths, such that changes to forest structure and diversity hypothesized by some scholars, discussed above, are elucidated.

2. Materials and methods

2.1. Derivation of studied samples

We re-examined a sub-set of soil cores retrieved in 2008–2009 from directly underneath present-day *terra firme* and fluvial (river bluff) forest of western and central Amazonia (Fig. 1). A total of 109 sites distributed over seven regions provided the cores. The regions are (Fig. 1): 1) Porto Velho to Manaus (PV-M), a long 450-km interfluvial transect running between these two cities in the central Amazon Basin (ten out of 13 *terra firme* sites originally sampled were studied), 2) Los Amigos (LA), located in the LA biological research station in south-eastern Peru above the confluence of the Madre de Dios and Los Amigos Rivers, 120 km

upriver from Puerto Maldonado (Pitman, 2010) (four of 11 sampled river bluff sites), and 3) Tefe, located on the southern side of the Amazon river in the central Basin (three fluvial and two interfluvial sites out of ten sampled). As a baseline for comparison, we re-analyzed phytoliths from the archaeological site of Teotônio, an important preceramic/ceramic-phase occupation located on a river bluff on the Upper Madeira River in Brazil just south of Porto Velho (Almeida and Neves, 2014; McMichael et al., 2015b; Watling et al., 2018).

We previously reconstructed histories of vegetation, fire, and soil modification from charcoal, phytolith, and geochemical data from the PV-M, Tefe, and LA samples (McMichael et al., 2012a,b; McMichael et al., 2015b; Piperno et al., 2015). Based on direct phytolith dating of these and other Amazonian terrestrial soil cores, the phytolith records cover at least the past several thousand years of vegetation history (McMichael et al., 2012b; Piperno et al., 2015; below). We were testing beliefs advanced by some scholars regarding regional-scale forest clearance and agriculture across Amazonia, discussed above, but found little to no evidence for long-term human occupation, agriculture, forest clearing, or other significant vegetation change in interfluvial locales and in some of the riverine areas we sampled. Frequencies of phytoliths from grasses and other early successional taxa (*Heliconia*, sedges) were absent to rare (0–6%) from the bottom to the top of many of the soil cores, while phytoliths indicative of closed, mature forest dominated (>90%) in many samples. No grass phytoliths at all were observed in many samples in extended slide scans of thousands of phytoliths.

Further, no association existed between palm phytolith frequencies and evidence of vegetation disturbance, and palm frequencies were never so high as to suggest that a dense concentration – something like a local grove or orchard – was present. Many *terra firme* samples lacked evidence for significant growth of major economic palms such as the peach palm (*Bactris gasipaes* Kunth) and *Astrocaryum* species despite their high visibility in phytolith profiles (we note that *Astrocaryum* is a hyperdominant today (ter Steege et al., 2013) predicted to have had extensive human utilization in Levis et al. (2012, 2017). No *terra preta*, *terra mulata* (the latter modified brown earths thought to be relictual prehistoric fields [Arroyo-Kalin, 2010]), or cultural artifacts such as stone tools or their debitage and ceramics were found in any sample. In sum, results indicated that the forests we studied were not in a state of recovery from significant pre-Columbian settlement and vegetation modification.

Table 1
Phytolith Potential in Some Economic Plants.

| Family | Species | Phytolith Production | Taxonomic Value |
|------------------|--|----------------------|--------------------------------------|
| Anacardiaceae | <i>Anacardium occidentale</i> L. | R | None |
| Anacardiaceae | <i>Spondias mombin</i> L. | C (L), Absent (S) | None |
| Annonaceae | <i>Annona glabra</i> L. | Absent | N.A. |
| Annonaceae | <i>Annona montana</i> Macfad. | Probably Absent to R | Probably None |
| Annonaceae | <i>Annona muricata</i> Linn | Absent (L and Stem) | N.A. |
| Annonaceae | <i>Annona mucosa</i> Jacq. | Probably Absent to R | Probably None |
| Annonaceae | <i>Annona squamosa</i> L. | Absent (S) | N.A. |
| Bignoniaceae | <i>Crescentia cujete</i> L. | R | Probably None |
| Chrysobalanaceae | <i>Couepia guienensis</i> Aubl. | Probably A | Family to a small number of families |
| Euphorbiaceae | <i>Hevea brasiliensis</i> Müll.Arg. | R | None |
| Fabaceae | <i>Inga edulis</i> Mart. | C to R | Probably None |
| Lecythidaceae | <i>Bertholletia excelsa</i> Bonpl. | Probably Absent to R | Probably None |
| Malvaceae | <i>Theobroma cacao</i> L. | R | None |
| Malvaceae | <i>Theobroma bicolor</i> Humb. & Bonpl. | R | None |
| Malvaceae | <i>Theobroma subincanum</i> Mart. | Probably Absent to R | Probably None |
| Malvaceae | <i>Theobroma speciosum</i> Willd. ex Spreng. | Probably Absent to R | Probably None |
| Rubiaceae | <i>Genipa Americana</i> L. | Absent | N.A. |

Notes: C = phytoliths common in the plant, R = Rare. N.A. = not applicable. L = leaf analyzed, S = seed, unless otherwise noted leaves were analyzed. Production was considered absent if small amounts of silicified fragments were observed. Taxa where phytolith production in leaves is absent or rare are unlikely to have production in fruits or seeds.

2.2. Palm phytolith analysis and identification

To examine with greater resolution the issue of forest management, this study presents a more granular analysis of modern and ancient palm phytoliths. We sought to identify the presence and possible human enrichment of three species of palms of considerable economic importance today and among those thought to have high densities in modern vegetation resulting from prehistoric enrichment (Levis et al., 2012, 2017): *Oenocarpus bataua* Mart., *O. bacaba* Mart., and *Euterpe precatoria* Mart. All three are hyperdominant species today (ter Steege et al., 2013): (a “hyperdominance” means the three species are among the 227 calculated by ter Steege et al. (2013) to account for more than half the trees in Amazonia). We utilized recent intensive studies of Amazonian palm phytolith morphology and size by Morcote-Ríos et al. (2016) that provided new identification techniques, as well as our own new analyses of the modern palm flora. Morcote-Ríos et al. (2016) analyzed 92 species in 29 genera of Amazonian palms, distinguishing eight phytolith sub-types that effectively went beyond the previously standard binary categories spherical (now termed globular) and conical for identification in the family (e.g., Tomlinson, 1961; Piperno, 1988, 2006). Morcote-Ríos et al. (2016) found that a type they named “globular echinate with short acute projections” (hereafter, GESP) (Fig. 2, left) has a limited distribution, occurring widely in the genera *Oenocarpus* and *Euterpe* and just four others (*Chelyocarpus*, *Syagrus*, *Manicaria*, and *Prestoea*), some of which are smaller groups with more circumscribed geographical and habitat distributions. Furthermore, their data indicated that GESP size in *Oenocarpus* and *Euterpe* is often larger than in other genera. For example, average diameters in *Oenocarpus* and *Euterpe* of up to 26 μm and 19 μm , respectively, were recorded, whereas in *Chelyocarpus ulei*, it was 12 μm . Further, individual GESP phytoliths greater than 20 μm in size very likely originated from either *Oenocarpus* or *Euterpe* (Gaspar Morcote-Ríos, pers. comm. to DRP, 2018).

We analyzed 16 species of Amazonian palms from all GESP-producing genera including most in addition to *Oenocarpus* and *Euterpe* spp. that were possibly distributed in the vicinity of sites studied here, based on their modern distributions (Table 2, modern distributions discussed below). Findings reported here are as reported in Morcote-Ríos et al. (2016) who used samples of the same species collected from different locations of Amazonia than those studied here. Average phytolith size and range in *O. bataua* and *O. bacaba* and maximum phytolith size in *E. precatoria* and *E. oleraceae* are much larger than in the other four GESP-producing genera, and phytoliths exceeded 20 μm in size only in *Oenocarpus* and *Euterpe* (Table 2). Based on this information, we developed and tested an approach that we believe could, with considerable

sensitivity, evaluate the distributions of *O. bataua*, *O. bacaba* and/or *E. precatoria* in terrestrial soil and other paleoecological contexts. We re-analyzed phytoliths from Amazonian terrestrial soils originally reported on in McMichael et al. (2012a) and Piperno et al. (2015), this time separately identifying, counting, and sizing GESP phytoliths. If any GESP reached a maximum size of 20 μm or greater, a likely presence of either or both *Oenocarpus* and *Euterpe* was indicated, and possible presence of *O. bataua*, *O. bacaba* and/or *E. precatoria* was suggested, realizing that further information on phytolith size is needed to make a definitive species-specific identification. Average GESP size provided additional information and GESP percentage frequencies through time spoke to questions of possible palm enrichment through human manipulation. If, on the other hand, GESP phytoliths did not reach a size of 20 μm or more, we considered that none of the three species of interest contributed to the samples, or at least were sparse in past landscapes. To ensure adequate coverage of GESP presence and size, we scanned at least 3000 phytoliths from every sample.

