Review of Palaeobotany and Palynology Research Article

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Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions II: southwestern Amazonian forests

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Abstract:

Accurate archaeological and palaeoenvironmental reconstructions using phytoliths relies on the study of modern reference material. In eastern Acre, Brazil, we examined whether the five most common forest types present today were able to be differentiated by their soil phytolith assemblages, and thus provide analogues with which to compare palaeoecological assemblages from pre-Columbian earthwork sites in the region. Surface soils and vegetation from dense humid evergreen forest, dense humid evergreen forest with high palm abundance, palm forest, bamboo forest and fluvial forest were sampled and their phytoliths analysed. Relative phytolith frequencies were statistically compared using Principal Components Analyses (PCAs). We found the major differences in species composition to be well-represented by the phytolith assemblages as all forest types, apart from the two sub-types of dense humid evergreen forest, could be differentiated. Larger phytoliths from the sand fraction were found to be more ecologically diagnostic than those from the silt fraction. The surface soil phytolith assemblages we analysed can therefore be used as analogues to improve the accuracy of archaeological and palaeoecological reconstructions in the region.

Key words: Phytoliths, palaeoecology, archaeology, southwest Amazonia

1. Introduction

In the mid-20th century, cultural ecologists proposed that the characteristics of soils, cyclical climatic changes, and the scarcity of protein presented limitations to cultural evolution in the Amazon tropical forest (Steward, 1948; Meggers, 1954; Gross, 1975). According to this vision, population density would have remained low, and humans had to adapt to tropical environments without modifying it substantially. In

1. Introduction

In the mid-20th century, cultural ecologists proposed that the characteristics of soils, cyclical climatic changes, and the scarcity of protein presented limitations to cultural evolution in the Amazon tropical forest (Steward, 1948; Meggers, 1954; Gross, 1975). According to this vision, population density would have remained low, and humans had to adapt to tropical environments without modifying it substantially. In the following decades, the cultural ecology paradigm lost its strength as scholars from different fields pointed to diverse forms of landscape modifications – plant management, soil mulching and earth moving for building mounds, raised fields, fish weirs, roads and dams – that would have impacted the environment and allowed a substantial increase in population density starting around 2,000 years ago (Roosevelt, 1980; Smith, 1980; Posey and Balée, 1989; Denevan, 2001; Erickson and Balée, 2006; Schaan, 2008; Iriarte et al., 2010; Schaan 2012; Rostain, 2013).

However, despite a growing body of literature emphasizing indigenous agency over the landscape, the extent to which human societies modified tropical landscapes is still a matter of debate, since the Amazon basin encompasses different types of environments which were differentially occupied in the past. While some argue that pre-Columbian landscape transformation was far more extensive in floodplains and highly seasonal regions (e.g. McMichael et al., 2012a; Piperno et al., 2015; Bush et al., 2015), others believe that the terra firme interfluves, which make up over 90% of Amazonia, were also transformed considerably (e.g. Heckenberger et al., 2003; Clement et al., 2015; Stahl, 2015).

In southwestern Amazonia (Acre state, Brazil), the discovery of over 450 geometrically-patterned earthworks (“geoglyphs”) situated in recently-deforested interfluvial areas (Pärssinen et al., 2009; Saunaluoma & Schaan, 2012; Schaan et al., 2012) has sparked questions over both the nature and size of the population that built them, and the extent to which they transformed the environment for the construction and use of the sites. In a recent paper, McMichael et al. (2014) modelled remote sensing data from the area to predict that the geoglyphs were originally constructed near the edges of bamboo (*Guadua*)-dominated forests. Bamboo forests today cover 161,500 km^2 of southwestern Amazonia (de Carvalho et al., 2013) and are much more open than other types of forest in the region, owing to the aggressive nature of the bamboos which kill trees and restrict sapling growth (Griscom and Ashton, 2006). Phytoliths from sediment cores in northern Acre close to the border with Amazonas state suggests that these forests have been around for most of the Holocene (McMichael et al., 2013). However, a recent study (Carson et al., 2014) suggests that in some areas further south, forest expanded after many prehistoric earthworks were built. It is unclear whether current forest distribution and composition mirrors that at the time of the geoglyph builders, however knowing this information is essential for understanding past human impact on the environment. If the geoglyph sites were once under bamboo forest then the task of forest clearance could have been facilitated by exploiting bamboo die-off events and the naturally more open environment afforded by this forest type. On the other hand, dense humid evergreen forest would have required much more labour to clear, especially with stone axes (Carneiro, 1979; Denevan, 2006). Also important is the question of what environmental legacy, if any, was left by these populations after the region was abandoned around the time of European Contact.

Palaeoecological studies are currently being conducted in Acre are aiming to answer these questions and to shed light on debates about the resilience of Amazonian ecosystems, the importance of an anthropogenic component in their conservation, and how to promote sustainable exploitation of forest resources.

The proxy we are using in these investigations is phytolith analysis. Phytoliths are opal silica bodies produced in the leaves, stems and inflorescences of plants (Piperno, 2006) and they have several advantages for investigating human-environment relationships in the study area. Firstly, they are an essential tool for reconstructing vegetation histories in interfluvial regions because, unlike pollen, they survive very well in terrestrial soils, including in the highly oxidised, acidic soils that characterise much of Amazonia and Acre (Piperno and Becker, 1996; Quesada et al., 2011). Secondly, as phytoliths are released into the soil where the plant dies and decomposes, they provide a highly localised signature of the vegetation in a given place, particularly beneficial for investigating the spatial extent of a vegetation type or past anthropogenic impact.

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Our ability to interpret fossil phytolith assemblages, and thereby contribute to archaeological and ecological debates, relies on their comparison with phytolith assemblages present underneath standing modern vegetation. Given the complexity and heterogeneity of neotropical ecosystems (Moran, 1993; Piperno and Pearsall, 1998a), area-sensitive appraisals of the types of vegetation present and the ability for these to be distinguished by phytoliths are necessary to allow more accurate and finer-grained interpretations of fossil assemblages. This study is the second of a series of papers aimed at characterising phytolith assemblages from Amazonian vegetation types (Dickau et al., 2013), and is similar to studies that have been conducted in other regions of the neotropics (Piperno, 1988) and tropical Africa (Alexandre et al., 1997; Runge, 1999; Bremond et al., 2005; Barboni and Bremond, 2009; Mercader et al., 2011; Aleman et al., 2012; Novello et al., 2012).

In this study, we determined whether different modern vegetation formations present today in the geoglyph region can be differentiated by their surface soil phytolith assemblages with the view to using them as analogues to compare with assemblages from archaeological and palaeoecological contexts. The work involved (i) selecting appropriate forest types to study and determining species composition within these forests, (ii) analysing their phytolith composition, and (iii) evaluating the relationship between surface phytolith composition and forest composition. This research provides an improved understanding of the sensitivity of phytoliths to vegetation variability and their usefulness in palaeoecological reconstructions, and offers some insites into phytolith production and deposition mechanisms.

2. Study area

2.1 Climate and geology

The climate of Acre state is characterised by seasonal precipitation ranging from 1566–2425 mm/year (average 1944 mm/year) (Duarte, 2005), with the east being drier than the west. Most rainfall occurs during the rainy season (October to April), while the dry season (June to August), can bring severe droughts (Aragão et al., 2007).

The state is situated between two geological formations: the Andes to the west and the Brazilian shield to the southeast. The orogeny of the Andes continues to form the relief, soils and hydrological basins through the uplift, deposition and re-working of sediments (Silveira et al., 2008). Acre's "eroded washboard" relief is gently undulating with closely and regularly spaced hills over the majority of the state, only becoming steeper upstream from the major rivers. The soils are for the most part sandy clay sediments belonging to the Solimões Formation, which were formed by Andean uplift between the end of the Miocene and the Pliocene (Westaway, 2006). Like the majority of Amazonian soils, they are highly acidic, shallow and poorly drained, which gives them a low agricultural potential (Silveira et al., 2008). Many rivers drain the state in a north easterly direction, the largest of which are the Juruá and the Purus, which carry heavy sediment loads due to their meandering forms. Floodplains and terraces comprised of more fertile alluvial soils flank the Juruá, Purus, and Acre rivers, but are either absent or very limited along the smaller rivers (*ibid.*).

2.2. Archaeological background

Despite initial investigations as part of PRONOPABA (Programa Nacional de Pesquisas Arqueológicas na Bacia Amazônica) in the 1970s, the archaeological significance of the geoglyphs remained unrecognised until they were re-discovered by chance during a commercial flight in the 1990s (Ranzi, 2003). Since then, increasing deforestation in the region and the use of free satellite imagery provided by Google Earth (Ranzi et al., 2007) has led to the discovery of over 450 geoglyphs – geometric ditched enclosures that vary in size from less than one to 15 hectares.

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Radiocarbon dates place the geoglyph culture(s) in the Formative Period in Amazonia (1000 BC – AD 1491) and demonstrate a proliferation in site building at the turn of the Christian Era. The latest date so far obtained is from Fazenda Colorada, which had continuous human activity between 25–342 cal AD, and an additional later phase dated 1244–1378 cal AD, while dates from other sites indicate several episodes of use during the first millenium AD (Schaan et al., 2012).

Excavations at several geoglyph sites since 2008 have revealed repeated patterns in their archaeological records. Most notable are the absence of artefacts deposited in the spaces enclosed by the banks and ditches, and the paucity of cultural material found at the sites in general. Such observations have led archaeologists to suggest ritual or ceremonial, rather than habitational, functions for the geoglyphs (Saunaluoma and Schaan, 2012).

