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Research paper

Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions

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ABSTRACT

The interpretation of Neotropical fossil phytolith assemblages for palaeoenvironmental and archaeological reconstructions relies on the development of appropriate modern analogues. We analyzed modern phytolith assemblages from the soils of ten distinctive tropical vegetation communities in eastern lowland Bolivia, ranging from *terra firme* humid evergreen forest to seasonally-inundated savannah. Results show that broad ecosystems – evergreen tropical forest, semi-deciduous dry tropical forest, and savannah – can be clearly differentiated by examination of their phytolith spectra and the application of Principal Component Analysis (PCA). Differences in phytolith assemblages between particular vegetation communities within each of these ecosystems are more subtle, but can still be identified. Comparison of phytolith assemblages with pollen rain data and stable carbon isotope analyses from the same vegetation plots show that these proxies are not only complementary, but significantly improve taxonomic and ecosystem resolution, and therefore our ability to interpret palaeoenvironmental and archaeological records. Our data underline the utility of phytolith analyses for reconstructing Amazon Holocene vegetation histories and pre-Columbian land use, particularly the high spatial resolution possible with terrestrial soil-based phytolith studies.

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1. Introduction

The accurate reconstruction of vegetation history is fundamental for addressing current debates regarding the nature and scale of human impacts on ecosystems over time. For example, there is significant debate about how much pre-Columbian humans altered parts of the Amazon in the past, with characterizations of the region ranging from 'cultural parkland' to 'pristine wilderness' (Denevan, 1992; Meggers, 1992; Denevan, 2001; Heckenberger et al., 2003; Meggers, 2003; Erickson and Balée, 2006; Mayle et al., 2007; McKey et al., 2010; Iriarte et al., 2012). In the tropics, silica bodies can be preserved in terrestrial and lacustrine sediments, and serve as a useful proxy for palaeo-vegetation and palaeoenvironmental reconstructions, along with other proxies like pollen, stable carbon isotopes, charcoal, and grass cuticles (e.g. Guillet et al., 1988; Pessenda et al., 1998; Alexandre et al., 1999; de Freitas et al., 2001; Wooller, 2002; Aleman et al., 2012; Loader et al., 2012; Calegari et al., 2013). Our ability to interpret fossil phytolith assemblages, and therefore address palaeoenvironmental and archaeological questions, relies on comparisons with appropriate modern analogues. The systematic sampling and analysis of soils underneath standing vegetation provide important information on phytolith deposition with regards to representation, dispersal, and abundance (Piperno, 2006).

As part of a project investigating pre-Columbian human impacts on the landscape in the Bolivian Amazon, we analyzed 56 modern phytolith assemblages from soils beneath ten distinctive tropical vegetation communities. Using these data, we tested whether vegetation communities can be statistically distinguished based on their residual phytolith signature or assemblage; i.e., the phytoliths left behind in the underlying soils after the decay of vegetation. We compared these results with carbon stable isotope data from the same soil samples and previously published pollen rain data (Gosling et al., 2005, 2009; Burn et al., 2010; Jones et al., 2011) collected in artificial pollen traps within the same sample plots. Because of their complementary nature, the combined use of phytolith and pollen analyses is becoming standard for the reconstruction of palaeoenvironments worldwide (e.g. Kurmann, 1985; Piperno et al., 1990; Kealhofer and

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Penny, 1998; Horrocks et al., 2000; Denham et al., 2003; Piperno and Jones, 2003; Iriarte et al., 2004; Parker et al., 2004; Iriarte, 2006; Li et al., 2010; Iriarte et al., 2012).