2.3. Modern palm distributions and abundance

In evaluating the palm data, we also inferred which *Oenocarpus*, *Euterpe* and other GESP-producing species could have occurred at sites studied based on the considerable information available on their modern distributions. Modern palm surveys of Amazonian forest provide the following details (e.g., Balslev et al., 2016; Cintra et al., 2005; Henderson, 1995; Kahn and de Castro, 1985; Montufar and Pintaud, 2006; Levis et al., 2012; Noblick, 2017). *O. bataua* and *E. precatoria* are widespread in Amazonia and can occur in all regions studied here, while *O. bacaba* is not found at significant distances south of the Amazon River. The latter occurs in the Tefe and possibly some PV-M areas and is not expected at Los Amigos. Two other species of *Oenocarpus* not examined here, *O. minor* Mart. and *O. balickii* F. Kahn, are expected in the Tefe/PV-M and Los Amigos study regions, respectively. *Euterpe oleraceae*, another species of considerable economic importance today and possibly in prehistory (Morcote-Ríos and Bernal, 2001) occurs along river margins and in river deltas and is not expected on well-drained soils studied here. With regard to the four non-*Oenocarpus*/*Euterpe* genera that produce GESP phytoliths, *Prestoea* is a mainly Andean genus with one lowland species, *Prestoea schultzeana* (Burret) H.E. Moore, occurring in northeastern Peru, and it is not expected here. *Chelyocarpus*, also a western Amazonian plant, occurs in the Los Amigos region (the species *C. ulei*) and is not expected at PV-M or Tefe. *Syagrus* is a large genus with its center of distribution in central and eastern Brazil considerably south of the study regions (Noblick, 2017). Two species, *S. inajai* (SPRUCE) Becc. and *S. sancona* H. Karst., are reported from regions studied here in central and

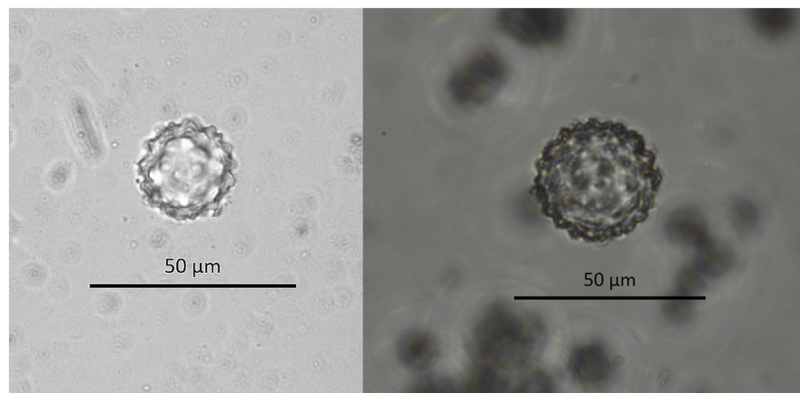


Fig. 2. Left, a GESP phytolith from a modern leaf of *Oenocarpus bataua*; Right, a GESP phytolith from PV-M 127 A, 0–20 cm b.s.

Table 2
GESP Phytolith Size in Modern Palms.

| Species | Mean Size GESp μm | Range | n |
|--|------------------------------|----------|----|
| <i>Chelyocarpus dianeurus</i> (Burret) H.E. Moore | 9.4 | 6–12 | 20 |
| <i>Chelyocarpus ulei</i> Dammer | 8.3 | 6–11, 14 | 20 |
| <i>Euterpe oleracea</i> Mart. | 8.8 | 5–24, 34 | 20 |
| <i>Euterpe precatoria</i> var. <i>precatoria</i> Mart. | 9.2 | 5–38 | 20 |
| <i>Manicaria saccifera</i> Gaertn. | 6.9 | 3–9 | 20 |
| <i>Oenocarpus bacaba</i> Mart. | 14.2 | 7–33, 38 | 20 |
| <i>Oenocarpus bataua</i> Mart. | 16.6 | 8–31, 32 | 20 |
| <i>Oenocarpus mapora</i> H.Karst. | 8.8 | 7–17 | 20 |
| <i>Prestoea ensiformis</i> (Ruiz & Pav.) H.E.Moore | 8.5 | 7–12 | 20 |
| <i>Prestoea schultzeana</i> (Burret) H.E.Moore | 7.3 | 5–10 | 20 |
| <i>Prestoea tenuiramosa</i> (Dammer) H.E.Moore | 6.7 | 5–10 | 20 |
| <i>Syagrus botryophora</i> (C. Martius) C. Martius | 9.2 | 7–13 | 20 |
| <i>Syagrus comosa</i> (Mart.) Mart. | 7.1 | 5–13 | 20 |
| <i>Syagrus coronata</i> (Mart.) Becc. | 8.6 | 7–10, 14 | 20 |
| <i>Syagrus inajai</i> (SPRUCE) Becc. | 11.2 | 6–17 | 20 |
| <i>Syagrus sancona</i> H. Karst. | 7.1 | 3–9 | 20 |

Notes: All specimens analyzed are leaves we sampled from vouchered specimens housed at the herbaria of the Missouri Botanical Garden and Smithsonian National Museum of Natural History. The number for Range after the comma indicates the largest phytolith observed on extended scanning of the slide.

western Amazonia, respectively, where they are among the most infrequently occurring palms (Cintra et al., 2005; Kahn and de Castro, 1985; Noblick, 2017). *Manicaria* largely occurs in swamps and other water-logged habitats across Amazonia.

In way of more detailed information on palm composition and abundance in the study regions, the following examples are discussed. In well-drained *terra firme* forest at Reserve Ducke in central Amazonia 25 km north of Manaus, *O. bataua*, *O. bacaba*, and *E. precatoria* were recorded, respectively, in 5, 11, and 8 out of 20 100 × 10 m plots studied within a 6400-ha area (Cintra et al., 2005). The maximum adult abundance per plot was 25, 2, and 9 individuals, respectively. Of 29 palm species recorded, *O. bataua*, *O. bacaba*, and *E. precatoria* were the 5th, 8th, and 9th most common, respectively. The average abundance of adults of the three species per 200 ha was 2, 0.95, and 1, respectively. *O. minor* and *Syagrus inajai* occurred in 10 and six plots, respectively, with maximum abundances per plot of 3 and 2 individuals, respectively, and *S. inajai* was the only species of that genus observed. In mature *terra firme* and secondary river bluff forest in the Purus-Madeira interfluvium, located 40–115 km west of the sampling locales in this study, Levis et al. (2012) recorded *O. bacaba*, *O. bataua* and *E. precatoria* in 5, 5, and 6 plots, respectively, out of 11 surveyed in six different sites (plot size 250 × 40 m). The maximum abundance per plot was 20, 94, and 157 individuals, respectively. The highest occurrences by far of *O. bataua* were in one area where soil charcoal, which was not dated, was abundant, suggesting increased growth in disturbed forest. Highest abundances by far of *E. precatoria* occurred in an area with nearby archaeological evidence and where undated soil charcoal was also common. That study did not describe palms not considered economically useful. In sum, this and other information indicates that the three palms emphasized in this study are among the most common in Amazonian forest today where they occur, but often do not exist in dense stands. They are also unevenly distributed across space within and between areas surveyed.

2.4. Non-palm woody phytolith analysis

As a final endeavor, we undertook a re-analysis of non-palm woody phytolith types initially reported in Piperno et al. (2015) that frequently occurred in the sand fractions of soils. These types were not yet represented in modern reference collections, and they were apparently from a large diversity of forest taxa. To better discriminate them, provide information on arboreal diversity and

forest structure through time, and identify possible enrichment of preferred tree species, we undertook a detailed review of our existing modern reference collection comprising over 2000 species of tropical plants. In doing so, we recognized a phytolith type from the family Boraginaceae that was occurring in the soils in addition to one from another genus of Annonaceae. We also sub-categorized phytoliths such as elongated forms, circumscribing their distributions in the modern flora, and we began expanding Amazonian species representatives in the collections (phytolith images and descriptions follow in Results).