2.3. Vegetation formations in Acre

Figure 1 is a map of modern vegetation formations in the study area. Botanical inventories conducted in eastern Acre have shown that its forests have floristic similarities with drier formations of the Central Amazon; and, although less diverse than forests near Manus, their alpha diversity is higher than roughly half of similar inventories throughout Amazonia (Silveira et al., 2008). In contrast to the dense forests present in the Central Amazon however, most of Acre is covered by forms of open forest which allow greater light penetration to the understory and the growth of bamboo, palms and other monocots (*ibid.*).

The First Catalogue of the Flora of Acre (Daly and Silveira, 2008) distinguishes five broad categories of forest type in the state. The first is open arborescent bamboo (*Guadua werberbaueri*) forest already mentioned in section 1. In some regions, bamboo also occurs alongside dense forest or on alluvial soils, and together these formations with bamboo make up 59% of the forest cover of Acre (Acre, 2000). Palm forest is the second dominant type of open forest in Acre and it can also be found intermixed with dense forest. As implied by the name, palms characterise the vegetation, with some genera such as *Attalea* and *Astrocaryum* determining the open character of the forest due to their large leaves which shade the soil and reduce tree sapling growth. Like bamboo forests, palm forests occur on a variety of different soil types, including waterlogged alluvium (Silveira et al., 2008). Patches of dense forest occur in the lowlands of southeast Acre in interfluvial zones, often separated by areas of palm and bamboo forest. The floristic make-up of these dense humid evergreen forests is very different to the dense submontane formations found further west (Acre, 2000). Fluvial forests occur along the floodplains and banks of many of Acre's rivers, though they do not reach as large proportions as those found in the lower courses of the tributaries of the Amazon river. There are several sub-types of fluvial forest that dominate according to the depth and duration of flooding (annually or supra-annually) and the age of the accumulated sediments (Silveira et al., 2008). Epiphytes are known to be particularly abundant and diverse in fluvial forests (*ibid.*).

3. Methods

3.1. Vegetation and field sampling methods

3.1.1 Site selection

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3.1.1 Site selection

All of the formations currently found in the geoglyph region were sampled for their surface soils. These included bamboo forest, palm forest, dense humid evergreen forest, dense humid evergreen forest with high palm abundance and fluvial forest (see Figure 1 for sample locations). The decision to sample fluvial forest was based less on archaeological questions and more on the fact that phytolith assemblages from these environments in Amazonia have not been previously tested.

For the bamboo and dense humid evergreen forests, sampling locations were based in plots with pre-existing botanical inventories monitored by the RAINFOR programme, an international collaborative project which has researched ecosystem dynamics across the Amazon since 2000, with the first plots in Acre set up in 1991 (www.rainfor.org). Species data was accessed with permission from www.forestplots.net (Lopez-Gonzalez et al., 2011) and soil samples taken along transects within the 1 ha plots. For all RAINFOR plots, trees >= 10 cm diameter at breast height (DBH), or above buttresses and deforities were inventoried and identified to genus or species.

As there are not currently any monitored plots with detailed inventories situated in Acre's palm or fluvial forests, sampling locations were chosen and species presence recorded in the field for trees >= 10 cm DBH. The palm forest sampled in this analysis is an area for which botanical inventories are currently being created in collaboration with UFAC (Universidade Federal do Acre) and timber extractors working in nearby reserves. A narrow strip of forest located on the floodplains of the Rio Andira was chosen for the fluvial forest samples based on ease of accessibility. This small river (*riozinho*) is a tributary of the Purus, which has its origin in the Peruvian sub-Andes and drains the Brazilian states of Acre and Amazonas in a northeasterly direction before eventually joining with the Solimões/Amazon river west of Manaus. Every year between December and April, the waters of the Rio Andira rise as high as 15 m, completely covering the forest floor and often flooding the adjacent highway.
Naming, location and species data for all of the forest plots are provided in Table 1.

Figure 1: Map of vegetation formations and plot locations

Table 1: Naming, location and species data for all forest plots

3.1.2. Surface soil sampling

Ten samples were collected from each vegetation community listed in Table 1. The RAINFOR plots (POR-01, POR-02 and RFH-1) all measured 1 ha in area, though the area dimensions differed from 25 x 400 m in the bamboo forest to 10 x 1000 m in the dense humid evergreen forests. Samples were therefore taken every 50 m in the bamboo forest and every 100 m in the dense humid evergreen forests to ensure that the entirety of the transects were sampled (See Table 2). In the palm and fluvial forests, samples were taken every 50 m and species presence data recorded along the length and up to roughly 5 m either side of the transect.

Table 2: Key of sample abbreviations

During sampling, care was taken to remove the leaf litter layer (A_0) so as not to bias the phytolith assemblage with recently-fallen plant material. Around 300 ml of the top 2–3 cm of the exposed A_1 surface was sampled. All ten samples from each vegetation plot were processed and their phytolith assemblages recorded.

3.2. Phytolith methods

3.2.1. Laboratory methods

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The A-fraction was analysed under 500x magnification and a minimum of 200 phytoliths counted per sample. In contrast, all of the phytoliths present on the C-fraction slide were counted and scanned under 200x magnification. Only those phytoliths with some taxonomic significance were recorded.

3.2.2. Phytolith identification

Phytolith identification was carried out using a range of published atlases from the neotropics, tropical Africa, Asia and Australasia (Piperno, 1988; Kondo et al., 1994; Piperno and Pearsall, 1998b; Boyd et al., 1998, Runge, 1999; Lu and Liu, 2003; Wallis, 2003; Chandler-Ezell et al., 2006, Piperno, 2006; Iriarte and Paz, 2009; Mercader et al., 2009; Watling and Iriarte, 2013; Dickau et al., 2013). Morphotypes were also checked against the University of Exeter phytolith reference collection, made up of over 500 modern neotropical plant specimens.

Table 3 lists all of the morphotypes found in the vegetation formations, their taxonomic affiliations and abbreviations for the PCA graphs. Figure 2 provides photographs of selected morphotypes under discussion. Many of the phytoliths listed were already described in detail in Dickau et al. (2013), therefore this section will be limited to describing those that were found only in the present study.

Table 3: List of phytoliths encountered, their taxonomic association and PCA codes
Plate I: Plate of selected phytolith morphotypes

Of the bamboo phytoliths encountered here, several were not reported by Dickau et al. from forest formations in Bolivia. Rondeloid/saddeloid phytoliths, as their name suggests, combine aspects of rondel and saddle phytoliths and are diagnostic to bamboos (Piperno and Pearsall 1998b). Another type of bamboo saddle, distinguishable from those produced by the Chloridoideae, was also identified on account of its size and cuboid-like ("blocky") appearance (*ibid.*). Tall and collapsed saddles were here grouped into a single category due to the fact that many phytoliths exhibited both characteristics. The morphotype here called "Cross (blocky)" refers to cross shaped phytoliths that belong to variants 3, 8 or 10, and these again are produced by many members in the bamboo subfamily (Iriarte, 2003). Chusquoid bodies, small phytoliths that appear like collapsed saddles in side view but are very narrow in planar view and rondels with spikes along their top side were also found, again diagnostic to bamboos (Piperno and Pearsall, 1998b).

The Poaceae in general produce bulliform (fan-shaped) phytoliths that are generally of little taxonomic significance below family level, however the "bulliform(bamb)" is distinguishable by having flared protrusions along the "fan" edge and is believed to be diagnostic to bamboo (Sase and Hosono, 2001). The phytoliths here called "UID (poac) 1 and UID (poac) 2" are grass short cells whose taxonomic affiliations are unknown apart from to the family level. UID (poac) 1 is a long, trapezoidal phytolith which has a ridged top and a narrow bottom plane with sinuous edges. UID (poac) 2 has psilate surface decoration and a highly regular, globular morphology. To our knowledge, these morphotypes have not been described previously.

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Many eudicot phytoliths were encountered in the forest soils. Among those not described by Dickau et al. were the stippled bodies produced in the reproductive structures of *Tetragastris spp.* (Burseraceae). These phytoliths exhibit sinuous to hexagonal edges, stippled decoration and a central domed protuberance (Piperno, 1989; Watling and Iriarte, 2013). *Ficus spp.* (Moraceae) produces circular hairbases with distinctive striations that run outwards from the centre of the hairbase to its periphery (Piperno 2006). Diagnostic to woody dicots in general, ISTs (irregular stippled tracheids) are a highly distinctive form of tracheid with irregular stippled surface direction (Runge, 1999; Dickau et al., 2013). Highly regular cylindrical versions of ISTs (named here IST (cyl)) with denser stippling were also distinguished in this study, often occurring in the same assemblage as the irregular forms. The phytoliths called here "UID (arb)" are also tracheid-types and were counted separately, as the diagnostic potential of tracheids seems promising but is still under investigation (Dickau et al., 2013). UID (arb) 1 has irregularly-spaced finger-like protrusions emanating from its surface and is globular to cylindrical in form, while UID (arb) 2 appears as a large plate with angular and nodular protuberances. Vesicular infillings are bodies consisting of concentric laminations of silica (Strömberg, 2003; 2004). While their diagnostic significance has not been well-researched, their presence has so far only been recorded in arboreal taxa (Watling and Iriarte, 2013). Articulated silicified anticlinal epidermal cells ("jigsaw puzzle pieces") also have their origin in arboreal taxa (Piperno, 2006). Finally, two unknown but highly distinctive hair base types were also recorded. UID hairbase 1 is a heavily silicified infilling of the base of a multi-celled, armed hair similar to those produced by Asteraceae (Piperno, 1988). Occasionally, both the hair and hairbase were found still articulated, but the presence of the hairbase alone was more common. UID hairbase 2 is stellate in shape and has highly folded, angular decoration. The taxonomic origin of this phytolith is unknown but is most likely to be arboreal.

