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Quantifying local-scale changes in Amazonian forest cover using phytoliths

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Abstract

The ecosystem services and immense biodiversity of Amazon rainforests are threatened by deforestation and forest degradation. A key goal of modern archaeology and paleoecology in Amazonia is to establish the extent and duration of past forest disturbance by humans. Fossil phytoliths are an established proxy to identify the duration of disturbance in lake sedimentary and soil archives. What is not known, is the spatial scale of such forest disturbances when identified by phytoliths. Here we use phytolith assemblages to detect local-scale forest openings, provide an estimate of extent, and consider long-term forest recovery. We use modern phytolith assemblages of 50 Amazonian lakes to i) assess how phytolith assemblages vary across forest cover at 5 spatial scales (100 m, 200 m, 500 m, 1 km, 2 km), ii) model which phytolith morphotypes can accurately predict forest cover at 5 spatial scales, and iii) compare phytoliths with pollen to quantify their relative ability to detect forest cover changes. DCA results show phytolith assemblages could be used to differentiate low, intermediate, and high forest cover values, but not to distinguish between biogeographical gradients across Amazonia. Beta regression models show Poaceae phytoliths can accurately predict forest cover within 200 m of Amazonian lakes. This modern calibration dataset can be used to make quantitative reconstructions of forest cover changes in Amazonia, to generate novel insights into long-term forest recovery. Combining phytoliths and pollen provides a unique opportunity to make qualitative and quantitative reconstructions of past vegetation changes, to better understand how human activities, environmental and climatic changes have shaped modern Amazonian forests.

Highlights

- Beta regression models at 5 spatial scales show that Poaceae grass phytoliths are a reliable predictor of forest cover within 200 meters of Amazonian lakes
- Phytoliths reflect local scale forest cover whereas pollen reflects biogeographical gradients and forest cover at larger spatial scales
- Our modern calibration dataset can be used to quantify past forest cover changes in Amazonia (to research long-term forest recovery)

Keywords: Amazon, beta regression, forest cover, landscape reconstruction, palaeoecology, phytoliths

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Introduction

Amazonia supports the largest remaining rainforest in the world and therefore plays an important role in global terrestrial carbon uptake and harbors a rich biodiversity (Hubau et al. 2020, Myers et al. 2000, Phillips and Brienen 2017, Santoro et al. 2020). High deforestation rates, however, threaten Amazonian rainforests (Gatti et al. 2021, Mitchard, 2018). While forest recovery will be crucial for mitigating global climate change and preserving ecosystem functions, the best practices for forest restoration remain uncertain (da Cruz et al. 2021). An understanding of past disturbances informs present day management decisions and frames current scientific discourse. Palaeoecology provides insight into long-term (>100 years) forest recovery, while taking life-history into account (Åkesson et al. 2023, 2021, Bush and Colinvaux 1988, Cole et al. 2014, Loughlin et al. 2018), and therefore offers unique insights that supplement those of modern ecological studies (Poorter et al. 2021, 2016).

Palaeoecological studies are increasingly performed with phytoliths, which are inorganic silica structures inside the vegetative and reproductive tissues of plants that can be preserved in soils and sediments after plants decay (Piperno, 2006). Phytoliths are a useful proxy to detect human disturbances in forested settings (Åkesson et al. 2021, Piperno, 1990, Piperno et al. 2021, Watling et al. 2023). In Amazonia, phytolith research (Åkesson et al. 2021) reflects that successional trajectories can be similar in the short-term (20 years), but different species compositions may establish after 50-100 years of recovery, depending on the type, intensity, or frequency of the disturbance (Fernandes Neto et al. 2019, Moran et al. 2000, Uhl et al. 1988). Repeated disturbances may result in persistent vegetation changes (Chazdon, 2003, Fernandes Neto et al. 2019, McMichael, 2021, McMichael et al. 2022, Rappaport et al. 2018). Several Amazonian forests still bear the marks of human activities from the pre-contact period (prior to 1492 CE) because the vegetation is enriched with useful plant species (Bodin et al. 2020, Maezumi et al. 2018).

Unlike fossil pollen, the highest taxonomic resolution in phytoliths is among monocotyledonous taxa. Phytoliths are produced in abundance by several cultivars (maize, banana, squash), grasses and palms, making them a promising tool to detect cultivation practices and palm enrichment or depletion (Iriarte, 2003, Morcote-Ríos et al. 2016, Piperno, 2009, Piperno et al. 1985). The low taxonomic resolution of dicotyledonous arboreal phytoliths prevents the reconstruction of forest composition changes (Watling et al. 2016), but biomass and tree cover density can be detected using phytolith analysis (Bremond et al. 2005, Witteveen et al. 2023).

Although phytoliths can be recovered from fossil teeth (Ciochon et al. 1990), ceramics (Piperno et al. 1985, Saul et al. 2013), and soils (Astudillo, 2018, Crifò and Strömberg 2020, Hill et al. 2023, Iriarte et al. 2010, McMichael et al. 2015, Piperno and Becker 1996), lake sedimentary archives offer the best temporal resolution, and hence the best opportunity to study the trajectories of ecological processes (Åkesson et al. 2023, Neumann et al. 2009, Paduano et al. 2003). Lake sediments also allow high temporal resolution reconstructions using color (Moy et al. 2002), X-Ray Florescence (SS) (Morlock et al. 2021) and other biological proxies, e.g., pollen, diatoms and Non-pollen palynomorphs (Bush and Colinvaux, 1988, Loughlin et al. 2021, Miras et al. 2015) that provide holistic views of paleoenvironments and landscapes (Åkesson et al. 2023, Carson et al. 2015, Neumann et al. 2009, Raj et al. 2015).

Recently, models have been developed to quantify past forest cover changes around Amazonian lakes using the abundance of Poaceae pollen (Blaus et al. 2023, Whitney et al. 2019). In flooded savannas, Whitney et al. found long-distance transport of pollen, making spatial analyses problematic. However, in closed forest setting Poaceae pollen is seen to be an accurate predictor of even small-scale forest clearance within one km of a lake (Blaus et al 2023). Because phytoliths are not adapted to transportation, and tend to fall close to the parent plant, i.e. leaf and branch fall (Piperno, 2006, Strömberg et al. 2018), they often provide an even more local signal of the vegetation than pollen (Plumpton et al. 2019). Combining pollen and phytoliths in a multiproxy approach to quantify deforested landscapes in Amazon would thus provide a new level of detail in vegetation disturbance reconstructions.

Phytolith transportation and deposition determine the spatial scale of the relationship between phytolith assemblages and the surrounding vegetation (Aleman et al. 2014, Piperno 2006, Plumpton et al. 2019). Phytoliths are transported and deposited into lake sediments via rivers, runoff, and to a lesser extent through aerial transport (Aleman et al. 2014). Vegetation type can also determine the spatial signal, because open habitats allow the aerial transportation of (burnt) phytoliths but closed-canopy settings may hamper it (Aleman et al. 2014). Therefore, biogeographical gradients in Amazon may affect the relationship between phytolith assemblages and forest cover, through different forest types (Oliveira-Filho et al. 2021, Stropp et al. 2009, Ter Steege et al. 2006). The effect of nearby vegetation on the spatial signal of phytolith assemblages from lake sediments, however, has never been studied in Amazonia.

Here we assess if phytolith assemblages vary across biogeographic gradients within Amazonia and can detect local-scale forest openings, to begin quantifying long-term forest recovery. We use modern phytolith assemblages of 50 Amazonian lakes to i) assess how phytolith assemblages vary across forest cover at 5 spatial scales (100 m, 200 m, 500 m, 1 km, 2 km), ii) model which phytolith morphotypes can accurately predict forest cover at 5 spatial scales, and iii) compare phytoliths with pollen in their ability to quantify forest cover changes to assess how a multiproxy approach can be used to quantify forest recovery through time.

Materials & Methods

Site description

A total of 50 lakes in the Amazon basin (Eva et al. 2005) were used to calibrate phytolith assemblages to forest cover changes. Sediment samples were collected with a Universal corer or Colinvaux-Vohnout

piston corer (Table S1) (more details can be found in Blaus et al. 2023, Bush et al. 2021). Sites were divided into biogeographical regions: northwestern (NW), southwestern (SW), East, (Gentry 1988, Ter Steege et al. 2013, 2000) and savanna (located in Roraima, Brazil) (Blaus et al. 2023). Sampling sites included permanent lakes, floodplains, and oxbow lakes (Table S1) and the surrounding vegetation included evergreen tropical rainforests (n=41) and savannas (n=9) (Fig. 1). Mean annual temperature, mean annual precipitation, and dry quarter precipitation were derived from CHELSA (at 30 arc sec, ~1 km resolution), using climatological data from 1981-2010 (Karger et al. 2017). Digital elevation models from Shuttle Radar Topography Mission (SRTM) data were used to generate elevation data at 1 km resolution (Jarvis et al. 2008). All sites were in the lowlands (0 to 180 meters above sea level), with a mean temperature between 25-27 °C. Annual precipitation ranged between 600 and 2200 mm, with the highest precipitation ranges in northwestern (NW) Amazon and the lowest in the savanna sites. Seasonality was lowest in NW Amazon and highest in the savanna sites.

