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Holocene increases in palm abundances in north-western Amazonia

Britte M. Heijink¹  | Crystal N. H. McMichael¹  | Dolores R. Piperno^{2,3} |
Joost F. Duivenvoorden¹ | Dairon Cárdenas⁴ | Álvaro Duque⁵

¹Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

²Department of Anthropology, Smithsonian National Museum of Natural History, Washington, DC, USA

³Smithsonian Tropical Research Institute, Balboa, Panama

⁴Herbario Amazónico Colombiano, Instituto Amazónico de Investigaciones Científicas Sinchi, Bogotá, Colombia

⁵Departamento de Ciencias Forestales, Universidad Nacional de Colombia Sede Medellín, Medellín, Colombia

Correspondence

Crystal N. H. McMichael, Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1090 XH Amsterdam, The Netherlands
Email: c.n.h.mcmichael@uva.nl

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Abstract

Aim: In Amazonia, 227 of c. 16,000 tree species account for half the individual trees (termed 'hyperdominant' species), and a disproportionate number of these species are palms. Our objectives are to show how and whether palm abundance has changed through the Holocene. Here, we reconstruct a detailed fire and vegetation history from north-western Amazonia, with a focus on changes in palm abundances, and compare our results with regional data.

Location: Amacayacu, Colombia.

Taxon: Amazonian palms.

Methods: We performed charcoal and phytolith analysis on soil cores, and obtained ages of past fires using ¹⁴C dating. We measured charcoal abundances and the relative abundances of phytoliths (silica-based microfossils) for all samples. We used these data to reconstruct changes in fire and vegetation, and compared these data with the species composition of palms in the modern forest.

Results: Seven ¹⁴C dates from charcoal in three cores provided fire ages ranging from 1630 to 2450 calibrated years before present. Charcoal was absent from one-third of the cores. Palm phytoliths from genera such as *Iriarte*, *Socratea*, and *Astrocaryum* have increased through time, while genera such as *Euterpe*, *Hyospathe*, and *Oenocarpus* have remained relatively stable and similar to modern levels. Overall, palm abundances were negatively correlated with charcoal measurements. Decorated sphere phytoliths, produced from unknown arboreal taxa were positively correlated with charcoal presence and abundance.

Main conclusions: Palms have increased at Amacayacu and other forest plots through time, but the increases are largest in north-western Amazonia. The presence of fire, however, dampens the increase in palms through time. When compared with reconstructions from other Amazon regions, our results suggest that increases in palm abundances in the late Holocene occurred both in the presence and absence of direct pre-Columbian human influence, and that response was strongest in north-western Amazonia when human influence was minimal.



KEYWORDS

Amazonia, Arecaceae, charcoal, fire, forest age, hyperdominant, palms, phytoliths, soil, tropical forests

1 | INTRODUCTION

The Amazonian rainforest (~6-million-km²) hosts the largest and most diverse tropical rainforest in the world, and provides global ecosystem services, such as carbon sequestration and water cycling (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000; Slik et al., 2015). There is an estimate of ~16,000 tree species >10 cm diameter at breast height (dbh) in Amazonia, and 227 of these species, termed hyperdominants, compose 50% of the individual trees in the forest (ter Steege et al., 2013). Many hypotheses have been put forward to explain patterns of forest composition in tropical forests, including abiotic and biotic regulation (Clark, Palmer, & Clark, 1999; Tuomisto, Ruokolainen, & Yli-Halla, 2003; Wright, 2005), neutral dynamics (Hubbell, 2001), and climatic refugia (Haffer, 1969; though see Colinvaux et al., 1996). A recent hypothesis is that the pre-Columbian inhabitants of Amazonia have played a large role in shaping modern forest composition throughout the Basin (Levis et al., 2017; McMichael, Matthews-Bird, Farfan-Rios, & Feeley, 2017). Humans have been present in Amazonia during the entire Holocene (Lombardo, Denier, May, Rodrigues, & Veit, 2013; Roosevelt et al., 1996), and they have been cultivating maize in some regions since at least 6500 cal yr BP (Brugger et al., 2016; Bush et al., 2016; Bush, Piperno, & Colinvaux, 1989).

One of the main ways that the pre-Columbian inhabitants of Amazonia affected the forests was through the use of fire (e.g. Bush, Silman, McMichael, & Saatchi, 2008). Fire rarely occurs in the aseasonal forests of the Amazon without a human ignition source (Bush et al., 2008; Malhi et al., 2008), and many rainforest trees lack fire adaptation (Uhl & Kauffman, 1990). A single fire can cause 40% species turnover in Amazonian forests, and repeated burns can cause 100% species turnover (Barlow & Peres, 2008). Charcoal that has resulted from past fires is commonly found in Amazonian soils (Hammond, ter Steege, & Borg, 2006; McMichael, Piperno, et al., 2012; Piperno & Becker, 1996; Saldarriaga & West, 1986; Sanford, Saldarriaga, Clark, Uhl, & Herrera, 1985; Santos et al., 2000), and most dates from these analyses indicate that fire events increased in frequency over the last 2,500 years (McMichael & Bush, 2019).

Based in part on modern indigenous forest usage, it is postulated that pre-Columbian people in Amazonia also domesticated a large number of plant species, and planted, protected, and transported numerous other useful plants, resulting in significantly altered forest composition that are still visible today (Junqueira, Shepard, & Clement, 2010; Levis et al., 2018; Thomas, Alcázar Caicedo, McMichael, Corvera, & Loo, 2015). Palms are one of the most economically important plant groups in Amazonia (Clement et al., 2015), and are also disproportionately abundant components of the 227 hyperdominant tree species (ter Steege et al., 2013). Pollen and phytolith analyses have shown that pre-Columbian people increased

palm densities at many known archaeological sites (Maezumi et al., 2018; McMichael et al., 2015; Watling et al., 2017). Increases in palm taxa through time, however, may also occur without human promotion. *Iriartea deltoidea* is the fifth commonest tree in Amazonia (a hyperdominant species), and several western Amazonian pollen records have documented its increase in abundance over the last 8,000 years (Bush & McMichael, 2016). An initial increase in *Iriartea* occurred ca. 6,500 years ago, but pollen percentages reached their highest levels over the last 3,000 years, particularly in areas containing little to no evidence of human activity (Bush & McMichael, 2016).

The 1,170 forest plots that are used to assess Amazonian biodiversity (ter Steege et al., 2013), and the subset of several hundred that are censused repeatedly and used to measure carbon dynamics (Fauset et al., 2015; Johnson et al., 2016), are disproportionately located in areas with high densities of archaeological sites (McMichael et al., 2017). Thus it is likely that past human activity has affected the long-term ecology in many of the studied forest plots. There are very few data, however, from directly within the forest plots to link forest composition with past human activity (McMichael, Piperno, et al., 2012; McMichael et al., 2015; Piperno & Becker, 1996; Piperno, McMichael, & Bush, 2019). The existing data are from plots in the central or southwestern parts of the Amazon (Figure 1). Recent data from a Peruvian forest plot and two other regions of western Amazonia indicate that in *terra firme* and fluvial forests in those portions of Amazonia, prehistoric populations did not enrich and influence the abundance of two important palm genera, *Oenocarpus* and *Euterpe*, both hyperdominant species today (Piperno et al., 2019). There are currently no data, however, on the past fire or vegetation history from forest plots in north-western Amazonia (Figure 1), the wettest and most diverse area of the basin (Gentry, 1988a, 1988b; ter Steege et al., 2006).