2.5. Chronology of the phytolith records

Direct dating of phytoliths of these and terrestrial soil cores from other Amazonian regions indicate that the records span at least the past several thousand years with the oldest phytoliths usually found at the deepest depths (Piperno and Becker, 1996; McMichael et al., 2012b; Piperno et al., 2015; Tables 3 and 4). It is not possible to date a single or a few phytoliths representing a discrete moment of time as it is with charcoal. A ¹⁴C phytolith age represents the mean age of all the phytoliths present in a particular soil assemblage and will contain a mixture of somewhat younger and older phytoliths. Therefore, it is often unrealistic to expect close dating conformity between charcoal and phytoliths from the same levels. Burned phytoliths can be identified (Piperno, 2006), however, and when a substantial number of burned phytoliths co-occur with charcoal in a given stratigraphic level, assessing phytolith age in that context on the basis of charcoal age may be possible. We explore, in this study, employing that strategy for the first time.

3. Results

3.1. Porto Velho to Manaus

The PV-M transect runs through well-drained *terra firme* forest about 20 to 60 km west of the Madeira River. *Terra preta* and archaeological sites concentrated along the river are from 20 to 80 km east of some of the sites sampled. We sampled all PV-M sites at 20-cm intervals, including for phytolith dating. The letters A and B for site numbers in the table for PV-M and other regions examined denote different cores randomly collected within a 100 m radius of the selected GPS point for each site. At PV-M, we dated phytolith assemblages in the uppermost 20 cm to 1600–2400 cal BP. At the

Table 3
GESP Palm Results from PV-M.

| Site | Level cm b.s., Phytolith ¹⁴ C cal BP | LO/E | % GESP | Mean | Range | GEE |
|----------------|---|------|----------|------|-----------|-----|
| PV-M 118 A | 0–20 | Yes | <1 | 13.2 | 10–16, 21 | No |
| PV-M 118 A | 60–80 | Yes | 1 | 17.2 | 11–26, 41 | Yes |
| PV-M 118 B | 0–20 | Yes | 1 | 17.5 | 10–26 | Yes |
| PV-M 118 B | 20–40 | Yes | 2 | 17.4 | 9–32 | No |
| PV-M 121 B | 0–20, 4530–4420 | Yes | 5 | 10.8 | 8–20 | Yes |
| PV-M 121 B | 20–40, 4780–4420 | Yes | 5 | 15.5 | 11–23 | Yes |
| PV-M 121 B | 60–80, 4420–4250 | Yes | 6 | 18.4 | 13–25 | Yes |
| PV-M 123 A + B | 0–20, 2486–2308* | Yes | <1 | 17.7 | 15–22 | No |
| PV-M 123 A + B | 20–40, 2765–2499** | Yes | 1 | 19.5 | 9–35 | Yes |
| PV-M 123 A + B | 40–60 | Yes | <1 | 17.7 | 11–32 | Yes |
| PV-M 124 A | 0–20, 1720–1560 | No | <1 | 11.8 | 8–16 | Yes |
| PV-M 124 A | 40–60 | Yes | 1 | 18.8 | 14–24 | Yes |
| PV-M 124 A | 60–80, 6860–6670 | Yes | 1 | 15.6 | 13–19, 24 | No |
| PV-M 124 B | 0–20 | No | <1, Rare | N.R. | N.R. | No |
| PV-M 124 B | 20–40 | Yes | <1, Rare | 13.2 | 9–22 | Yes |
| PV-M 124 B | 60–80 | Yes | 1 | 16.8 | 13–24 | Yes |
| PV-M 125 A | 0–20 | No | <1, Rare | 15.6 | 8–19 | No |
| PV-M 125 A | 60–80 | No | <1, Rare | 13.7 | 8–19 | Yes |
| PV-M 127 A | 0–20 | Yes | 1 | 17.2 | 9–22 | Yes |
| PV-M 127 A | 20–40 | Yes | 1 | 15.6 | 8–26 | Yes |
| PV-M 127 A | 60–80 | Yes | 2 | 17.8 | 11–28 | Yes |
| PV-M 128 A | 0–20, 2000–1880 | Yes | 1 | 12.9 | 8–19, 25 | Yes |
| PV-M 128 A | 20–40 | Yes | 2 | 15.6 | 10–22 | Yes |
| PV-M 128 B | 0–20, 2000–1880 | Yes | 1 | 13.4 | 8–20, 25 | Yes |
| PV-M 128 B | 20–40 | Yes | 1 | 17.9 | 11–32 | Yes |
| PV-M 130 A | 0–20 | No | <1, Rare | 11.8 | 8–15 | Yes |
| PV-M 130 A | 20–40 | No | <1, Rare | 13.2 | 8–18 | Yes |
| PV-M 130 A | 60–80 | No | <1, Rare | 11.7 | 8–17 | No |
| PV-M 131 A | 0–20 | No | <1 | 12.3 | 9–18 | No |
| PV-M 131 A | 20–40 | No | <1, Rare | 11.0 | 8–15 | No |
| PV-M 131 A | 60–80 | No | <1, Rare | 11.8 | 8–16 | No |
| PV-M 131 B | 0–20 | No | <1 | 10.7 | 8–14 | No |
| PV-M 131 B | 20–40 | No | <1 | 11.9 | 8–18 | No |
| PV-M 131 B | 40–60 | No | <1 | 12.6 | 8–18 | Yes |

Notes: All Phytolith date ranges in two sigma calibrated years. * (Beta-520792), ** (Beta-520793). For Sites 123 and 128 the phytolith dates are for 0–20 cm A and B combined (Beta-368021). For the % GESP column, a Rare noted after percentages indicates GESP phytoliths were very rarely observed in extended scans of 3000 phytoliths. Ten GESP phytoliths were sized in each sample unless they were rarely observed; N.R. indicates not recorded. For the range of size column (Range), the value after the comma is the largest GESP phytolith observed in extended scans of the slide outside of the calculation for mean size.

lowest depth sampled, 60–80 cm, we obtained a phytolith age of 6860–6670 cal BP (Table 3) (all phytolith dates with the exception of Los Amigos, which was sampled in closer depth intervals [see below], used phytoliths aggregated from a 20-cm level). Therefore, as in other Amazon regions studied in this way (McMichael et al., 2012b), the uppermost 20 cm is relevant to the last few thousand years of prehistory when indigenous cultural impacts are thought to have been greatest in Amazonia. That soil depth will also contain phytoliths from the last 500 to 600 years (see the phytolith date from Los Amigos, below). The bottom-most date indicates that the sequences cover at least 7000 years and probably more. Depths from 20 to 60 cm should often contain phytoliths of an age in-between the oldest and most recent, realizing soil disturbances from roots and other factors may prevent an ideal stratification. Phytolith dates from the 0–20, 20–40, and 60–80 cm levels of Site 121 interestingly overlapped in the ca. 4400 cal BP period (Table 3), with interpretations below. Burned phytoliths were absent to rare in most sites. When we found them in substantial number in the same levels with dated charcoal, however, we further assessed phytolith age based on charcoal age.

Table 3 provides the results of the palm analysis. In the PV-M soils, GESP phytoliths were readily identified morphologically and

occurred at all sites, albeit sometimes very rarely. Large ($\geq 20 \mu\text{m}$) GESP phytoliths, likely derived from *Oenocarpus* and/or *Euterpe* (hereafter, LO/E), occurred in six out of nine sites analyzed (Table 3) (Fig. 2, right). In addition to the modern distributional information on other GESP-producing genera that probably rules them out from representation (*Prestoea*, *Chelyocarpus*, and *Manicaria*), phytolith size in them as well as others that may have been present (*Syagrus inajai*), is considerably smaller than in *Oenocarpus* or *Euterpe* (Table 2). Average GESP size between 15 and 18 μm in some samples with LO/E further indicates *Oenocarpus* and/or *Euterpe* (hereafter, O/E) presence. Except for site 121, discussed below, overall GESP percentages were low, from <1 to 2%, throughout, showed no trend for an increase in abundance through time that suggested enrichment, and sometimes tended to be somewhat more frequent in number at greater depth (Table 3). At site 124, for example, LO/E was present in the deepest level with a phytolith date of 6860–6670 cal BP and also above at 40–60 cm, but was not observed in the 0–20 cm level with a phytolith date of 1720–1560 cal BP. A reduction in phytolith size also points to a change in palm composition in 0–20 cm with loss or reduced frequency of LO/E.