Data preparation

From each of the 50 lakes, 0.5 or 1 cm^3 of sediment was subsampled from the top (0-1 cm) of the sediment core and prepared for phytolith analysis. Organic material was removed by boiling the samples four times in 33% H_2O_2. After the third and fourth time, 10% HCl and $KMnO_4$ were added, respectively. Clay was removed by decanting the samples. After washing the samples with ethanol, Bromoform (specific gravity 2.3) was added to extract the phytoliths from the sediment. Finally, phytoliths were mounted on slides using Naphrax. Phytolith slides were counted and identified at 630x-1000X magnification with a Zeiss Axioscope 5, using the latest literature and nomenclature (Collura and Neumann, 2017, Huisman et al. 2018, Morcote-Ríos et al. 2016, Neumann et al. 2019, Piperno 2006, Piperno and McMichael, 2023, 2020, Witteveen et al. 2022). The phytolith sum varied between 233-744 total phytoliths and included a minimum of 200 arboreal phytoliths for forested sites or 200 non-grass phytoliths for savanna sites.

Forest cover was calculated using the Global Forest Change v1.8 database that contains pixels with percentages of forest cover (from 0% to 100%) (Hansen et al. 2013). In this spatial data product, pixels were classified as forested, if canopy heigh exceeded 5 m, based on Landsat satellite imagery with a spatial resolution of 30 m (Hansen et al. 2013). Using this database, forest cover was calculated for 5 buffers (100 m, 200 m, 500 m, 1 km, 2 km) around the perimeter of each of the 50 lakes using Google Earth Engine (Gorelick et al. 2017). Lake perimeters were defined using the JRC Global Surface Water Mapping Layers v1.3 (Pekel et al. 2016), lake water bodies were delineated, and these pixels were summed and masked from further analyses. Pixels > 40% water were classified as water/lake pixels. Next, other pixels in each buffer were classified as forest or non-forest, with pixels containing > 50% of forest cover classified as forested. Because the forest cover

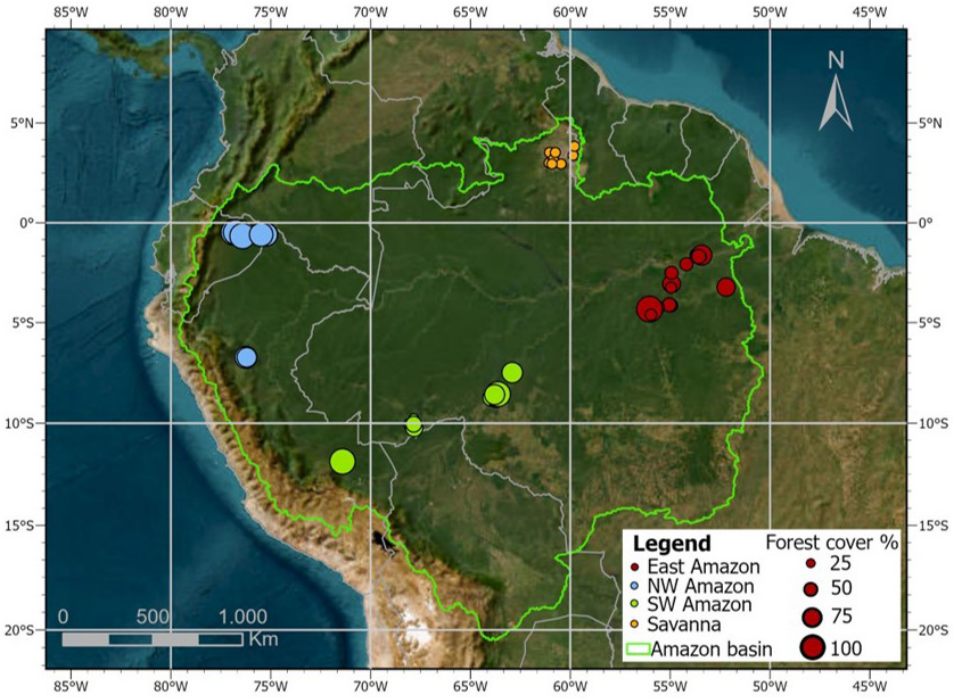

Figure 1. Map of the Amazon basin (Eva et al. 2005) containing the 50 lakes used to calibrate phytolith assemblages with forest cover. Sites are color-coded by biogeographic region and symbol size reflects the forest cover (%) within 200 m of each lake. NW = northwestern, SW = southwestern

dataset is based on 2000 CE, the forest cover loss from 2000 to 2019 CE was summed and subtracted from the forest cover dataset to obtain the number of forested pixels representative of 2019 CE, when most lakes were sampled for phytoliths. Finally, the proportion of forest cover was calculated by dividing the forested pixels by the total number of pixels in each buffer (excluding the lake water bodies).

Data analysis

Phytoliths were grouped according to morphotype or taxonomic group (Table S2). Detrended Correspondence Analysis (DCA) was used to assess the major (dis)similarity between samples, using phytolith abundances. To assess how environmental variables were related to the differences between phytolith assemblages, forest cover, elevation (Jarvis et al. 2008), mean annual temperature, mean annual precipitation and the precipitation of the dry quarter (Karger et al. 2017) were fitted on DCA sites scores as vectors. Beta regression models (Cribari-Neto and Zeileis, 2010) were developed to predict the proportion of forest cover pixels in the landscape, using phytolith taxa in proportions. We ran models with a variety of arboreal and palm phytoliths, grass phytoliths, and a combination of grass phytoliths and pollen. The performance of each model was assessed using pseudo-R^2-values, p-values of the beta regression coefficients for the predictor variables, and AIC values. Furthermore, the ability to predict forest cover within 200 m of Lake Kumpak[a] was assessed for five beta regression models, using the proportion of forest cover for the years 1983 and 2014 (Fig. S5). To calculate forest cover at two time points, polygons were drawn within 200 m of Lake Kumpak[a] using Google Earth, with aerial image overlays that were collected in 1983 and 2014 (Fig. S5) (Åkesson et al. 2021). The age-depth model of Lake Kumpak[a] is based on 7 radiocarbon dates in the last 2415 years and has a constant deposition, therefore, this sediment record provides an excellent opportunity to test the beta regression models. Statistical analyses were performed in R (R Development Core Team 2017) using the "rioja" (Juggins and Juggins, 2019), "betareg" (Cribari-Neto and Zeileis, 2010) and "vegan' (Oksanen et al. 2013) packages. Figures were plotted using ESRI ArcGIS Pro Version 3.1.1 software and the "ggplot2" (Wickham et al. 2016) and "viridisLite" (Garnier, 2018) packages in R.

Results

Forest cover

Forest cover ranged between 0.02-100% (Fig. 2) and was positively correlated for each of the buffer sizes (100 m, 200 m, 500 m, 1 km, 2 km) (Fig. S2). Few sites had a forest cover between 10-20%, but forest cover values between 20-100% were well represented. The sites located in the savanna had the lowest forest cover (0-10%), whereas sites in the NW Amazon had the highest percentages of surrounding forest cover (75% - 99%). Sites in the southwestern (SW) and East Amazon were more variable in forest cover percentage and ranged from 24-90%. Because buffer sizes were

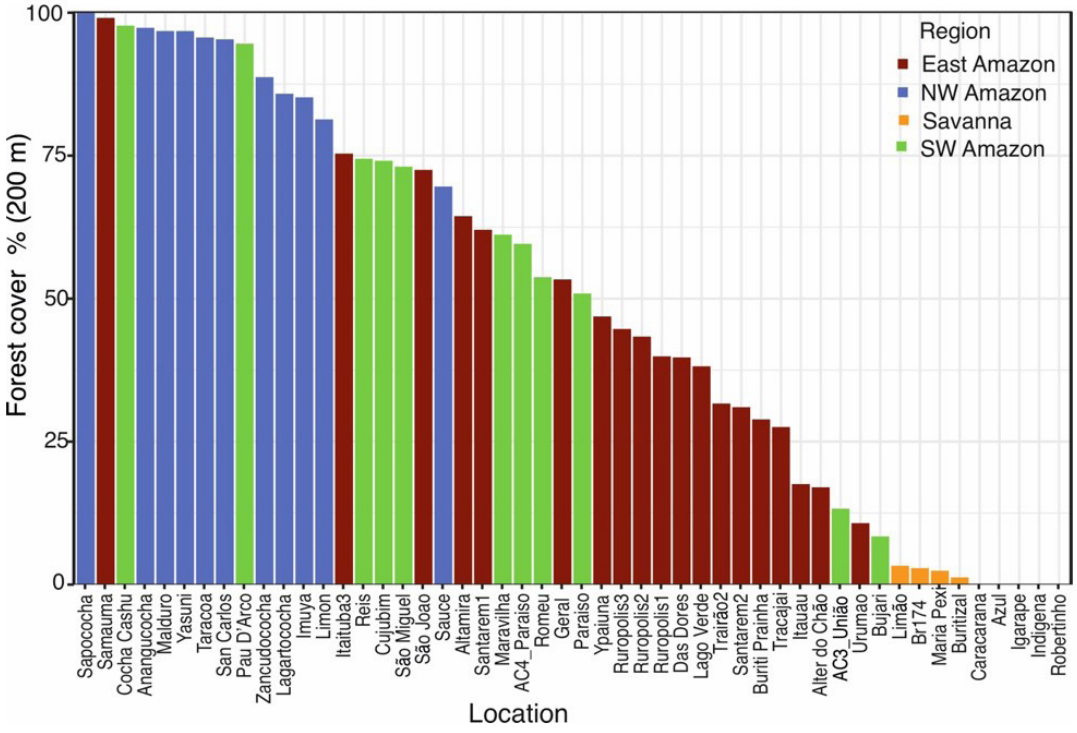

Figure 2. The percentage of forest cover (based on the amount of forested pixels) within 200 m radius of 50 Amazonian lakes. Sites are color-coded based on assigned biogeographic regions (Blaus et al. 2023)

correlated, subsequent analyses are shown for a single buffer size (200 m) and other buffer sizes are in the supplementary material.