Here, we reconstruct the spatial and temporal patterns of past fire and vegetation change, with a focus on palms, from the Amacayacu forest plot (Colombia) in north-western Amazonia (Figure 1). We determine the timings of the most recent fires, the extent of past fire and vegetation change within the forest plot, and whether the observed vegetation changes were related to past fires. We contrast our results from Amacayacu with existing data on fire and vegetation history from other western Amazonian sites (Figure 1), and place our results in the context of modern hyperdominance patterns and carbon storage potential.

2 | MATERIALS AND METHODS

2.1 | Site description and field sampling

Amacayacu National Natural Park (S 3°48'32.76", W 70°16' 4.079") is located in the most southern part of Colombia (Figure 1) and

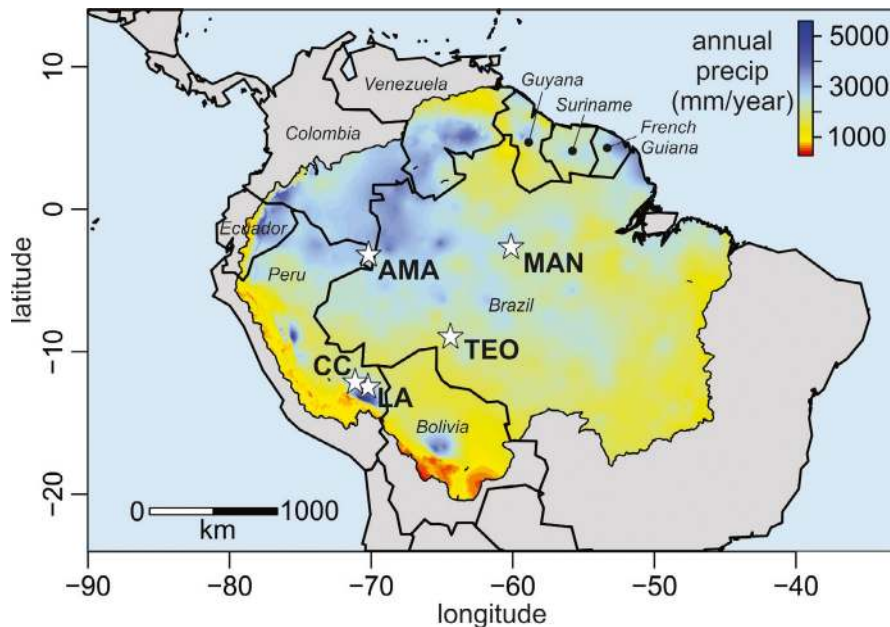


FIGURE 1 Map of Amazonia showing Amacayacu (AMA) and other sites discussed in the text. Annual precipitation for Amazonia is shown (Hijmans, Cameron, & Parra, 2005). CC, Cocha Cashu; LA, Los Amigos; MAN, Manaus; TEO, Teotônio

consists of both *terra firme* and seasonally inundated tropical forests. Amacayacu National Park receives c. 3,200 mm of rain per year, with a dry season of less than 100 mm of precipitation per month from June to September. The mean temperature is 25.8°C and does not change significantly throughout the year (Rudas Lleras, Prieto Cruz, Taylor, & Ortiz, 2005). Fire is not a natural component in this region (Bush et al., 2008), and is known to have been absent from the plot for at least 12 years (A. Duque, personal observation).

The 25-ha Amacayacu Forest Dynamics Plot (hereafter Amacayacu) (−3.8091, −70.2678) was established in 2007 as part of the Center for Tropical Forest Science—Forest Global Earth Observatory (Anderson-Teixeira et al., 2015). The Amacayacu plot was established on a transitional area between low dissected tertiary plains of the Pebas formation (Hoorn, 1994) and waterlogged soils on low terraces of the former alluvial plain. The plot is located c. 1.5 km north of the Amazon River, ranges between 88.5 and 110.9 metres above sea level, and includes a depression that remains swampy in a small portion of the plot for a few months, but not in every year. The swampy area is seasonally flooded due to the interaction of poor drainage of soils at the bottom part of internal valleys, the drainage of streamlets during the wet season, and the high seasonal level of the Amazon River's water table (Zuleta et al., 2018). The 25-ha plot has been divided in three main topographic habitats: ridges, slopes, and valleys, which represent 25.1%, 30.7%, and 44.2% of the total area, respectively (Zuleta, Duque, Cardenas, Muller-Landau, & Davies, 2017).

All woody plants with a dbh ≥ 1 cm at the 25-ha Amacayacu forest plot were tallied, mapped and identified. The plot harbors around 1,200 tree species, which makes of it one of the most diverse places on Earth (Duque et al., 2017). *Eschweilera coriacea*, *Eschweilera itayensis*, *Eschweilera rufifolia*, *Otoba glydicarpa*, *Guarea pubescens* and *Rinorea lindeniana* are important species in terms of basal area and abundance within the plot (Ellison et al., 2019). Soils in Amacayacu are acid (pH = 3.9 ± 0.1), with low contents

of phosphorous ($p = 8.9 \pm 0.1$), and low total exchangeable bases (TEB = 1.2 ± 0.5) (Zuleta et al., 2018). No known archeological sites are found within 50 km of Amacayacu. The nearest recorded archeological site is Igarapé Takana, which is 51 km away and has ^{14}C dates c. 1230 cal yr BP (Morcote-Rios, Raz, Giraldo-Cañas, Franky, & León Sicard, 2013). The first European voyage down the Amazon River by Francisco Carvajal in 1541, however, describes the chiefdom of Aparia-the-Greater (Medina, 1934). This site is c. 20–30 km upriver from the forest plot location. Amacayacu National Park is currently inhabited by the Tikuna indigenous community and the forest plot is within walking distance of the Amazon River.

In January 2018, 12 soil cores were collected around the perimeter of the 25-ha forest plot. For each core, soils were collected at 10 cm intervals to a total depth of 80 cm or groundwater level. All of the cores were analyzed for charcoal (fire history) ($N = 96$ samples), and 10 of the cores were analyzed for phytoliths (vegetation history) ($N = 80$). Within a 5-m radius of each core site, we also collected 7–10 pinch samples from the soil surface. The pinch samples were combined into one surface sample per core site ($N = 10$), and used to reflect the modern vegetation.

