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Soil phytolith assemblages reflect palm community composition in western Amazonia

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ABSTRACT

Humans have domesticated and used palms in tropical forests for millennia. The extent to which past human palm use affects modern tropical systems remains relatively unexplored due to lack of a good fossil record. However, palms produce an array of phytoliths, which are siliceous cell structures that preserve well in the soil even after the organic plant material has decayed. Phytoliths vary in morphology and can be identified to group level and sometimes even to species. We analyzed if palm phytolith assemblages sampled from the soil reflect palm species compositions and abundances in 63 western Amazonian transects. Principal coordinate analysis (PCoA) and Mantel tests showed that palm communities and phytolith assemblages had similar turnover patterns. Negative binomial generalized linear models indicated that the abundances of nine of the 13 common palm genera were significantly related to a combination of soil cation concentrations, grass phytolith percentages, and palm phytolith PCoA axis scores. These results suggest that phytoliths have potential as quantitative indicators of changes in palm abundances in paleoecological and archaeological reconstructions.

1. Introduction

Palms are among the most common and ecologically important plant groups in tropical forests (e.g., Balslev et al., 2016; Eiserhardt et al., 2011; Seibert, 1950). Many species of palms are used for food, construction, fuels, fabrics, and medicine, though usage of species varies between Indigenous tribes and groups (Bernal et al., 2011; De la Torre et al., 2008; Macía et al., 2011; Smith, 2014; Wallace, 1853). Palm distributions tend to be driven by local-scale soil and topographic gradients (Balslev et al., 2016; Balslev et al., 2017; Balslev et al., 1987; Macía and Svenning, 2005; Svenning, 2001; Svenning et al., 2009; Svenning, 1999). The abundances of palms are particularly high in Amazonia compared with African or Asian rainforests (Muscarella et al., 2020). It has been suggested that a combination of environmental and human factors are responsible for the high abundances of palms in Amazonian forests (Zuquim et al., 2023).

People have lived in Amazonia for over 13,000 years and have heavily relied on palms since that time (Clement, 2006; Oliver, 2008; Roosevelt, 2013). Some archaeological sites in Amazonia contain evidence of palm enrichment (Iriarte, 2024; Iriarte et al., 2020; Montoya et al., 2020; Pärssinen et al., 2021; Politis, 2009; Robinson et al., 2021; Witteveen et al., 2024b). The Teotonio archaeological site, which has some of the oldest Amazonian Dark Earths found anywhere in the Amazon, shows *Attalea* Kunth (palm) cultivation occurring as early as 8000 years ago (Watling et al., 2018). The peach palm (*Bactris gasipaes* Kunth) has been domesticated over the last millennia in Amazonia (Clement, 1988; Clement et al., 2009). Other records, however, have documented the depletion of palm abundances. *Iriartea deltoidea* Ruiz and Pavon has been shown to decrease in abundance because of pre- and post-Columbian human exploitation (Åkesson et al., 2021; Bush and McMichael, 2016; Clark et al., 1995). *Mauritia flexuosa* Lf is another example. Some *M. flexuosa* swamps around Iquitos (Peru) are

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increasingly dominated by male palms because the females get cut when the fruits are harvested (Endress et al., 2013; Horn et al., 2012). When females are not cut, the male–female ratio of individuals in *Mauritia* swamps is more balanced (Montúfar et al., 2021). The role of past human activity in shaping palm distributions is complex, depends on the species, and can include either enrichment or depletion of local populations (Åkesson et al., 2021; McMichael, 2021; Montoya et al., 2020).

Paleoecological investigations paired with botanical inventories can assess whether legacies of past human activities affect modern palm abundances (McMichael et al., 2023a; McMichael et al., 2023b). Pollen and phytoliths retrieved from lake sediments are commonly used in paleoecological reconstructions to assess how past human activities have affected Amazonian vegetation (including palm abundances) (Iriarte et al., 2020; Maezumi et al., 2018; Maezumi et al., 2023; McMichael et al., 2023a). In terrestrial soils, pollen grains degrade from oxidation but silica-based phytoliths typically preserve (Piperno, 2006). Phytoliths recovered in paleoecological and archaeological studies can detect (and potentially quantify): i) cultivation of many Amazonian crops such as maize and squash, ii) disturbances and forest openings, and iii) forest management, including palm use (Morcote-Ríos et al., 2015; Piperno, 2006; Piperno, 2011; Watling et al., 2016; Watling et al., 2018; Witteveen et al., 2023). Modern phytolith assemblages found in surface soils or sediments can also help to distinguish biome types, various forms of land use, forest modification, and forest characteristics (including palm forests) at local and landscape scales (Bremond et al., 2005a; Bremond et al., 2008; Dickau et al., 2013; Watling et al., 2016; Witteveen et al., 2024a; Witteveen et al., 2023).

While phytoliths have been used to estimate past environmental parameters such as biome type (Bremond et al., 2005a; Bremond et al., 2008), biomass, or forest cover (Witteveen et al., 2025), they have not been used to quantify changes in past palm community composition. Palms are prolific phytolith producers, and palm phytoliths can be used to identify sub-tribes, genera, and occasionally species of palms in Amazonia (Huisman et al., 2018; Morcote-Ríos et al., 2016; Witteveen et al., 2022). Here we assess the degree to which phytolith assemblages collected from surface soil samples reflect local palm diversity and abundances in western Amazonia. We specifically ask: i) how are palm communities and palm phytolith assemblages structured across biogeographic regions and soil gradients in Amazonia, and ii) can phytolith assemblages be used to predict palm abundances?

2. Materials and methods

2.1. Site description and sample collection

To answer our research questions, we used a subset from a published dataset of 546 transects (5 m × 500 m, i.e. 0.25 ha) collected across western Amazonia from 1995 to 2012 (Balslev et al., 2019). Each transect was inventoried for palm species abundances, and surface soil samples were analyzed for relevant variables (e.g., pH, texture, concentrations of base cations and other elements). The soil samples (0–10 cm depth, excluding the surface leaf litter layer) were collected at three locations along each transect (one close to each end and one close to the center). Each surface soil sample was composed of five sub-samples taken from the corners and the center of a 5 m × 5 m subunit. In preparation for laboratory processing, all leaf litter and stones were removed from the soil samples, which were then air-dried and stored in cotton or plastic bags or plastic bottles.