Phytolith assemblages across a gradient of forest cover

In the 50 lake samples, 85 phytolith morphotypes were present including 21 arboreal types, 22 palms, 34 grasses, 8 herbs and 4 unknowns. These morphotypes were merged into 24 groups for further analysis (Fig. S3, Table S2). Phytoliths of sites with high and intermediate forest (>20%) generally contained < 30% Poaceae, whereas sites with low forest cover (<10%) contained 35-70% of Poaceae phytoliths. Cyperaceae were common in the savanna sites but virtually absent from the other (forested) sites. Overall, arboreal phytoliths were more common in highly forested sites and rare in sites with low forest cover. Rugose SPHEROID phytoliths were generally higher in sites with >50% forest cover, and ornate SPHEROID was highest (>20%) in sites with a forest cover >75% while this morphotype was absent from sites with low forest cover (<10%). CONICAL phytoliths from palms like *Iriartea deltoidea, Socratea exorrhiza, Bactris* and *Geonoma* were common in high forested sites, which were all located in NW Amazon. SPHEROID palm phytoliths were highest in sites where the vegetation was (i) a 'palm swamp' (Igarapé, Buritizal Prainha) or (ii) palms were an abundant component of the landscape (Ypaiuna, Urumao, Anangucocha), which was generally in sites with intermediate forest cover (20-60%). SPHEROID palm phytoliths occurred 5-40% in sites with forest cover >75% but were below <10% abundance in sites with low forest cover <10% (except Igarapé).

Several phytolith morphotypes were more common in specific regions: CONICAL palm phytoliths were most common in NW Amazon, SPHEROID palm phytoliths were more common in East Amazon, granulate SPHEROID in Para (Brazil), *Bambusoideae* grasses were more common in Acre, and *Pooideae* in Rondonia (Fig. S3).

Drivers behind different phytolith assemblages

DCA results indicates that phytolith assemblages correspond to changes in forest cover (Fig. 4a), but

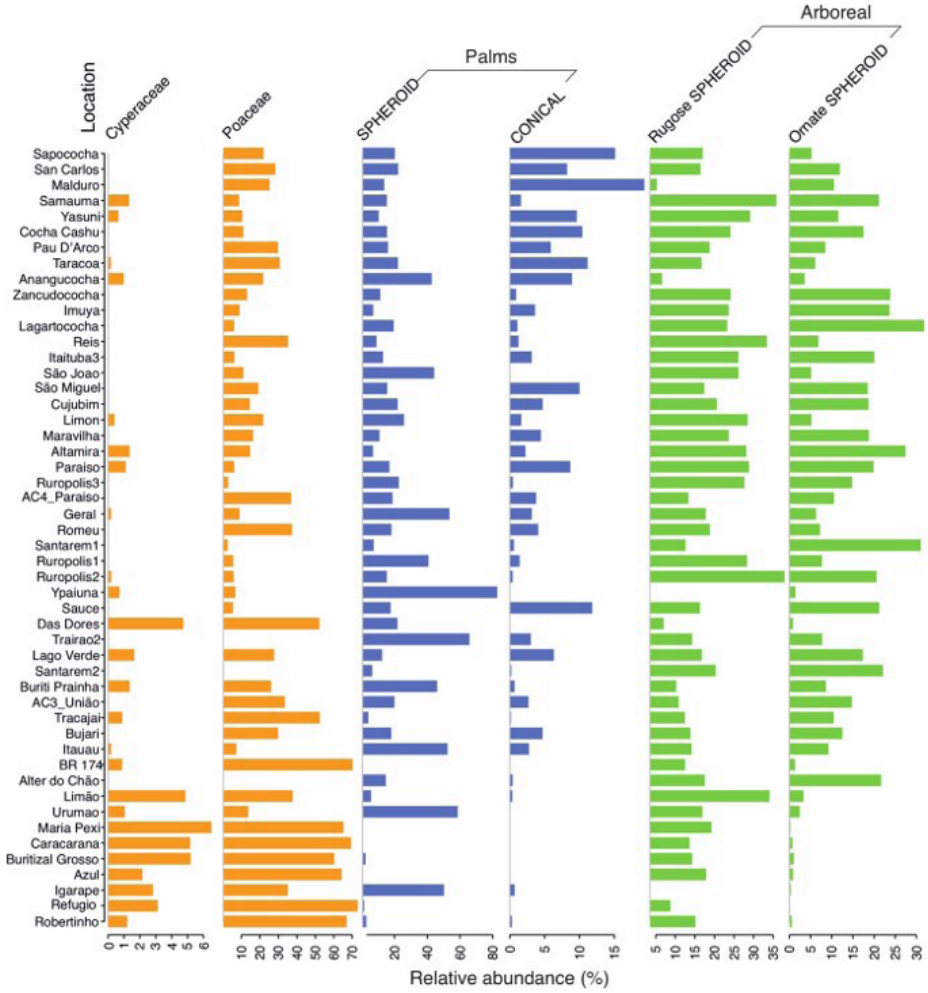

Figure 3. Phytolith diagram showing the relative abundance (in %) of Cyperaceae and Poaceae (orange), palms (blue) and arboreal morphotypes (green). Sites are sorted by the percentage of forest cover within 200 m of each lake, from high (top) to low (bottom).

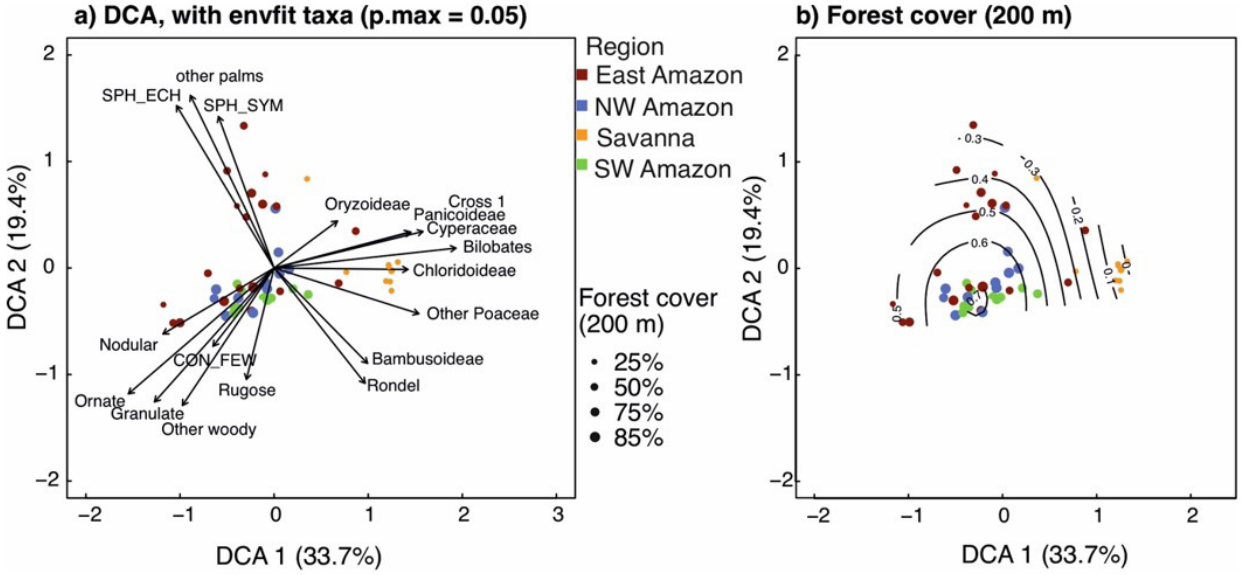

Figure 4. DCA of the phytolith assemblages from 50 Amazonian lakes showing a) significant site-taxa relationships and b) (dis)similarity across forest cover within 200 m. Sites are color-coded by assigned biogeographic region and sizes reflect forest cover within 200 m.

not linearly to environmental gradients (Fig. S4). DCA1 shows the main variation in phytolith assemblages is between sites with low forest cover (<10%) and other sites, whereas DCA2 separated sites with high palm abundances and intermediate forest cover (25%-75%) from other sites. Correspondingly, sites with low forest cover were common in Poaceae and Cyperaceae, sites with intermediate forest cover were abundant in SPHEROID palm phytoliths and sites with high forest cover were abundant in arboreal phytoliths (and CONICAL palms). Savanna sites were low in forest cover, most sites in East Amazon had intermediate forest cover and high forest cover was mostly in sites in NW Amazon. 18 phytolith groups were able to significantly separate sites with high, intermediate, and low forest cover (Fig. 4b).