The presence of more than one phytolith type in individual palm species enabled further assessment of which genera may be

Table 4
GESP Phytoliths from Tefe, Los Amigos, and Teotonio.

| Site | Level cm b.s., Phytolith ¹⁴ C cal BP | LO/E | % GESP | Mean μ m | Range | GEE |
|-----------|---|------|----------|--------------|-------------|-----|
| Tefe 143B | 0–20 | Yes | 4 | 16.3 | 12–20, 27 | Yes |
| Tefe 143B | 20–40 | Yes | 3 | 15.6 | 12–19.4, 33 | Yes |
| Tefe 143B | 40–60 | Yes | 3 | 13.8 | 10–22.9, 24 | Yes |
| Tefe 143B | 60–80 | Yes | <1, Rare | 13.7 | 10–26 | Yes |
| Tefe 144B | 0–20 | Yes | 3 | 18.8 | 12–31 | Yes |
| Tefe 144B | 20–40 | Yes | 2 | 16.4 | 10–25 | Yes |
| Tefe 144B | 40–60 | Yes | 1 | 20 | 9–33 | Yes |
| Tefe 144B | 60–80 | Yes | <1 | 17.5 | 11–29 | Yes |
| Tefe 145A | 0–20 | Yes | 2 | 16.5 | 9–24, 25 | Yes |
| Tefe 145A | 20–40 | Yes | 1 | 13.2 | 8–21, 26 | Yes |
| Tefe 145A | 40–60 | Yes | 2 | 15.2 | 10–23, 26 | Yes |
| Tefe 145B | 0–20 | Yes | 3 | 16.1 | 10–27 | Yes |
| Tefe 145B | 20–40 | Yes | 3 | 13.1 | 9–19, 23 | Yes |
| Tefe 145B | 60–80 | Yes | 3 | 16.9 | 8–23, 32 | Yes |
| Tefe 146A | 0–20 | Yes | 2 | 18.6 | 12–33 | Yes |
| Tefe 146A | 20–40 | No | 2 | 12.3 | 9–18 | Yes |
| Tefe 147A | 0–20 | Yes | 2 | 13.3 | 9–17, 26 | Yes |
| Tefe 147A | 20–40 | Yes | <1 | 18.9 | 9–34 | Yes |
| Tefe 148A | 0–20 | Yes | 2 | 14.5 | 11–19, 24 | Yes |
| Tefe 148A | 20–40 | Yes | <1 | 12.9 | 8–22 | Yes |
| Tefe 148A | 60–80 | No | <1, Rare | 13.5 | 10–18 | Yes |
| LA 8 | 4–17 | Yes | <1, Rare | 16.7 | 11–25 | Yes |
| LA 8 | 17–35.5 | Yes | <1, Rare | 13.2 | 8–18, 31 | Yes |
| LA 8 | 44–54.5 | Yes | <1 | 17.3 | 11–27,28 | Yes |
| LA 9 | 0–4, 960–830* | Yes | <1 | 16.3 | 8–21, 29 | No |
| LA 9 | 4–22.5, 3076–2864** | No | 1 | 9.2 | 8–13,18 | Yes |
| LA 9 | 58–69.5, 5032–5016*** | No | 5 | 12.2 | 8–17.5 | Yes |
| Teotonio | 30–40 | Yes | 5 | 12.6 | 7–18, 46 | Yes |
| Teotonio | 50–60** | Yes | 3 | 13.7 | 9–19, 26 | Yes |
| Teotonio | 100–110 | Yes | 6 | 10.2 | 8–15.5, 23 | Yes |
| Teotonio | 110–120*** | No | 2 | 9.7 | 8–13.3 | Yes |

*(Beta-302597), **(Beta-520794), *** (Beta-520795), At Teotonio **Charcoal date of 1480 cal BP; ***Charcoal date of 3375 cal BP.

represented. In *O. bataua* and *O. bacaba* “globular echinate elongated” (GEE), for example, phytoliths co-occur with and are present in considerably higher frequencies than GESPs (Morcote-Ríos et al., 2016; this study). In sites where LO/E GESPs do not occur or are rare (e.g., 130, 131), no to rare GEE presence is a further indication of the absence or sparse presence of those two *Oenocarpus* species (Table 3). Where LO/Es occur but where GEEs were not observed (118 A, 0–20 cm; 124 A, 60–80 cm) a data point is provided indicating that GESPs phytoliths may not be from the two *Oenocarpus* species and suggest *Euterpe* instead.

Site 121 is notable because it is the only one out of 13 studied in the entire transect with definitive evidence for a human presence in the form of maize phytoliths, and one of two sites with elevated phytolith percentages from weeds typical of human forest clearings (McMichael et al., 2012a; Piperno et al., 2015). Maize occurred in the 20–40 cm level of 121B and elevated herbaceous frequencies with high percentages of burned phytoliths (39% burned) including some from maize were also found there and above at 0–20 cm (17% burned) in contrast to 0% burned below 40 cm. This burning trend is also evident at 121 A. LO/E and GEE phytoliths co-occurred in all levels and GESPs frequencies were higher than in other sites, persistently reaching 5–6%. This trend might point to a human enrichment of the palms or their increased growth following human disturbance during the past few thousand years. Overlapping phytolith ages of 4000 BP from 0 to 60 cm (Table 3) may well be a result of soil mixing in the column generated by the past farming and clearance. A charcoal age of 1248 ± 38 cal BP obtained from 0 to 20 cm at 121D (McMichael

et al., 2012a) makes it reasonable to infer that some of the phytoliths at 0–20 cm are that old and those from 20 to 40 cm with maize are earlier, not unreasonably a few thousand years older considering the direct phytolith ages. That a valid measure of GESPs frequency or size changes through time can be obtained remains unlikely, due to the apparent soil mixing, but GESPs percentages are elevated compared with other PV-M localities.

In sum, GESPs phytoliths were straightforwardly recognizable through their morphology. They occurred in every site examined from the PV-M transect, but not always of a size indicating LO/E presence. Even if all of the LO/E phytoliths are from *O. bataua*, *bacaba*, and/or *E. precatoria*, the results indicate heterogeneity in their distributions across space in the past, as in the present day. The results also show evidence for the past significant enrichment or increase following human disturbance, possibly present at only a single locality sampled.

3.2. Tefe and Los Amigos

The area around the town of Tefe, located just south of the Amazon River 590 km west of Manaus, has a known archaeological history and *terra preta* is found nearby sites studied here. Sampling occurred over a c. 50 km² area encompassing river bluff and *terra firme* forest. Charcoal was present in many intervals in most river bluff cores and charcoal dates ranged from 2730 to 500 cal yr B.P. Charcoal of modern age was also found in the uppermost levels of two sites studied here, 144 and 145. Tefe river bluff soils contained elevated amounts of phytoliths from early successional herbaceous

taxa (grasses, *Heliconia*, sedges), with some showing evidence of burning (McMichael et al., 2012a; Piperno et al., 2015). Although we did not identify crop plants, the data probably reflect human firing and possible forest clearing and other human disturbances in the past. Direct phytolith dates are not yet available. Associations of high frequencies of burned phytoliths with dated charcoal was possible at two sites, 141 and 144. In the latter at 0–20 cm, a post-bomb charcoal date was obtained, whereas at 141 at 60–80 cm, the charcoal date was 1914 ± 53. Given the disturbance and frequent fire activity documented at Tefe, it is possible that charcoal fragments were subjected to frequent movement in the profiles. Future phytolith dating will establish how ancient the oldest phytoliths are at Tefe and best inform chronological trends.

This study considered three of the river bluff forests (sites 144–146) and two *terra firme* forests (sites 147, 148) (Table 4). All five sites examined had GESP and LO/E phytoliths, and GEE phytoliths occurred in all samples (Table 4). GESP percentages ranged from <1 to 3%. As at PV-M, GESP-producing species other than O/E can probably be ruled out on the basis of phytolith size, their distributions today, or both. From the bottom to top of sequences at some sites, a trend is apparent for GESP frequency and size increase and/or appearance of LO/E towards the top. This trend suggests a possible human-induced change in the palms' abundance.

At Los Amigos, a high abundance of Brazil nut trees occurs in the *terra firme* forests of the region (Foster, 2001). This raises the possibility of pre-Columbian activity there, as the species was almost certainly promoted and dispersed in prehistory (Shepard and Ramirez, 2011). Historical accounts provide evidence of rubber tapping in the 19th century in the forests along the Los Amigos River studied here (Pitman, 2010). *Syagrus sancona* and *Chelyocarpus ulei* occur in the region, but phytolith size does not suggest their presence. We did not sample palm swamps of the area in this study, probably ruling out *Manicaria*. Two study locations had LO/E phytoliths (Table 4). We dated a phytolith sample from the uppermost 4 cm of soil from Site 9 to 960–830 cal BP (Table 4). This date indicates that the phytoliths span the late prehistoric, historic, and modern eras. We obtained phytolith dates of 3076–2864 and 5032–5016 cal BP from 4 to 22.5 and 58 to 69.5 cm b.s., respectively, indicating a clear stratigraphic and chronological separation of the phytoliths with depth. GESP frequencies were low (<1–1%), save in the bottom level from Site 9, where a peak of burned phytoliths also occurred (McMichael et al., 2012a). However, phytolith size did not indicate LO/E presence in the bottom level. The GESP phytolith size increase at Site 9 at 0–4 cm instead suggests that O/E entered that locality during the past 960 years.