3.3. Quantitative analyses

A- and C-fractions were treated separately and the relative percentage abundances were calculated relative to the sum in each fraction. A-fractions were counted to a sum of 200, following standard procedure (Pearsall, 2000), whereas the entire C-fraction was analysed for each assemblage and their totals ranged from 8 to 5016. Dickau et al. (2013) determined that, given the lower diversity of C-fraction assemblages, key compositional differences were demonstrated among samples containing a minimum of 50 phytoliths. Thus, 50 was chosen as the minimum cut-off value for the calculation of percent abundances, although the presence of individual morphotypes was noted on the frequency diagrams. Likewise, C-fractions samples with < 50 phytoliths were excluded from multivariate analysis. Diagrams showing relative phytolith frequencies were created using C2 software (Juggins, 2010).

Principal components analysis (PCA) was chosen as the most appropriate unconstrained ordination method for analysing the phytolith data set. Given the analyses of Dickau et al. (2013) whose samples included more diverse vegetation formations than the present study, we assumed similarly short environmental gradients were represented in this study. A- and C-fractions were also treated separately for PCA. Prior to analysis, all relative frequencies were square root transformed as a means of normalising the data and reducing asymmetry (Legendre and Birks, 2012). The components were extracted using a covariance matrix as opposed to a correlation matrix, as the variables were standardised measurements (Borcard et al., 2011). The resulting factor scores from the PCA were then plotted graphically for each group of samples from the forest plots. Both the PCAs and the resulting factor score graphs were created using IBM SPSS Statistics 20 software.

4. Results

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Figure 3: A-fraction relative frequency diagram
Figure 4: C-fraction relative frequency diagram

4.1.1. Dense humid evergreen forest (POR-01)

As expected, the majority of phytoliths encountered in the dense humid evergreen forest plot were arboreal types. In the A-fraction, globular granulates averaged 57% of total phytoliths present and represented by far the largest input of arboreal phytoliths. Globular psilate phytoliths and vesicular infillings were consistently present in low levels (~2%), while MFBs, tracheids and sclereids also added to the total arboreal sum which averaged 62%. Despite it being the most abundance species in the vegetation plot, only one *Tetragastris*-type phytolith was encountered in all of the samples. As these phytoliths are produced only in the seeds of the tree, its under-representation in the phytolith assemblages is not surprising. In contrast, palm presence in the samples is over-represented (average 30%), as palm phytoliths are produced abundantly by all parts of the plant. Palm abundance is negatively correlated with arboreal taxa and the two fluctuate considerably based on the spatial location of the phytolith assemblage, presumably its proximity to a palm tree. In particular, the area covered by samples POR-01-6 to POR-01-8 (500–700 m) had higher amounts of small (A-fraction) and large (C-fraction) globular echinates, undoubtedly reflecting an area more dominant in palm in this part of the vegetation community.

Understory taxa, for which data was not recorded in the botanical inventories, were represented in low numbers in the A-fraction phytolith assemblages and consist of plants from the Marantaceae (average 3%), Bambusoideae (average 1.5%), and to a lesser extent, Panicoideae (average 0.5%). All three of these groups are also present in the C-fraction but here, interestingly, the bulliforms (split into grass- and bamboo-type) account for around 50% of the total phytoliths in the assemblages. Such disparity in the representation of grasses and bamboos between the A- and C-fractions must be a result of a lower tendency of arboreal taxa to produce large phytoliths, even though a reasonable diversity of the latter are still represented. These include Annonaceae faceted bodies, anticlinal epidermal cells, tracheary elements, MFBs and quantities of UID hairbase 1 that were unrepeated in the other vegetation plots. It is also of interest to note that three of the ten samples yielded <50 C-fraction phytoliths and so had to be excluded from the relative abundance calculations.

4.1.2. Dense humid evergreen forest with palm (POR-02)

The relative frequencies of A-fraction phytoliths from the dense humid evergreen forest with palm do not differ substantially from those from the dense humid evergreen forest (POR-01). This may reflect the proximity (2 km) of the two plots and that they share seven of their ten most abundant species (Table 1). Total palm abundance averaged 31%, compared with 30% in POR-01, and arboreal taxa 62%, compared with 63% in POR-01, with the two still showing a strong negative correlation with each other. While these and other very minor differences with POR-01 can be observed in the A-fraction, they are not enough to be significant.

The C-fraction assemblages, like those from POR-01, are largely dominated by grass and bamboo bulliforms showing again the over-representation of the larger phytoliths in these taxa. Large globular echinates are also consistently moderately abundant coinciding with high numbers of *Euterpe precatoria* in the plot inventory (see section 5.2). Annonaceae faceted phytoliths are less abundant than in POR-01, reflecting the situation in the species inventory. Similarly, the *Ficus* hairbase in POR-02-8 likely reflects the presence of *F. trigona* in the plot. Tracheids, sclereids and MFBs are present throughout the samples, as are (rarely) Asteraceae and *Mendoncia*. Although not reaching the same frequencies as UID hairbase 1 in POR-01, UID hairbase 2 was similarly found restricted to this vegetation formation. Phytoliths that occurred sporadically in the transect include the IST (cyl) tracheid type and those

and bamboo bulliforms showing again the over-representation of the larger phytoliths in these taxa. Large globular echinates are also consistently moderately abundant coinciding with high numbers of *Euterpe precatoria* in the plot inventory (see section 5.2). Annonaceae faceted phytoliths are less abundant than in POR-01, reflecting the situation in the species inventory. Similarly, the *Ficus* hairbase in POR-02-8 likely reflects the presence of *F. trigona* in the plot. Tracheids, sclereids and MFBs are present throughout the samples, as are (rarely) Asteraceae and *Mendoncia*. Although not reaching the same frequencies as UID hairbase 1 in POR-01, UID hairbase 2 was similarly found restricted to this vegetation formation. Phytoliths that occurred sporadically in the transect include the IST (cyl) tracheid type and those from the seeds of Marantaceae, again reflecting the highly localised nature of phytolith deposition.

4.1.3. Bamboo forest (RFH-01)

Unsurprisingly, the bamboo forest plot was characterised by high relative frequencies of bamboo phytoliths in the assemblages. Average total bamboo in the A-fraction was 15%, a sum consistent with bamboo forest plots sampled on the Acre/Amazonas border by McMichael et al. (2013). Tall/collapsed saddles were the most abundant bamboo phytolith type, others including blocky saddles and crosses, chusquoid bodies, 2-spiked bodies and bamboo bulliforms present in the A-fraction. Rondel frequencies can be seen to mirror very well other bamboo phytolith frequencies in this plot which suggests that many of them may have originated from bamboo. If this association is correct, bamboo relative frequencies would almost double in most of the samples. Bamboo was even more represented in the C-fraction, where the bulliforms averaged 89% of the total assemblage, and the counts themselves were well above those from any of the other plots (averaging 3973 compared to 202 for the fluvial forest which had the second highest C-fraction counts). Such a pattern is arguably a highly diagnostic aspect of bamboo forest phytolith assemblages.

The A-fraction assemblages also had the highest, though still relatively low, frequencies of true (i.e. non-bamboo) grasses of all vegetation plots (average 1.8%). This is most likely due to the openness of the forest formation, in which *Guadua* acts aggressively to kill old trees and restrict new tree growth, thus creating large canopy openings (Griscom and Ashton 2006). UID (poac) morphotypes are seen to occur exclusively in this formation, while Marantaceae is almost absent in all samples bar RFH-01-7.

The remainder of the phytolith assemblages consist of palm and arboreal phytoliths, with palm phytoliths outnumbering the arboreal (average 40% compared to 29%). Again, this could be attributed to more open conditions are often colonised by palms. Although difficult to see in Figure 4 due to the dominance of bamboo bulliforms, large globular echinates were present in most of the C-fraction samples, generally in lower numbers than in the humid evergreen forest samples, but exceptionally high (n = 140) in RFH-01-2. *E. precatoria* is the third most abundant species in the inventory (Table 1). There were also very high numbers of Asteraceae present in the assemblages which far exceeded counts in samples from other forests. Due to a lack of liana and understory species data recorded for the forest plots, we cannot say from which group of plants (herb or liana) the Asteraceae phytoliths belong. Slightly elevated counts of *Mendoncia* show that lianas are more common in this forest and they may be a secondary growth component of this disturbed type of forest ((Balée, 1990)). ISTs were also very abundant in a few of the C-fraction samples. In contrast to the humid evergreen forests, globular psilates and vesicular infillings were rarely present in the A fraction, whereas UID (arb) 1 was present in consistent frequencies and only in this vegetation community, suggesting an origin for the phytolith in a tree species not found as abundantly in the other plots.

4.1.4. Palm forest (EST)

As expected, palm phytoliths made up the majority of the assemblages from the palm forest plot (average 65%), most coming from species producing globular echinate forms. Arboreal phytoliths average 28%, the lowest of all the plots studied here, with non-globular granulates contributing relatively little to the A fraction arboreal count. The true grass input to the phytolith assemblages is similar (average 1.2%) to the bamboo forest, which is expected since palm forests are also a type of open forest. Bamboo frequencies remain low throughout (1.1%) and are comparable with those from the humid evergreen and fluvial forest types. Both true grass and bamboo bulliforms are present in the C fraction, however all of the palm forest C fractions contributed < 50 phytoliths (average: n = 27), and as such were excluded from both the relative frequency and Principal Components Analyses. Dickau et al (2013) found

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4.1.5. Fluvial forest (RAND)

Phytolith assemblages from the fluvial forest plot also show some interesting patterns that are unique to this vegetation community. The arboreal phytolith input (average 68% when outlier RAND-6 is excluded) is the highest of all the vegetation plots, even the humid evergreen forests. While globular granulates again make up the bulk of the arboreal count, high numbers of sclereids were also present in the samples (average 6% compared to < 1% in the other forest plots). Conversely, palms are least abundant in the fluvial forest plot (average 11.3%), with the exception of sample RAND-6 in which globular echinates totalled nearly 100% of the assemblage (count excluded in calculation of average), the most extreme example of localised phytolith deposition in the study.