Here we use a subset of 63 transects (Fig. 1), selected so as to obtain representative samples of previously identified gradients in palm communities, geographical regions, habitat types, and environmental (climatic and soil) characteristics (Balslev et al., 2019; Tuomisto et al., 2016) (Appendix 1). The soil samples that were collected at the center of the selected transects were analyzed for phytoliths. These ranged in elevation from 78 to 487 m above sea level. The average annual precipitation across the transect locations ranged from 1377 to 5734 mm per year, with an average of 2462 mm year-1 (Karger et al., 2017). The mean annual air temperature across the transect locations was approximately 26 °C. The full array of soil properties and environmental characteristics for each transect can be found in Appendix 1 and Balslev et al. (2019).

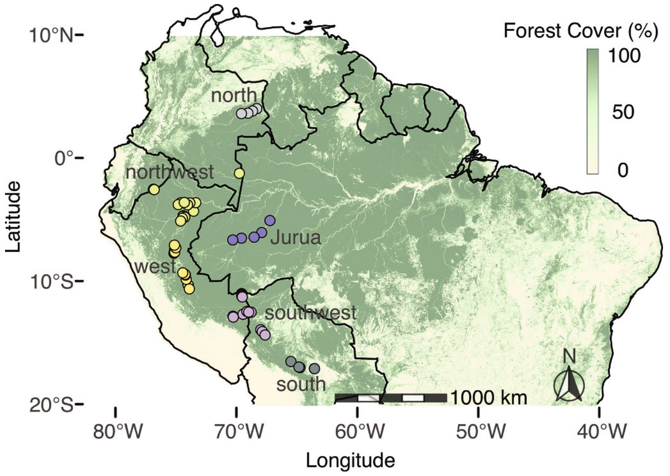

Fig. 1. Locations of the transects used in the present paper across western Amazonia ($N = 63$), color coded and labeled by geographical region (sensu ter Steege et al., 2013). The transects were inventoried for palms, and corresponding soil samples were analyzed for base cations and phytoliths. The background map is fractional tree cover in 2021 (GLOBMAP FTC) derived from MODIS spectra (Liu et al., 2024).

2.2. Phytolith analysis

Phytoliths were extracted from 1 cm^3 of each surface soil sample ($N = 63$) using standard laboratory techniques (Piperno, 2006). Samples were soaked in beakers with enough 33% H_2O_2 to submerge the samples, then heated until reactions are completed (while keeping enough H_2O_2 in the beaker). Afterwards, samples were centrifuged and washed in 10% HCl and $KMnO_4$ to remove organic material, carbonates, and humic acids. The samples were decanted to remove any clay particles, and then bromoform ($CHBR_3$, specific gravity of 2.3) was added to the sediment to separate the phytoliths and microspheres from the remaining soil material. The extracted phytoliths were then mounted on slides using Naphrax. The samples were unfortunately not able to be rotated for a three-dimensional inspection of phytoliths.

Phytoliths were identified using a Zeiss Axioscope at a magnification of 1000X using immersion oil. A minimum of 300 phytoliths were counted per sample, including at least 100 non-arboreal phytoliths. The total counts of the samples varied between 300 and 602, with an average of 400 phytoliths per sample being counted (Appendix 1). Phytolith morphotypes were identified using the latest literature and published guides (Chen and Smith, 2013; Morcote-Ríos et al., 2016; Piperno, 2006; Piperno and McMichael, 2020; Piperno and McMichael, 2023; Witteveen et al., 2022). Plants that produce phytoliths, including palms, typically also produce a variety of morphotypes (Piperno, 2006). The array of phytolith morphotypes produced by the palm species found in the vegetation transects were classified according to Witteveen et al. (2022) (Table 1, Appendix 2).

2.3. Data analysis

To prepare the data for ordination and regression analyses, we divided the 63 transects into six geographic regions (Fig. 1) based loosely on the biogeographic regions of ter Steege et al. (2013). Earlier studies have found soil base cation concentration to be strongly related to palm species abundances (Cámara-Leret et al., 2017; Tuomisto et al.,

Table 1
The palm genera found across the 63 transects and the phytolith morphotypes they produce. The number of species per genus and the number of individuals per genus (# individuals) across all 63 plots are shown alongside the phytolith morphotypes produced by each genus. Phytolith morphotypes with an asterisk (*) have variants that are genus specific. For images of each phytolith morphotype, see Appendix 2. Morphotypes are classified according to Witteveen et al. (2022) unless otherwise denoted.

Genus or species	# species	# individuals	Phytolith morphotypes
CONICAL PALM PHYTOLITH PRODUCERS			
Aiphanes Willd.	4	84	CON_TAB + CON_ECH
Astrocaryum G. Mey	9	4559	CON_FEW + CON_ECH + CON_ECH_PRO + CON_TAB
Bactris Jacq. ex Scop.	22	6688	CON_FEW + CON_ECH_PRO*
Chamaedorea Willd.	3	296	CON_FEW + CON_ECH + CON_TAB
Desmoncus Mart.	5	477	Conical (Morcote-Ríos et al., 2016)
Geonoma Willd.	13	13,481	CON_BAS*
Iriartea deltoidea Ruiz & Pav.	1	1726	CON_FEW + CON_FEW_OBL*
Iriartella H. (Mart.)H. Wendl.	2	236	Conical (Morcote-Ríos et al., 2016)
Socratea exorrhiza Wendl.	1	2427	CON_FEW + CON_FEW_CIR*
Wendlandiella gracilis Dammer	1	292	Unreferenced – assumed to create CON_FEW + CON_ECH + CON_TAB as it is closely related to *Chamaedorea*
Wettinia Poepp. ex Endl.	4	37	CON_TAB + CON_ECH
SPHERICAL PALM PHYTOLITH PRODUCERS			
Aphandra Barfod	1	5	Unreferenced – assumed to create SPH_ECH + SPH_SYM as it is closely related to *Phytelephas*
Attalea Kunth	8	6243	Large_SPH_ECH* + Large_SPH_TUB* + SPH_ECH + ELL_ECH + SPH_TUB
Chelyocarpus ulei Dammer	1	16	SPH_ECH + SPH_ACU_S (Morcote-Ríos et al., 2016)
Cocos nucifera L.	1	1	SPH_SYM (Fenwick et al., 2011)
Elaeis oleifera (Kunth) Cortés	1	2	ELL_ECH + SPH_ECH
Euterpe Mart.	2	5610	SPH_ACU_LARGE* + SPH_SYM* + SPH_ECH + ELL_ECH + EUT_SPH*
Hyospathe elegans Mart.	1	700	ELL_ECH + SPH_ECH + REN
Lepidocaryum tenue Mart.	1	461	SPH_ECH (Morcote-Ríos et al., 2016)
Mauritia flexuosa L.f.	2	104	SPH_SYM* + SPH_ECH + ELL_ECH
Mauritiella Burret	2	420	SPH_ECH + ELL_ECH + SPH_ACU_SMA
Oenocarpus Mart.	5	2695	SPH_ECH + ELL_ECH + SPH_ACU* + SPH_TUB* + SPH_SYM + SPH_ROU
Pholidostachys H. Wendl. ex Benth. & Hook. f.	1	3	ELL_ECH + REN (Morcote-Ríos et al., 2016)
Phytelephas Ruiz & Pav.	2	2232	SPH_ECH (Morcote-Ríos et al., 2016)
Prestoea schultzeana (Burret) H.E. Moore	1	79	PRE_SPH + SPH_ACU_S + ELL_ECH + REN (Morcote-Ríos et al., 2016)
Syagrus sancona (Kunth) H. Karst	1	45	SPH_ECH + ELL_ECH + SPH_ACU_S (Morcote-Ríos et al., 2016)