3.3. Archaeological comparison: the Teotônio site

Teotônio is an important archeological site located on a river bluff on the Upper Madeira River in Brazil just south of the town of Porto Velho that was occupied from about 9500 cal BP through the historic period. It contains *terra preta* as old as 6500 cal BP, among the most ancient yet found (nearby sites in the Upper Madeira have *terra preta* dated to about 8000 cal BP (Almeida and Neves, 2014; McMichael et al., 2015a; Watling et al., 2018). Teotônio should provide a clear picture of how a stable and sizeable human presence in Amazonia is represented in palm and other phytolith records.

Soils for phytoliths were originally sampled every 10 cm to a depth of 140 cm in an area of the site with *terra preta* that contained abundant pottery sherds, charcoal, and macrofossils, particularly in its upper layers (for additional details, see Almeida and Neves, 2014 and McMichael et al., 2015b). Early polychrome pottery occurs in the upper levels. Two charcoal dates from the soils examined are 3375 cal BP and 1480 cal BP at

110 cm and 50–60 cm, respectively. Teotônio had by far the highest frequencies of palms of all types of any site considered here and in other terrestrial soil work, exceeding 30–40% in all but the lowermost level at 110–120 cm, which was not *terra preta* soil (McMichael et al., 2015b). The latter sample nonetheless demonstrated palm frequencies (18%) higher than in terrestrial soils. Palm frequencies increased through time to reach ≥70% at ca. 1480 BP and after. Recent macrobotanical evidence from the site indicates cf. *Oenocarpus* seed fragments occurred in *terra firme* contexts dated based on associated charcoal to within the ca. 6500 to 1000 cal BP period (Watling et al., 2018). Carbonized remains of the Brazil nut were also found. Analyzing phytoliths from a different area of the site than this study, Watling et al. (2018) also found high overall palm frequencies of 40 to 75%. They identified Euterpeae (*Oenocarpus*/*Euterpe*) phytoliths from the bottom to the top of the long ca. 9000 year-old preceramic occupation sequence they studied, although the method of identification was unclear.

In four levels from our previous work re-studied here, we found LO/E phytoliths in three levels with *terra preta*, and not in the 110–120 cm level without it (Table 4). GESP percentages reaching 5–6% were higher than at most PV-M and Tefe sites, and GEE phytoliths co-occurred with LO/Es.

3.4. Non-palm woody phytolith types

As reported in Piperno et al. (2015), the sand fractions of Neotropical terrestrial soils (50–250 μm size fraction) contain high numbers of large-sized phytoliths not yet represented in modern reference collections that appear to be from a diverse array of woody taxa. We re-evaluated the sand fractions of Piperno et al. (2015), re-examining and expanding modern reference collections to identify previously unrecognized taxa and sub-characterizing phytolith types. We also utilized the review of phytoliths in bark and wood of African plants by Collura and Neumann (2017). Tables 5 and 6 show the results.

At PV-M, a high diversity of woody taxa is represented in all sites and levels studied. Some of the forms or variations of them are present at Tefe and Teotônio. Included are mature forest taxa from the Annonaceae and Boraginaceae that are not dietary items today and not in lists of species considered to have been manipulated in Levis et al. (2012, 2017). In Annonaceae, the genus *Gutteria* is represented by irregular forms, *Gutteria* and/or *Oxandra* by elongates, and *Unonopsis* and/or *Oxandra* by sphericals (e.g., Fig. 3, left and see Piperno, 1988, Figs. 75, 76). In Boraginaceae, *Cordia* is currently indicated (Fig. 3, right) with more work needed to ascertain if the phytoliths are more widely distributed in the family in areas studied here. Phytoliths possibly but not yet definitely from Neotropical *Trema* and/or *Celtis*, based on analysis of African representatives of the genera (Collura and Neumann, 2017), are present in some sites, reaching levels of 6–9% in two of the sites (Fig. 4). *Trema* is a pioneer shrub or small tree of forest gaps while *Celtis* can be a tree of established forest or a liana. Types of elongated phytoliths called Arboreal Elongates (curved, tapered, with striations or stipulate decorations) are present in most samples, sometimes reaching high frequencies (Figs. 5 and 6). They appear to have restricted distributions, being found so far in such trees as *Mabea*, *Cordia*, *Brosimum* and a few other Moraceae, the Chrysobalanaceae, and also *Mendoncia*, a liana). Elongates characterized as having “pavement” decorations (P in the Elongate Other category) are found in a few samples and are tentatively identified as *Ficus* based on the Collura and Neumann (2017) study. *Ficus* are free-standing trees or epiphytic strangler figs on others. Sclereids, produced in a variety of woody taxa, are present at most sites. The categories Forest A to Forest E represent several phytoliths with distinctive appearances (Figs. 7–9). Forest A, B, and C are present in

Table 5
Sand Phytoliths from PV-M.

| | Annonaceae | | Boraginaceae | Forest | | | | | Arboreal Elongate | | | Sclereid | Stipulate | | T or C? | Large | Depth | n | |
|------|------------|------|--------------|--------|----------|----|----|------|-------------------|---------|------------|----------|-----------|--------|---------|-------|-------|-------|----------|
| | Irr. | Sph. | | A | B | C | D | E | Curved | Tapered | Other | | Irr. | Elong. | | | | | Tracheid |
| 118A | 6, E | 0 | * | 6 | 36, J, K | 2 | 2 | * | 4 | 30 | 4, N | 0 | 0 | 4 | 4 | 2 | 0–20 | 50 | |
| 118A | 8, E | 0 | 2 | 4 | 26, K | 2 | 2 | 10 | 0 | 40 | 2 | 0 | 0 | 2 | 0 | 2 | 20–40 | 50 | |
| 118A | 8, E | 0 | 1 | | 15, J, K | 9 | 8 | 13 | 1 | 32 | 2, S | | | | | 6 | 40–60 | 70 | |
| 118B | 22, E | 2 | 4 | 24 | 36, K | 2 | 2 | * | 8 | * | *, STR. | * | 0 | * | 0 | 0 | 0–20 | 50 | |
| 118B | * | 0 | * | * | * | * | 0 | * | * | * | *, STR. | * | 0 | * | * | 0 | 20–40 | N.C. | |
| 118B | * | 0 | * | * | * | * | 0 | * | * | * | *, STR. | * | 0 | * | * | 0 | 40–60 | N.C. | |
| 119A | 3 | 0 | 3 | 3 | 26, J | 15 | 10 | 0 | 1 | 4 | 3, STR. | 4 | 4 | 4 | 0 | 20 | 0–20 | 50 | |
| 119B | 5, E | 0 | 6 | 2 | 24, K, J | 0 | * | 4 | 5 | 48 | 6, N | 0 | 0 | 0 | * | 0 | 0–20 | 100 | |
| 119B | 4, E | 0 | 15 | 5 | 13, K, J | 1 | 0 | 7 | 5 | 41 | 5, N | 1 | 3 | 0 | 0 | 0 | 20–40 | 100 | |
| 121A | 10, E | 0 | 6 | * | 10, K | 4 | 0 | 0 | 26 | 20 | 10, I | 8 | 0 | 4 | 2 | 0 | 0–20 | 50 | |
| 121A | 0 | 0 | * | 0 | * | * | * | * | * | * | * | 0 | * | 0 | 0 | * | 20–40 | N.C. | |
| 121B | 3 | 0 | 3 | 0 | 20, K | 3 | 0 | 10 | 9 | 20 | 3, P | 10 | 7 | 7 | 3 | 2 | 0–20 | 30 | |
| 121B | * | 0 | * | * | * | * | * | * | * | 0 | *, STR. | * | 0 | 0 | * | 0 | 20–40 | N.C. | |
| 121B | 0 | 0 | 4 | 0 | 22 | 16 | 24 | 12 | 2 | 6 | 2, P | 2 | 0 | 0 | 0 | 10 | 40–60 | 50 | |
| 121B | 3, E | 0 | 13 | 0 | 19 | 18 | 10 | 13 | 1 | 6 | 7, P | 4 | 0 | 1 | 2 | 3 | 60–80 | 70 | |
| 124A | 0 | 2 | 2 | 4 | 16, K | 2 | 0 | 2 | 12 | 30 | 2 | 4 | 12 | 4 | 2 | 8 | 0–20 | 50 | |
| 124A | 2 | 2 | 2 | 6 | 29, K, J | 2 | 2 | 4 | 4 | 18 | 4, N | 4 | 2 | 2 | 0 | 18 | 20–40 | 50 | |
| 124B | 3, E | 1 | 1 | 5 | 10, K | 3 | 2 | 6, D | 1 | 31 | 3, I, S | 3 | 10 | 2 | 0 | 19 | 0–20 | 100 | |
| 124B | 2 | 0 | 0 | 2 | 10, K | 0 | 0 | 0 | 4 | 52 | 4, N, STR. | 2 | 8 | 2 | 0 | 10 | 20–40 | 50 | |
| 127A | 2 | 0 | 4 | 12 | 22 | 4 | 0 | 0 | 14 | 16 | * | 8 | 6 | 0 | 10 | 2 | 0–20 | 50 | |
| 127A | 2 | 0 | 40 | 6 | 32 | 0 | 0 | 4 | 4 | 4 | 4 | 2 | 0 | 0 | 0 | 2 | 20–40 | 50 | |
| 127A | 0 | 0 | 30 | 2 | 20 | 2 | 2 | 0 | 12 | 10 | 6 | 2 | 4 | 0 | 0 | 10 | 60–80 | 50 | |
| 127B | 0 | 0 | 9 | 16 | 25, K, J | * | 0 | 1 | 9 | 8 | 0 | 12 | 6 | 3 | 6 | 5 | 0–20 | 100 | |
| 127B | 1 | * | 38 | 7 | 8, K | 2 | 0 | 0 | 8 | 2 | 0 | 6 | 1 | 1 | 0 | 26 | 40–60 | 100 | |
| 128A | 4 | 2 | 8 | 10 | 28 | 2 | * | 0 | 16 | 12 | 2 | 10 | 4 | 2 | 0 | 0 | 0–20 | 50 | |
| 128B | 2 | 2 | 8 | 6 | 26 | * | 0 | 0 | 24 | 10 | 0 | 4 | 8 | 2 | 2 | 6 | 0–20 | 50 | |
| 128B | 2 | 0 | 14 | 6 | 38, K | 6 | 0 | 0 | 16 | 8 | 2 | 6 | 8 | 4 | 0 | 0 | 20–40 | 30 | |
| 130A | 6, E | 1 | 0 | 42 | 34, K, J | 3 | 0 | 1 | 1 | 0 | *, STR. | 0 | 1 | 1 | 9 | 1 | 0–20 | 70 | |
| 130B | *, E | 0 | * | * | * | * | * | 0 | 0 | * | * | * | * | 0 | 0 | 0 | 0 | 20–40 | N.C. |
| 131A | 28, E | 4 | 0 | 0 | 29, K | 14 | 2 | *, D | 4 | 4 | 0 | * | 6 | 0 | 0 | 9 | 0–20 | 50 | |
| 131A | 12, E | 0 | 0 | 2 | 22, K | 12 | 4 | 6, D | 2 | 18 | 0 | 2 | 10 | 0 | 0 | 10 | 20–40 | 50 | |