Phytoliths from the forest understory were dominated by Marantaceae globular nodular forms which made up (average) 20% of the total sum, compared to < 3% in the humid evergreen forests and probably represents wet-adapted taxa of the family. Cyperaceae cones and one Oryzeae scooped bilobate were also recorded, reflecting the wet nature of the vegetation community. UID (poac) 2 is most common in the fluvial forest samples, but a lack of understory species data hinders our ability to narrow down the species that produced them. *Heliconia* was also found, along with high frequencies of Strelitziaceae phytoliths, the presence of these monocots likely representing the highly disturbed nature of the vegetation community. The grass and bamboo phytolith inputs remain low in the A fraction (average 0.6% and 1.3% respectively), but make up around one third of the C fraction counts (average 30%). Unusually, despite the large numbers of Marantaceae phytoliths in the A fraction, few phytoliths from the family made it to the C fraction. Asteraceae platelets, however, reach the highest relative frequencies here than any of the other vegetation plots. Annonaceae faceted bodies were also present, despite the absence of the family in the species inventory (see section 5.1). Other arboreal phytoliths in the C fraction consist mainly of ISTs, again much higher than relative frequencies in other plots, MFBs, sclereids and other tracheid types.

4.2. Principal components analyses

The PCAs that were run both the A- (Figure 5) and C-fraction (Figure 6) assemblages show that their differences can be separated statistically. The only exception is with the dense humid evergreen forest and dense humid evergreen forest with high palm abundance, whose factor scores overlap considerably.

Figure 4: A fraction PCA and factor scores
Figure 5: C fraction PCA and factor scores

In the A-fraction, axes PCA1 and PCA2 together accounted for 62% of the total variance in the dataset. Bamboo and palm forests plot negatively on PCA1 (46%) and humid evergreen and fluvial forest types plot positively. The axis is strongly correlated (negatively) with phytoliths from Poaceae and (positively) with arboreal forms (globular granulate, globular nodular, sclereids etc), showing that greatest variance in the dataset is explained by the difference between grassy to more forested vegetation communities (open to dense forests). PCA2 (16%) separates bamboo from palm forest phytoliths. Overall, the bamboo, palm and fluvial forests are well separated by the analysis, with the exception of some overlapping samples

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In analysis of the C-fractions, PCA1 (33%) separates bamboo forest assemblages from all other forest types. This is almost wholly driven by bamboo bulliform phytoliths which consistently dominated the assemblages. PCA2 (29%) separates the bamboo and fluvial forests from the humid evergreen forests, with sub-types of the latter again indistinguishable. Phytoliths common to fluvial forest assemblages, IST phytoliths, Asteraceae, Annonaceae and Marantaceae nodular bodies, are key components of PCA2. Both the bamboo and fluvial forests are more open than the humid evergreen forests and plot on the negative axis, suggesting that PCA2 represents a gradient of density of vegetation communities. The dense humid evergreen forests are characterised by the presence of a range of different arboreal phytolith types. The palm forest is again noted for its lack of larger phytoliths, and had to be excluded from the PCA.

5. Discussion

5.1. Distinguishing between vegetation formations

This study set out to test whether modern forest formations in eastern Acre, Brazil, could be distinguished by their phytolith signatures. The results show that significant differences do exist between the phytolith assemblages from humid evergreen, bamboo, palm and fluvial forest that would allow their differentiation in the fossil phytolith record. We also found that phytoliths are unable to pick up subtler differences in species composition, as seen in the statistical overlap of assemblages from dense humid evergreen and dense humid evergreen with high palm forests. Forest types, particularly fluvial forest, were better separated on account of the C-fraction phytoliths, as shown by the tighter clustering of subsamples and less spatial overlap in the PCA. It is possible that this could be due to the exclusion of the palm forest samples from the analysis; however, the lack of larger phytoliths produced by this vegetation community is a diagnostic feature of itself. These findings support those from lowland Bolivia which also showed that vegetation formations were more easily differentiated by the C-fraction phytoliths (Dickau et al., 2013), reinforcing the advantages of analysing the silt-sized and sand-sized phytoliths separately.

The analyses we used also help us to determine which phytoliths might be associated to which vegetation formations. Dense humid evergreen forests are characterised by the presence of globular psilate phytoliths and vesicular infillings in the A-fraction, large globular echinate, hairbase phytoliths and anticlinal epidermal cells in the C-fraction, and tracheary elements in both. Bamboo forests are associated with bamboo short cells and the almost complete dominance of bamboo bulliforms in the C-fraction, while palm forest A-fractions are dominated by globular echinate phytoliths and have true grass percentages comparable to those from bamboo forests. Finally, fluvial forests are characterised by globular granulate, globular nodular and sclereid phytoliths in the A-fraction and Annonaceae, Asteraceae and IST phytoliths in the C-fraction, the latter two morphotypes also having high absolute (though not relative) counts in bamboo forest. The high frequencies of tracheary element phytoliths (particularly scereids, IST/(Cyl)s) in the fluvial forest is noteworthy and leads us to suggest that tree species adapted to fluvial ecosystems may deliberately produce more of these phytoliths as structural support for the xylems which have to deal with a high degree of water stress. Phytolith assemblages high in tracheary elements were similarly found to be produced by marine-adapted plants in southeast India (Kumari and Kumarasamy, 2014). Further studies of surface soils under similar fluvial forests are necessary to corroborate these findings, which could be of use to palaeoecologists tracking the extent of flooded forests in the past (Whitney et al., 2011).

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This study has also shown good correlations between phytolith surface soil assemblages and species inventory data, indicating that they are a result of relatively recent deposition. In the case of the fluvial forest, where we would expect alluvial transport of phytoliths to be a concern, the uniqueness of the phytolith data indicates limited mixing of phytoliths from other forest formations in the drainage basin. It is highly possible, however, that some of the phytoliths originated in other similar flooded forests upstream from the vegetation plot. This could explain the high frequencies of Annonaceae phytoliths despite the absence of the family in the forest plot, as well as the presence of globular echinates which are not produced by the species of palm recorded in the inventory (*Bactris maraja*). The Annonaceae family is a common component of fluvial and inundated environments: in a study of fluvial forest species on the floodplains of the River Juruá, *Annona spp.* (Annonaceae) was recorded as strongly dominating in the plot with the highest mean high water levels (Campbell et al., 1992).

As predicted, both over- and under-representation of plant taxa was apparent in the phytolith data. One example of under-representation was of *Tetragastris altissima* (Burseraceae) in the dense humid evergreen forests. Only one seed phytolith from this species was recovered from both vegetation plots, despite it being the most abundant species in the inventories. Over-representation of globular echinate phytoliths also occurred in the palm forests to the extent that other phytolith types were “swamped” in the A-fraction counts. When over-representation is suspected in phytolith assemblages it is usually common practice to extend the total count to > 200 morphotypes to counteract this effect (Pearsall, 2000). However, as the aim of this study was to calculate relative phytolith frequencies from the plots and directly compare these both graphically and statistically, a closed sum of 200 was maintained.

5.2. Implications for archaeology and palaeoecology

The ultimate goal of our study was to see whether surface soil phytolith assemblages could help provide accurate analogues for phytolith assemblages from archaeological and palaeoecological contexts in the region. We have shown that the differences between the phytolith datasets are sufficient for this purpose and that surface soil studies can also reveal interesting insights regarding phytolith deposition mechanisms and phytolith/ecosystem relationships. Due to problems with taxonomic resolution and visibility of eudicot phytoliths, our data do not reflect the floristic diversity of the forests that were sampled – something that pollen analysis does much better (Pearsall, 2000). However, we have shown that comparing the percentage inputs of even a relatively small sample of phytolith morphotypes in different forest formations produces significant and useful results. In addition, our research has identified four phytolith morphotypes that have not previously been described (UID (poac) 1 and 2, and UID hairbase 2). We have also been able to suggest taxonomic affiliations for large globular echinate phytoliths. *Euterpe oleracea* Mart. was previously seen by Watling and Iriarte (2013) to produce unusually large globular echinate phytoliths similar to those encountered here (d > 50μm), and given the abundance these morphotypes in the dense humid evergreen forest plots where *E. precatoria* is the second most dominant species, it raises the possibility that these phytoliths could be diagnostic to genus level. Detailed studies comparing all *Euterpe* spp. and other palms in the region are necessary test this hypothesis. Studies into phytoliths from modern plant material are also required to help increase taxonomic resolution of phytolith data among arboreal species in general.

The extent to which different phytolith types preserve over time is an important issue to consider when comparing assemblages from deep soil horizons with those from modern surface soils. While Piperno (1988) showed that the presence of free iron and aluminium oxides in highly weathered tropical soils, like those of Acre, may enhance phytolith durability by becoming absorbed into the phytoliths and thus hindering their dissolution, we would still expect a degree of differential preservation among the current phytolith suite. It has been noted previously that those phytoliths which are formed as casts of cells and cell wall incrustations, such as epidermal

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The distinction of four important forest types in the region by their phytoliths is a considerable step forward for archaeologists and palaeoecologists interested in landscape histories over time and space. Phytoliths will play a crucial role in testing the hypothesis of McMichael et al. (2014), as bamboos do not produce diagnostic pollen grains and we have shown in this study that phytoliths assemblages from bamboo forests are easily recognisable. The importance of palms and the role of humans in driving their past and present distributions has also been widely discussed in the literature (Kahn, 1988; Clement, 1999; Morcote-Ríos and Bernal, 2001). While it is unknown to what extent Acre’s palm forests are relics of old secondary forests after human manipulation, knowing the phytoliths that they produce is important to compare with assemblages from archaeological contexts that may be similar. In addition, the promising data we retrieved from the fluvial forest could also be useful to archaeologists looking to trace human impact in these environments. The floodplains of the Amazon basin have long been recognised as highly sought-after locations for planting crops due to the annual replenishment of soil fertility caused by annual flooding (Lathrap, 1970; Roosevelt, 1980; Denevan, 2001). With more studies of phytolith assemblages from floodplain environments, it may be possible to detect some of these pre-Columbian land-use strategies.