2016), so we calculated for each of the 63 soil samples the sum of the concentrations of the exchangeable base cations calcium, magnesium, and potassium (hereafter: base cation concentration). The base cation concentrations were measured from the center soil sample of each transect. The sum of the base cations was then $\log_{10}$-transformed for analysis. We calculated the number of palm genera (palm richness) and individuals (palm abundance) for each transect (Table 1). Kruskal-Wallis Tests were used to determine if palm richness or abundance varied significantly between regions. We calculated the total number of palm individuals that produce the two main types of palm phytoliths (conical and spheroid) for each plot. Following standard palaeoecological protocol, we then calculated for each phytolith morphotype its proportion out of the total number of phytoliths counted for each sample.

Only the percentages of palm phytoliths were used in ordination analysis to directly compare phytolith percentages with vegetation abundances. Note that we did not recalculate palm phytolith percentages but used the percentage of each morphotype out of *all* phytolith morphotypes in our ordination analyses. This was done to account for the fact that other vegetation types were present in the landscape, but to minimize their influence in palm phytoliths and palm (plant) relationships. We generated two distance matrices using the Bray-Curtis distance metric, one on palm abundance data and the second on the percentages of palm phytolith morphotypes ($n = 25$ types, see Appendices 1 and 2). We used a Mantel test with 999 permutations to test if the two distance matrices were correlated with each other. Principal coordinate analysis (PCoA) was used to illustrate the patterns in among-transect differences separately for palm species abundances and for phytolith morphotype abundances. To facilitate the interpretation of the ordinations, their visualizations include specific symbols for habitat type, base cation concentration, and geographic region.

To test if phytoliths can reconstruct past changes in palm abundances, we used negative binomial generalized linear models to predict the abundances of palm species based on the phytolith and soil data. We calculated the number of plots where each palm genus occurred, and only included genera that occurred in >10 transects. For each genus that met this criterion, we set up the negative binomial regression to predict the number of individuals at a site using as predictors the first two axes of the principal coordinate analysis (PCoA) on phytolith data, the percentage of grass phytoliths found in a sample, and the base cation concentrations. Because the phytolith data would be used for each of the predictions, we adjusted the resulting p-values from the generalized linear model using the Bonferroni correction. We assessed the relationships between the predictor variables and the palm abundances along the gradient of the predictors.

3. Results

A total of 26 palm genera were identified in the 63 transects (Appendix 1). The number of palm genera per transect ranged from 2 to 16 and most transects contained between six and eight genera (Fig. 2a). The abundance of palms ranged from 80 to 2533 individuals per transect (Fig. 2b), and Kruskal-Wallis tests indicated that there were no significant differences in the number of palm individuals or the number of palm genera between regions ($\chi^2 = 9.14$, df = 5, $p = 0.10$). Half of the palm genera (13 of 26) occurred in >10 of the 63 transects (>15%) (Tables 1, S1) and were used in further analyses. *Astrocaryum*, *Attalea*, *Bactris*, *Euterpe*, and *Geonoma* each occurred in over 80% of the sampled transects (Table S1). Other common palm genera were *Chamaedorea*, *Desmoncus*, *Iriartea*, *Oenocarpus*, and *Socratea*, which occurred in 40–80% of the sampled transects. These widely distributed palm genera also tended to have higher abundances in the transects (Table 1, Appendix 1).

Most palm genera occurred in more than one region (Fig. 3). *Astrocaryum*, *Attalea*, *Bactris*, *Euterpe*, *Geonoma*, *Oenocarpus*, and *Socratea* occurred in all regions but not in all transects. The abundances of all

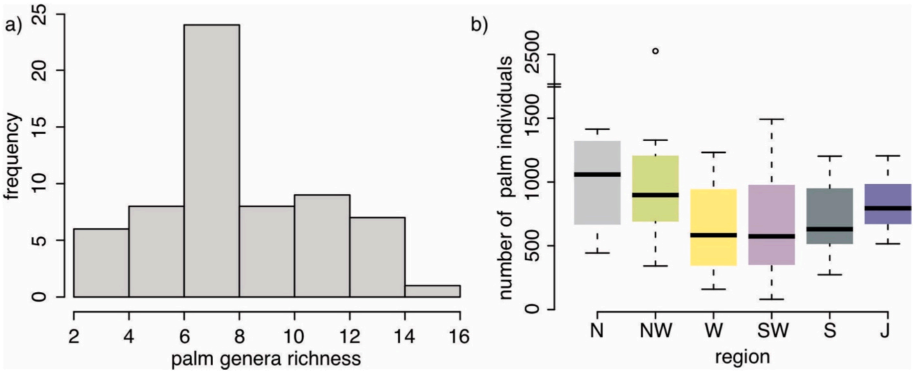

Fig. 2. a) Frequency distribution of the number of palm genera per transect, and (b) the number of palm individuals found per transect in each of the geographic regions shown in Fig. 1. Abbreviations of geographic regions: N = north, NW = northwest, W = west, SW = southwest, S = south, J = Jurua.