2.2 | Laboratory analysis

Charcoal analysis was performed on 20–50 mg of soil for all soil core samples ($N = 96$). Samples were boiled for 15 min in 3% H_2O_2 (hydrogen peroxide) followed by rinsing and sieving of the remaining material at 500 μm . Charcoal fragments were identified using an Axiophot Stereo microscope, and photographed using a Fuji camera. Image J software was used to calculate the surface area of each charcoal fragment in each samples (Abramoff, Magalhaes, & Ram, 2004). We then converted the surface area (mm^2/ml^3) of each fragment to volume (mm^3/ml^3) using Weng's (2005) equation, and derived the volume of charcoal per cubic centimeter of soil by dividing by the initial volume of the sample.



Phytoliths were prepared in using standard laboratory techniques (Piperno, 2006), using 1 cm³ of soil. We added 56,000 microspheres to each sample at the onset of processing to calculate phytolith concentration in the soils. We used H₂O₂, HCl, and KMnO₄ to remove carbonates, organic material, and humic acids. Bromoform (CHBr₃) with a specific gravity of 2.3 g/cm³ was added to the remaining sediment to separate the phytoliths and microspheres from the remaining soil material. We used Naphrax to mount the phytoliths on microscope slides. All phytoliths were identified using a Zeiss Axio Scope.A1 microscope with a 1,000× magnification in oil using differential interference contrast. Slides were counted until 200 arboreal phytoliths and a total of 300 phytoliths was reached (Aleman, Canal-Subitani, Favier, & Bremond, 2014). Counts ranged from 300 to 567 for all samples. We used Piperno (2006) for identification of grass and arboreal phytoliths. For each palm species occurring in Amacayacu, we identified the phytolith morphotypes they produce using recently published reference guides (Huisman, Raczka, & McMichael, 2018; Morcote-Ríos, Bernal, & Raz, 2016) and the phytolith reference collection at the University of Amsterdam.

2.3 | Data analysis

We dated all charcoal fragments >1 mm³. The charcoal fragments were submitted to DirectAMS (Seattle, WA, USA) for radiocarbon dating. The 'Bchron' package (Parnell, 2016) for R (R Development Core Team, 2013) was used to calibrate the radiocarbon dates using the SHCal13 calibration curve (Hogg et al., 2013), and to generate cumulative probabilities of fire events. We discuss our results in the context of ¹⁴C dated charcoal fragments documented in other forest plots (Los Amigos and Cocha Cashu in Peru, and Manaus in Brazil) (McMichael, Piperno, et al., 2012; McMichael et al., 2015; Piperno & Becker, 1996; Figure 1).

Charcoal ages do not necessarily correspond with ages of phytoliths at the same depth intervals. 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. However, direct dating of phytoliths from terrestrial soil cores such as those from other Amazonian regions indicate phytolith records span at least the past several thousand years with the oldest phytoliths usually found at the deepest depths (e.g. Piperno, McMichael, & Bush, 2015; Piperno et al., 2019).

For charcoal metrics, we calculated the total charcoal abundance per core, and the total charcoal abundance per depth interval (across the plot), though we make no assumptions that charcoal fragments found at a given depth interval are of equivalent age across the plot. For each core, we also calculated the proportion of depth intervals containing charcoal.

For phytoliths, we calculated the relative percentage of all phytolith types found within each sample at Amacayacu, and determined the phytolith morphologies for each of the palm species >1cm dbh occurring in the Amacayacu forest plot. We performed detrended correspondence analysis to look for patterns of vegetation (dis)similarity within and between depth intervals and cores. We also calculated the trends (% in uppermost sample—% in basal sample) and magnitude of change (maximum %—minimum %) of palm and arboreal phytolith types within each core (McMichael et al., 2015). We determined whether the trend and magnitude of change metrics for the phytolith types were associated with the charcoal metrics using Spearman rank correlation tests.

We also discussed the phytolith metrics in the context of those reported from the Los Amigos, Cocha Cashu, and Manaus forest plots (McMichael, Piperno, et al., 2012; McMichael et al., 2015; Piperno & Becker, 1996; Figure 1). The phytoliths from previously studied forest plots were analyzed before the characterization of specific palm morphotypes, thus we only discussed regional comparisons at the level of total palms (Arecaceae).

3 | RESULTS

3.1 | Fire history

Only seven charcoal fragments found at Amacayacu were large enough for ¹⁴C AMS dating, and these originated from three of the 12 soil cores (Table 1). The dated charcoal fragments indicated that fires occurred from 1630 to 1710 cal yr BP (calibrated years before present) at the AMA 6 site, at 1850 cal yr BP at the AMA 10 site, and at c. 2450 cal yr BP at the AMA 15 site (Table 1, Figure 2).

Charcoal fragments were found in 8 out of 12 cores and 24 out of 95 samples (Figure 2, Table S1). Abundances of charcoal within the samples ranged from 0 to 18.60 mm³ charcoal per cm³ soil. No core contained charcoal in all depth intervals, and very little charcoal was present at depths greater than 60 cm (Figure 2c). Charcoal was most abundant between depths of 10 and 40 cm (Figure 2c). Cores 15 and 6 contained most of the charcoal found within the plot, and Core 10 also had a piece large enough for ¹⁴C AMS dating

TABLE 1 Calibrated ages of ¹⁴C dates obtained from soil cores within the Amacayacu, Colombia forest plot. The dates corresponding to the highest probability were chosen as the most likely calibrated age

Core	Depth (cm)	¹⁴ C age (yr BP ±SD)	Calibrated age (cal yr BP)
AMA 6	0–10	1792 ± 32	1630
AMA 6	10–20	1833 ± 24	1710
AMA 6	20–30	1773 ± 27	1660
AMA 6	30–40	1825 ± 27	1710
AMA 10	40–50	1925 ± 28	1830
AMA 15	50–60	2467 ± 27	2460
AMA 15	50–60	2470 ± 27	2440