Notes: For Annonaceae: Irr = irregular faceted forms from *Guatteria*; E = some phytoliths were elongated faceted forms from *Guatteria* and/or *Oxandra*, and Sph = spherical faceted forms from *Unonopsis* and/or *Oxandra*. For T or C?, phytoliths are possibly from *Trema* and/or *Celtis*. For Arboreal Elongates under Other: some are: I = Irregular; S = serrated edge; P = Pavement; N = Notched; STR = Striations. For Forest E: D = some are decorated. For Forest B: J = some with shapes similar to large jigsaws; K = some have knobbed surface decorations. Forest categories A–E do not necessarily represent the same types of phytoliths as in Table 1 of Piperno et al., 2015. For samples where counts are not provided (N.C. = no counts), additional analysis is needed to achieve representative counts; taxa denoted with an asterick were observed and it cannot be said that taxa without a designation did not occur. Forest B phytoliths were present in significant frequencies and in 130B, 20–40 cm Forest A phytoliths were also present in high frequencies. In samples with sample count number provided, * indicate phytoliths were observed in the sample and are <1% of the count.

Table 6
Sand Phytoliths from Tefe and Teonio. See Notes to Table 5.

| | Annonaceae | | Boraginaceae | Forest | | | | | Arboreal Elongate | | | Sclereid | Stipulate | | T or C? | Large | Depth | n |
|------------|------------|------|--------------|--------|-------|---|----|-------|-------------------|---------|----------|----------|-----------|--------|---------|-------|-------|-----|
| | Irr. | Sph. | | A | B | C | D | E | Curved | Pointed | Other | | Irr. | Elong. | | | | |
| Tefe 140 A | 6, E | 4 | 2 | 0 | 30, J | 8 | 8 | 4, D | 8 | 8 | 0 | 4 | 0 | 0 | 8 | 8 | 0–20 | 50 |
| Tefe 140A | 4, E | 2 | * | 0 | 20, J | 6 | 6 | 6, D | 10 | 10 | 10, STR. | 12 | 0 | 0 | 14 | 0 | 20–40 | 50 |
| Tefe 140A | 0 | 2 | * | 0 | 22, J | 2 | 6 | * | 24 | 22 | 2, P | 20 | 0 | 0 | 0 | 0 | 40–60 | 50 |
| Tefe 141A | 8 | 2 | 0 | 0 | 24, J | 6 | 4 | 16, D | 12 | 18 | 0 | 0 | 2 | 2 | 0 | 6 | 0–20 | 50 |
| Tefe 141A | 8, E | 0 | 12 | 0 | 24, K | 6 | 8 | 2 | 10 | 28 | 2 | 0 | 0 | 0 | 0 | 0 | 20–40 | 50 |
| Tefe 142A | 2 | 6 | 0 | 0 | 58, J | 0 | 0 | 0 | 6 | 12 | 0 | 0 | 10 | 6 | 0 | 0 | 0–20 | 50 |
| Tefe 142A | 2, E | 2 | * | 0 | 64, K | * | 4 | 4 | 4 | 10 | 6, N | 0 | * | * | 0 | 4 | 20–40 | 50 |
| Tefe 143 B | 2 | 4 | 2 | 8 | 38, J | 4 | 0 | 10, D | 12 | 12 | 4, STR. | 2 | 0 | 0 | 2 | 0 | 0–20 | 50 |
| Tefe 143 B | 17, E | 0 | 0 | 4 | 25 | 0 | 0 | 16, D | 6 | 2 | *, STR. | 4 | 8 | 18 | 0 | 0 | 20–40 | 50 |
| Tefe 143 B | 8 | 0 | 10 | 0 | 52 | 0 | 2 | 4, D | 2 | 2 | 2, S | 2 | 10 | 0 | 0 | 0 | 40–60 | 50 |
| Tefe 144 B | 0 | 0 | 3 | 0 | 19, J | 7 | 13 | 33, D | 0 | 2 | 0 | 0 | 7 | 4 | 0 | 12 | 0–20 | 100 |
| Tefe 145 A | 4, E | 0 | 2 | 0 | 42, J | 8 | 0 | 22, D | 6 | 6 | 2, P | 8 | 0 | 0 | 0 | 2 | 0–20 | 50 |
| Tefe 145 A | 4, E | 0 | 26 | 0 | 30 | 2 | 0 | 10, D | 2 | 8 | 4, P | 10 | * | 0 | * | 4 | 20–40 | 50 |
| Teonio | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 | 18 | 6 | 0 | 2 | 54 | 8 | 2 | 30–40 | 50 |
| Teonio | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 2 | 16 | 4 | 0 | 10 | 44 | 6 | 6 | 40–50 | 50 |
| Teonio | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 2 | 18 | 2, STR. | 0 | 26 | 32 | 10 | 0 | 50–60 | 50 |
| Teonio | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 2 | 4 | 6 | 0 | 0 | 10 | 50 | 6 | 10 | 70–80 | 50 |

most samples, and the B category that is often present in high frequencies encompasses in itself at least eight discrete forms.

Importantly at PV-M, there is little suggestion that the taxonomic diversity indicated by the phytolith record decreases or increases through time, or that particular taxa show increases at

the expenses of others or appear later in time. Rather, the various types, including non-dietary genera from Annonaceae and Boraginaceae, are maintained throughout the sequences and indicate stable forest structure, composition, and biodiversity. A caveat is that the phytolith data from this study of modern plants

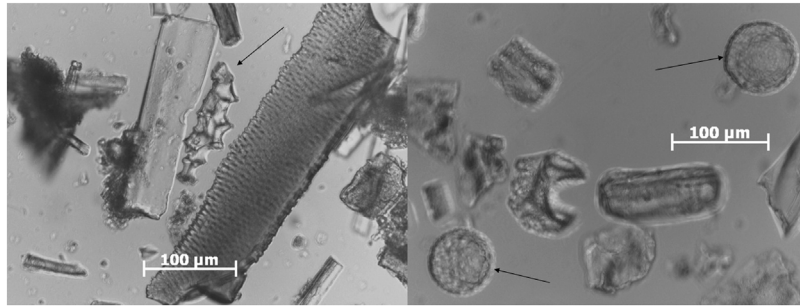


Fig. 3. Left, the arrow points to an Annonaceae elongated faceted phytolith from PV-M 124B, 0–20 cm b.s.; Right, arrows point to Boraginaceae spherical cystoliths from PV-M 119B, 20–40 cm b.s. They have subtle surface decorations.