Other modern phytolith soil studies from specific vegetation communities have been undertaken in the tropics or subtropics (Boyd et al., 1998), but the majority of these are from tropical Africa (Alexandre et al., 1997b; Runge and Runge, 1997; Runge, 1999; Bremond et al., 2005; Barboni et al., 2007; Mercader et al., 2011; Aleman et al., 2012; Novello et al., 2012). Only a limited number have been done in the South American tropics and subtropics (Piperno and Becker, 1996; Alexandre et al., 1999; Borba-Roschel et al., 2006; Iriarte and Paz, 2009). Our study represents the first time that phytoliths, pollen, and stable carbon isotopes have been combined from the same plots to characterize modern vegetation communities in the Neotropics. Given the heterogeneity of vegetation and high floristic diversity of the Amazon region, the characterization of modern phytolith assemblages from defined vegetation communities provides clear advantages for taxonomic resolution in interpreting assemblages from tropical environments of the past.

2. Study area

Ten distinctive vegetation communities – six forest types and four savannah types – were chosen for analysis (Table 1). Nine of these came from within or near the Noel Kempff Mercado National Park (NKMNP) in northeastern Bolivia, on the southern margin of Amazonia (Fig. 1). The 15,230 km² park and surrounding areas contain a wide

Table 1

Vegetation plots sampled.

diversity of ecosystems, ranging from humid evergreen rain forests to seasonally dry forests and savannahs. Eight vegetation communities were selected from established, one hectare, permanent vegetation study plots where detailed botanical inventories exist (Mostacedo and Killeen, 1997; Killeen, 1998; Killeen and Schulenberg, 1998; Panfil, 2001; Killeen et al., 2003; SALVIAS, 2004). Rectangular plots, measuring 20 m \times 500 m unless their configuration needed to be altered to accommodate the shape of the vegetation community, were established in visually homogenous vegetation types, and did not adjoin one another. Savannah vegetation was inventoried by Killeen and others using a point intercept method, documenting all taxa in 20 m perpendicular transects along a 500 m base line. In forest vegetation plots, all freestanding stems >10 cm d.b.h. (diameter at breast height, ca. 1.2 m) were recorded. Forbs, grasses, vines, and small lianas were not systematically inventoried in the forest plots; however, some data on these taxa and their general vegetation associations is available from a checklist of the vegetation in NKMNP produced during a Rapid Assessment Program (RAP) of the park (Killeen et al., 1998) (See Table S1 in the Supplementary information). Within the park, there is no recent history of significant human alteration to the vegetation other than rubber (Hevea brasiliensis) tapping in the early 20th century and the selective logging of mahogany (Swietenia macrophylla) prior to the establishment of the park in 1988 (Killeen and Schulenberg, 1998). A forest dominated by cusi (Attalea speciosa) palm comprised an additional vegetation community sampled outside the park, hereafter referred to as terra firme palm forest (TF Palm Forest). No vegetation inventory exists for this sample site.