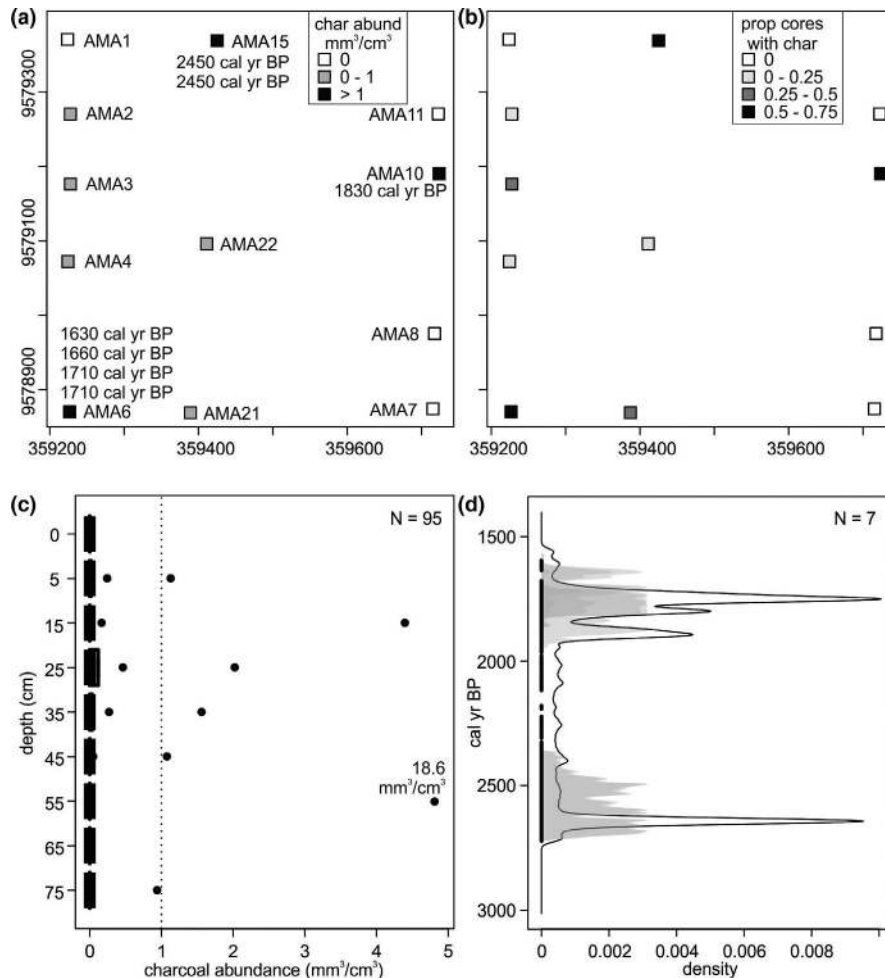


FIGURE 2 Charcoal data from the forest plot in Amacayacu, Colombia: (a) charcoal abundances per core and spatial configuration of the ¹⁴C AMS dated charcoal fragments (Table 1); (b) proportion of samples per core containing charcoal presence; (c) charcoal abundances per depth interval across the plot. The dashed vertical line indicates size limit of charcoal fragments for ¹⁴C AMS analysis—all fragments above that size were ¹⁴C AMS dated; (d) summed cumulative probability distribution of ¹⁴C AMS dated charcoal fragments. Note that ages are not inferred for undated charcoal fragments. Panels a and b are shown in UTM projected coordinate system

(Figure 2, Table S1). Another five cores contained trace amounts of charcoal, where even the combined volume of charcoal for a given depth interval was too small for ¹⁴C AMS dating (Figure 2, Table S1). Four of the 12 cores lacked any charcoal in any of the depth intervals (Figure 2, Table S1).

3.2 | Modern palms and phytoliths

Palms comprised 3.6% (5,137) of the 143,835 stems >1 cm dbh in the 25 ha Amacayacu forest plot, and 9.2% of the 14,714 stems that are >10 cm dbh. There were 16 identified palm species from 11 genera occurring within the plot (Table 2), of which 14 species are useful to humans, and six are hyperdominant (Clement et al., 2015; Henderson, Galeano-Garces, & Bernal, 1997). *Astrocaryum*, *Bactris*, *Euterpe*, *Geonoma*, *Hyospathe*, *Iriarte*, *Oenocarpus*, and *Socratea* were the most common palm genera in the plot (Table 2). Of those, *Astrocaryum*, *Euterpe*, *Iriarte*, and *Socratea* all have species that are hyperdominant (sensu ter Steege et al., 2013; Table 2). *Oenocarpus minor* was well-represented in the plot but is neither hyperdominant nor useful to people, though *Oenocarpus bataua*, an economically important species, is not abundant (Table 2).

The soil surface samples contained 12 phytolith morphotypes known to be produced by the palm species found in the plot (Table

S2), and two morphotypes that have not been identified (star palm and 'other' palm, Figures S2 and S3). *Astrocaryum*, *Bactris*, *Geonoma*, *Iriarte*, and *Socratea* were the most common genera in the plot that produce conical palm phytoliths (Table 2 and Table S2). These genera accounted for 60% of the total palm abundance in the plot. *Euterpe*, *Oenocarpus*, and *Hyospathe* were the most common genera that produce globular echinate palm phytoliths (Tables 2 and Table S2), and composed about 40% of the total palm individuals in the plot. Only *Euterpe precatatoria* produced globular granulate phytoliths, and only *Geonoma* produced Conical Variant 4 phytoliths, making those morphotypes diagnostic to specific taxa.

3.3 | Vegetation change at Amacayacu

We identified 23 total phytolith morphotypes within the soil samples, including six arboreal, 14 palm, and four grass morphotypes. No evidence of maize or squash cultivation was found in any of the samples. *Heliconia* phytoliths, which also indicate an open canopy, were absent in all samples. Samples were dominated by arboreal morphotypes (78.3% ± 12.7%), and only 8 of 91 samples contained any grass phytoliths (Figure 3). When grass phytoliths occurred in a sample, they never exceeded 1.3% of the total assemblage, indicating no significant forest clearing.



TABLE 2 Palm species occurring in the 25 ha Amacayacu research plot. Columns indicate whether the species is hyperdominant (HD) (ter Steege et al., 2013) or reported as being useful to people (X is from Clement et al., 2015, X* is from Henderson et al., 2006). The abundance of individuals >2 cm dbh within the plot, the percentage of total individuals within the plot >2 cm dbh, and whether the species produces phytoliths within the general conical or echinate groups (see further details on phytolith classifications in Table S2) are also shown

Species	HD	Useful	Abundance	Percent total	Conical	Echinate
<i>Astrocaryum ferrugineum</i>	X	X	590	0.410	X	
<i>Attalea butyracea</i>	X	X*	11	0.008		
<i>Bactris concinna</i>		X*	3	0.002	X	
<i>Bactris maraja</i>		X*	865	0.601	X	
<i>Bactris simplicifrons</i>			15	0.010	X	
<i>Bactris unknown sp</i>			68	0.047	X	
<i>Chamaedorea pinnatifrons</i>		X*	10	0.007	X	
<i>Desmoncus giganteus</i>		X*	1	0.001	X	
<i>Euterpe precatoria</i>	X	X*	540	0.375		X
<i>Geonoma deversa</i>		X*	722	0.502	X	
<i>Geonoma maxima</i>		X*	38	0.026	X	
<i>Geonoma stricta</i>		X*	41	0.029	X	
<i>Geonoma unknown sp</i>			92	0.064	X	
<i>Hyospathe elegans</i>		X*	857	0.596		X
<i>Iriartea deltoidea</i>	X	X*	452	0.314	X	
<i>Oenocarpus bataua</i>	X	X*	4	0.003		X
<i>Oenocarpus minor</i>			521	0.362		X
<i>Socratea exorrhiza</i>	X	X*	307	0.213	X	
Total			5,137	3.571		