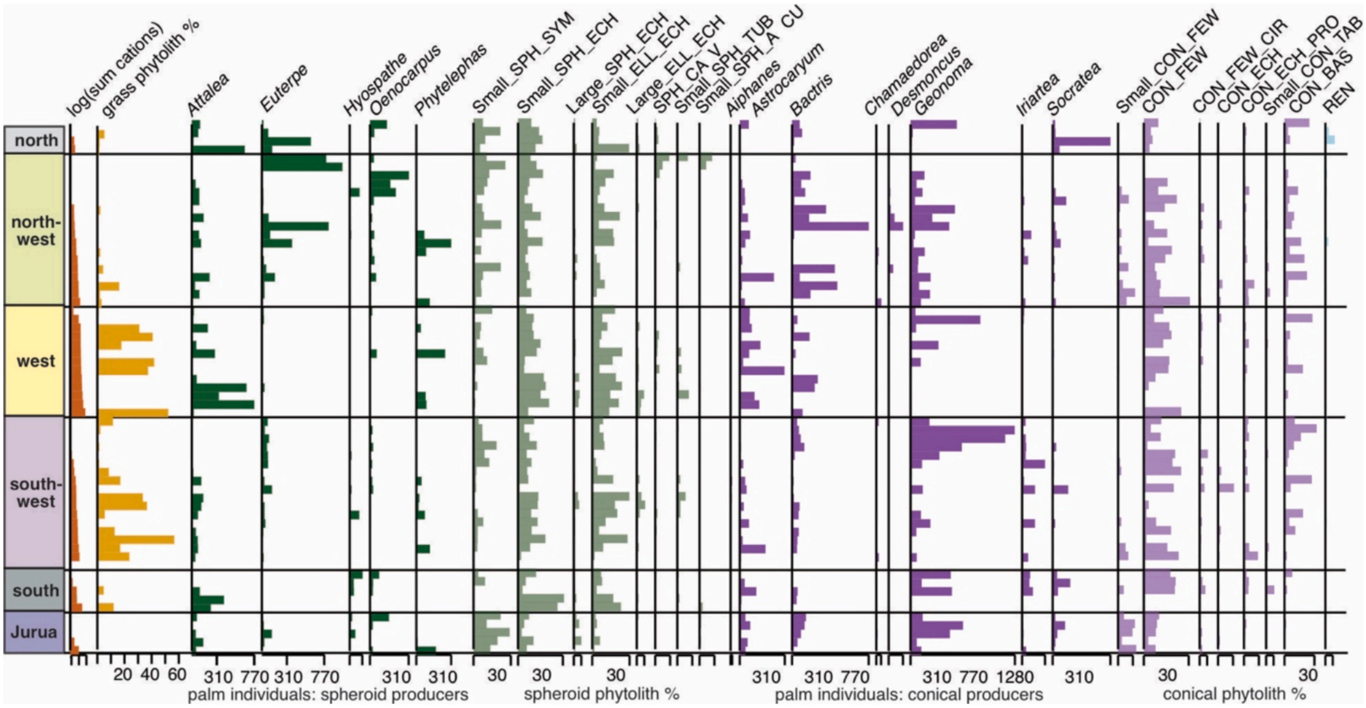

Fig. 3. Abundances of palms and palm phytoliths in 63 transects across western Amazonia (for locations, see Fig. 1). Palm compositions are shown to the left of the regional classification and palm phytolith compositions to the right. Within each region, transects are sorted by soil base cation concentration (orange bars). Grass phytolith abundances are shown for comparison, and are colored yellow. Palm genera are colored green or purple according to which of two major groups of palm phytoliths they produce (spheroid or conical, respectively), and the phytolith types are colored accordingly. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

genera were locally variable both between transects within a region and between regions (Fig. 3). The strongest gradient in palm genus turnover (PCoA Axis 1) was associated with soil base cation concentration (Fig. 4). Most of the transects located on non-inundated terra firme soils (TF) were in the lower left quadrant of the PCoA plot, but two floodplain transects from the southern region also fell in this quadrant. Floodplain and terrace transects primarily fell in the upper two quadrants of the PCoA plot, and the restinga and white sand transects in the lower right quadrant (Fig. 4).

The phytolith assemblages contained 24 morphotypes associated with palms. In addition, there were 16 phytolith morphotypes associated with dicotyledonous trees (hereafter arboreal), 22 associated with Poaceae, several associated with *Heliconia* and Asteraceae, and some unknowns (Appendix 1–2). Arboreal phytoliths ranged from 1% to 83% (Fig. S1). Arboreal phytolith abundances varied within regions, but northwestern Amazonia and the Jurua regions typically had the highest abundances of arboreal phytoliths (Fig. S1). Poaceae phytoliths were absent from 13 samples (22%) and ranged from < 1% to 55% where they occurred, exceeding 20% in eleven samples from floodplain and terra firme forests primarily in the west and southwest regions (Figs. 3, S1). The most common grass types were rondels and tall saddles. *Heliconia* phytoliths occurred in 33 samples (57%) and Asteraceae phytoliths in 7 samples (12%), but their occurrences did not show geographic patterns (Appendix 1). Cyperaceae phytoliths were only found in two samples and in abundances less than 1%. Zingiberales phytoliths occurred in most samples, but never in abundances over 2%. Both conical and spheroid palm phytoliths were present in all samples, and ranged from 7% to 86% of the total phytolith assemblage (Fig. S1).