Calibrating phytolith assemblages to forest cover changes

The beta regressions indicated that phytolith proportions were able to predict forest cover, based on AIC values, p-values and pseudo-R2 values of the model predictors (Table S2 and S3). Arboreal and palm phytoliths were able to predict forest cover as one group (arboreal, palms) and two groups (SPHEROID, CONICAL morphotypes) at five buffer sizes (100 m, 200 m, 500 m, 1 km, 2 km). Models with higher R2 values had lower AIC values (Table S2 and S3). Generally, models performed better with increasing buffer sizes (Table S3). Models with the best R2 values included two arboreal and two palm phytolith groups, and models with the lowest AIC values included 'rugose SPHEROID' and 'ornate SPHEROID' arboreal phytoliths. The model 'palms + arboreal', 'Poaceae' and 'Poaceae + Cyperaceae' had intermediate AIC and R2 values. Rugose SPHEROID and SPHEROID palms were not significant in models 3 and 4 (Table 1).

Predicting forest cover changes through time

To test the performance of our models, we applied 5 beta regression models to predict forest cover changes near Lake Kumpak[a] and compared our results to pollen estimates (Blaus et al. 2023). Within 200 m around the lake, aerial images reveal 78% forest cover in 1983 and 88% forest cover in 2014 (Fig. S5). The 'Poaceae model' accurately predicts ca. 80% forest cover around this period and predicts an increase in forest cover from 1983 to 2014 (Fig. 6). In comparison, models containing arboreal and palm phytoliths predict a higher proportion of forest pixels within 200 m of the lake. Also, the increase in forest cover from 1983 to 2014 is not predicted by models containing arboreal and palm phytoliths (Fig. 6b).

Discussion

In this study, we showed that phytolith assemblages from 50 Amazonian lakes can be used to predict forest cover. Previously, phytoliths from terrestrial soils have been shown to differentiate rainforests from savanna (Dickau et al. 2013). Our results indicate similar capacities for phytoliths from lake sediments. Also, we demonstrate that phytolith assemblages from lake sediments reflect forest cover changes and differentiate deforested landscapes from highly forested sites. This modern calibration dataset can be used to make quantitative reconstructions of forest cover changes in Amazonia, and generate novel insights into long-term forest recovery.

Table 1. Pseudo-R^2 values, model coefficients and AIC values for six beta regressions used to predict forest cover values (the proportion of forest pixels) within 200 m of 50 Amazonian lakes. P-values are given for significant predictor variables.

MODEL	MORPHOTYPES	DF	AIC	PSEUDO-R2	COEFF
1	**Poaceae (P < 0.001)**	3	-80.829909	0.3520617	0.9311196
2	**Arboreal (P < 0.001) + palms (p= 0.00171)**	4	-77.6631	0.330868	-2.54171
3	**CONICAL (P < 0.001)** + SPHEROID palms (p= 0.275)	4	-81.028842	0.3109237	-1.3174533
4	Rugose SPHEROID (p= 0.20844) + **Ornate SPHEROID (p= 0.00314)**	4	-68.925295	0.2009910	-1.5212419
5	**Arboreal (P < 0.001)**	3	-69.0147	0.176061	-1.5491
6	**Rugose SPHEROID (p= 7.19e-05) + Ornate SPHEROID (P < 0.001) + CONICAL (P < 0.001) + SPHEROID palms (p= 0.001338)**	6	-111.420252	0.5471110	-3.9841141

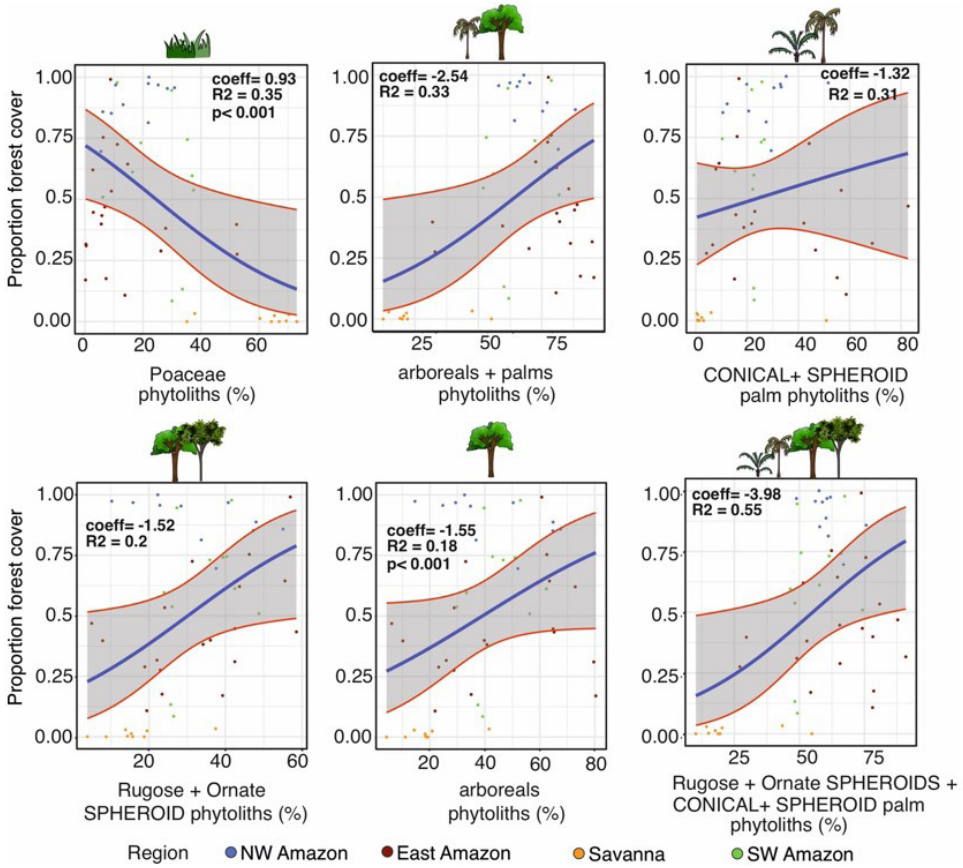

Figure 5. Six beta regression models were used to predict forest cover values (the proportion of forest pixels) within 200 m of 50 Amazonian lakes, using different phytolith groups/types. Sites are color-coded by assigned biogeographic region. Pseudo-R^2 values, model coefficients and p-values are shown.

We aimed to assess the spatial scale at which phytolith assemblages (can) predict forest cover changes across five buffer sizes (100 m, 200 m, 500 m, 1 km, 2 km, Fig. S2). We found that forest cover was highly correlated (>0.8) between these buffers. Comparisons of phytolith assemblages with satellite imagery and photographs showed the local vegetation growing within 200 m of each lake was well represented for most sites. For example, the palm swamp vegetation at sites Igarapé and Buritizal Prainha and the deforested landscape at Limão (Fig. S6), were appropriately reflected in the lake samples. The combination of grass (<30%), palm and arboreal phytoliths in the intermediate and high forested sites likely indicated that the lakeshore vegetation and a small fraction of the forest beyond it was captured

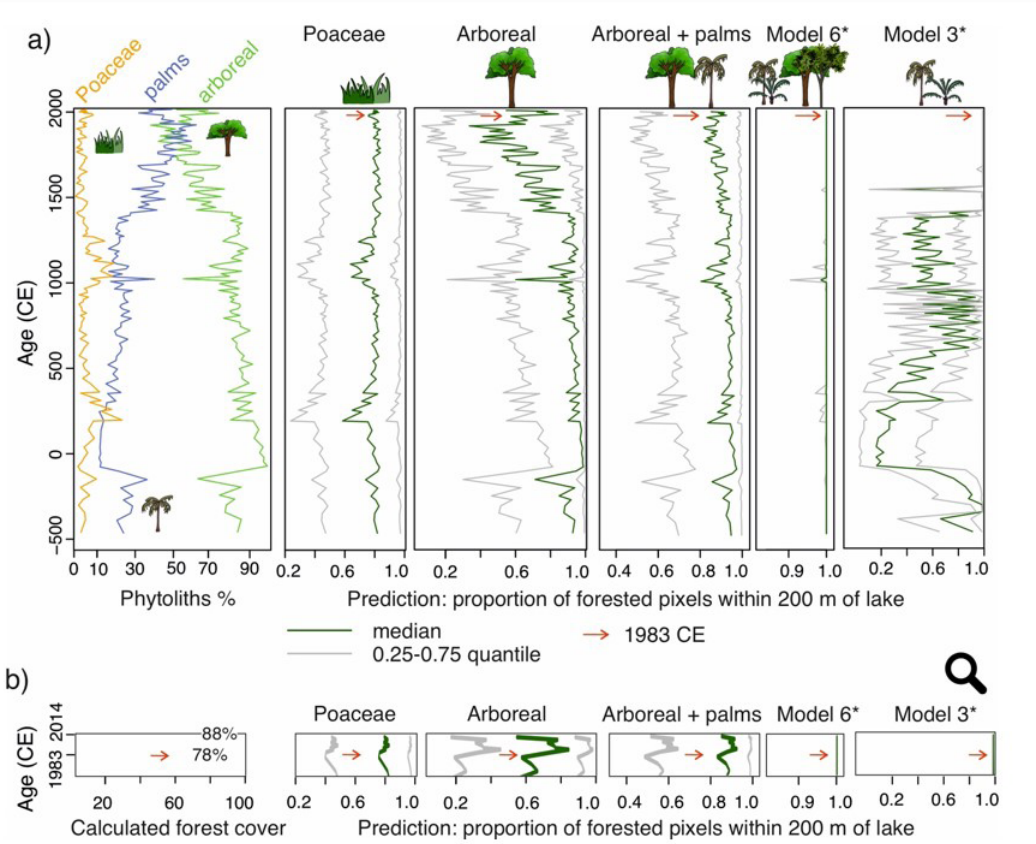

Figure 6. a) The predicted proportion of forest cover within 200 m of Lake Kumpak[a] based on Poaceae (orange), palms (blue) and arboreal (green) phytoliths (Åkesson et al. 2021). Median (dark green), 0.25 and 0.75 quantiles (grey) are shown for each model. Models 3 and 6 refers to Table 1. The red arrow indicates the year 1983, which is shown in detail in b) where the calculated forest cover for 1983 and 2014 CE (based on aerial images, Fig. S5) are compared to the predicted forest cover for the period 1983 to 2014.