Our data also have relevance for ecologists seeking to test the resilience of southwestern Amazonian ecosystems to both climate and human impact. Phytolith studies can now be conducted within the forest plots themselves in order to trace their development and longevity in their current locations and see to what extent humans have either interfered with, or helped to form, their character. Phytolith depth profiles may provide information on long-term changes in forest composition due to climate in areas where pollen analysis from lake coring is not possible.

The data from modern vegetation formations sampled in this study provide a baseline from which archaeological and palaeoecological phytolith assemblages from eastern Acre can now be compared. Work conducted since 2011 in the geoglyph region has included the stratigraphic sampling of soil profiles both within and outside of the sites to track the types of vegetation present before, during and after their use, and the degree of human impact on the landscape (Watling et al. unpublished data). Statistical comparisons of these data with those from these modern analogues will be crucial in characterising vegetation change within these landscapes and ultimately contribute to our understanding of the nature and scale of pre-Columbian impact by the geoglyph builders.

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List of figures and tables

Figure 1: Map of vegetation formations and plot locations

Table 1: Plot and species data for sampled vegetation formations

Plot name	Code	Forest type	Alt (masl)	Slope	Most common tree species	
Seringal Porongaba 1	POR-01	Dense humid evergreen	176	< 5°	*Tetragastris altissima* (Burseraceae)	7.3
(10°49'19.01"S, 68°46'15.75"W)		forest			*Euterpe precatoria* (Arecaceae)	5.7
					Pausandra trianae (Euphorbiaceae)	5.5
					Pseudolmedia murure (Moraceae)	3.6
					Siparuna decipiens (Siparunaceae)	3.5
					Bracteanthus glycycarpus (Monimiaceae)	2.8
					Eschweilera coriacea (Lecythidaceae)	2.6
					Inga sp. (Fabaceae)	2.1
					Psychotria sp. (Rubiaceae)	2.1
					Guarea kunthiana (Meliaceae)	1.9
					Total:	37.1
Seringal Porongaba 2	POR-02	Dense humid evergreen forest with palm	268	< 5°	*Tetragastris altissima* (Burseraceae)	9.5
(10°47'51.97"S, 68°46'23.67"W)					*Euterpe precatoria* (Arecaceae)	8.3
					Pseudolmedia laevis (Moraceae)	3.6
					Pausandra trianae (Euphorbiaceae)	2.9

Seringal Porongaba 2	POR-02	evergreen forest with palm	268	< 5°	*Tetragastris altissima* (Burseraceae)	9.5
(10°47'51.97"S, 68°46'23.67"W)					*Euterpe precatoria* (Arecaceae)	8.3
					Pseudolmedia laevis (Moraceae)	3.6
					Pausandra trianae (Euphorbiaceae)	2.9
					Inga sp. (Fabaceae)	2.9
					Eschweilera sp. (Lecythidaceae)	2.4
					Micropholis sp. (Sapotaceae)	2.4
					Iriartea deltoidea (Arecaceae)	2.2
					Brosimum sp. (Moraceae)	2.2
					Siparuna decipiens (Siparunaceae)	2.2
					Total:	38.5
Reserva Florestal Humaita	RFH	Bamboo forest	268	< 5°	*Trichilia sp.* (Meliaceae)	10.3
(9°45'1.90"S, 67°40'18.80"W)					*Quararibea guianensis* (Malvaceae)	6.3
					Euterpe precatoria (Arecaceae)	5.7
					Sorocea briquetii (Moraceae)	3.8
					Pseudolmedia laevis (Moraceae)	3.5
					Aptandra sp. (Olacaceae)	2.7
					Aspidosperma vargasii (Apocynaceae)	2.4
					Celtis schippii (Cannabaceae)	2.2
					Licania sp. (Chrysobalanaceae)	2.2
					Heisteria nitida (Olacaceae)	1.9
					Total:	41.0
					Species present	
Estranjero 4 (10°29'3.72''S, 67°55'43.54W)	EST	Palm forest	222	< 5°	Arecaceae: *Astrocaryum sp.*, *Attalea phalerata, Bactris maraja, Euterpe precatoria, Oenocarpus bacaba, Phytolephas macrocarpa* , Socratea sp.*	
					Bignoniaceae: *Jacaranda copaia*	
					Cecropiaceae: *Cecropia sciadophylla*	
					Fabaceae: *Amburanca cearensis, Apuleia leiocarpa, Tachigali sp., Dialium guianense*	
					Malvaceae: *Ceiba pentandra, Theobronia icaco*	
					Moraceae: *Brosimum guianensis, Clarisa biflora*	
					Meliaceae: *Cedrela*	

					sclaudophylla
					Fabaceae: *Amburanca cearensis, Apuleia leiocarpa, Tachigali sp., Dialium guianense*
					Malvaceae: *Ceiba pentandra, Theobronia icaco*
					Moraceae: *Brosimum guianensis, Clarisa biflora*
					Meliaceae: *Cedrela odorata*
					Lauraceae: *Ocotea sp.*
					Lecythidaceae: *Bertholetti excelsa*
Rio Andira	RAND	Fluvial forest	157	< 5°	Arecaceae: *Bactris maraja*
(9°43'29.80''S, 68°7'28,39''W)					Clusiaceae: *Garcinia sp.**
					Combretaceae: *Terminalia amazonica*
					Dichapetalaceae: *Tapura sp.*
					Euphorbiaceae: *Hevea brasiliensis, Mabea sp.*
					Fabaceae: *Andira sp., Copaifera sp., Inga sp., Macrolobium sp.*
					Lecythidaceae: *Gustava sp.*
					Moraceae: *Brosimum guianense, Ficus trigona*
					Meliaceae: *Melia sp., Trichilia sp.*
					Myristicaceae: *Virola surinamensis*
					Myrtaceae: *Eugenia sp.*
					Polygonaceae: *Coccoloba sp.*
					Rubiaceae: *Calycophyllum sp., Simira sp.*
					Sapotaceae: *Pouteria sp.*

Caption for Table 1:
* Denotes most dominant species in the EST and RAND plots

Table 2: Key of sample abbreviations

Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position
POR-01	1	0m	POR-02	1	0m	RFH-01	1	0m	EST	1	0m	RAND	1	0m
	2	100m		2	100m		2	50m		2	50m		2	50m
	3	200m		3	200m		3	100m		3	100m		3	100m
	4	300m		4	300m		4	150m		4	150m		4	150m
	5	400m		5	400m		5	200m		5	200m		5	200m

Table 2: Key of sample abbreviations

Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position	Plot	Sample	Position
POR-01	1	0m	POR-02	1	0m	RFH-01	1	0m	EST	1	0m	RAND	1	0m
	2	100m		2	100m		2	50m		2	50m		2	50m
	3	200m		3	200m		3	100m		3	100m		3	100m
	4	300m		4	300m		4	150m		4	150m		4	150m
	5	400m		5	400m		5	200m		5	200m		5	200m
	6	500m		6	500m		6	250m		6	250m		6	250m
	7	600m		7	600m		7	300m		7	300m		7	300m
	8	700m		8	700m		8	350m		8	350m		8	350m
	9	800m		9	800m		9	400m		9	400m		9	400m
	10	900m		10	900m		10	450m		10	450m		10	450m

Table 3: List of phytoliths encountered, their taxonomic association and PCA codes

Phytolith type	Fraction	Association	References	PCA code	Plate
Bilobates	A	Panicoideae	1-6	Bilob	
Polylobates	A	Panicoideae	1-6	Plob	
Crosses	A	Panicoideae	5-12	Cross	
Saddles	A	Chloridoideae	2, 3, 5, 6, 13	Sad	
Rondels/trapezoids	A	Poaceae	2, 3, 5, 6	Rond	
Tall rondels	A	Poaceae	5, 6, 13	Trond	
Rondeloid/saddeloid	A	Bambusoideae	5	RondSad	
Tall/collapsed saddles	A	Bambusoideae	5-7, 15, 16	TCSad	1
Saddles (blocky)	A	Bambusoideae	5	SadBlck	
Crosses (blocky)	A	Bambusoideae	5-12	Chusq	
Chusquoid bodies	A	Bambusoideae	5, 6	TwoSRond	
Two-spiked bodies	A	Bambusoideae	5	BambBull	
Oryzeae scooped bilobates	A	Oryzeae	1, 17	Oryz	
Olyreae irreg/complex	A	Olyreae	5, 18	Olyr	2
Bulliforms	C	Poaceae	6, 7	Bull	
Bulliforms (bamb)	A, C	Bambusoideae	35	BambBull	3
UID (poac) 1	A	Poaceae		UIDPoac1	4
UID (poac) 2	A	Poaceae		UIDPoac2	5
Heliconia troughed body	A	*Heliconia*	6, 19, 20	Helic	
Cyperaceae cones	A	Cyperaceae	13, 21-24	CypCon	
Marantaceae globular nodular	A	Marantaceae	23	GlobNod	
Marantaceae seed	C	Marantaceae	23	MarSeed	6
Marantaceae nodular	C	Marantaceae	23	MarNod	7
Strelitziaceae druse	A	Strelitziaceae	18	Streliz	8
Globular echinate	A	Arecaceae	6, 13, 18, 26-27	GlobEch	
Large globular echinate	C	Arecaceae	29	LGlobEch	9
Palm hats	A	Arecaceae	6, 13, 18, 26-28	Hat	