The relative abundances of palm phytolith morphotypes varied within and between regions, and sometimes the association with specific palm genera observed in the transect were clear. For example, small ellipsoidal echinate (Small_ELL_ECH) palm phytoliths tended to occur in

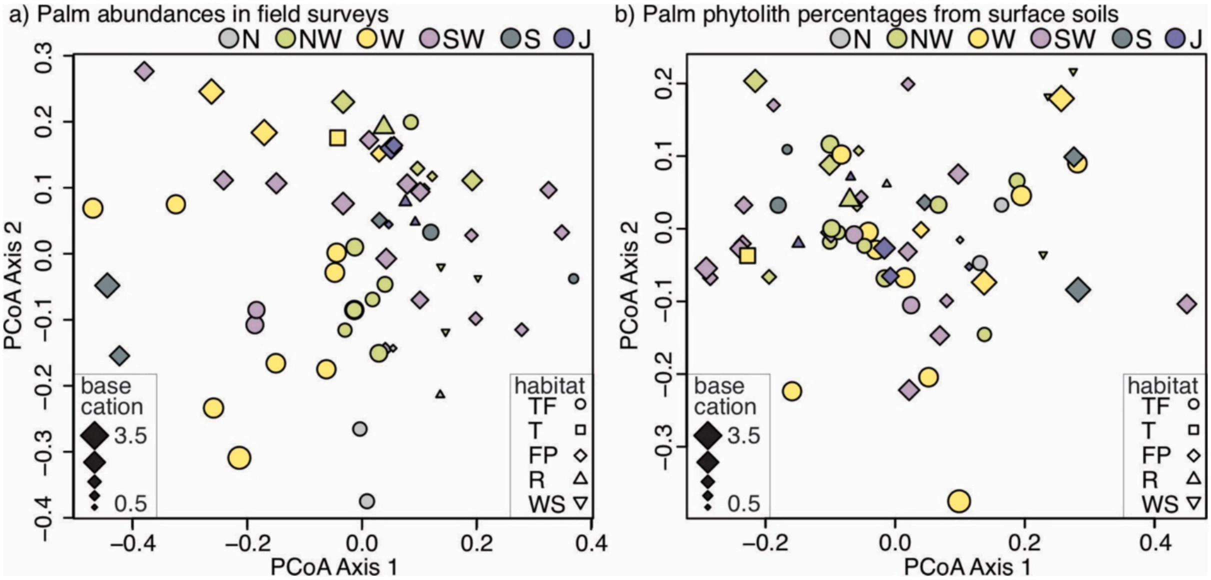

Fig. 4. Principal coordinates analysis (PCoA) of the a) abundances of palm genera and b) abundances of palm phytolith types from 63 transects across western Amazonia. Each point represents a transect and is color-coded by geographic region (N = north, NW = northwest, W = west, SW = southwest, S = south, J = Jurua) as shown in Fig. 1. Symbols indicate habitat type (TF = terra firme, T = terrace, FP = floodplain, R = restinga, WS = white sand), and symbol sizes are proportional to the $\log_{10}$-transformed soil base cation concentration (sum of calcium, magnesium, and potassium).

transects with high abundance of *Attalea* palms (Fig. 3). In the southwest region, there was a turnover from *Euterpe/Oenocarpus* in the transects on cation-poor soils to *Attalea/Phytelephas* on cation-rich soils, and a turnover in the corresponding soil samples from Small_SPH_ECH phytoliths to Small_ELL_ECH phytoliths (Fig. 3). Except for the south and Jurua regions, transects with elevated levels of *Geonoma* palms also contained elevated abundances of CON_BAS phytoliths (Fig. 3). CON_FEW phytoliths were common and abundant in the soils regardless of the abundances of the palm genera that produced them (*Astrocaryum*, *Bactris*, *Iriartea*, *Socratea*).

In PCoA, Axis 1 was clearly correlated with soil base cation concentration when the analysis was based on palm inventories, but not when it was based on palm phytolith assemblages (Fig. 4). The phytolith assemblages also did not show as clear structure related to region or habitat type as the palm inventories did. Nevertheless, the Mantel test between Bray-Curtis dissimilarities as calculated with palm inventories versus palm phytolith assemblages showed a significant and positive correlation ($r = 0.382$, $p < 0.001$, Fig. S2). In addition, increasing abundance of palms producing conical and spheroid phytoliths (the two main groups of palm phytoliths) in the inventories was associated with an increase in the percentage of these types of phytoliths in the corresponding soil samples (Fig. 5). The slopes of the best fit lines were similar for conical and spheroid phytoliths, although the intercept was higher for conical than spheroid phytoliths.

None of the palm genera tended to increase with increasing grass phytolith percentages. Overall palm abundances were highly variable in transects containing low abundances of grass phytoliths, but transects with higher percentages of grass (Poaceae) phytoliths were negatively related to palm abundances (Fig. 5). Out of the 16 samples with grass abundances >10%, 14 came from the west and southwest regions but they were evenly distributed between floodplain and terra firme transects (Fig. 3, Appendix 1).

To test if palm abundances are predictable with phytolith data, we modeled the abundances of the 13 palm genera observed in >10 transects with negative binomial generalized linear models. As predictors, we used Axes 1 and 2 values from the PCoA based on palm phytolith assemblages, total grass phytolith percentages, and the $\log_{10}$-transformed base cation concentrations (sum of Ca, Mg, K). The total abundances of the “spheroid phytolith producing palm” genera and “conical phytolith producing palm” genera were analyzed in a similar way. In all models, at least one of the predictor variables was significant, except for *Astrocaryum*, *Desmoncus* and “spheroid phytolith producing palms” (Fig. 6). PCoA Axis 1 was a significant predictor for nine genera (Fig. 6). Positive PCoA Axis 1 scores were associated with increased abundances of *Euterpe*, *Oenocarpus*, *Hyospathe*, *Socratea, Iriartea*, *Geonoma*, and