(Fig. 2). Therefore, a spatial scale of 200 m was chosen for the beta regression models.

Pollen assemblages reflect biogeographical gradients in Amazonia (Bush et al. 2021), and likewise, *Bambusoideae* and *Pooideae* phytoliths are mostly found in SW Amazon (Carvalho et al. 2013, Watling et al. 2020), Fig S3). We also hypothesize that the high abundance of CONICAL (and CON_FEW) phytoliths in NW Amazon reflects the local abundances of *Iriartea deltoidea* (Henderson et al. 2019, Ter Steege et al. 2013). Unlike pollen, the taxonomic resolution of phytoliths, however, does not allow biogeographical gradients and Amazon forest types to be distinguished. Instead, phytoliths seem well-suited to detect local disturbances (Åkesson et al. 2021, Astudillo, 2018, Heijink et al. 2023, McMichael et al. 2015, 2022, Piperno, 2006, Piperno et al. 2021, Witteveen et al. 2023) and forest cover (Bremond et al. 2005, Witteveen et al. 2023). In support, our DCA results show that phytolith assemblages from highly forested sites (like Samauma and Cocha Cachu) are more similar to each other than sites in the same biogeographical region (Fig. 3). Also, palm swamp sites are grouped regardless of their location (Fig. 3). Thus, phytolith assemblages can differentiate low, intermediate, and high forest cover, which seems a stronger driver of phytolith assemblages than biogeographical gradients.

In line with our hypothesis, several phytolith morphotypes were able to accurately model forest cover changes (Figs. 5). Previous studies showed that arboreal and palm phytoliths could predict tree cover in tropical African forests (at mid or low elevations) (Barboni et al. 2007). In contrast, our beta regression models showed Poaceae phytoliths were most accurate in predicting forest cover surrounding Lake Kumpak[a] (Fig. 6). Prior research indicated Poaceae phytoliths are most sensitive to detect deforestation and gradients of land-use (Watling et al. 2023, Witteveen et al. 2023). The model with two types of arboreal (rugose and ornate SPHEROID) and two palm (CONICAL and SPHEROID) phytoliths showed the highest pseudo-R^2 values (at 200 m and 1 km), but likely resulted in an overfitted model, because CONICAL palm phytoliths were associated with highly forested sites in this dataset, and SPHEROID palm phytoliths with sites containing intermediate forest cover estimates (25%-75%).

The performance of our beta regression models is likely affected by palm abundances. Palms can be a part

of the forested landscape but are also known to grow well in disturbed or deforested areas (Henderson et al. 2019, Muscarella et al. 2020, Salm, 2005, Smith, 2014). When applying the beta regression models to paleo settings, the increase in a few palm trees may disproportionally lead to high palm phytolith abundances, which could lead to a decrease in other arboreal phytoliths although forest cover is not impacted/lowered. This balance likely explains why model 'Arboreal' predicts a large decrease in forest cover after 1005 CE and around ca. 150 BCE, when palm phytoliths increase (Åkesson et al. 2021) (Fig. 6).

Several Amazonian lakes had lower arboreal or Poaceae phytolith abundances than expected based on their estimated forest cover, possibly caused by local flooding conditions influencing sedimentary deposition or local vegetation. First, high abundances of arboreal phytoliths were found at low forested sites Santarem1, Santarem2 and Alter do Chão. However, these arboreal phytoliths were mostly granulate SPHEROID that probably corresponded to local flood forest vegetation (Figs. S3, S7). Second, the high abundance of Poaceae at Das Dores is likely because this site was a floodplain with extensive Poaceae vegetation on the lakeshore (Fig. S7).

Pollen and phytolith models showed similar trends in their predicted forest cover for the last 2200 years around Lake Kumpak[a] (Fig. 7). Episodes of reduced forest cover aligned with evidence of past cultivations and burning events, which gave us confidence in the ability of phytoliths to predict forest cover. Both models predicted that most of the lake catchment was forested (>80%) in the late-Holocene, and that deforestation occurred around ca. 1005 CE and 192 CE (Fig. 7). Around 150 BCE, however, phytoliths predicted a decrease in forest cover within 200 m of Lake Kumpak[a] that was not predicted within 1km of the lake but coincided with increased *Cecropia* pollen (Åkesson et al. 2021). Combined, we interpreted these results to represent (three periods of) increasing human impact through time. Deforestation was small scale, occurring within 200 m of the shore c. 150 BCE before expanding to c. 1 km or more c. 190 CE. Around 1005 CE as much as half of the forest cover within 1 km of the lake was removed. These results also supported the interpretation of a mosaic of deforestation instead of widespread deforestation (and reforestation) due to past human activities (Bush et al. 2021). Comparing forest cover reconstructions with the pollen and phytolith assemblages (Åkesson et al. 2021) showed that past human activities probably had a more significant impact on forest composition than on forest cover near Lake Kumpak[a]. This example showed the potential of combining phytolith and pollen data to reconstruct local vegetation and environmental changes at different spatial scales, improving understanding of how past human activities changed Amazonian forests.

Some limitations in this study that may be addressed in future research. Firstly, our estimates of forest cover may be improved. We used a dataset where the proportion of forest pixels is based on tree species >5 m in height (Hansen et al. 2013), which includes forests in various stages of succession but can also include flooded forests or swamp forests. We hypothesize that the calibration of arboreal and

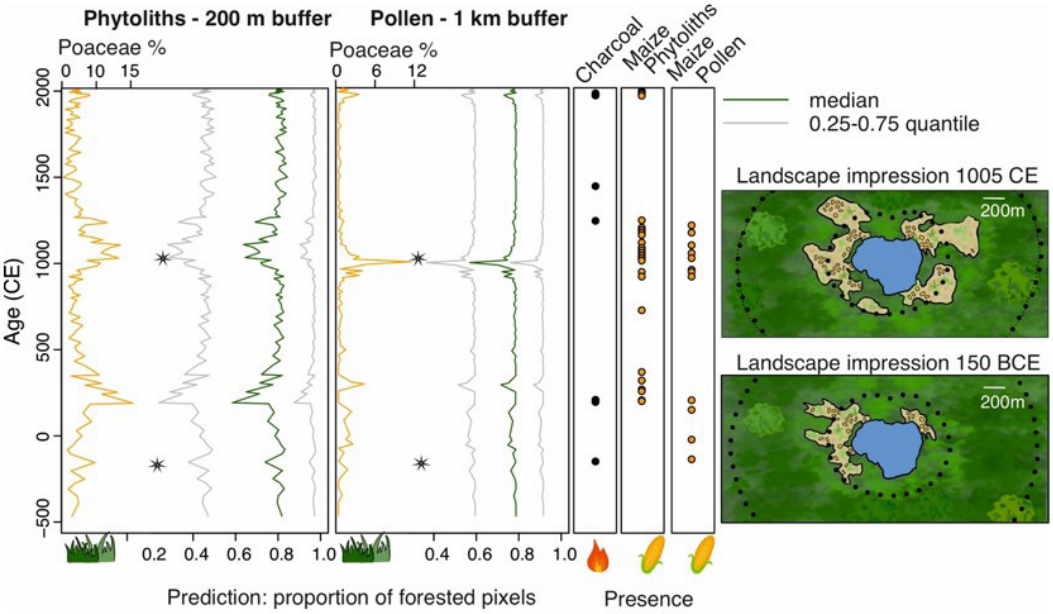

Figure 7. The predicted forest cover within 200 m and 1 km of Lake Kumpak[a] based on beta regression models using Poaceae phytoliths and pollen, respectively, covering the last 2200 years. An impression of the landscape is given for c. 150 BCE and 1005 CE, based on the model predictions (indicated with a star). The presence of charcoal fragments and maize phytoliths and pollen are shown for comparison.

palm phytoliths to forest cover estimates will be improved if flooded, swamp, and early successional forests are excluded or filtered out. Certainly, the incorporation of higher resolution satellite imagery, Light Detection and Ranging (LiDAR) or Unmanned Aerial Vehicle (UAV) imagery would all offer substantive improvements in forest cover estimates. Furthermore, in future studies, phytolith assemblages could be calibrated with other aspects of forest structure or vegetation type using remote sensing, LiDAR and UAV imagery (Witteveen et al. 2023), to better distinguish forest types (Oliveira-Filho et al. 2021). For example, we hypothesize that *Mauritia flexuosa* swamps may be detected and quantified using palm phytoliths based on UAV imagery and SPH_SYM morphotypes. Improving estimates of forest cover to distinguish between early successional and mature forests would be an important improvement to understand long-term forest recovery. Finally, our calibration dataset may be improved by including more low-forested sites (10-20%), because our dataset was skewed towards sites with a high forest cover (Figs. 1, S1).