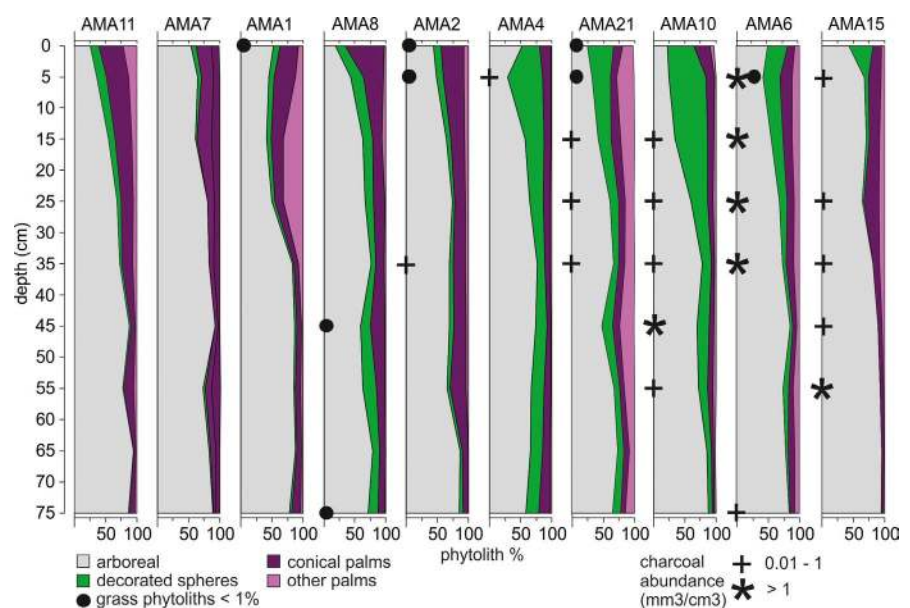


FIGURE 3 Stratigraphic diagram of arboreal, palm, and grass phytoliths found in the ten soil cores analyzed from the Amacayacu forest plot in Colombia

All 10 cores contained >75% rugose sphere (arboreal) phytoliths (Figure S4) at depths below 40 cm (Figure 3). These are produced in a limited number of woody species, including members of Acanthaceae, Burseraceae, Chrysobalanaceae, Euphorbiaceae, and Moraceae. The Chrysobalanaceae produce by far more of these types than other families, where they are found in small numbers in a few species. Eight of the 12 cores analyzed for phytoliths contained increased conical palm abundances in the upper 20 cm of soils compared with lower depths (Figure 3). The globular echinate or other non-conical phytoliths ('other palms' in Figure 3) do not increase through time like the conical palm phytoliths. The detrended correspondence analysis indicated that overall palm abundance and composition were the main drivers of variation among phytolith samples in all cores (Figure S1). Samples in the upper depth intervals that had higher palm abundances clustered on the positive end of DCA Axis 1, whereas samples deeper in the cores that had lower palm abundances and higher percentages of arboreal taxa were clustered on the negative end (Figure S1).

Eight of the 10 soil cores also showed increases in decorated sphere phytoliths in the upper portions of the cores compared with the deeper portions (Figure 3 and Figure S1). Decorated sphere phytoliths are a type of arboreal taxa (Figure S5), and indicated a change in the composition of trees towards the present. Samples with high abundances of decorated spheres trended towards the negative end of DCA Axis 2, and those samples also had high abundances of globular echinate variant 1 (GE var 1), conical with basal projections (conical var 4), and large globular echinate with short projections (GE var 4; Figure S1). Another forest phytolith type, Annonaceae, was also found in samples with high palm abundances on the positive side of DCA Axis 1. The Annonaceae were also on the positive side of DCA Axis 2, and were associated with the conical palms, reniform echinate palms, and several types of globular echinate palm phytoliths (Figure S1).

The within-core trend and magnitude of change metrics agreed with the DCA. Trend values indicated that arboreal phytolith types (rugose spheres) decreased through time, from 5% (AMA4) to 70% (AMA10; Figure 4). Decorated spheres, however, increased towards the modern time in nine out of 10 soil cores (Figure 3 and Figure S1). Trend values of decorated spheres were almost twice as high in AMA21, AMA10, AMA6, and AMA15 compared with the other cores that contained little to no charcoal (Figure 4). Trend values also indicated that palms producing globular echinate phytoliths and conical phytoliths increased in frequency towards the present day in 9 out of 10 soil cores. Trends seen in the conical palm phytoliths, however, were of a larger magnitude than in the globular echinate phytoliths (Figure 4).

The magnitude of change values for the soil cores collected at Amacayacu were also large, and because grasses never exceeded 1.3% of the assemblage, shifts occurred basically between arboreal and palm taxa. Magnitude of change values for rugose spheres ranged from 40% to 70% (Figure 4b). The values for decorated spheres were >25% in cores AMA4, AMA21, AMA10, AMA6, and AMA15, and were <17% in all other cores that contained less

charcoal. The magnitude of change values for the globular echinate and conical palm phytoliths ranged from 10% to 60% (Figure 4). The magnitude of change values, like the trend of change values, were higher in the conical palm phytoliths compared with the globular echinate palm phytoliths.

The Spearman Rank correlation tests indicated that the trend values for conical phytoliths and globular echinate phytoliths were not associated with charcoal abundances or with the proportion of samples per core containing charcoal (Table 3). The trend values for decorated spheres (Figure 4 and Figure S5), which reflect arboreal taxa, were significantly and positively correlated with charcoal abundance and the number of samples per core containing charcoal (Table 3). The magnitude of change values were also significantly and negatively correlated for decorated spheres and all (total) palms, though significance was not seen in the individual palm groups (Table 3).