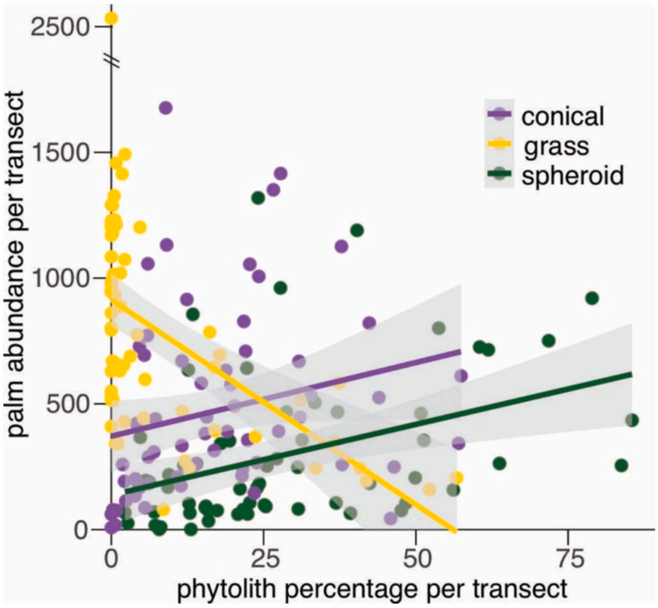

Fig. 5. Percentages of phytoliths collected from surface soil samples compared with palm abundances across 63 western Amazonian transects. Conical and spheroid palm phytolith percentages are calculated based on the total number of palm phytoliths found in the sample, and are compared with the abundances of palm genera that produce those types of phytoliths. Grass phytolith percentages are calculated out of the total number of phytoliths counted, and are compared with the total palm abundance for the transect. The best fit regression line (using a general linear model) and confidence intervals are shown for all three phytolith groups.

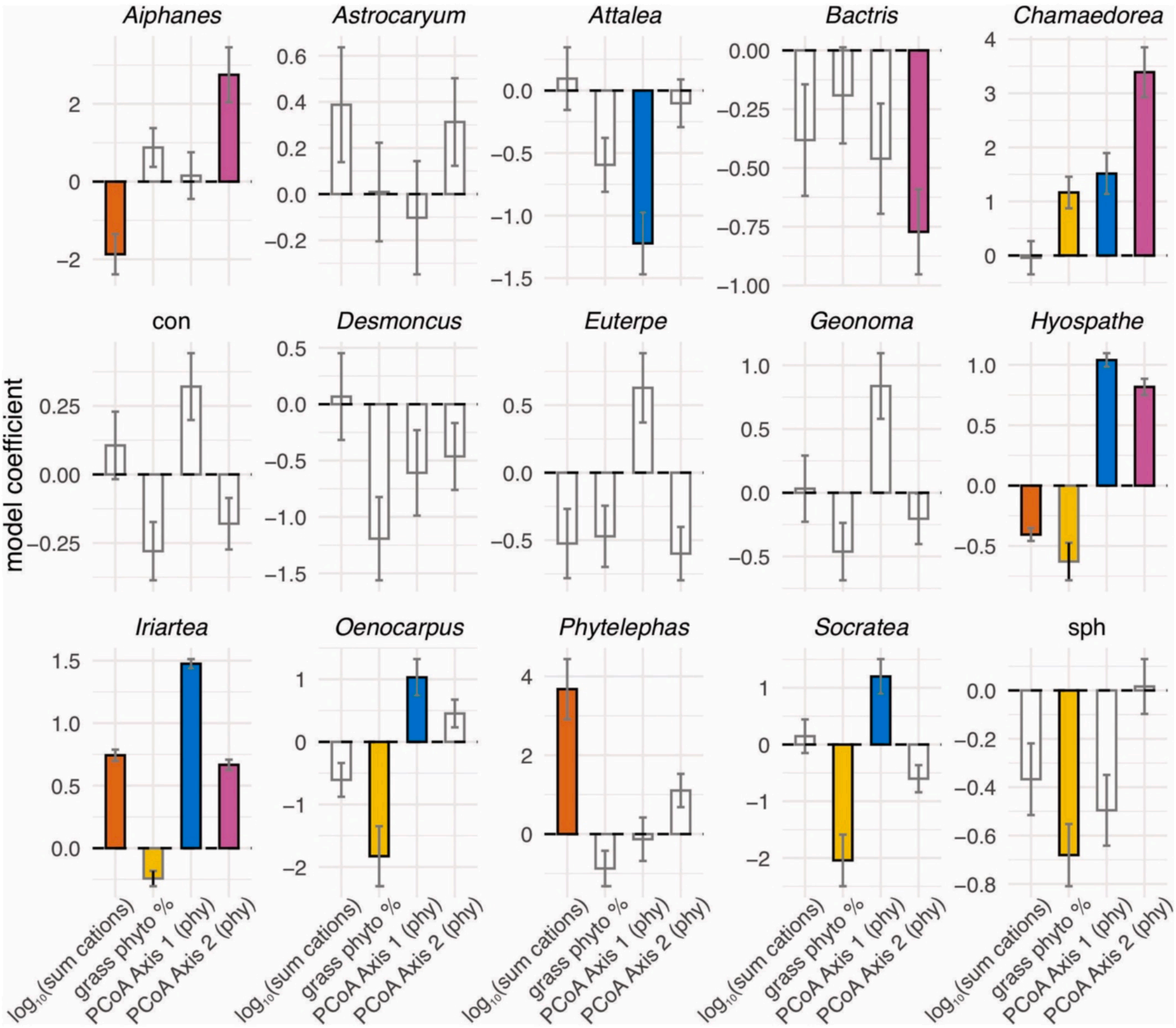

Fig. 6. Model coefficients and significance values for variables (phytolith PCoA Axis 1, phytolith PCoA Axis 2, grass phytolith percentages, and $\log_{10}$-transformed base cation concentrations) used to predict the abundances of palms in western Amazonia. Predictor variables are shown along the x-axis and model coefficient values from the negative binomial generalized linear model are shown on the y-axis. Unfilled bars indicate non-significant predictors in the model, filled bars significant predictors. Each variable is given a different color for visual clarity. Each palm genus was modeled separately, and additional models were run for all palm genera that produce conical phytoliths together (con), and for all palm genera that produce spheroid phytoliths together (sph).

“conical phytolith producing palms” (Fig. 7). Negative PCoA Axis 1 scores were associated with increased abundances of *Attalea* and *Chamaedorea* (Fig. 7). Positive PCoA Axis 2 scores were related to increased abundances of *Hyospathe*, *Aiphanes*, and *Chamaedorea*. Negative PCoA Axis 2 scores were related to increased abundances of *Bactris*, *Euterpe*, *Iriartea*, *Phytelephas*, and *Socratea* (Fig. 7). Base cation concentration was a significant predictor for five species (Fig. 6). Low cation values were associated with increased abundances of *Aiphanes*, *Hyospathe*, and *Oenocarpus*, while high cation values were associated with high abundances of *Iriartea* and *Phytelephas* (Fig. 7).