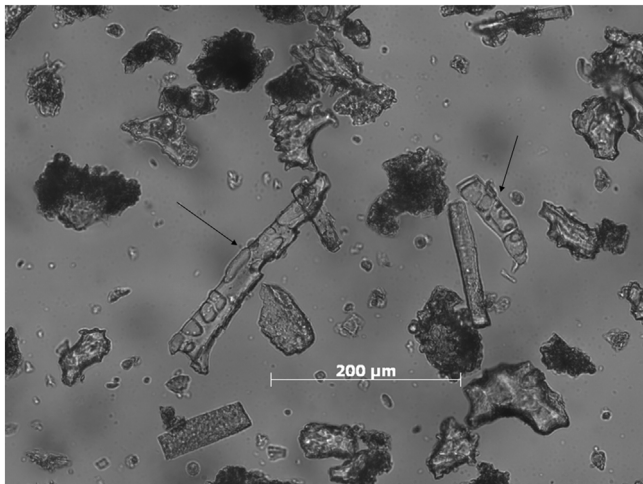


Fig. 4. Arrows point to possible phytoliths from the bark of *Trema* and/or *Celtis*. Collura and Neumann (2017) describe similar phytoliths as “elongate scalariform”.

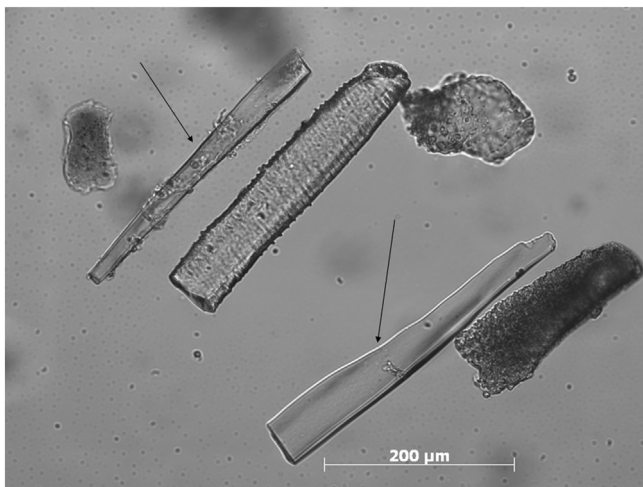


Fig. 5. Arrows point to typical elongated phytoliths with one tapered end present at the sites. They are very long, smooth and solid, and may have weathered-looking surface marks.

indicate that the phytolith record cannot document several major useful species, and thus past presence/absence or changes in frequencies of those taxa upon human manipulation is not assessable (Table 1).

At Tefe, river bluff forest from six sites, 140–145, covering an area about 25 km², were examined. We commonly observed

sponge spicules at the sites reflecting their riverine localities. A diversity of woody phytoliths also occurs at Tefe through time (Table 6); however, the assemblages show significant differences compared with PV-M. Forest B phytoliths frequently differ from those at PV-M, for example, whereas Forest E types have the same shapes as at PV-M but at times have different surface decorations, and they can occur at far higher frequencies at Tefe (Fig. 10). Some elongate types found at PV-M do not occur at Tefe and Forest A phytoliths were not observed at most Tefe localities. The differences between Tefe and PV-M may reflect differing forest compositions at riverine and interfluvial localities and/or a greater human influence on the Tefe forests. With regard to the LA sites, their sand fractions have not yet been examined.

The results from Teotônio demonstrate marked differences compared with both PV-M and Tefe. Not present are the Annonaceae and Boraginaceae along with five other phytolith types recorded in the other two regions. Another type, Forest E, occurs below the *terra preta* but not within it. Forest B phytoliths are present in far fewer frequencies and less diversity at Teotônio than at PV-M and Tefe. Rather, two phytolith categories, elongate and irregular stipulate, of the same types found at PV-M and Tefe dominate Teotônio assemblages (Fig. 6), reaching frequencies of 32–54% (Table 6). Phytoliths possibly from *Trema* or *Celtis* are also consistently represented in significant frequencies.

4. Discussion

Forest management in the past, as in the present, likely involved activities on different intensity scales from planting, to removing non-useful species, to pruning, to encouraging or sparing useful species. The subtle characteristics of some of these strategies pose challenges for paleoecological detection. This study tested approaches designed to detect the presence and management of three palm species of considerable economic importance. The approaches employed here also examined at a finer level whether human modification influenced the distribution of some non-palm woody species in forests through time. They utilized recent and new information on palm phytolith morphology and size, together with reported modern distributions of relevant genera and species. Palm phytoliths are among the most prolifically produced, preserved, and diagnostic. In terrestrial soils such as these, a local source area is known, permitting reconstructions from well-defined tracts of landscapes without complicating influences from factors such as long-distance transport that can occur in lake sediment records. These characteristics, plus data from paleoecological and modern phytolith records (the latter from surficial soils underneath tropical forest), indicate that they effectively track changes in palm abundance and can document a significant enrichment, or decrease, in the past.

In surficial soils underneath inventoried forest on Barro Colorado Island, Panama, for example, palm phytolith

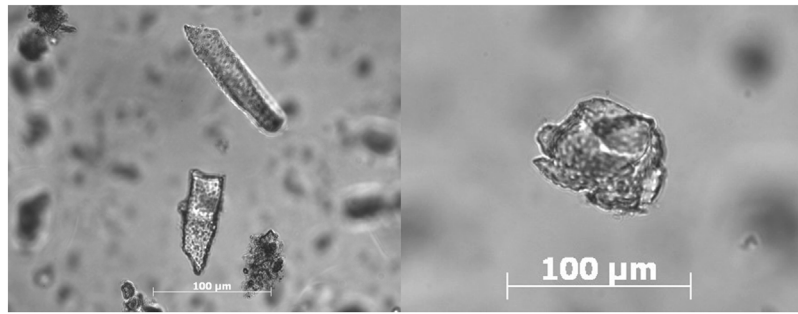


Fig. 6. Left, Two elongate stipulate phytoliths from Teotonio, 30–40 cm b.s. The surfaces have small rounded protuberances; Right, an irregular stipulate phytolith from Teotonio, 50–60 cm b.s. The irregular stipulates can take on a variety of different shapes in the sites (see also Fig. 7).

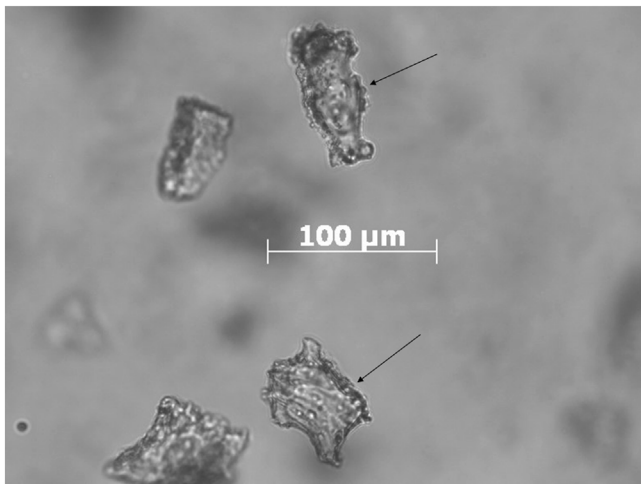


Fig. 7. Top arrow points to an irregular stipulate phytolith and bottom arrow to a typical Forest A phytolith from PV-M 130B, 20–40 cm. It is irregular in shape with thin facets crossing the phytolith horizontally.

percentages were 1% where density was 10/ha and individuals were dispersed and 8% where the palms grew in clumps (Piperno, 1988; Piperno et al., 2015). In an inventoried *terra firme* forest in Bolivia, palm frequency in the vegetation was 12% and in the surficial soils was 33% (Dickau et al., 2013). Although other Amazonian forests with surficial phytolith records were not inventoried, they showed significantly increased palm frequencies where palms were obviously a greater component of the vegetation (Dickau et al., 2013; Watling et al., 2016). In paleoecological profiles representing a gradient of human disturbance across western Amazonia, palm percentages clearly increase where other associated disturbance gradients in the sequences are higher (McMichael et al., 2015b).

In this study, we identified readily palm types both in terrestrial soils and in an archaeological site. Results indicate an uneven distribution of the three palm species across the landscapes, as today (see Methodology Section 2.1), with little to no evidence for an increase and human enrichment in prehistory in the PV-M *terra firme* forests or at localities studied at LA. Riverine Tefe sites showed some trend for increase of the palms through time possibly suggesting a human influence. As more precise information on these and other palm phytolith characteristics accumulates from analyses of modern flora, data from ancient contexts will become more revealing. As palm occurrence and frequency from inventoried modern forests are increasingly compared with surficial soil phytolith assemblages, reconstructions and interpretations will be improved further. Will it be possible, for example, to estimate not only overall abundance but density per hectare of palms in the past with such information?