Phytolith taxonomy is continually improving (Piperno and McMichael, 2023, 2020, Witteveen et al. 2022) and as more taxa are identified from phytoliths the potential to capture biogeographical gradients will improve. To this end, future research should expand modern reference material from the bark, fruits, and seeds of tree (and palm) species across Amazonia. The abundance of various palm and arboreal phytoliths is highly variable among soil samples from forested sites (Barboni et al. 1999, Heijink et al. 2023, 2020, McMichael et al. 2015, 2022, Piperno et al. 2021). In this study, for example, granulate SPHEROID was higher in the Para region and sites with intermediate forest cover, while ornate SPHEROID was highest in highly forested sites. It is possible that these sites differ in their habitat (shrub or hardwood trees) and tree species composition, which may be reflected by different phytolith assemblages, but it is not known which tree species produce granulate SPHEROID phytoliths and the taxonomic resolution of ornate SPHEROID is low (Piperno and McMichael, 2023, 2020).

Our results show phytolith assemblages from lake sediments, like terrestrial soils (Dickau et al. 2013), can distinguish savanna from tropical forests, and reflect differences in local forest cover. Our dataset can be used to begin quantifying deforested landscapes in Amazonian rainforests, using Poaceae phytoliths. Combined with Poaceae pollen, a multiproxy approach can be used to reconstruct forest cover within 1 km (Blaus et al. 2023) of Amazonian lakes. The integration of pollen and phytolith assemblages can shed light on species compositional and forest cover changes during long-term forest recovery. Such insights are necessary to understand successional trajectories and ecological legacies from pre-contact and post-colonial human activities (McMichael, 2021).

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Data Availability Statement

Phytolith assemblages will be uploaded in the Neotoma database (www.neotomadb.org).

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Table S1. List of lakes and general characteristics of lake properties and climate variables.

Table S2. Phytolith groups, the morphotypes included in those groups, their taxonomic representation and the original literature this morphotype was published first.

Table S3. AIC values, df, pseudo-R2 squared values and coefficients for the beta regression models used to predict forest cover values of 50 Amazonian lakes, with different phytolith groups/types.

Figure S1. Forest cover percentages for 100 m, 500 m, 1 km, and 2 km buffers around each of the 50 Amazonian lakes where phytoliths were identified and quantified.

Figure S2. Correlation matrix of forest cover values for 100 m, 200 m, 500 m, 1 km, and 2 km buffers around 50 Amazonian lakes used in the study.

Figure S3. Phytolith diagram showing morphotypes that were used to run the Detrended Correspondence Analysis.

Figure S4. DCA showing the variability of phytolith assemblages across environmental gradients within a 200m buffer size of 50 Amazonian lakes.

Figure S5. Aerial images of Kumpaka, which were used to estimate forest cover in 1983 and 2014.

Figure S6. Google Earth images and photographs giving an impression of the palm swamps growing near the lakeshore of sites Limaõ and Igarapé.

Figure S7. Photographs showing the lakeshore vegetation consisting of palms, grasses and flooded forests.

References

Åkesson, C.M., McMichael, C.N.H., León-Yánez, S. & Bush, M.B. (2023) Late-Holocene maize cultivation, fire, and forest change at Lake Ayauchi, Amazonian Ecuador. Holocene, 33,

550–561. https://doi.org/10.1111/1365-2745.13501

Åkesson, C.M., McMichael, C.N.H., Raczka, M.F., Huisman, S.N., Palmeira, M., Vogel, J., Neill, D., Veizaj, J. & Bush, M.B. (2021) Long-term ecological legacies in western Amazonia. Journal of Ecology, 109, 432–446. https://doi.org/10.1111/1365-2745.13501

Aleman, J.C., Canal-Subitani, S., Favier, C. & Bremond, L. (2014) Influence of the local environment on lacustrine sedimentary phytolith records. Palaeogeography, Palaeoclimatology, Palaeoecology, 414, 273–283. https://doi.org/10.1016/j.palaeo.2014.08.030

Astudillo, F.J. (2018) Soil phytoliths as indicators of initial human impact on San Cristóbal Island, Galápagos. Palaeogeography, Palaeoclimatology, Palaeoecology, 490, 522–532. https://doi.org/10.1016/j.palaeo.2017.11.038

Barboni, D., Bonnefille, R., Alexandre, A. & Meunier, J.-D. (1999) Phytoliths as paleoenvironmental indicators, west side Middle Awash Valley, Ethiopia. Palaeogeography, Palaeoclimatology, Palaeoecology, 152, 87–100. https://doi.org/10.1016/S0031-0182(99)00045-0

Barboni, D., Bremond, L. & Bonnefille, R. (2007) Comparative study of modern phytolith assemblages from inter-tropical Africa. Palaeogeography, Palaeoclimatology, Palaeoecology, 246, 454–470. https://doi.org/10.1016/j.palaeo.2006.10.012

Blaus, A., McMichael, C.N.H., Raczka, M.F., Herrick, C., Palace, M., Witteveen, N.H., Nascimento, M.N. & Bush, M.B. (2023) Amazonian pollen assemblages reflect biogeographic gradients and forest cover. Journal of Biogeography, https://doi.org/10.1111/jbi.14701

Bodin, S.C., Molino, J.F., Odonne, G. & Bremond, L. (2020) Unraveling pre-Columbian occupation patterns in the tropical forests of French Guiana using an anthracological approach. Vegetation History and Archaeobotany. https://doi.org/10.1007/s00334-019-00767-w

Bremond, L., Alexandre, A., Hély, C. & Guiot, J. (2005) A phytolith index as a proxy of tree cover density in tropical areas: calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon. Global and Planetary Change, 45, 277–293. https://doi.org/10.1016/j.gloplacha.2004.09.002

Bush, M.B. & Colinvaux, P.A. (1988) A 7000-year pollen record from the Amazon lowlands, Ecuador. Vegetatio, 76, 141–154. https://doi.org/10.1007/BF00045475

Bush, M.B., Correa-Metrio, A., van Woesik, R., Collins, A., Hanselman, J., Martinez, P. & McMichael, C.N.H. (2021) Modern pollen assemblages of the Neotropics. Journal of Biogeography, 48, 231–241. https://doi.org/10.1111/jbi.13960

Bush, M.B., Nascimento, M.N., Åkesson, C.M., Cárdenes-Sandí, G.M., Maezumi, S.Y., Behling, H., Correa-Metrio, A., Church, W., Huisman, S.N., Kelly, T., et al. (2021) Widespread reforestation before European influence on Amazonia. Science, 372, 484–487. https://doi.org/10.1126/science.abf3870

Carson, J.F., Watling, J., Mayle, F.E., Whitney, B.S., Iriarte, J., Prümers, H. & Soto, J.D. (2015) Pre-Columbian land use in the ring-ditch region of the Bolivian Amazon. The Holocene, *25*, pp.1285-1300. https://doi.org/10.1177/0959683615581204

Carvalho, A.L. de, Nelson, B.W., Bianchini, M.C., Plagnol, D., Kuplich, T.M. & Daly, D.C. (2013) Bamboo-dominated forests of the southwest Amazon: detection, spatial extent, life cycle length and flowering waves. PLoS ONE, 8, e54852. https://doi.org/10.1371/journal.pone.0054852

Chazdon, R.L. (2003) Tropical forest recovery: Legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics, 6, 51–71. https://doi.org/10.1078/1433-8319-00042

Ciochon, R.L., Piperno, D.R. & Thompson, R.G. (1990) Opal phytoliths found on the teeth of the extinct ape Gigantopithecus blacki: implications for paleodietary studies. Proceedings of the National Academy of Sciences USA, 87, 8120–8124. https://doi.org/10.1073/pnas.87.20.8120

Cole, L.E.S., Bhagwat, S.A., & Willis, K.J. (2014) Recovery and resilience of tropical forests after disturbance. Nature Communications, 5, 1–7. https://doi.org/10.1038/ncomms4906

Collura, L.V. & Neumann, K. (2017) Wood and bark phytoliths of West African woody plants. Quaternary International, 434, 142–159. https://doi.org/10.1016/j.quaint.2015.12.070

Cribari-Neto, F., & Zeileis, A. (2010) Beta regression in R. Journal of Statistical Software, 34, 1–24. https://doi.org/10.18637/jss.v034.i02

Crifò, C. & Strömberg, C.A.E. (2020) Small-scale spatial resolution of the soil phytolith record in a rainforest and a dry forest in Costa Rica: applications to the deep-time fossil phytolith record. Palaeogeography, Palaeoclimatology, Palaeoecology, 537, 109107. https://doi.org/10.1016/j.palaeo.2019.03.008

da Cruz, D.C., Benayas, J.M.R., Ferreira, G.C., Santos, S.R. & Schwartz, G. (2021) An overview of forest loss and restoration in the Brazilian Amazon. New Forests, 52, 1–16. https://doi.org/10.1007/s11056-020-09777-3

Dickau, R., Whitney, B.S., Iriarte, J., Mayle, F.E., Soto, J.D., Metcalfe, P., Street-Perrott, F.A., Loader, N.J., Ficken, K.J. & Killeen, T.J. (2013) Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions. Review of Palaeobotay and Palynology, 193, 15–37. https://doi.org/10.1016/j.revpalbo.2013.01.004

Eva, H.D., Huber, O., Achard, F., et al. (2005) A proposal for defining the geographical boundaries of Amazonia, synthesis of the results from an expert consultation workshop organized by the European Commission in collaboration with the Amazon Cooperation Treaty Organization-JRC Ispra, 7-8 June 2005. European Commission.