4. Discussion

Palm distributions in western Amazonia are linked to regional-scale climatic gradients and local-scale soil and topographic gradients (Balslev et al., 2016; Balslev et al., 2017; Balslev et al., 1987; Macía and Svenning, 2005; Svenning, 2001; Svenning et al., 2009; Svenning, 1999; Zuquim et al., 2023). The abundances of the 26 palm genera that occurred across our 63 sampled sites were driven primarily by soil base cation concentration (Fig. 4a), which agrees with previously published analyses of the sites (Cámara-Leret et al., 2017; Tuomisto et al., 2016). Though the principal coordinate analysis of the phytolith assemblages did not show an obviously similar pattern with soil cation concentrations as the plants (Fig. 4), the Mantel test showed that phytolith dissimilarity significantly increased alongside increasing palm dissimilarity (Fig. S2). Basically, the relationship between vegetation and phytolith assemblages was not due to random chance, so phytoliths are reliable though not necessarily highly accurate predictors of palm abundances.

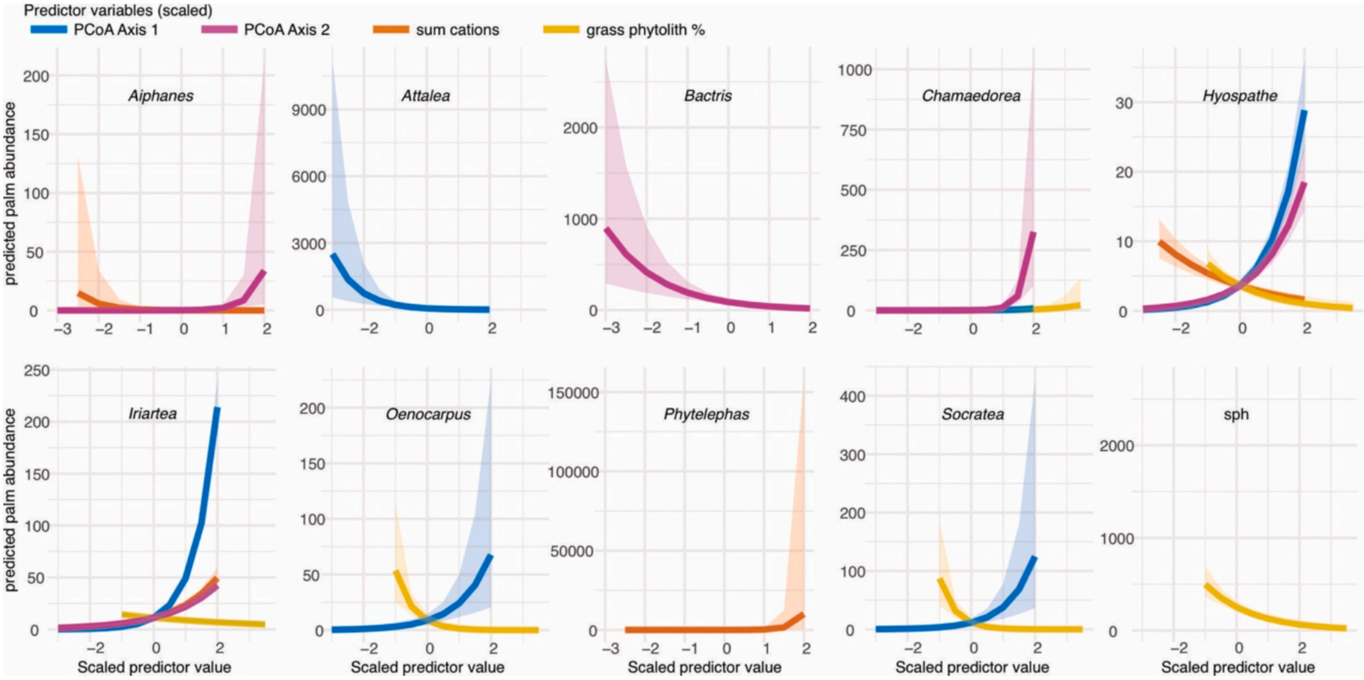

Fig. 7. Predictions of the abundances of palm genera that were found in at least 10 of 63 transects inventoried across western Amazonia. The last panel shows the predictions of total abundance of all palms producing conical phytoliths (sph). Analyses were done with negative binomial generalized linear regression models using as predictor variables Axis 1 and 2 values from palm phytolith assemblage PCoA, percentage of grass phytoliths, and the $\log_{10}$-transformed sum of soil base cation concentrations. Predictor variables are shown with a standardized scale (zero mean and unit variance). Only statistically significant (according to Bonferroni-corrected p-values) relationships are shown.

4.1. Interpreting phytolith data

The palm phytoliths were present and abundant across all transects (Fig. 3) and increased in abundance when the number of palms producing them increased in the landscape (Fig. 5). Previous analysis of phytoliths from herbarium specimens have shown that while palm phytoliths are not diagnostic to species, certain morphotypes can be associated with clusters of species or genera (Table 1) (Huisman et al., 2018; Morcote-Ríos et al., 2016; Piperno, 2006; Witteveen et al., 2022). Phytolith analysis from surficial soils in southwestern Amazonia and the Guiana Shield have shown that palm-dominated forests contain high abundances of palm phytoliths (Watling et al., 2016; Witteveen et al., 2023). Our analysis shows that these patterns can also be detected on larger geographic scales and at finer taxonomic organization levels. Examples include the higher percentages of CON_BAS phytoliths that were documented in transects containing high densities of *Geonoma* palms (Fig. 3). Higher abundances of Small_ELL_ECH phytoliths were also found in transects that had the highest abundances of *Attalea* palms. CON_FEW phytolith percentages typically tracked the presence and abundance of *Bactris* or *Iriartea* palms.

The percentages of grass phytoliths also provided useful information about palm composition and abundances in the landscape. Grass phytolith percentage was a significant predictor in models of *Oenocarpus*, *Iriartea*, *Socratea*, *Hyospathe*, *Chamaedorea* and spheroid palm abundances (Figs. 6–7). The most common grass phytolith morphotypes encountered in the samples were rondels (RON) and tall saddles (SAD_TAL) (Appendix 1), which are often produced by bamboos. Of the 11 samples that contained over 20% grass phytoliths, five were from floodplain sites (Fig. 5). Four of the six terra firme sites report *Guadua glomerata* (bamboo) and other Poaceae in the field notes.