4 | DISCUSSION

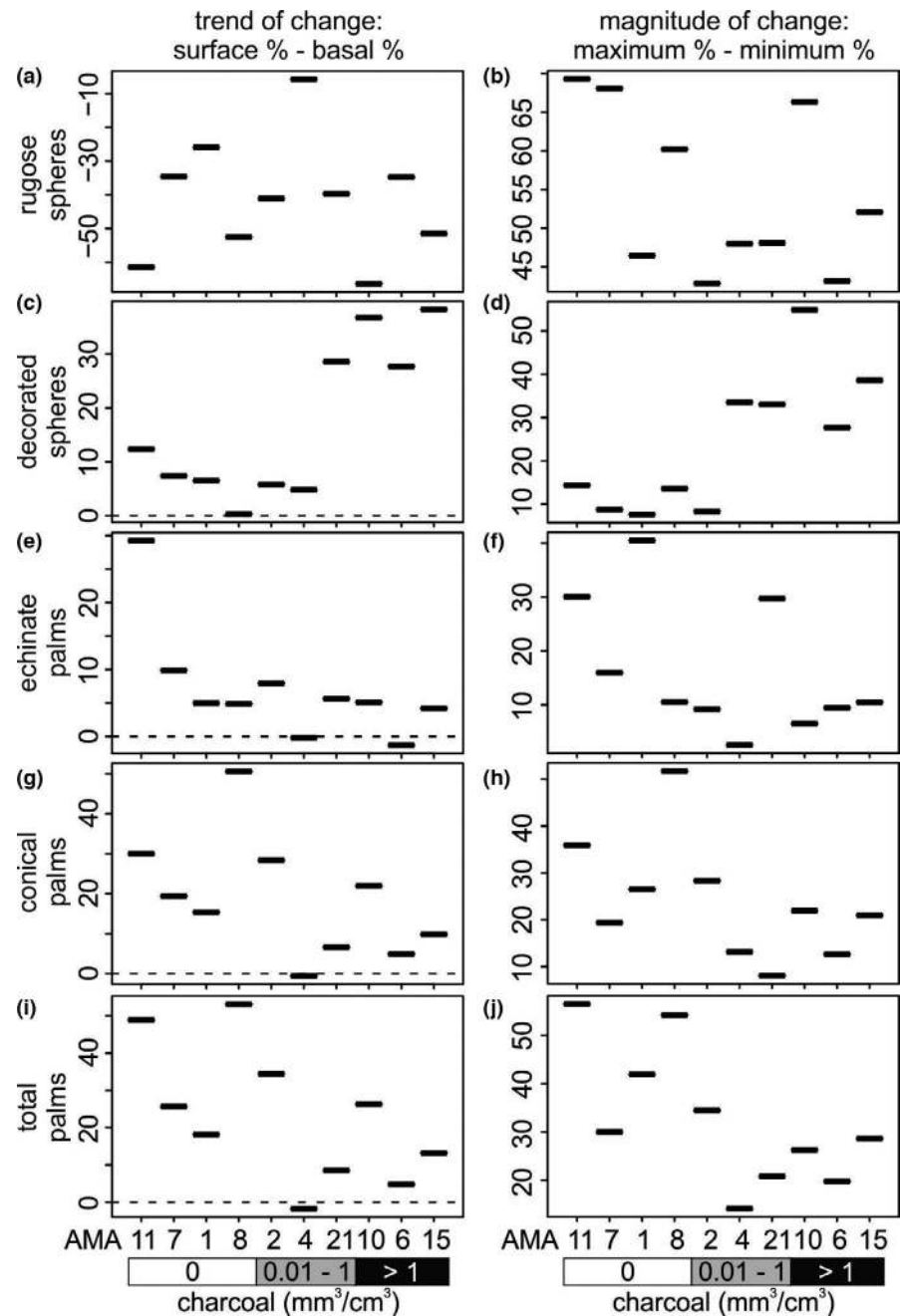
4.1 | The history of Amacayacu

We made every attempt to date the most recent fire possible at Amacayacu, and we dated every fragment of charcoal recovered that was large enough for ^{14}C AMS analysis. Our data suggest that the Amacayacu forest plot has not burned since 1630 cal yr BP (Table 1). The fires from 1630 to 1710 cal yr BP did not spread through the entire plot, and earlier fires at 1830 cal yr BP and 2450 cal yr BP were also localized across the plot (Figure 2). We do not infer any age-depth relationships for charcoal; however, several patterns are evident in our dataset. The most recent fires of 1630–1710 cal yr BP were recorded from site AMA6. Evidence of these fires was consistent in the upper 40 cm of soils (Table 1), indicating differential percolation rates through the upper soil layers. Dated charcoal fragments from deeper layers of soils (i.e. 40–60 cm) were consistently older and stratigraphically intact (Table 1). Although the stratigraphy of soils is always coarser than lake sediments, we do not believe bioturbation was problematic in our assessments because of arrangement of charcoal dates (Table 1), and distinct changes of phytolith assemblages noted between depth intervals of the soil cores (Figure 3).

Humans were the likely ignition source of the fires occurring at Amacayacu. Fire rarely if ever occurs without a human ignition source in the aseasonal forests of Amazonia (Bush et al., 2008; Malhi et al., 2008), including areas such as Amacayacu (Figure 1). Further, isotopic records from stalagmites indicate that the last 4,000 years, which encompasses the period of fires at Amacayacu, was the wettest period of the Holocene in western Amazonia (van Breukelen, Vonhof, Hellstrom, Wester, & Kroon, 2008). The frequency of ^{14}C dated archaeological material from Amazonian Dark Earths (Glaser & Birk, 2012; Glaser & Woods, 2004) and geoglyphs (Pärssinen, Ranzi, Saunaluoma, & Siirinen, 2003; Ranzi, Feres, & Brown, 2007; Schaan et al., 2012), and ^{14}C dated soil charcoal fragments, has increased since 2500 cal yr BP in Amazonia (McMichael & Bush, 2019).



FIGURE 4 Trend of change and magnitude of change metrics for phytoliths from ten soil cores collected at Amacayacu forest plot. Soil cores are ordered from those containing no charcoal (left side) to those containing the highest amounts of charcoal (right side) (see Table S1 for details)



Although the fire events likely originated from some type of human source, there was no evidence of past agriculture or canopy openings in the Amacayacu forest plot. Grass phytoliths were found in only four of eight soil cores despite counts of over 300 phytoliths per sample, and grass abundances never exceeded 1.3% (Figure 3). These combined results indicated that the forest canopy was not opened during the fire events, or at all during the last 5,000–7,000 years of the Holocene, which is the time period usually captured with phytoliths in Amazonian soil cores collected to 1 m in depth (McMichael, Piperno, et al., 2012; Piperno et al., 2015).

Even though the canopy at Amacayacu has not been opened on significant spatial scales (i.e. >100s of meters) for the last several thousand years, the composition of the forest has changed (Figures

3 and 4). The changes in forest composition happen in both the presence and absence of fire, but their trajectories of change differ. The cores containing charcoal had larger increases in decorated sphere phytoliths through time than those that lacked charcoal (Figures 3 and 4). Decorated sphere phytoliths have several types of surface patterns (e.g. Figure S5), and our ongoing work is aiming to categorize them into discrete types and link them with specific taxa. What is known is that the decorated spheres are primarily produced by arboreal taxa (D. R. Piperno, personal observation). The increases in decorated spheres over the mid- to late-Holocene could thus be either from compositional changes in the canopy or understory trees.

The soil cores that contained the largest increases in palm abundances were the ones that lacked charcoal (Figures 2–4). These

	Charcoal abundance			Proportion of samples with charcoal		
	Rho	S	p	Rho	S	p
Trends of change						
Decorated spheres	0.71	48.41	.02	0.70	49.63	.02
Echinate palms	-0.48	244.45	.16	-0.49	245.76	.15
Conical palms	-0.49	246.51	.15	-0.51	248.90	.13
Total palms	-0.49	246.51	.15	-0.51	248.90	.13
Magnitude of change						
Decorated spheres	0.69	51.51	.03	0.75	41.24	.01
Echinate palms	-0.52	250.64	.12	-0.58	260.44	.08
Conical palms	-0.52	250.64	.12	-0.55	255.20	.10
Total palms	-0.65	272.30	.04	-0.71	282.47	.02