Heliconia troughed body	A	*Heliconia*	6, 19, 20	Helic	
Cyperaceae cones	A	Cyperaceae	13, 21-24	CypCon	
Marantaceae globular nodular	A	Marantaceae	23	GlobNod	
Marantaceae seed	C	Marantaceae	23	MarSeed	6
Marantaceae nodular	C	Marantaceae	23	MarNod	7
Strelitziaceae druse	A	Strelitziaceae	18	Streliz	8
Globular echinate	A	Arecaceae	6, 13, 18, 26-27	GlobEch	
Large globular echinate	C	Arecaceae	29	LGlobEch	9
Palm hats	A	Arecaceae	6, 13, 18, 26-28	Hat	
Globular granulate	A	Woody eudicot	6, 30, 31	GlobGran	
Globular psilate	A	Woody eudicot	13	GlobPsi	
MFBs	A, C	Woody eudicot	6, 7	MFB	
Tetragastris stippled	A	*Tetragastris*	25	Tetra	10
Annonaceae faceted	C	Annonaceae	6, 7	Ann	
Ficus hairbase	C	*Ficus*	7	FicHB	11
Mendoncia	C	*Mendoncia*	7	Mend	12
Asteraceae platelets	C	Asteraceae	6, 7, 32	Ast	
Tracheids	A, C	Woody eudicot	6, 7	Trach	
Sclereids	A, C	Woody eudicot	6, 31	Scler	
IST	C	Woody eudicot	6, 13, 26, 31	IST	13
IST (cyl)	C	Woody eudicot		ISTCyl	14
UID (arb) 1	A	Woody eudicot		UIDArb1	15
UID (arb) 2	A	Woody eudicot		UIDArb2	16
Vesicular infillings	A	Woody eudicot	33, 34	Vesic	17
Anticlinal epidermis	C	Woody eudicot	7	AntEp	18
UID hairbase 1	C	Woody eudicot		UIDHB1	19
UID hairbase 2	C	Woody eudicot		UIDHB2	20

Caption for table 3:
References: 1. Metcalfe, 1960; 2. Twiss et al., 1969; 3. Brown, 1984; 4. Fredlund and Tieszen, 1994; 5. Piperno and Pearsall, 1998b; 6. Piperno, 2006; 7. Piperno, 1988; 8. Piperno, 1984; 9. Pearsall, 1978; 10. Pearsall, 1982; 11. Pearsall and Piperno, 1990; 12. Iriarte, 2003; 13. Kondo et al., 1994; 14. Zucol, 1999; 15. Lu, et al., 1995; 16. Lu et al., 2006; 17. Chaffey, 1983; 18. Watling and Iriarte, 2013; 19. Tomlinson, 1961; 20. Prychid et al., 2003; 21. Ollendorf, 1992; 22. Honaine et al., 2009; 23. Metcalfe, 1971; 24. Wallis, 2003; 25. Piperno, 1989; 26. Runge, 1999; 27. Tomlinson, 1961; 28. Bozarth et al., 2009; 29. Dickau et al., 2013; 30. Amos, 1952; 31. Scurfield et al., 1974; 32. Bozarth, 1992; 33. Strömberg, 2003; 34. Strömberg, 2004; 35. Sase and Hosono, 2001

Plate I: Plate of selected phytolith morphotypes encountered in the study
Caption for Plate I:
1. Tall/collapsed saddle; 2. Olyreae irregular/complex body; 3. Bamboo bulliform; 4. UID (poac) 1; 5. UID (poac) 2; 6. Marantaceae seed phytolith; 7. Marantaceae nodular body; 8. Strelitziaceae druse; 9. Large globular echinate; 10. Tetragastris body; 11. Ficus hairbase; 12. Mendonica; 13. Irregular stipulate tracheid (IST); 14. IST(cylindrical); 15. UID (arb) 1; 16. UID (arb) 2; 17. Vesicular infilling; 18. Anticlinal epidermis; 19. UID (hairbase) 1; 20. UID (hairbase) 2.

Figure 2: Relative frequency diagram of A fraction

Plate I: Plate of selected phytolith morphotypes encountered in the study
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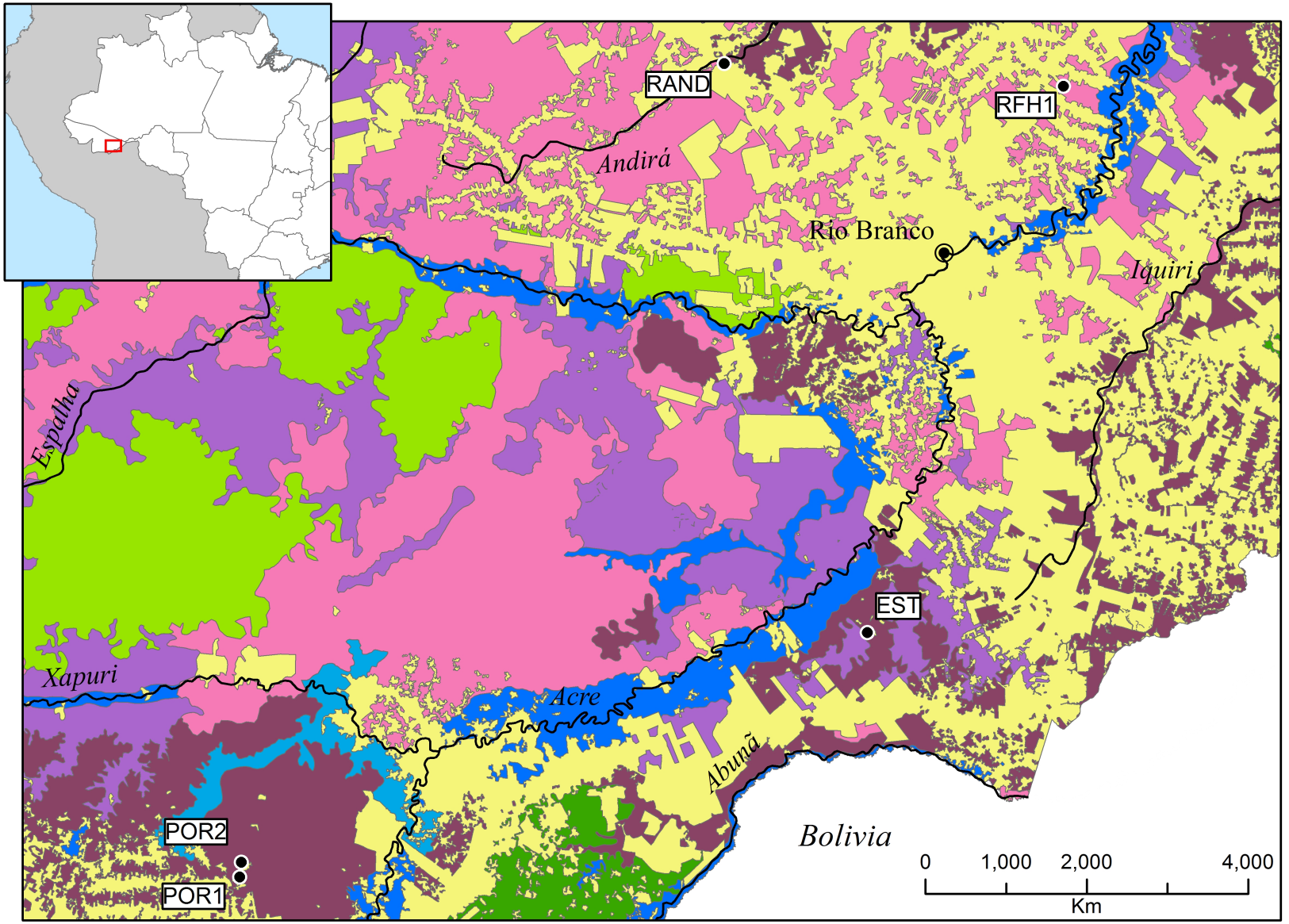
Figure 2: Relative frequency diagram of A fraction
Caption for figure 3:
+ = Frequency = < 2%