Above a threshold of about 10%, increasing percentage of grass phytoliths typically indicated lower overall abundances of palms in the transects (Fig. 5). Previous work in western Amazonia has shown that canopy gaps that fill with an abundance of bamboos result in regrowing forests that are depauperate in palm richness and abundance (Ziccardi et al., 2021). *Guadua* species dominate areas of the southwestern Amazonian landscape (Carvalho et al., 2013) and physically repress the successful recruitment of other tree species (Griscom and Ashton, 2006). So it is likely that the samples containing high percentages of bamboos had low palm abundances and thus low palm phytolith percentages. Bamboos, however, produce large amounts of RON and SAD_TAL phytoliths (Piperno, 2006). The high production of phytoliths by bamboos and other grasses indicative of canopy opening (e.g., from Panicoid grasses) could potentially reduce palm phytolith percentages to the point to where the correspondence with palm abundances is masked.

One of the main advantages of phytolith analysis is that they reflect local scale patterns of plant composition. Phytoliths collected from Amazonian lake sediments are suggested to reflect a ca. 250 m radius of vegetation around the lake (Witteveen et al., 2024a) and soils are believed to reflect an even smaller area (mainly <100 m) (McMichael et al., 2023a; Piperno, 1985). We obtained a statistically significant positive correlation between the palm phytolith assemblages and palm composition, which was measured on 5 m × 500 m (0.25 ha) transects. Our results support that the appropriate scale of interpretation for soil phytoliths is <1 ha. The local scale representation of phytoliths makes them ideal for calibration studies with local vegetation (e.g., forest plots or vegetation transects) (Watling et al., 2016) or with remote sensing data (Witteveen et al., 2025). The lack of phytoliths showing patterns in broad scale biogeography across Amazonia (Fig. 3) also agrees with previous work (Witteveen et al., 2024a). The taxonomic limitations of phytolith identification and analyses likely obscure the ability to detect regional biogeographic trends in palm diversity. The analysis of the large arboreal phytoliths found in the coarse fractions of soils may provide an avenue to begin unraveling regional differences in vegetation composition (Piperno et al., 2021; Piperno et al., 2024; Watling et al., 2016).

4.2. Estimating past palm abundances in the landscape

Parameterizing relationships between phytoliths (or any microfossil) and aspects of the modern environment is the first step in quantitative predictions of change through time (commonly called 'transfer functions') in paleoecological sequences (e.g., Birks, 2003; Huntley, 1990; Huntley and Prentice, 1988). Phytolith-based transfer functions have been used to estimate past temperature and precipitation in temperate regions (e.g., Liu et al., 2021; Lu et al., 2007; Song et al., 2022). In the tropics, ecosystem characteristics such as forest cover or biomass (Witteveen et al., 2024a; Witteveen et al., 2025), the ratios of C3 and C4 grasses (e.g., Bremond et al., 2008), tree cover (Bremond et al., 2005a) and grass water stress (Bremond et al., 2005b) have been quantified through time using phytolith-based transfer functions. To our knowledge, however, no studies have yet predicted aspects of palm communities using phytoliths.

Several considerations should be made when attempting to reconstruct palm abundances at a given site. The level of identification of the phytoliths needs to be standardized between the calibration dataset of surface soil samples (with paired vegetation data) and the test dataset (the paleoecological or archaeological samples). The source area being measured in the calibration should be comparable with that in the test datasets. Further, a 1:1 relationship between soil phytolith assemblages and palm assemblages cannot exist because of: i) differential phytolith productivity between species and plant parts, ii) multiple species producing the same morphotypes of phytoliths, iii) varying palm to non-palm tree ratios in the landscape (and not all trees produce phytoliths), iv) soil surface samples containing phytoliths that have accumulated over decades and potentially centuries (Piperno, 2006; Watling et al., 2016). Even given these issues and considerations, previous studies have shown that phytoliths can distinguish biomes and local habitat variability in Amazonia (Dickau et al., 2013; Watling et al., 2016; Witteveen et al., 2023).

The significant relationship found with the ordination analysis and Mantel test (Fig. S2) allowed us to generate negative binomial regression models that used principal coordinates analysis axis 1 and 2, soil base cation concentration, and grass phytolith abundances to predict palm abundances (Figs. 6–7). Of the 13 commonest palms encountered in the vegetation surveys, the regressions predicting their abundances were significant in nine genera. The association of palm communities with soils (Fig. 4a) allows us to narrow down the taxonomic identification of the phytoliths. For example, certain phytoliths can be identified to either the *Attalea* and *Oenocarpus* genus. *Attalea* abundances were higher on richer soils; *Oenocarpus* abundances were higher on poorer soils (Fig. 3). *Oenocarpus* is also related to the amount of grass phytoliths (representing forest openness) (Fig. 6). Thus, if the soil cation and grass phytolith information about a site is known, it can help with predicting the amount of *Attalea* versus *Oenocarpus* individuals.

Although 63 samples can only represent a tiny part of the heterogeneity of palm communities across Amazonia, our study shows that there are strong relationships between palm phytoliths and palm composition in the modern landscape (Figs. 3, 5–7). The phytolith assemblages in this study can be used as a calibration dataset to begin quantifying aspects of palm assemblages and their past changes (via soil core samples). We are expanding our database of phytolith-environment relationships and will continue the development of the regression models. Palms are one of the plant groups that are most widely used by people in the tropics (Bernal et al., 2011), and have been so for thousands of years (Clement, 1988; Clement et al., 2015). The ability to estimate changes in palm diversity and the abundances of different palm genera through time provides a new way to measure human influence and the ecological legacies of past people on modern tropical landscapes.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Crystal N. H. McMichael reports financial support was provided by European Research Council. Henrik Balslev reports financial support was provided by Natur og Univers. Henrik Balslev reports financial support was provided by European Commission. Hanna Tuomisto reports financial support was provided by Research Council of Finland. Hanna Tuomisto reports financial support was provided by Aarhus University Research Foundation. Hanna Tuomisto reports financial support was provided by Danish National Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2025.105443.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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