TABLE 3 Spearman correlation tests between charcoal metrics and phytolith metrics measured in the ten soil cores from Amacayacu forest plot. Rho represents Spearman's rho and S represents the test statistic (sum of all squared rank differences)

data suggest that genera producing conical phytoliths, such as *Astrocaryum*, *Bactris*, *Geonoma*, *Iriarte*, and *Socratea*, have all increased at Amacayacu during the Holocene in the absence of fire. These data also corroborate previous findings from lake sediment records that show *Iriarte* pollen increased in abundance over the last 2,500 years, and did so with a greater magnitude when human influence (i.e. fire or cultivation) was absent or minimal (Bush & McMichael, 2016). The abundance of globular echinate palms increased at eight of the ten soil cores, though had lower trend and magnitude of change values than the conical palm phytoliths (Figures 3 and 4). These data suggest that genera such as *Euterpe*, *Oenocarpus*, and *Hyospathe* have been present in the Holocene landscape around Amacayacu in similar abundances as they are found today, though small increases in abundances were found in cores AMA11, AMA7, and AMA1. Like the conical palm phytoliths, the cores with increasing levels of globular echinate palms had little to no charcoal (Figure 3), even though Spearman correlation tests were non-significant (Table 3). Because the palms do not seem to be associated with the fire events, and there is no other evidence for canopy openings or cultivation of crops, it is unlikely that the changes in palm abundances were a result of direct human activity at Amacayacu. Therefore, as in other Amazonian regions studied using improved palm identification criteria (Piperno et al., 2019), prehistoric human influences do not appear to have caused increases in now-hyperdominant palm taxa such as *Oenocarpus* and *Euterpe*.

It is also interesting to note that the Annonaceae phytoliths occurred in samples containing high abundances of conical palm phytoliths (Figure S1). *Guatteria*, *Unonopsis*, and *Oxandra* are the genera of Annonaceae that produce the diagnostic phytoliths seen in our samples (Piperno, 2006; Piperno et al., 2019). These genera rarely contain species that are useful to people (sensu Clement et al., 2015; Levis et al., 2017; Levis et al., 2018). The co-occurrence of these Annonaceae phytoliths alongside the increasing palm phytoliths further suggests that these changes in the forests at Amacayacu were not a direct result of human action.

Hunting, which usually extends several kilometers away from an occupation site (Peres, 2000; Peres, Emilio, Schietti, Desmoulière, &

Levi, 2016), affects the seed dispersal and predation of many palms (Wright & Duber, 2001; Wright et al., 2000; Wyatt & Silman, 2004). If seed dispersers are lost due to hunting pressure, then local palm abundances may decrease. If seed predators are lost, palm abundances may increase, despite the loss of seed dispersers (Wright & Duber, 2001; Wright et al., 2000). For people living without guns, which would have been the case in pre-Columbian times, the sphere of influence for hunting can be 10–15 km (Bush et al., 2015; Peres, 2000). The nearest known archaeological site is Igarapé Takana (Morcote-Rios et al., 2013), located 51 km from Amacayacu, outside of the known sphere of influence. The forest plot, however, is located only c. 1.5 km north of the main Amazon River channel. The pre-Columbian chiefdom of Aparia-the-Great, which was described in the earliest European account (Medina, 1934), likely lies somewhere between 20 and 30 km away from Amacayacu and was also on the Amazon River channel. Thus, it may be possible that indirect pre-Columbian human influence affected the palm abundances in Amacayacu.

4.2 | Regional trends of fire and vegetation change in western Amazonia

Besides Amacayacu, there are only three other records of fire and vegetation history from within the western Amazonian forest plots that are used to estimate biodiversity and carbon storage. The Los Amigos and Cocha Cashu forest plots are located within 160 km of each other in south-western Amazonia, and the Manaus forest plot (KM 41) is located in the central Amazon north of the main river channel (Figure 1). All four plots show fire activity primarily during the last 3,000 years (Figure 5), a period of climatic wetness in western Amazonia (van Breukelen et al., 2008). The timings of these past fire events across the four plots are coincident with: (a) an increase in archaeological site density across Amazonia (McMichael & Bush, 2019), (b) the trans-Amazon transition to agriculture (Piperno, 2011), and (c) an increase in archaeological site density across the entirety of South America (Goldberg, Mychajliw, & Hadly, 2016). Thus it is likely that the fires

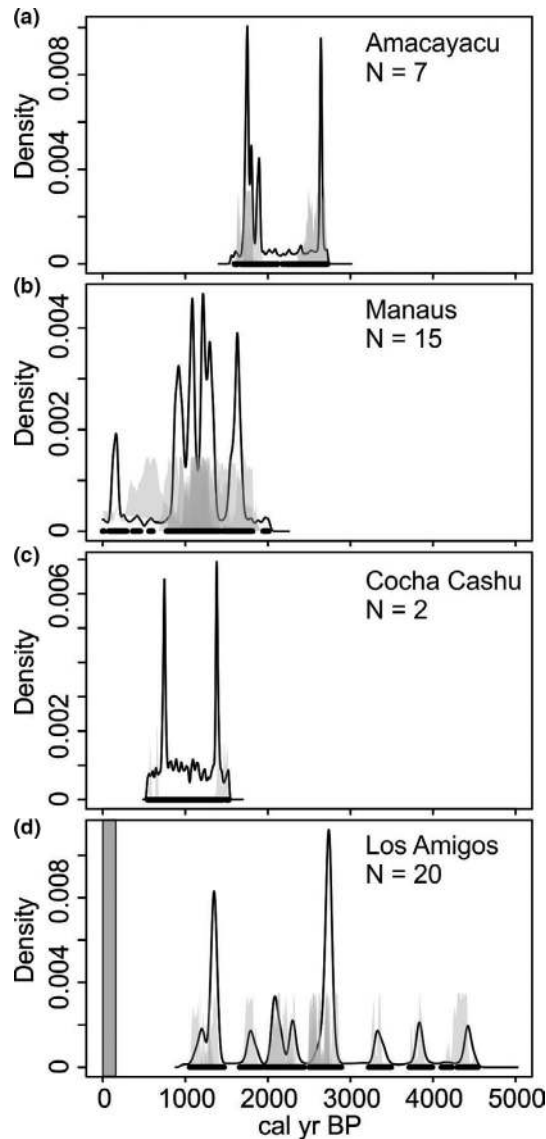


FIGURE 5 Comparison of fire history based on dated ^{14}C charcoal fragments from (a) Amacayacu, (b) Manaus, (c) Cocha Cashu, and (d) Los Amigos forest plots in Amazonia. See Figure 1 for plot locations

documented at the four forest plots were of human origin. Over the last 3,000 years, however, fire has occurred less frequently at Amacayacu and Cocha Cashu than at Manaus and Los Amigos

(Figure 5; McMichael, Correa Metrio, & Bush, 2012; McMichael et al., 2015; Piperno & Becker, 1996). The Amacayacu forest plot has also experienced a longer fire-free interval than any of the other plots surveyed.