Fernandes Neto, J.G., Costa, F.R.C., Williamson, G.B. & Mesquita, R.C.G. (2019) Alternative functional trajectories along succession after different land uses in central Amazonia. Journal of Applied Ecology, 56, 2472–2481. https://doi.org/10.1111/1365-2664.13484

Garnier, S. (2018) ViridisLite: Default color maps from'matplotlib' (lite version). R Package Version 0.3. 0. Available at: https://cran.r-hub.io/web/packages/viridisLite/index.html

Gatti, L. V, Basso, L.S., Miller, J.B., Gloor, M., Gatti Domingues, L., Cassol, H.L.G., Tejada, G., Aragão, L.E.O.C., Nobre, C., Peters, W., et al. (2021) Amazonia as a carbon source linked to deforestation and climate change. Nature, 595, 388–393. https://doi.org/10.1038/s41586-021-03629-6

Gentry, A.H. (1988) Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences USA, 85, 156–159. https://doi.org/10.1073/pnas.85.1.156

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017) Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment, 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Hansen, M.C., Potapov, P. V, Moore, R., et al. (2013) High-resolution global maps of 21st-century forest cover change. Science, 342, 850–853. https://doi.org/10.1126/science.1244693

Heijink, B.M., Mattijs, Q.A., Valencia, R., Philip, A.L., Piperno, D.R. & McMichael, C.N.H. (2023) Long-term fire and vegetation change in northwestern Amazonia. Biotropica, 55, 197–209. https://doi.org/10.1111/btp.13175

Heijink, B.M., McMichael, C.N.H., Piperno, D.R., Duivenvoorden, J.F., Cárdenas, D. & Duque, Á. (2020) Holocene increases in palm abundances in north-western Amazonia. Journal of Biogeography, 47, 698–711. https://doi.org/10.1111/jbi.13721

Henderson, A., Galeano, G. & Bernal, R. (2019) Field guide to the palms of the Americas. Princeton University Press.

Hill, J., Black, S., Araujo-Murakami, A., et al. (2023) An assessment of soil phytolith analysis as a palaeoecological tool for identifying pre-Columbian land use in Amazonian rainforests. Quaternary, 6, 33. https://doi.org/10.3390/quat6020033

Hubau, W., Lewis, S.L., Phillips, O.L., et al. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature, 579, 80–87. https://doi.org/10.1038/s41586-020-2035-0

Huisman, S.N., Raczka, M.F. & McMichael, C.N.H (2018) Palm phytoliths of mid-elevation Andean forests. Frontiers of Ecology and Evolution, 6, 1–8. https://doi.org/10.3389/fevo.2018.00193

Iriarte, J. (2003) Assessing the feasibility of identifying maize through the analysis of cross-shaped size and three-dimentional morphology of phytoliths in the grasslands of southeastern South America. Journal of Archaeological Science, 30, 1085–1094. https://doi.org/10.1016/S0305-4403(02)00164-4

Iriarte, J., Glaser, B., Watling, J., Wainwright, A., Birk, J.J., Renard, D., Rostain, S. & McKey, D. (2010) Late Holocene Neotropical agricultural landscapes: phytolith and stable carbon isotope analysis of raised fields from French Guianan coastal savannahs. Journal of Archaeological Science, 37, 2984–2994. https://doi.org/10.1016/j.jas.2010.06.016

Jarvis, A., Guevara, E., Reuter, H.I. & Nelson, A.D. (2008) Hole-filled SRTM for the globe: version 4: data grid. Available at: https://research.utwente.nl/en/publications/hole-filled-srtm-for-the-globe-version-4-data-grid

Juggins, S. & Juggins, M.S. (2019) Package 'rioja.' Available at: https://cran.r-project.org/web/packages/rioja/index.html

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P. & Kessler, M. (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data, 4, 1–20. https://doi.org/10.1038/sdata.2017.122

Loughlin, N.J.D., Gosling, W.D., Mothes, P. & Montoya, E. (2018) Ecological consequences of post-Columbian indigenous depopulation in the Andean–Amazonian corridor. Nature Ecology and Evolution, 2, 1233–1236. https://doi.org/10.1038/s41559-018-0602-7

Loughlin, N.J.D., Mayle, F.E., Otano, N.B.N., O'Keefe, J.M.K., Duncan, N.A., Walker, J.H. & Whitney, B.S. (2021) Insights into past land-use and vegetation change in the Llanos de Moxos (Bolivia) using fungal non-pollen palynomorphs. Journal of Archaeological Science, 130, 105382. https://doi.org/10.1016/j.jas.2021.105382

Maezumi, S.Y., Alves, D., Robinson, M., de Souza, J.G., Levis, C., Barnett, R.L., Almeida de Oliveira, E., Urrego, D., Schaan, D. & Iriarte, J. (2018) The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. Nature Plants, 4, 540–547. https://doi.org/10.1038/s41477-018-0205-y

McMichael, C.H., Piperno, D.R., Neves, E.G., Bush, M.B., Almeida, F.O., Mongeló, G. & Eyjolfsdottir, M.B. (2015) Phytolith assemblages along a gradient of ancient human disturbance in Western Amazonia. Frontiers in Ecology and Evolution 3, 1–15. https://doi.org/10.3389/fevo.2015.00141

McMichael, C.N.H. (2021) Ecological legacies of past human activities in Amazonian forests. New Phytologist, 229, 2492–2496. https://doi.org/10.1111/nph.16888

McMichael, C.N.H., Vink, V., Heijink, B.M., Witteveen, N.H., Piperno, D.R., Gosling, W.D. & Bush, M.B. (2022) Ecological legacies of past fire and human activity in a Panamanian forest. Plants, People, Planet. https://doi.org/10.1002/ppp3.10344

Miras, Y., Beauger, A., Lavrieux, M., Berthon, V., Serieyssol, K., Andrieu-Ponel, V. & Ledger, P.M. (2015) Tracking long-term human impacts on landscape, vegetal biodiversity and water quality in the Lake Aydat catchment (Auvergne, France) using pollen, non-pollen palynomorphs and diatom assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology, 424, 76–90. https://doi.org/10.1016/j.palaeo.2015.02.016

Mitchard, E.T.A. (2018) The tropical forest carbon cycle and climate change. Nature, 559, 527–534. https://doi.org/10.1038/s41586-018-0300-2

Moran, E.F., Brondizio, E.S., Tucker, J.M., da Silva-Forsberg, M.C., McCracken, S. & Falesi, I. (2000) Effects of soil fertility and land-use on forest succession in Amazonia. Forest and Ecology Management, 139, 93–108. https://doi.org/10.1016/S0378-1127(99)00337-0

Morcote-Ríos, G. & Bernal, R., Raz, L. (2016) Phytoliths as a tool for archaeobotanical, palaeobotanical and palaeoecological studies in Amazonian palms. Botanical Journal of the Linnean Society, 182, 348–360. https://doi.org/10.1111/boj.12438

Morlock, M.A., Vogel, H., Russell, J.M., Anselmetti, F.S. & Bijaksana, S. (2021) Quaternary environmental changes in tropical Lake Towuti, Indonesia, inferred from end-member modelling of X-ray fluorescence core-scanning data. Journal of Quaternary Science, 36, 1040–1051. https://doi.org/10.1002/jqs.3338

Moy, C.M., Seltzer, G.O., Rodbell, D.T. & Anderson, D.M. (2002) Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. Nature, 420, 162–165. https://doi.org/10.1038/nature01194

Muscarella, R., Emilio, T., Phillips, O.L., et al. (2020) The global abundance of tree palms. Global

Ecology and Biogeography, 29, 1495–1514. https://doi.org/10.1111/geb.13123

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. Nature, 403, 853–858. https://doi.org/10.1038/35002501

Neumann, K., Fahmy, A., Lespez, L., Ballouche, A. & Huysecom, E. (2009) The Early Holocene palaeoenvironment of Ounjougou (Mali): phytoliths in a multiproxy context. Palaeogeography, Palaeoclimatology, Palaeoecology,, 276, 87–106. https://doi.org/10.1016/j.palaeo.2009.03.001