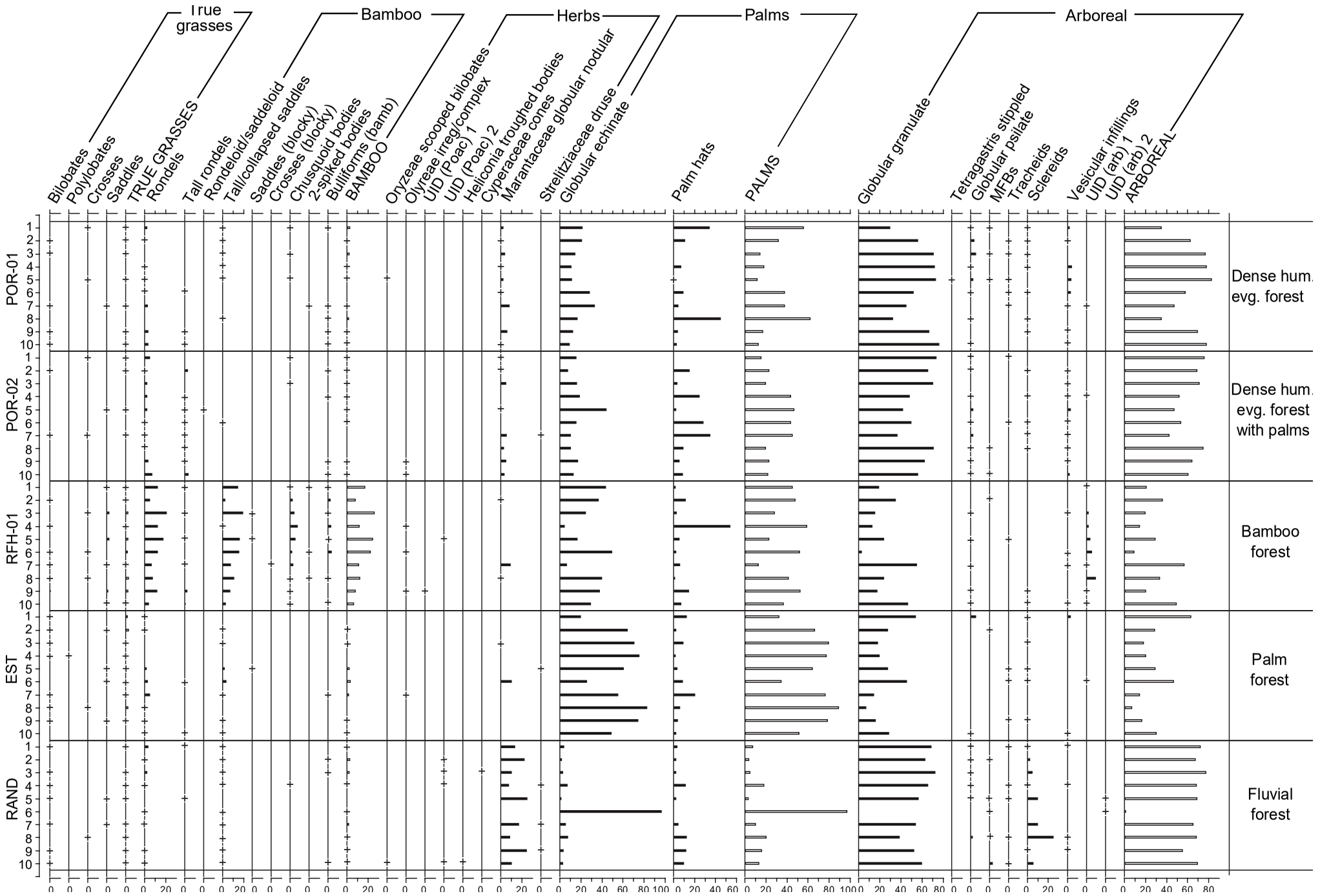
Figure 3: Relative frequency diagram of C Fraction
Caption for figure 4:
+ = Frequency = < 2%
X = Presence of phytoliths in a sample where $n < 50$

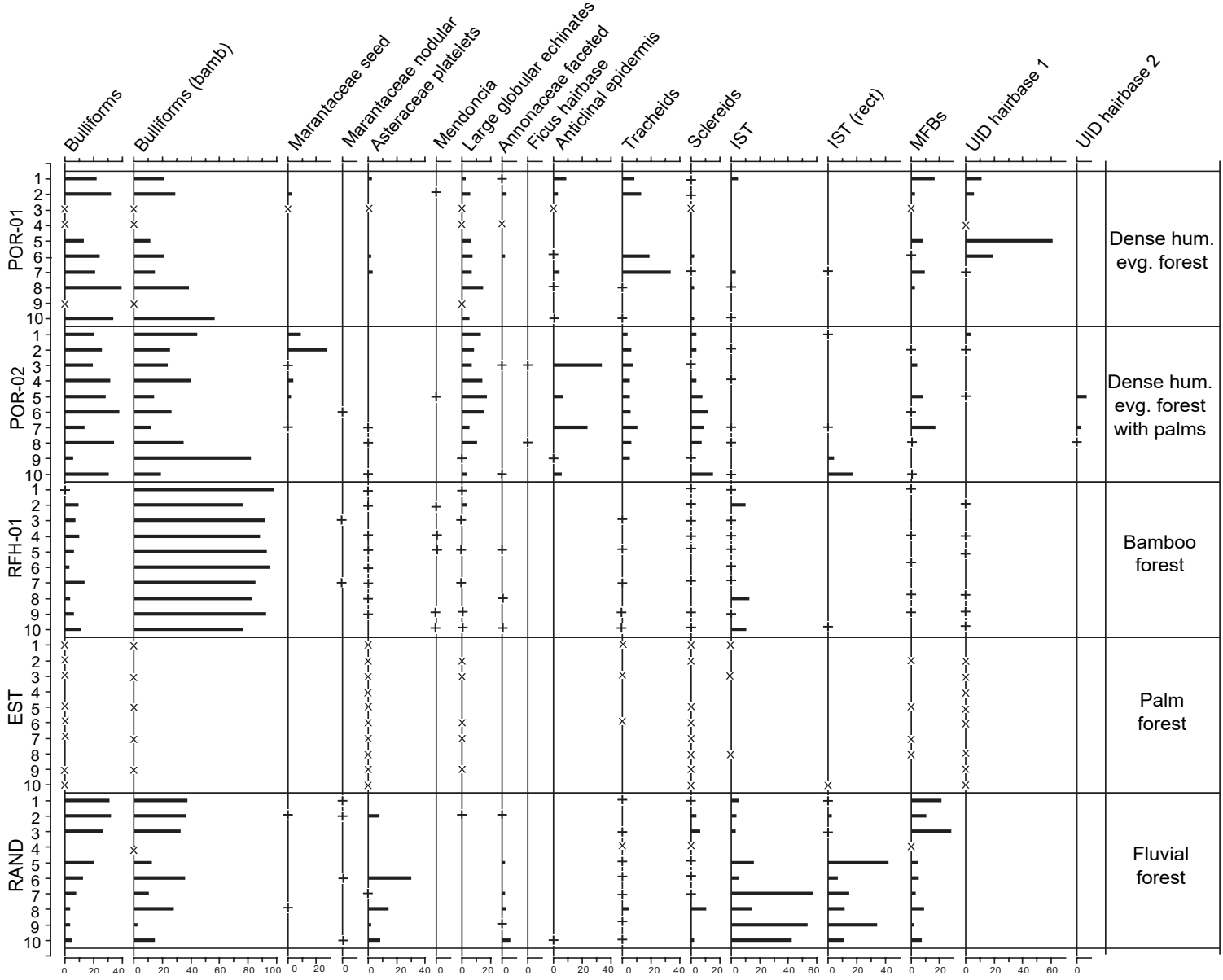
Figure 4: A fraction PCAs and loading plots
Figure 5: C fraction PCAs and loading plots