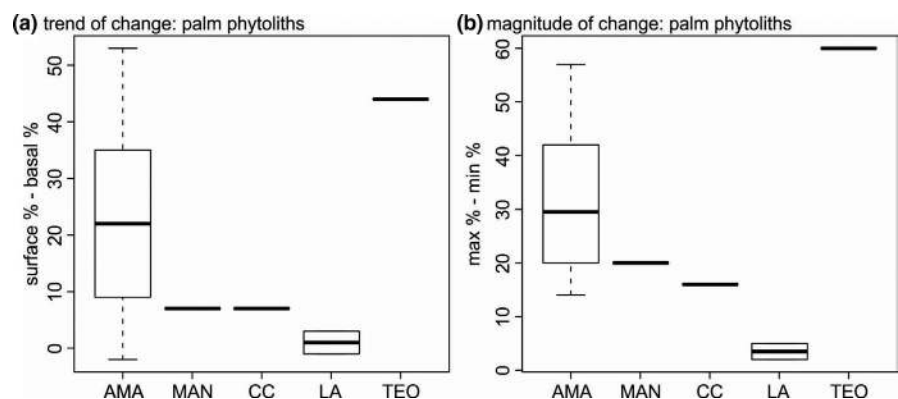
Though the four plots differ in their time since the last fire and their fire return interval (Figure 5), there are some similarities in their vegetation histories. Phytolith data from all four plots lack evidence of past maize, squash, or rice cultivation (McMichael et al., 2015; Piperno & Becker, 1996). The phytolith assemblages from Los Amigos and Manaus, however, which have more recent and frequent fire, contain evidence of localized and short-lived canopy openings that occurred in the past (McMichael, Piperno, et al., 2012; Piperno & Becker, 1996). Amacayacu and Cocha Cashu contain no evidence of past forest openings (Figure 3; McMichael et al., 2015).

Increases in palm abundances through time (trend of change values) were seen in all four plots, though to a much less degree at Los Amigos (Figure 6). The trend of change values, and the overall fluctuations in palm abundance (magnitude of change values), were significantly higher at Amacayacu compared with the other forest plots, and nearly reached levels documented at an excavated archaeological site in the Teotônio region of Brazil (Figures 1 and 6). In contrast to Amacayacu, however, the Teotônio site has been occupied for 2,000 years, and contains evidence of pottery, soil modifications, recurrent fires, maize cultivation, and palm cultivation (Almeida & Neves, 2014; McMichael et al., 2015; Watling et al., 2018).

4.3 | The rise of Amazonian palms

The synthesized data across the four forest plots and the Teotônio archaeological site show an overall increase in palms through time (Figure 6), but the mechanisms driving those increases vary between regions, and are not dependent on human intervention. At Teotônio, people cultivated palms. In places where past human influence is minimal, such as the forest plots, wetter conditions in Amazonia during the last 4,000 years (van Breukelen et al., 2008) would have also allowed palm genera such as *Iriarte*, *Socratea*, *Astrocaryum*, *Bactris*, and *Geonoma* to increase their abundance (Figures 3 and 4). The increases in palm abundances documented

FIGURE 6 Trend of change and magnitude of change values for palm phytoliths across four forest plots and an archaeological site in western Amazonia. Palm phytolith abundances and metrics are shown for the Amacayacu (AMA), Manaus (MAN), Los Amigos (LA), and Cocha Cashu (CC) forest plots, and are compared with the Teotônio archaeological site (TEO) (Figure 1)



within the forest plots are highest in north-western Amazonia compared with the south-western and central regions (Figures 1 and 6). This is the most aseasonal setting of all plots surveyed, and has the lowest levels of fire. These patterns mirror the variation observed in *Iriarte* pollen records across western Amazonia (Bush & McMichael, 2016), collectively suggesting that changes in precipitation and seasonality have had marked effects on the distribution and relative abundances of Amazonian palms in the Holocene.

The palms are a major component of the modern hyperdominant species pool (ter Steege et al., 2013), meaning that they are among the most abundant trees in the Amazonian forest. Palm percentages range from 1% to 25% of all stems >10 cm dbh from the four forest plots where we have data on fire and vegetation histories (Amacayacu, Los Amigos, Cocha Cashu, and Manaus) (Lopez-Gonzalez, Lewis, Burkitt, Baker, & Phillips, 2009; Lopez-Gonzalez, Lewis, Burkitt, & Phillips, 2011). Palm percentages are lowest in the Los Amigos plot (c. 1%), which has the most intensive and recurrent fire history. Palm percentages range from 10% to 25% in the other three plots that have not experienced recent or recurrent fire events. Our results suggest that palms, which have been present in Amazonian forests for millions of years (e.g. Couvreur & Baker, 2013; Janssen & Bremer, 2004; Roncal et al., 2015), have increased in relative abundances, including in sites that lack recent or recurrent fire or evidence of past forest clearing (Figures 3, 4, and 6). Though likely largely climate-driven, three of the four forest plots are located within a day's walk of a major river, it is possible that people increased palm abundances by dropping seeds as they passed through. Regardless of the mechanisms driving the 'rise of palms' in the Holocene, the exact timings remain unknown, though phytoliths found in the upper 1 m of soil usually date to the mid- or late-Holocene, e.g. the last 6,000–5,000 years (Piperno et al., 2015, 2019). The rise of the palms in Amazonia also continues in the modern era. *Astrocaryum* has increased its range size in a 'colonization front' in recent decades (Charles-Dominique et al., 2003), though the mechanisms driving this expansion remain unclear.

Amazonian forests contain up to 17% of all the carbon in the terrestrial biosphere (Feldpausch et al., 2012; Zhao & Running, 2010). The rise of the palms seen in our datasets suggests that this carbon storage potential may have changed over time. Palms are one of the most abundant plant groups in Amazonia, yet their contribution to aboveground biomass and primary productivity in the modern system remain poorly understood (Goodman et al., 2013). The long-term increases in palm abundances seen in the phytolith records from the north-western Amazonian forests at Amacayacu could reflect changes in carbon storage in two ways. One possibility is that the canopy components of the forests (both palms and arboreal taxa) have remained relatively stable through time, and the palm phytolith increases represent a change in the mid- to late-Holocene understory density. An alternative, however, is that the relative abundances of larger canopy palms have significantly increased over the last few thousand

years while the abundances of arboreal taxa (large trees) have decreased. Both of these scenarios suggest that carbon storage potential has changed over the last few thousand years. Further empirical data in both modern and past contexts are needed to test these ideas and begin assessing long-term patterns of carbon dynamics in Amazonian forests.

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DATA AVAILABILITY STATEMENT

Upon publication all charcoal and phytolith data will be uploaded to DataDryad.

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ORCID

Britte M. Heijink  <https://orcid.org/0000-0001-7359-5023>

Crystal N. H. McMichael  <https://orcid.org/0000-0002-1064-1499>

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BIOSKETCH

Britte M. Heijink is a MSc student in the Ecology & Evolution Program in the Institute for Biodiversity and Ecosystem Dynamics at the University of Amsterdam. Her primary research interests are palaeoecology and tropical ecology, and this work was part of an ongoing project to reconstruct fire and vegetation histories within Amazonian forest plots led by Crystal McMichael (CNHM).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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