Neumann, K., Strömberg, C., Ball, T., Albert, R.M., Vrydaghs, L. & Cummings, L.S. (2019) International Code for Phytolith Nomenclature (ICPN) 2.0 International Committee for Phytolith Taxonomy. Supplementary Information : Glossary of Descriptive Terms. Annuals of Botany, XX. https://doi.org/10.1093/aob/mcz064

Oksanen, J., Blanchet, F.G., Kindt, R., et al. (2013) Package 'vegan.' Community ecology package, version 2, 1–295. Available at: Oliveira-Filho, A.T., Dexter, K.G., Pennington, R.T., Simon, M.F., Bueno, M.L., Neves, D.M., (2021) On the floristic identity of Amazonian vegetation types. Biotropica 53, 767–777. https://doi.org/10.1111/btp.12932

Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C. & Seltzer, G.O. (2003) A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. Palaeogeography, Palaeoclimatology, Palaeoecology, 194, 259–279. https://doi.org/10.1016/S0031-0182(03)00281-5

Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A.S. (2016) High-resolution mapping of global surface water and its long-term changes. Nature, 540, 418–422. https://doi.org/10.1038/nature20584

Phillips, O.L. & Brienen, R.J.W. (2017) Carbon uptake by mature Amazon forests has mitigated Amazon nations' carbon emissions. Carbon Balance and Management, 12, 1–9. https://doi.org/10.1186/s13021-016-0069-2

Piperno, D.R. (2009) Identifying crop plants with phytoliths (and starch grains) in Central and South America: a review and an update of the evidence. Quaternary International, 193, 146–159. https://doi.org/10.1016/j.quaint.2007.11.011

Piperno, D.R. (2006) Phytoliths: a comprehensive guide for archaeologists and paleoecologists. Rowman Altamira Press.

Piperno, D.R. (1990) Aboriginal agriculture and land usage in the Amazon Basin, Ecuador. Journal of Archaeological Science, 17, 665–677. https://doi.org/10.1016/0305-4403(90)90048-A

Piperno, D.R. & Becker, P. (1996) Vegetational history of a site in the central Amazon basin derived from phytolith and charcoal records from natural soils. Quaternary Research, 45, 202–209. https://doi.org/10.1006/qres.1996.0020

Piperno, D.R., Clary, K.H., Cooke, R.G., Ranere, A.J. & Weiland, D. (1985) Preceramic Maize in Central Panama: phytolith and pollen evidence. American Anthropologist, 87, 871–878. https://doi.org/10.1525/aa.1985.87.4.02a00090

Piperno, D.R. & McMichael, C. (2023) Phytoliths in modern plants from Amazonia and the Neotropics at large: II. Enhancement of eudicotyledon reference collections. Quaternary International, 655, 1–17. https://doi.org/10.1016/j.quaint.2023.01.010

Piperno, D.R. & McMichael, C. (2020) Phytoliths in modern plants from amazonia and the neotropics at large: implications for vegetation history reconstruction. Quaternary International, 565, 54–74. https://doi.org/10.1016/j.quaint.2020.10.043

Piperno, D. R., McMichael, C. H., Pitman, N. C., Andino, J. E. G., Ríos Paredes, M., Heijink, B. M. & Torres-Montenegro, L. A. (2021) A 5,000-year vegetation and fire history for tierra firme forests in the Medio Putumayo-Algodón watersheds, northeastern Peru. Proceedings of the National Academy of Sciences USA, 118(40), e2022213118. https://doi.org/10.1073/pnas.2022213118

Plumpton, H., Whitney, B. & Mayle, F. (2019) Ecosystem turnover in palaeoecological records: the sensitivity of pollen and phytolith proxies to detecting vegetation change in southwestern Amazonia. Holocene, 29, 1720–1730. https://doi.org/10.1177/0959683619862021

Poorter, L., Bongers, F., Aide, T.M., et al. (2016) Biomass resilience of Neotropical secondary

forests. Nature, 530, 211–214. https://doi.org/10.1038/nature16512

Poorter, L., Craven, D., Jakovac, C.C., et al. (2021) Multidimensional tropical forest recovery. Science, 374, 1370–1376. https://doi.org/10.1125/science.abh362

Raj, R., Chamyal, L.S., Prasad, V., Sharma, A., Tripathi, J.K. & Verma, P. (2015) Holocene climatic fluctuations in the Gujarat Alluvial Plains based on a multiproxy study of the Pariyaj Lake archive, western India. Palaeogeography, Palaeoclimatology, Palaeoecology, 421, 60–74. https://doi.org/10.1016/j.palaeo.2015.01.004

Rappaport, D.I., Morton, D.C., Longo, M., Keller, M., Dubayah, R. & dos-Santos, M.N. (2018) Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation. Environmental Research Letters, 13, 65013. https://doi.org/10.1088/1748-9326/aac331

Salm, R. (2005) The importance of forest disturbance for the recruitment of the large arborescent palm Attalea maripa in a seasonally-dry Amazonian forest. Biota Neotropica. https://doi.org/10.1590/S1676-06032005000100004

Santoro, M., Cartus, O., Carvalhais, N., et al. (2020) The global forest above-ground biomass pool for 2010 estimated from high-resolution satellite observations. Earth System Science Data Discussions, 2020, 1–38. https://doi.org/10.1594/PANGAEA.894711

Saul, H., Madella, M., Fischer, A., Glykou, A., Hartz, S. & Craig, O.E. (2013) Phytoliths in pottery reveal the use of spice in European prehistoric cuisine. PLoS ONE, 8, e70583. https://doi.org/10.1371/journal.pone.0070583

Smith, N. (2014) Palms and People in the Amazon. Springer.

Strömberg, C.A.E., Dunn, R.E., Crifò, C., Harris, E.B., 2018. Phytoliths in paleoecology: analytical considerations, current use, and future directions, in: Methods in Paleoecology (ed. by D.A. Croft, D.F. Su and S.W. Simpson), pp. 235–287, Springer. https://doi.org/10.1007/978-3-319-94265-0_12

Stropp, J., Ter Steege, H. & Malhi, Y., ATDN, RAINFOR. (2009) Disentangling regional and local tree diversity in the Amazon. Ecography, 32, 46–54. https://doi.org/10.1111/j.1600-0587.2009.05811.x

Ter Steege, H., Pitman, N.C.A., Phillips, O.L., et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature, 443, 444–447. https://doi.org/10.1038/nature05134

Ter Steege, H., Pitman, N.C.A., Sabatier, D., et al. (2013) Hyperdominance in the Amazonian tree flora. Science, 342. https://doi.org/10.1126/science.1243092

Ter Steege, H., Sabatier, D., Castelllanos, H., Van Andel, T., Duivenvoorden, J., De Oliveira, A.A., EK, R., Lilwah, R., Maas, P. & Mori, S. (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. Journal of Tropical Ecology, 16, 801–828. https://doi.org/10.1017/S0266467400001735

Uhl, C., Buschbacher, R. & Serrao, E.A.S. (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. Journal of Ecology, 663–681. https://doi.org/10.2307/2260566

Watling, J., Schmidt, M., Heckenberger, M., Lima, H., Moraes, B., Waura, K., & Kuikuro, A. (2023) Assessing charcoal and phytolith signals for pre-Columbian land-use based on modern indigenous activity areas in the Upper Xingu, Amazonia. The Holocene, *33*, 1176-1185. https://doi.org/10.1177/0959683623118306

Watling, J., Castro, M.T., Simon, M.F., Rodrigues, F.O., Brilhante de Medeiros, M., De Oliveira, P.E. & Neves, E.G. (2020) Phytoliths from native plants and surface soils from the Upper Madeira river, SW Amazonia, and their potential for paleoecological reconstruction. Quaternary International. https://doi.org/10.1016/j.quaint.2020.03.045

Watling, J., Iriarte, J., Whitney, B.S., Consuelo, E., Mayle, F., Castro, W., Schaan, D. & Feldpausch, T.R. (2016) Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions II: Southwestern Amazonian forests. Review of Palaeobotany and Palynology, 226, 30–43. https://doi.org/10.1016/j.revpalbo.2015.12.002

Whitney, B.S., Smallman, T.L., Mitchard, E.T.A., Carson, J.F., Mayle, F.E. & Bunting, M.J. (2019)

Constraining pollen-based estimates of forest cover in the Amazon: a simulation approach. Holocene, 29, 262–270. https://doi.org/10.1177/09596836188103

Wickham, H., Chang, W. & Wickham, M.H. (2016) Package 'ggplot2.' Create elegant data visualisations using the grammar of graphics. Version 2, 1–189. Available at: https://ggplot2.tidyverse.org/reference/ggplot2-package.html

Witteveen, N.H., Hobus, C.E.M., Philip, A., Piperno, D.R. & McMichael, C.N.H. (2022) The variability of Amazonian palm phytoliths. Review of Palaeobotany and Palynology, 300, 104613. https://doi.org/https://doi.org/10.1016/j.revpalbo.2022.104613

Witteveen, N.H., White, C., Martinez, SanchezB.A., Booij, R., Philip, A., Gosling, W.D., Bush, M.B. & McMichael, C.N.H. (2023) Phytolith assemblages reflect variability in human land use and the modern environment. Vegetation History and Archaeobotany, https://doi.org/https://doi.org/10.1007/s00334-023-00932-2

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