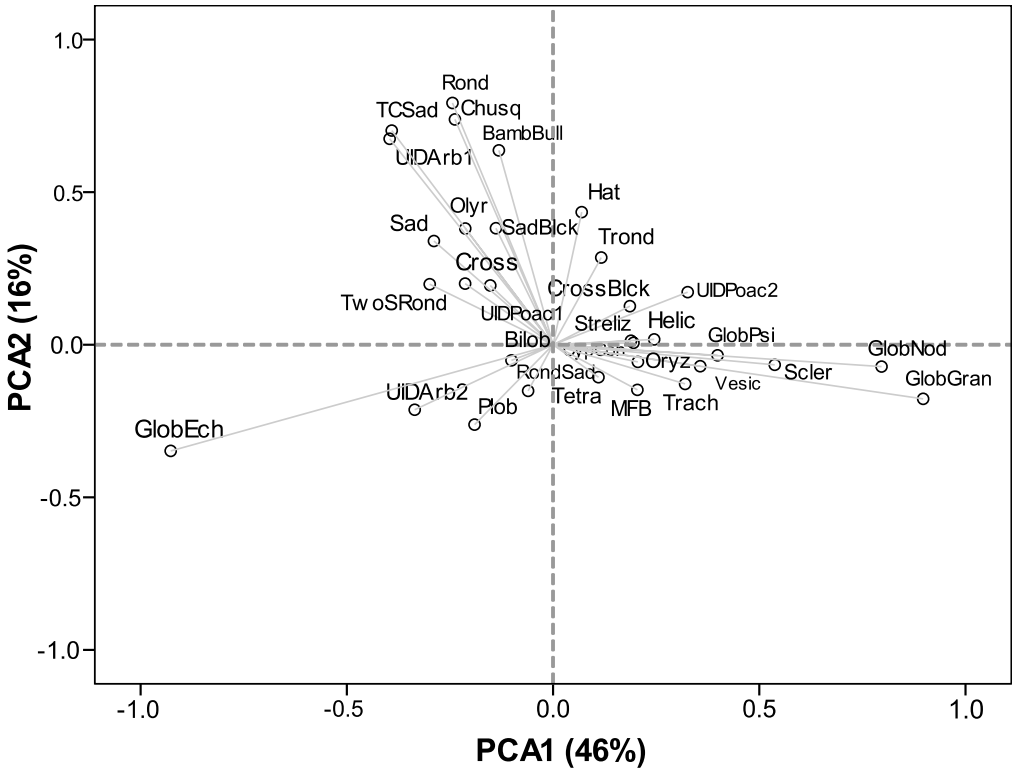


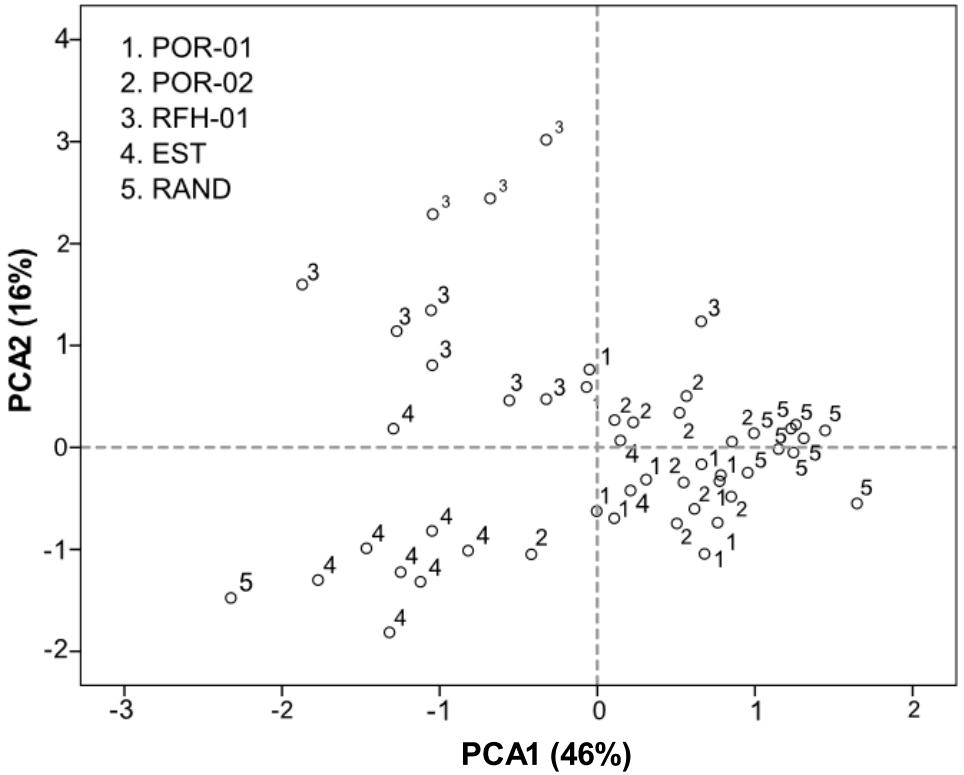
Legend

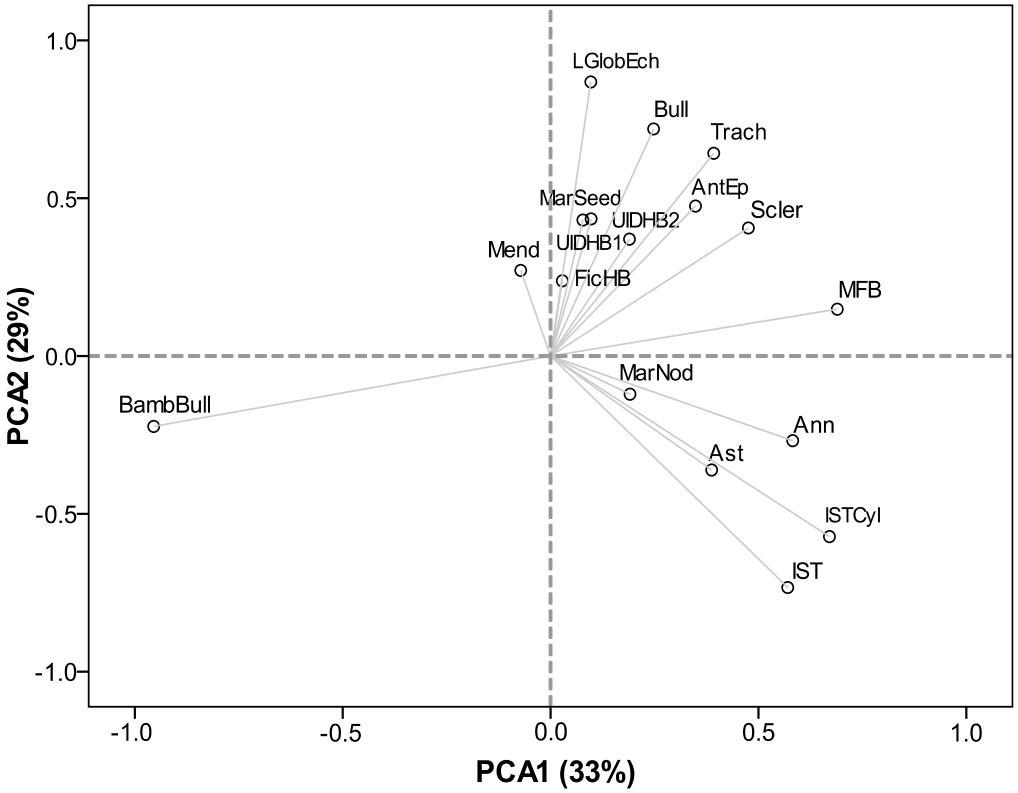
- Deforestation
- Bamboo Forest
- Bamboo Forest on Alluvial Soils
- Palm Forest
- Palm Forest on Alluvial Soils
- Dense Humid Evergreen Forest
- Bamboo / Dense Humid Evergreen Forest
- Palm / Dense Humid Evergreen Forest
- Rivers
- Vegetation Plots
- Capital City
- *River names*

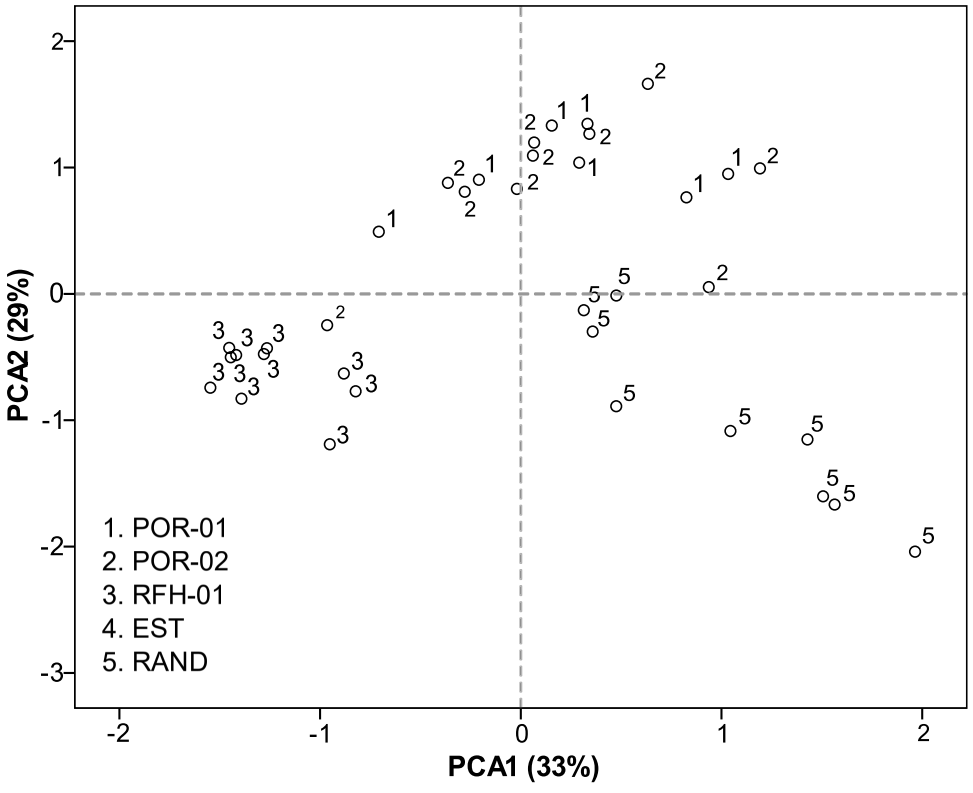

True grasses
Bamboo
Herbs
Palms
Arboreal
Bilobates
Polylobates
Crosses
Saddles
TRUE GRASSES
Rondels
Tall rondels
Rondeloid/saddeloid
Tall/collapsed saddles
Saddles (blocky)
Crosses (blocky)
Chusquoid bodies
2-spiked bodies
Bulliforms (bamb)
BAMBOO
Oryzeae scooped bilobates
Olyreae irreg/complex
UID (Poac) 1
UID (Poac) 2
Heliconia troughed bodies
Cyperaceae cones
Marantaceae globular nodular
Strelitziaceae druse
Globular echinate
Palm hats
PALMS
Globular granulate
Tetragastris stippled
Globular psilate
MFBs
Tracheids
Sclereids
Vesicular infillings
UID (arb) 1
UID (arb) 2
ARBOREAL
POR-01
POR-02
RFH-01
EST
RAND
Dense hum. evg. forest
Dense hum. evg. forest with palms
Bamboo forest
Palm forest
Fluvial forest


Bulliforms
Bulliforms (bamb)
Marantaceae seed
Marantaceae nodular
Asteraceae platelets
Mendoncia
Large globular echinates
Annonaceae faceted
Ficus hairbase
Anticlinal epidermis
Tracheids
Sclereids
IST
IST (rect)
MFBs
UID hairbase 1
UID hairbase 2
POR-01
POR-02
RFH-01
EST
RAND
Dense hum. evg. forest
Dense hum. evg. forest with palms
Bamboo forest
Palm forest
Fluvial forest


Rond
TCSad
Chusq
BambBull
UlDArb1
Hat
Olyr
Sad
SadBlck
Trond
Cross
CrossBlck
UlDPoac2
TwoSRond
UlDPoac1
Streliz
Helic
GlobPsi
Bilob
GlobNod
Oryz
Scler
RondSad
Vesic
GlobGran
UlDArb2
Tetra
Trach
Plob
MFB
GlobEch
PCA2 (16%)
PCA1 (46%)
1.0
0.5
0.0
-0.5
-1.0


1. POR-01
2. POR-02
3. RFH-01
4. EST
5. RAND
PCA2 (16%)
PCA1 (46%)


LGlobEch
Bull
Trach
AntEp
Scler
MarSeed
UlDHB2
UlDHB1
Mend
FicHB
MFB
MarNod
BambBull
Ann
Ast
lSTCyl
lST
PCA2 (29%)
PCA1 (33%)
1.0
0.5
0.0
-0.5
-1.0


1. POR-01
2. POR-02
3. RFH-01
4. EST
5. RAND
PCA2 (29%)
PCA1 (33%)
2
1
0
-1
-2
-3