Vegetation community	Abbreviation	Plot(s) sampled	Coordinates (deg, min, sec)	Elevation (m asl)	Slope (deg) ^a	Common taxa ^b
Terra Firme Humid	TF Evergreen	LF1	14 34 50 S, 60 49 48 W	235	0	Moraceae, Phenakospermum guianensis (Strelitziaceae),
Evergreen Forest	Forest	LF2	14 34 50 S, 60 49 48 W	235	0	Vochysiaceae, Arecaceae (esp. <i>Euterpe precatori</i>), Rubiaceae, Melastomataceae (esp. <i>Miconia</i> spp.), <i>Solanea eichleria</i> (Elaeocarpaceae), Fabaceae, Hippocrateaceae
Terra Firme Humid	TF Liana Forest	CH1	14 23 08 S, 61 08 52 W	202	5 S	Phenakospermum guianensis (Strelitziaceae), Fabaceae,
Evergreen Liana Forest		CH2	14 20 35 S, 61 09 37 W	212	0	Bignonaceae, Moraceae, Combretaceae, Anacardiaceae, <i>Talisia</i> sp. (Sapindaceae)
Seasonally-Inundated	SI Evergreen	LO1	14 24 15 S, 61 08 38 W	183	0	Rinoreocarpus ulei (Violaceae), Fabaceae, Melastomataceae
Evergreen Forest	Forest	LO2	14 24 15 S, 61 08 38 W	183	0	(esp. Miconia poeppigii), Annonaceae, Sapotaceae,
						Moraceae, Arecaceae
Terra Firme	TF	AC2	15 14 58 S, 61 14 42 W	263	0	Fabaceae (esp. Caesalpinia floribunda), Aspidosperma spp.
Semi-Deciduous Dry Forest	Semi-Deciduous Forest	CP1	14 32 23 S, 61 29 53 W	391	20 ^c	(Apocynaceae), Bignoniaceae (esp. <i>Tabebuia</i> sp.), Flacourtiacae, Anacardiaceae, <i>Combretum leprosum</i> (Combretaceae), and Malvaceae (Sterculiaceae and Tiliaceae)
Seasonally-Inundated Semi-Deciduous Dry Forest	SI Semi-Deciduous Forest	MV1	14 56 33 S, 61 08 23 W	190	0	Fabaceae (esp. Inga ingoides), Physocalymma scaberimum (Lythraceae), Hirtella gracilipes (Chrysobalanaceae), Moraceae, Annonaceae, Malpighiaceae
Terra Firme Attalea Palm Forest	TF Palm Forest	Cusi	15 13 48 S, 61 09 52 W	248	n/a	Attalea speciosa ^d
Terra Firme Woodland Savannah (Cerradão)	TF Wooded Savannah	FC2	14 35 10 S, 60 50 26 W	229	<1	Panicoideae grasses (esp. <i>Trachypogon plumosus</i>), Melastomataceae, Clusiaceae (esp. <i>Caraipa densifolia</i>), Fabaceae
Terra Firme Savannah (Cerrado)	TF Savannah	FC1	14 36 25 S, 60 51 23 W	204	0	Panicoideae grasses (esp. Paspalum stellatum and Andropogon virgatus), Myrtaceae (esp. Eugenia parviflora), Fabaceae, Borreria sp. (Rubiaceae), Dilleniaceae
Seasonally-Inundated	SI Savannah	TO1	14 43 41 S,6 1 08 16 W	170	n/a	Panicoideae grasses (esp. Mesosetum cayennense and Paspalum
Savannah		FT1	14 36 53 S, 60 51 59 W	198	0	<i>lineare</i>), Cyperaceae, <i>Synonganthus</i> spp. (Eriocaulaceae), Xyridaceae ^e
Beni Seasonally-Inundated	Beni SI	LL1	14 54 24 S, 64 27 03 W	164	0	Thalia geniculata (Marantaceae), Cyperus gigantus (Cyperaceae),
Savannah	Savannah	LI1	14 59 28 S, 65 35 19 W	162	0	Typha dominguensis (Typhaceae), Inga stenopoda (Fabaceae), Canna glauca (Cannaceae), Heliconia sp. (Heliconiaceae), Erythrina fusca (Fabaceae) ^f

^a Slope data for NKMNP from Panfil 2001.

^b See Burn et al., 2010; Gosling et al., 2005, 2009; Jones et al., 2011 for lists of taxa ranked by relative cover and relative frequency for LF1, LF2, CH1, CH2, LO1, LO2, AC2, FC1, FC2, and FT1. See SALVIAS (2004) online database for detailed inventories, as well as Killeen (1998).

^c Plot is situated on top of a granite inselberg 50–70 m above the surrounding forest: slope is down in all directions.

^d No vegetation inventory available; plot dominated by *Attalea speciosa*.

^e No quantitative vegetation data available for TO1. Common Taxa information for seasonally-inundated savannah is based only on FT1 plot.

^f A preliminary vegetation survey was done by Soto in 2010 (see Supplementary information). Not all stems were counted, but Soto assessed major taxa on a scale of Dominant (>50%), Abundant (20–50%), Frequent (10–20%), Occasional (2–10%), Few (<2%), and Rare (1–2 individuals).

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