With regard to the study of non-palm forest taxa, using more sensitive indices than previously (Piperno et al., 2015), data from this study again do not indicate significant alterations in forest structure or diversity due to human manipulation at PV-M or even possibly at Tefe, as the same array of woody taxa were maintained throughout the sequences. Of course, more subtle manipulation strategies involving few tree species and relatively little increase of individuals from a given species might go undetected, and there are major economic taxa silent in phytolith records. It is noteworthy, however, that in the PV-M analysis any suggestion of enrichment of palms in way of higher percentages of GESP phytoliths than in other sites in that study region took place in the setting-site 121—where some agriculture and forest clearance occurred. Forests managed to any significant degree require persistent human occupations nearby to carry out the frequent pruning, encouragement, enrichment, or planting that becomes management. Today in Amazonia and the Neotropics at large these forests are typically generated from fallows or home gardens (Miller and Nair, 2006; Peters, 2000). It is thus not surprising that clear paleo-ecological-based evidence for substantial palm

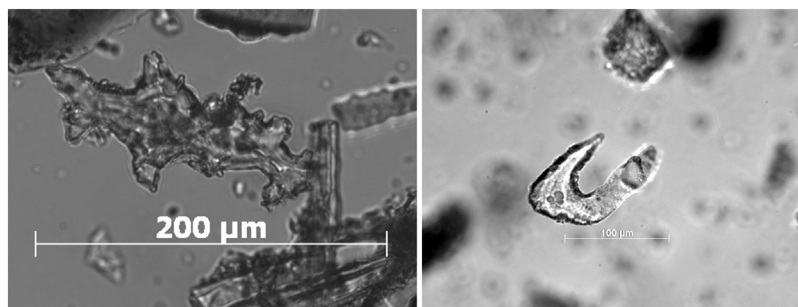


Fig. 8. Left, a Forest B phytolith from PV-M 124B, 0–20 cm with the “knobbed” surface decoration. Right, another type of Forest B phytolith from PV-M 128B, 0–20 cm.

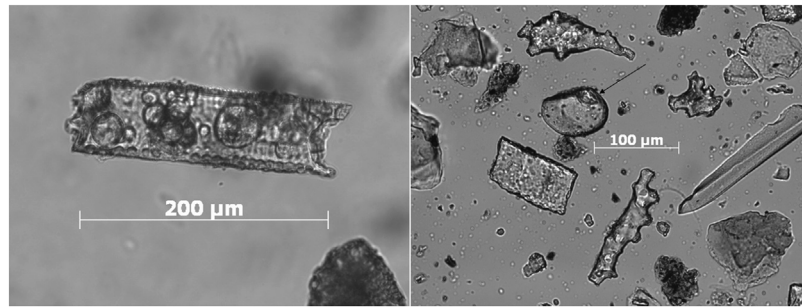


Fig. 9. Left, a Forest D phytolith from PV-M 128 A, 0–20 cm. It is elongated in shape and has circular depressions on the surface presumably created by pressure from adjoining cells pressing on it during formation. Right, arrow points to a Forest E phytolith from PV-M 119B, 0–20 cm. It is a three-quarter-complete sphere with a smooth surface decoration. Some Forest E types are one-half-complete spheres and some have more decorated surfaces. Above, to the right, and to the bottom right of the Forest E phytolith are two Forest B phytoliths and elongate forms (a tapered and an Elongate Other) are present as well.

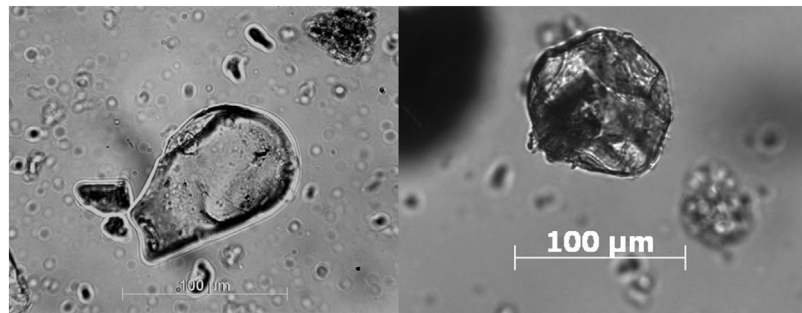


Fig. 10. Left, a Forest B phytolith from Tefe 144B, 0–20 cm that occurs at Tefe and not at PV-M. Right, a Forest E phytolith from Tefe 145A, 0–20 cm that has a number of surface facets unlike those at PV-M. It may eventually be placed in a separate category.

increase with possible enrichment in closed-canopy Amazonian forest beginning 2500 years ago comes from near a permanent occupation with extensive *terra preta* in the Santarém region of eastern Amazonia, which was well-occupied in late prehistory (Maizumi et al., 2018a).

Moreover, the locations of the Amazonian forest inventory plots used in Levis et al. (2017) to argue for a substantial prehistoric legacy are disproportionately located near areas with the highest abundances of archaeological sites, with many located in areas known to have been well-occupied in the past (e.g., near rivers; where *terra preta* and landscape alterations such as mounds, roads, and raised fields have been found) (McMichael et al., 2017). Apart from the issue of management, this study provides additional evidence that significant tree clearance for agriculture did not take place. The findings also support an increasing body of evidence that this activity occurred over a relatively small area of Amazonia in prehistory and probably did not have serious implications for global climate or forest structure.

With relation to Teotônio, whether the *terra preta* sampled there represents a trash midden or living area, or perhaps a house garden context is currently unclear. Nonetheless, all the contexts are sensitive to economic practices, and phytolith data, whereas documenting intensive palm use and likely management, importantly do not indicate exploitation of the wide array of non-palm woody taxa commonly found in the PV-M and Tefe terrestrial soils. This finding further suggests that many of those phytoliths are not from economic taxa. They likely instead represent an array of plants not routinely manipulated and that were stable components of diverse forests whose structures were not significantly impacted in prehistory. As we expand our modern reference collections, many of these taxa should be identified, generating information on species abundance and diversity through time that will be valuable to scholars studying the past and present Amazon alike, and also

better separating economic from non-economic taxa. Moreover, the diminished diversity of woody taxa at Teotônio may well speak to how a substantial cultural occupation of tropical forest can result in decreased biodiversity.

Finally, with regard to substantial human impact in Amazonia and what timeline should register its beginning, the late Holocene period at about 3000–2500 cal BP seems a suitable date. Certainly, at this time or shortly after, agriculture with major native and introduced crop plants was well-established and some landscapes were fundamentally altered by permanent settlements of considerable size and complexity. In the Amazon, as elsewhere in the tropical zones (Roberts et al., 2018 for a review), that human alterations of environments began well before the industrial era is thus clear. The extent to which significant human environmental modification extended across Amazonia in prehistory, however, requires further study. Available evidence in this study and elsewhere indicates that Amazonian forest experienced heterogeneous cultural impacts from sparse and localized, to intense and regional. Regardless, we believe that defining a beginning date is less critical at this juncture to the multi-disciplinary research community involved in Amazonia than filling in the considerable lacunae concerning the scale and intensity of prehistoric impacts and how they may influence ecosystems today.

5. Conclusions

This study permits answers or preliminary answers to the research questions posed. First, this and other research (Morcote-Rios and Bernal, 2001) shows that it is possible to identify the important palm genera *Oenocarpus* and *Euterpe* based on phytolith morphology and size characteristics, and to follow their presence and abundance through time in soil profiles. This capacity allows robust empirical study of hypotheses concerning prehistoric

human influences on their present distributions and abundances. Second, it appears possible, through study of the numerous distinctive phytoliths from non-palm woody plants that are well-preserved in the soil profiles, to follow significant changes in forest structure and diversity through time. Results from Amazonian localities studied here indicate that prehistoric human influences on the overall structure and diversity of *terra firme* forests and creation of palm hyperdominance in them were less influential than currently proposed by some Amazonian scholars.

Future modern reference work with additional species of *Oenocarpus* and *Euterpe* should allow a more definitive interpretation of which species are present in soils. Further work will also lead to identification of currently unknown woody phytolith taxa that were persistently common on landscapes through time. It will establish whether any derived from trees thought to have been commonly exploited and manipulated in prehistory (e.g., Levis et al., 2012, 2017). Present and future work is applicable to both terrestrial soil profiles and lake sediment cores, elucidating to a greater extent Amazonian vegetational history. This information will also increasingly inform ecological practices and guide conservation and restoration policies.

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